

# Comparing the effect of the interaction between fine and coarse scales and surround suppression on motion discrimination

**Ignacio Serrano-Pedraza**

Faculty of Psychology, Universidad Complutense de Madrid, Madrid, Spain  
Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, UK



**María J. Gamonoso-Cruz**

Faculty of Psychology, Universidad Complutense de Madrid, Madrid, Spain



**Vicente Sierra-Vázquez**

Faculty of Psychology, Universidad Complutense de Madrid, Madrid, Spain



**Andrew M. Derrington**

Faculty of Humanities and Social Sciences, University of Liverpool, Liverpool, UK



Our ability to discriminate motion direction in a Gabor patch diminishes with increasing size and contrast, indicating surround suppression. Discrimination is also impaired by a static low-spatial-frequency patch added to the moving stimulus, suggesting an antagonism between sensors tuned to fine and coarse features. Using Bayesian staircases, we measured duration thresholds in motion-direction discrimination tasks using vertically oriented Gabor patches moving at 2°/s. In two experiments, we tested two contrasts (2.8% and 46%), five window sizes (from 0.7° to 5°), and two spatial frequencies (1 c/deg and 3 c/deg), either presented alone or added to a static pattern. When the moving pattern was presented alone, duration thresholds increased with size at high contrast and decreased with size at low contrast. At low contrast, when a static pattern of 3 c/deg was added to a moving pattern of 1 c/deg, duration thresholds were similar to the case when the moving pattern was presented alone; however, at high contrast, duration thresholds were facilitated, eliminating the effect of surround suppression. When a static pattern of 1 c/deg was added to a moving pattern of 3 c/deg, duration thresholds increased about 4 times for high contrast and 2 times for low contrast. These results show that the antagonism between sensors tuned to fine and coarse scales is more complex than surround suppression, suggesting that it reflects the operation of a different mechanism.

## Introduction

There is a counterintuitive psychophysical result in motion perception: as the size of the stimulus increases, our ability to discriminate its direction of motion is impaired or facilitated depending on its contrast.

At high contrast, motion discrimination of a simple brief stimulus (Gabor patch) is impaired with increasing size (Tadin, Lappin, Gilroy, & Blake, 2003; Tadin & Lappin, 2005; Glasser & Tadin, 2010; Serrano-Pedraza, Hogg, & Read, 2011; see review in Nishida, 2011). This result is consistent with the reduced firing response found in some middle temporal (MT) neurons for large stimuli presented at high contrast (Pack, Hunter, & Born, 2005) and short durations (Churan, Khawaja, Tsui, & Pack, 2008). This impairment in direction discrimination has been explained as the operation of a perceptual mechanism called *surround suppression*, which is hypothesized to be the psychophysical counterpart of the center-surround antagonism present in the receptive fields of motion sensors of the visual-area MT (Allman, Miezin, & McGuiness, 1985a, 1985b; Tanaka et al., 1986; Born & Tootell, 1992; Tadin et al., 2003).

At low contrast, motion discrimination is facilitated with increasing stimulus size (S. J. Anderson & Burr, 1991; Watson & Turano, 1995; Tadin et al., 2003;

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Tadin & Lappin, 2005). This facilitation in motion discrimination has been explained as the operation of a perceptual mechanism called *spatial summation* (S. J. Anderson & Burr, 1991; Tadin et al., 2003). The presumed physiological basis of spatial summation is the increase in the size of the receptive fields that occurs with decreasing contrast (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Sceniak, Ringach, Hawken, & Shapley, 1999; Kapadia, Westheimer, & Gilbert, 1999; Nauhaus, Busse, Carandini, & Ringach, 2009). Interestingly, it has been found that MT surround modulation depends on the strength of the neuronal response: surround suppression is stronger for stimuli that elicit larger responses, and surround summation (facilitation) is stronger for stimuli that elicit smaller responses (Huang, Albright, & Stoner, 2008).

There is another counterintuitive psychophysical result in motion perception that shows that motion discrimination at short durations is impaired when the size of a complex stimulus that consists of a moving fine-scale (high-spatial-frequency) pattern added to a static coarse-scale (low-spatial-frequency) pattern increases (Derrington & Henning, 1987; Henning & Derrington, 1988; Derrington, Fine, & Henning, 1993; Serrano-Pedraza, Goddard, & Derrington, 2007; Serrano-Pedraza & Derrington, 2010; see the “Interaction across different spatial scales” section in Nishida, 2011). Although previous results are consistent with the idea that early processing by the human visual system analyses fine-scale and coarse-scale image features separately using motion sensors that are selective for spatial frequency and have localized receptive fields (S. J. Anderson & Burr, 1985, 1987, 1989, 1991; S. J. Anderson, Burr, & Morrone, 1991), these errors in motion discrimination can be explained by a model of motion sensing in which there is a subtractive interaction between motion sensors tuned to high spatial frequencies and those tuned to low spatial frequencies (Serrano-Pedraza et al., 2007).

To date, there has been no psychophysical study that compared duration thresholds for motion discrimination of simple and complex stimuli. Accordingly, our objective was to compare surround suppression with the interaction across different scales by measuring duration thresholds for motion discrimination. We performed two experiments in order to measure duration thresholds for fine- and coarse-scale patterns and the combination of motion signals from fine and coarse scales. We tested four types of stimulus: two simple—a moving fine-scale pattern (3 c/deg) and a moving coarse-scale pattern (1 c/deg)—and two complex—a moving fine-scale pattern added to a static coarse-scale pattern and a moving coarse-scale pattern added to a static fine-scale pattern. We chose those particular spatial frequencies for the complex stimulus

because previous studies have shown that the maximum effect was obtained when the test had a spatial frequency of 1 c/deg and the inducer had a spatial frequency of 3 c/deg (Henning & Derrington, 1988).

In the first experiment, we tested two spatial-window sizes—one very small ( $\sigma_{xy} = 0.35^\circ$ ) and the other large ( $\sigma_{xy} = 2.5^\circ$ )—and two contrasts—low (2.8%) and medium-high (46%). In the second experiment, we extended the first experiment to explore the effect of stimulus size on duration thresholds. The main results of both experiments suggest that for fine-scale motion at high contrast, the antagonism between sensors tuned to fine and coarse features produced a greater impairment of motion discrimination than surround suppression. However, for coarse-scale motion at high contrast, our results showed that the antagonism between sensors tuned to fine and coarse features facilitated motion discrimination. Simulations of the model proposed by Serrano-Pedraza et al. (2007) could explain the results for complex stimuli at high contrast, but not at low contrast.

## Methods

### Subjects

Five human subjects (aged 18–40 years) with experience in psychophysical experiments took part in the experiments (ISP, MGC, IP, AGS, and GEC). Subjects IP, AGS, and GEC were not aware of the purpose of the study. Subject GEC completed only half of Experiments 1 and 2. All subjects had normal or corrected-to-normal refraction and normal visual acuity. The experiments were carried out in a dark room, and a chin rest (UHCOTech HeadSpot, Houston, TX) was used to stabilize the subject’s head and to control the observation distance. To minimize tracking eye movements, the subjects were instructed to maintain fixation on a small cross ( $0.25^\circ \times 0.25^\circ$ ) in the center of the screen before the stimuli were presented. Experimental procedures were approved by the Universidad Complutense de Madrid Ethics Committee.

### Equipment

The stimuli were presented on a gamma-corrected 17-in. Eizo Flex Scan T565 monitor (Eizo Corp., Hakusan, Japan) under the control of a Mac Pro running Matlab (MathWorks, Natick, MA) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007; www.psychtoolbox.org) and 14 bits of gray-scale resolution

(Bits++ Cambridge Research Systems Ltd, Cambridge, UK). The monitor was gamma corrected using a Minolta LS-100 photometer (Konica Minolta Optics, Inc., Osaka, Japan) and had a resolution of  $800 \times 600$  pixels (horizontal  $\times$  vertical), a vertical frame rate of 150 Hz, and a mean luminance of  $61.9 \text{ cd/m}^2$ . It was observed binocularly from a distance of 91 cm. Stimuli were Gabor patches of  $512 \times 512$  pixels, with 8-bit range, and were presented at the center of the monitor screen in a square of 20 cm per side, subtending an area of  $12.6^\circ \times 12.6^\circ$ . The display's spatial resolution was 40 pixels per degree of visual angle, so the pixel size was  $0.025^\circ$ . The remainder of the screen was at the mean luminance.

## Stimuli

The stimuli (Gabor patches) used in the experiments were constructed using Matlab (MathWorks). Two different configurations for the stimuli were used: (a) a moving vertical Gabor patch of low (1 c/deg) or high (3 c/deg) spatial frequency (see Figure 1A and B), and (b) a complex stimulus composed of a moving vertical Gabor patch of high spatial frequency (3 c/deg) added to a static vertical Gabor patch of low spatial frequency (1 c/deg) or a moving vertical Gabor patch of low spatial frequency (1 c/deg) added to a static Gabor patch of high spatial frequency (3 c/deg; see Figure 1C

and D). The equation of a moving Gabor patch is as follows:

$$L(x, y, t) = L_0 \left[ 1 + m(t) \exp \left\{ -\frac{\hat{x}^2}{2\sigma_x^2} - \frac{\hat{y}^2}{2\sigma_y^2} \right\} \times \cos(2\pi\rho_1(\hat{x} - vt) + \phi_1) \right] \quad (1)$$

The equation of a complex stimulus is as follows:

$$L(x, y, t) = L_0 \left[ 1 + m(t) \exp \left\{ -\frac{\hat{x}^2}{2\sigma_x^2} - \frac{\hat{y}^2}{2\sigma_y^2} \right\} \times [\cos(2\pi\rho_1(\hat{x} - vt) + \phi_1) + \cos(2\pi\rho_2(\hat{x}) + \phi_2)] \right] \quad (2)$$

where  $\hat{x} = x\cos(\theta_0) + y\sin(\theta_0)$  and  $\hat{y} = -x\sin(\theta_0) + y\cos(\theta_0)$ ;  $x$  and  $y$  are on-screen position;  $L_0$  is mean luminance ( $L_0 = 61.9 \text{ cd/m}^2$ );  $\theta_0$  is the orientation, in degrees (all stimuli had a vertical orientation,  $\theta_0 = 0^\circ$ );  $\rho_1$  (see Equations 1 and 2) is the spatial frequency of the moving pattern and  $\rho_2$  (see Equation 2) is the spatial frequency of the static pattern, in cycles per degree (c/deg), both in the direction of  $\theta_0$ ;  $\phi_1$  and  $\phi_2$  are the phases of the patterns, in radians;  $\sigma_x$  and  $\sigma_y$  are the

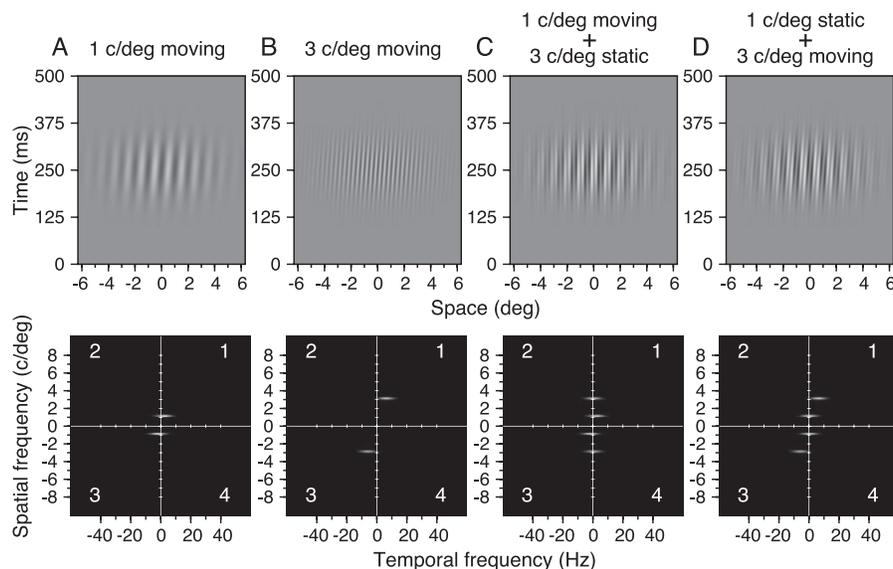


Figure 1. Examples of stimuli used in the experiments. The top panels show the space-time plots; the bottom panels show the Fourier spatiotemporal amplitude spectrum from the space-time plots on the top. (A) Moving Gabor patch of 1 c/deg (coarse-scale motion). (B) Moving Gabor patch of 3 c/deg (fine-scale motion). (C) Complex stimulus composed of a moving Gabor patch of 1 c/deg added to a static Gabor patch of 3 c/deg. (D) Complex stimulus composed of a moving Gabor patch of 3 c/deg added to a static Gabor patch of 1 c/deg. All examples have patterns moving rightward (see quadrants 1 and 3 of the spatiotemporal spectra) at a speed of  $2^\circ/\text{s}$  and a spatial Gaussian-window diameter of  $2\sigma_{xy} = 5^\circ$  and are presented in a temporal Gaussian window of duration  $2\sigma_t = 100 \text{ ms}$ .

spatial standard deviations of the Gaussian window, in degrees of visual angle ( $^{\circ}$ );  $v$  is the speed of the moving pattern, in degrees per second ( $^{\circ}/s$ ); and  $m$  is the Michelson contrast as a function of time given by

$$m(t) = M \exp\left\{-t^2/(2\sigma_t^2)\right\} \quad (3)$$

where  $\sigma_t$  is the temporal standard deviation, in milliseconds (ms), varied as described in the “Procedure” subsection, so as to find the duration threshold; and  $M$  is the peak contrast.

## Procedure

Each trial started with a fixation cross displayed at the center of the screen using a Gaussian temporal profile (see Equation 3) with a standard deviation of  $\sigma_t = 80$  ms truncated to give an overall duration of 500 ms. The cross disappeared before the presentation of the stimulus. The stimuli (see Equations 1 and 2) were presented using a Gaussian temporal function (see Equation 3) with a standard deviation controlled by an adaptive staircase procedure. The Gaussian temporal profile was truncated to give an overall duration of 500 ms, so each trial including the fixation cross lasted 1000 ms. Moving patterns always had a fixed speed of  $v = 2^{\circ}/s$ . The motion direction—leftward or rightward—was randomized, and the observer’s task was to indicate, by pressing a button on the ResponsePixx Handheld (VPixx Technologies Inc., Montreal, Canada, <http://www.vpixx.com>), the direction of each presentation. A new trial was initiated only after the observer’s response; thus, the experiment proceeded at a pace determined by the observer. No feedback about the correctness of responses was provided.

In Experiment 1, we measured duration thresholds for two types of stimuli: simple stimuli and complex stimuli. The simple stimuli were Gabor patches of moving patterns (see Figure 1A and B) of spatial frequency  $\rho_1 = 1$  c/deg (coarse-scale motion) and  $\rho_1 = 3$  c/deg (fine-scale motion), with two different Michelson contrast (2.8% and 46%) and two spatial window sizes: one small ( $\sigma_x = 0.35^{\circ}$ ,  $\sigma_y = 0.35^{\circ}$ ) and one large ( $\sigma_x = 2.5^{\circ}$ ,  $\sigma_y = 2.5^{\circ}$ ). The complex stimuli were Gabor patches with two patterns, one moving and one stationary.

We tested two complex stimuli: stationary  $\rho_2 = 3$  c/deg with moving  $\rho_1 = 1$  c/deg (see Figure 1C) and stationary  $\rho_2 = 1$  c/deg with moving  $\rho_1 = 3$  c/deg (see Figure 1D). Each pattern of the complex stimuli could have one of two different Michelson contrasts, 2.8% or 46%, and one of two spatial-window sizes, small ( $\sigma_x = 0.35^{\circ}$ ,  $\sigma_y = 0.35^{\circ}$ ) or large ( $\sigma_x = 2.5^{\circ}$ ,  $\sigma_y = 2.5^{\circ}$ ). Thus, in Experiment 1 we tested 16 conditions: 2 types of stimuli (simple and complex)  $\times$  2 spatial-frequency scales

(coarse and fine)  $\times$  2 contrasts (high and low)  $\times$  2 window sizes (small and large).

In Experiment 2, we measured duration thresholds for the same stimuli used in Experiment 1 but with the addition of intermediate spatial-window sizes ( $\sigma_{xy}$ ), in particular,  $0.35^{\circ}$ ,  $0.65^{\circ}$ ,  $1.35^{\circ}$ ,  $2^{\circ}$ , and  $2.5^{\circ}$ . Thus, in Experiment 2 we tested 40 conditions: 2 types of stimuli (simple and complex)  $\times$  2 spatial-frequency scales (coarse and fine)  $\times$  2 contrasts (high and low)  $\times$  5 window sizes.

Duration threshold, the minimum presentation time that is needed in order to discriminate the correct direction of motion, was defined as the value of  $2\sigma_t$  (see Equation 3), resulting in a performance of 82% correct. Duration thresholds were measured using adaptive Bayesian staircases (Treutwein, 1995) in a forced-choice direction-discrimination task. Between 5 and 9 min were required per duration-threshold estimation. The characteristics of the Bayesian staircases were as follows: (a) The prior probability-density function was uniform (Pentland, 1980; Emerson, 1986) with a starting duration of 200 ms. (b) We used the logistic function as the model likelihood function adapted from García-Pérez (1998, appendix A), with a spread value of 1 (with a delta parameter of 0.01, a lapse rate of 0.01, and a guess rate of 0.5). (c) The value of the temporal duration ( $2\sigma_t$ ) in each trial was obtained from the mean of the posterior probability distribution (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994). (d) The staircase stopped after 50 trials (Pentland, 1980; Anderson, 2003). (e) The final threshold was estimated from the mean of the final probability-density function. Three threshold estimations per condition were obtained for each subject. The conditions in each experiment were tested in different sessions, counter-balanced across subjects. Practice sessions were performed prior to the experiment.

## Results

### Experiment 1. Suppression and facilitation ratios for simple and complex stimuli

In Experiment 1, we measured duration thresholds for motion discrimination of simple and complex stimuli. We tested two spatial frequencies (coarse and fine motion scales), two contrasts (low and high), and two Gaussian window sizes (small and large). Figure 2 shows the duration thresholds (ms) as a function of the diameter ( $^{\circ}$ ) of the Gaussian spatial window. Figure 2a and b (gray panels) shows the results for high contrast (46%), and Figure 2c and d shows the results for low contrast (2.8%). White dots show the results for simple

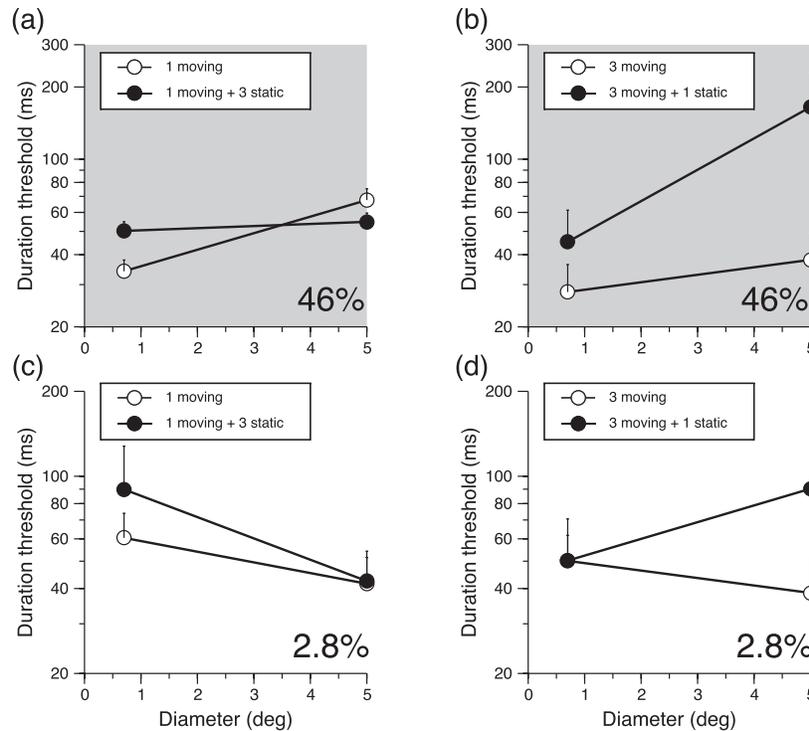


Figure 2. Results from Experiment 1. Each panel shows the duration thresholds ( $2\sigma_t$ ) for motion-direction discrimination as a function of the Gaussian-window diameter ( $2\sigma_{xy} = 0.7^\circ$  and  $2\sigma_{xy} = 5^\circ$ ). Gray panels (a and b) show results for high contrast (46%). White panels (c and d) show results for low contrast (2.8%). (a and c) Mean plus standard deviation of the duration thresholds of five subjects (IP, AGS, GEC, ISP, and MGC). White dots are results for moving Gabor patches of 1 c/deg. Black dots are results for coarse-scale moving complex stimuli of 1 c/deg added to static stimuli of 3 c/deg. (b and d) Mean plus standard deviation of the duration thresholds of four subjects (IP, AGS, ISP, and MGC). White dots are results for moving Gabor patches of 3 c/deg. Black dots are results for fine-scale moving complex stimuli of 3 c/deg added to static stimuli of 1 c/deg. Moving patterns always had a fixed speed of  $v = 2^\circ/s$ .

stimuli, and black dots show the results for complex stimuli.

Figure 2 (white dots) shows the results obtained with simple stimuli. These results replicate previous results (Tadin et al., 2003; Serrano-Pedraza et al., 2011). At high contrast (Figure 2a and b), duration thresholds increased with increasing size (two-sample  $t$  test for the two-tailed hypothesis where  $t_{0.05(2),8} = 2.306$ :  $t = -8.6442$ ,  $p < 0.0001$ , for 1 c/deg;  $t = -1.6269$ ,  $p = 0.1424$ , for 3 c/deg). At low contrast (Figure 2c and d), duration thresholds decreased with increasing size ( $t$  test  $t_{0.05(2),8} = 2.306$ :  $t = 2.2857$ ,  $p = 0.0516$ , for 1 c/deg;  $t = 1.054$ ,  $p = 0.3227$ , for 3 c/deg). Figure 3 shows the ratio between the duration thresholds for large and small Gaussian windows; these ratios show the strength of the suppression or facilitation as a function of contrast. Figure 3a (white bars) show the ratios for simple stimuli of 1 c/deg. For high contrast (46%), the ratio is higher than 1 (the dotted line shows the value that represents no effect), showing suppression. However, for low contrast (2.8%), the ratio is lower than 1, showing facilitation. For the conditions tested in the experiment, the suppression and facilitation found for coarse-scale motion (1 c/deg) are stronger than those

for fine-scale motion (3 c/deg; see Figure 3b, white bars).

Figure 2 (black dots) shows the results obtained with complex stimuli. For coarse-scale motion (Figure 2a and c; moving element of 1 c/deg and static element of 3 c/deg), the results are similar to those obtained with simple stimuli (Figure 2a and c, white dots). At high contrast there is a no significant suppression ( $t$  test  $t_{0.05(2),8} = 2.306$ :  $t = -1.5289$ ,  $p = 0.1648$ ), and at low contrast there is facilitation ( $t$  test  $t_{0.05(2),8} = 2.306$ :  $t = 2.7132$ ,  $p = 0.0265$ ). Figure 3a (black bars) shows the ratio of the duration thresholds for large and small windows. The bars show that the ratio for high contrast is close to 1, showing no effect of size on duration thresholds. For fine-scale motion (Figure 2b and d; moving element of 3 c/deg and static element of 1 c/deg), we see an interesting result: Direction discrimination is highly impaired with increasing size of the spatial window, for both high ( $t$  test  $t_{0.05(2),8} = 2.306$ :  $t = -4.041$ ,  $p = 0.003$ ) and low ( $t$  test  $t_{0.05(2),8} = 2.306$ :  $t = -5.6409$ ,  $p < 0.001$ ) contrast.

These results are in the same direction as previous results (Serrano-Pedraza et al., 2007; Serrano-Pedraza & Derrington, 2010). In effect, previous results have

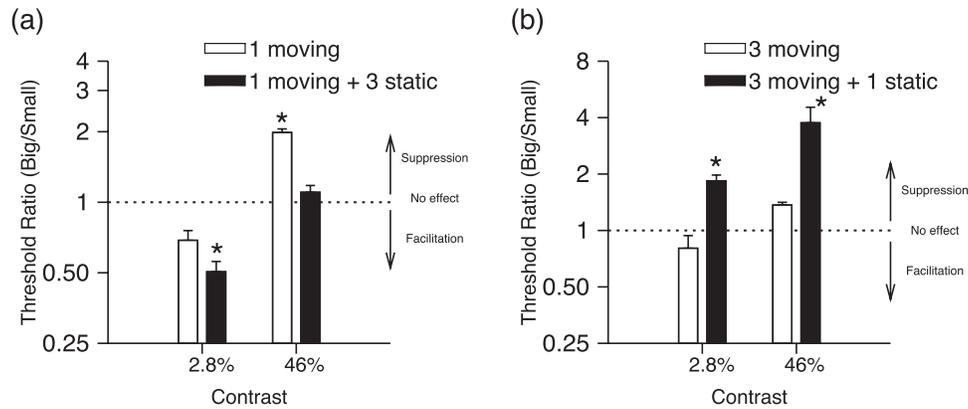


Figure 3. Ratios between duration thresholds of large ( $5^\circ$ ) and small ( $0.7^\circ$ ) Gaussian windows (large divided by small) as a function of contrast (2.8% and 46%). (a) Bars represent the mean plus or minus the standard error of the mean for the ratios of five subjects (see Figure 2a and c). White bars are results for moving Gabor patches of 1 c/deg. Black bars are results for complex stimuli composed of a moving element of 1 c/deg added to a static element of 3 c/deg. (b) Bars represent the mean plus or minus the standard error of the mean for the ratios of four subjects (see Figure 2b and d). White bars are results for moving Gabor patches of 3 c/deg. Black bars are results for complex stimuli composed of a moving element of 3 c/deg added to a static element of 1 c/deg. The dotted line represents a ratio that is equal to 1 (no effect of size). Note that values greater than 1 show suppression or impairment in motion discrimination, and values less than 1 show facilitation in motion discrimination. Asterisks (\*) correspond to significant differences between the duration thresholds used to compute the ratios. To test the differences, we used a two-sample *t* test for the two-tailed hypothesis and  $\alpha = 0.05$ . See text for particular values.

shown that the percentage of errors in direction discrimination increased with increasing size (Serrano-Pedraza & Derrington, 2010). Here we have shown that duration thresholds for veridical motion perception (a measure that can be related to the percentage of errors at short durations) are greater for the large window than for the small window. This result is present for high and low contrast. Interestingly, at high contrast and with a large spatial window (see Figure 2b), the duration thresholds for complex stimuli (black dots) are much higher than for simple stimuli (white dots).

Figure 3b (black bars) shows the ratio of the duration thresholds for large and small windows. The ratio is greater than 1 for both contrasts, although greater for high contrast (46%). Interestingly, the suppression ratio for high contrast is twice the highest ratio obtained with simple stimuli. This result shows that the impairment in motion discrimination with increasing size when a static coarse-scale pattern is added to a moving fine-scale pattern is greater than for a simple stimulus composed only of a moving fine-scale pattern (surround suppression; see Figures 2b and 3b). This result suggests that the antagonism between motion sensors tuned to fine and coarse features is stronger than the antagonism produced by surround suppression.

In sum, in Experiment 1 we have shown three new results:

(a) For high contrast, the direction discrimination of a fine-scale moving complex stimulus—a static coarse (1 c/deg) pattern added to a moving fine (3 c/deg)

pattern—is impaired with increasing size and is more strongly impaired than when the moving fine-scale pattern (3 c/deg) is presented alone (see Figure 2b).

(b) For low contrast, the direction discrimination of a fine-scale moving complex stimulus is also impaired with increasing size, but this result is opposite to the facilitation found for a fine-scale moving simple pattern (see Figure 2d).

(c) For high contrast, the direction discrimination of a coarse-scale moving complex stimulus—a static fine (3 c/deg) pattern added to a moving coarse (1 c/deg) pattern—is impaired for small sizes and is facilitated for large sizes, when compared with the duration thresholds obtained for a coarse-scale moving pattern (1 c/deg; see Figure 2a). The threshold ratios for the coarse-scale moving complex stimulus show that there is no effect of size on duration thresholds (see Figure 3, black bars, 46% contrast).

## Experiment 2. Effect of size on duration thresholds for simple and complex stimuli

Figure 2a (black dots) shows that there was no effect of size on duration thresholds when a static fine (3 c/deg) pattern was added to a moving coarse pattern (1 c/deg). However, we do not know if the duration thresholds are the same for intermediate sizes, and we have this same problem for the rest of conditions. Thus, the objective of Experiment 2 was to measure the duration thresholds using the same stimuli tested in

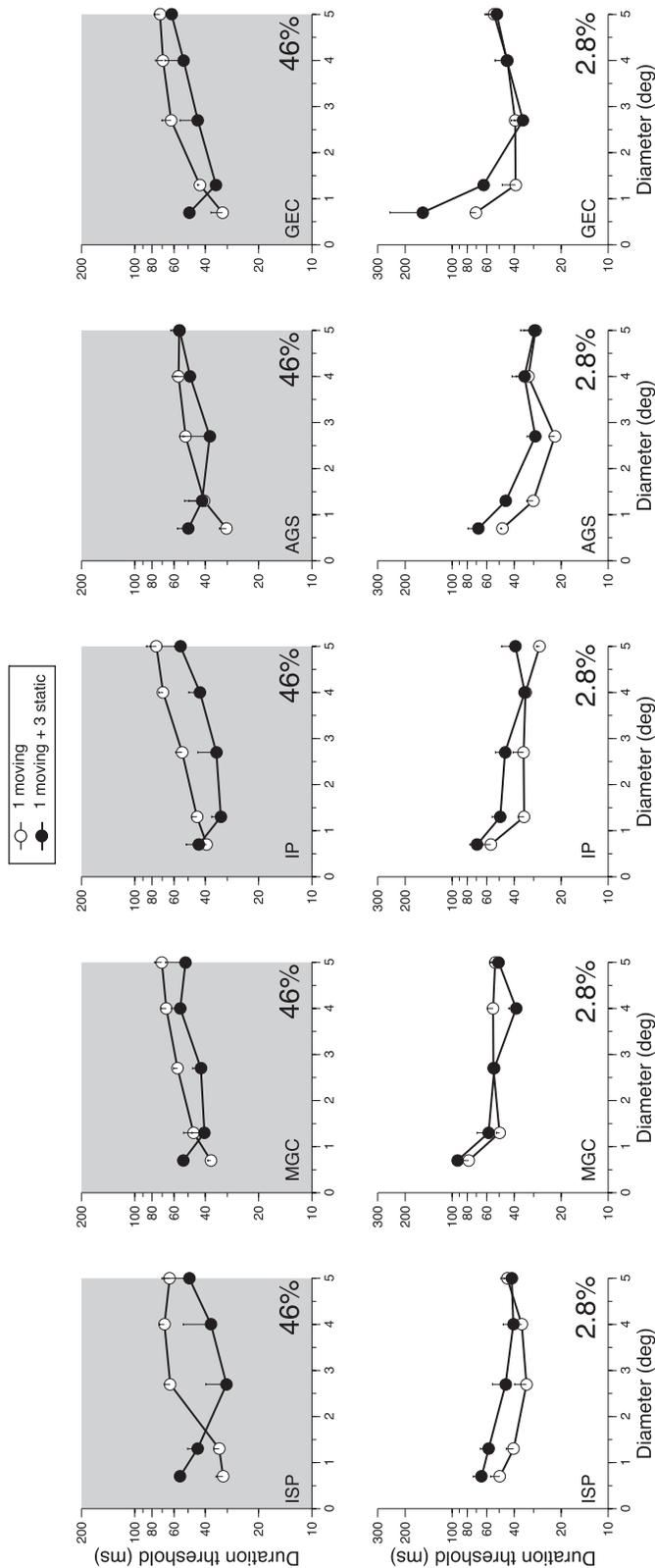


Figure 4. Results from Experiment 2 (coarse-scale motion) of five subjects (ISP, MGC, IP, AGS, and GEC). Each panel shows the duration thresholds ( $2\sigma_t$ ) for motion-direction discrimination as a function of the Gaussian-window diameter ( $2\sigma_{xy}$ ). Gray panels show results for high contrast (46%). White panels show results for low contrast (2.8%). The dots show the mean plus standard deviation of three duration thresholds. White dots are results for moving Gabor patches of 1 c/deg. Black dots are results for complex stimuli, composed of a moving element of 1 c/deg added to a static element of 3 c/deg. Moving patterns always had a fixed speed of  $v = 2^\circ/s$ .

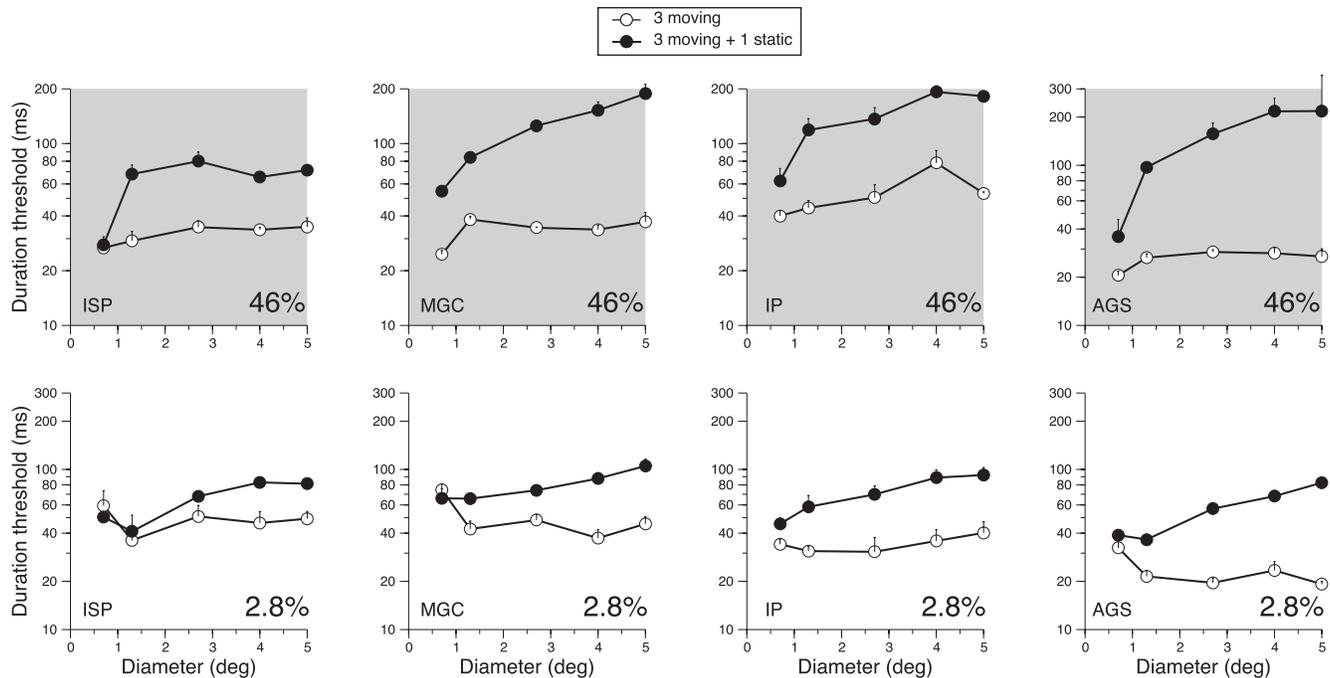


Figure 5. Results from Experiment 2 (fine-scale motion) of four subjects (ISP, MGC, IP, and AGS). Each panel shows the duration thresholds ( $2\sigma_t$ ) for motion-direction discrimination as a function of the Gaussian-window diameter ( $2\sigma_{xy}$ ). Gray panels show results for high contrast (46%). White panels show results for low contrast (2.8%). The dots show the mean plus standard deviation of three duration thresholds. White dots are results for moving Gabor patches of 3 c/deg. Black dots are results for complex stimuli, composed of a moving element of 3 c/deg added to a static element of 1 c/deg. Moving patterns always had a fixed speed of  $v = 2^\circ/s$ .

Experiment 1 but including intermediate spatial windows. In particular, we tested three more sizes ( $\sigma_{xy}$ ):  $0.65^\circ$ ,  $1.35^\circ$ , and  $2^\circ$ . The duration thresholds for the smallest ( $0.7^\circ$ ) and the largest ( $5^\circ$ ) windows are taken from Experiment 1.

Figures 4 and 5 show the results of Experiment 2 for the same subjects tested in Experiment 1. The panels show the duration thresholds for motion discrimination as a function of the spatial Gaussian-window diameter ( $2\sigma_{xy}$ ). Gray panels show the results for high contrast (46%), and white panels show the results for low contrast (2.8%).

Figure 4 shows the results for coarse-scale moving stimuli. White dots show the results for simple moving stimuli of 1 c/deg, and black dots for complex stimuli composed of a moving element of 1 c/deg added to a static pattern of 3 c/deg. The results for simple stimuli and high contrast show the duration thresholds increasing with increasing size. For complex stimuli and high contrast, we found very interesting results. The results have a U shape, where for window diameters close to  $3^\circ$  there is a reduction of the duration thresholds, or facilitation. Figure 6a shows the average of all subjects. The results clearly show that although there is surround suppression for moving stimuli of 1 c/deg (white dots), if we add a static pattern of 3 c/deg, then motion discrimination is facilitated. Figure 4 also

shows that for low contrast (white panels), the duration thresholds for both conditions (simple and complex stimuli) are similar, although for small sizes the impairment in motion discrimination is higher for complex stimuli (see average results in Figure 6c).

Figure 5 shows the results for fine-scale moving stimuli. White dots show the results for simple moving stimuli of 3 c/deg, and black dots for complex stimuli composed of a moving element of 3 c/deg added to a static pattern of 1 c/deg. The results for simple stimuli and high contrast show the duration thresholds increasing with increasing size; however, the increment is lower than for moving elements of 1 c/deg (see Figure 4, gray panels). For complex stimuli and high contrast, we found impairment in motion discrimination with increasing size, and the impairment was greater than with simple moving stimuli for all sizes (see average results in Figure 6b). For low contrast, we found that motion discrimination improved with increasing size for simple moving stimuli (see Figure 5, white panels, white dots). However, for complex stimuli, we found an interesting result: Duration thresholds increased with increasing window size. Thus, facilitation disappears when a static coarse-scale stimulus is added to a fine-scale moving stimulus (see Figure 5, white panels, black dots).

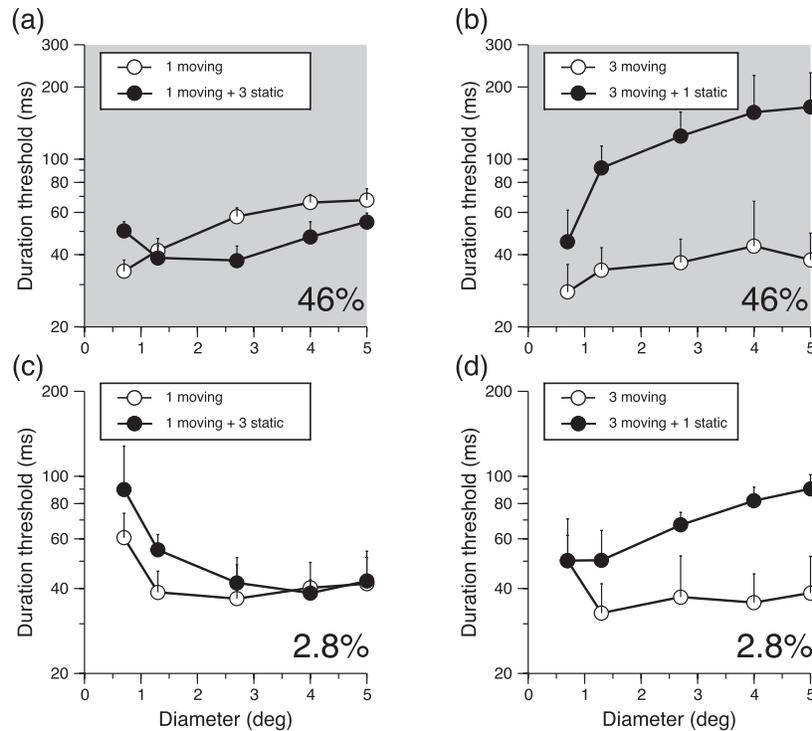


Figure 6. Average results from Experiment 2. Each panel shows the duration thresholds ( $2\sigma_t$ ) for motion-direction discrimination as a function of the Gaussian-window diameter ( $2\sigma_{xy}$ ). Gray panels (a and b) show results for high contrast (46%). White panels (c and d) show results for low contrast (2.8%). (a and c) Mean plus or minus standard error of the mean for the duration thresholds of five subjects (ISP, MGC, IP, AGS, and GEC; data from Figure 4). White dots are results for moving Gabor patches of 1 c/deg. Black dots are results for complex stimuli, composed of a moving element of 1 c/deg added to a static element of 3 c/deg. (b and d) Mean plus standard deviation of the duration thresholds of four subjects (ISP, MGC, IP, and AGS; data from Figure 5). White dots are results for moving Gabor patches of 3 c/deg. Black dots are results for complex stimuli, composed of a moving element of 3 c/deg added to a static element of 1 c/deg. Moving patterns always had a fixed speed of  $v = 2^\circ/\text{s}$ .

## Discussion

The results obtained with simple stimuli replicate previous results (Tadin et al., 2003; Tadin & Lappin, 2005; Glasser & Tadin, 2010; Serrano-Pedraza et al., 2011). At high contrast, duration thresholds increased with increasing size for moving coarse scales (1 c/deg) and for fine scales (3 c/deg). At low contrast, duration thresholds decreased with increasing size for both fine and coarse scales.

For the first time, we have measured duration thresholds for complex stimuli composed of fine and coarse scales. The duration-threshold measurements allowed us to characterize in stimulus terms a phenomenon that has been reported in performance terms in previous studies (Derrington & Henning, 1987; Henning & Derrington, 1988; Derrington et al., 1993; Serrano-Pedraza et al., 2007; Serrano-Pedraza & Derrington, 2010). In those studies, the authors fixed the presentation durations of the complex stimulus and measured the proportion of correct responses for direction discrimination as a function of the duration.

At very short durations (25 ms), when the coarse scales were static and fine scales were moving, the subjects obtained about 17% correct responses; this means that 83% of the time, the subjects reported a motion direction opposite to the true direction of motion (Serrano-Pedraza & Derrington, 2010). In this article, we have fixed the proportion of correct responses at 82%, so we are measuring duration thresholds for veridical motion perception. This procedure allowed us to compare previous results of surround suppression (Tadin et al., 2003) and interaction between spatial scales.

The results reported here show that at high contrast, duration thresholds for complex stimuli composed of moving fine features and static coarse features increase about 4 times (ratio of 3.75) with increasing size, and 2 times (ratio of 1.83) for low contrast. However, for simple stimuli, at low contrast we found a ratio of 0.68 for coarse scales and a ratio of 0.8 for fine scales, showing facilitation in both cases; and at high contrast we found a ratio of 1.98 for coarse scales and a ratio of 1.36 for fine scales. These ratios show that at high contrast, the antagonism between sensors tuned to fine

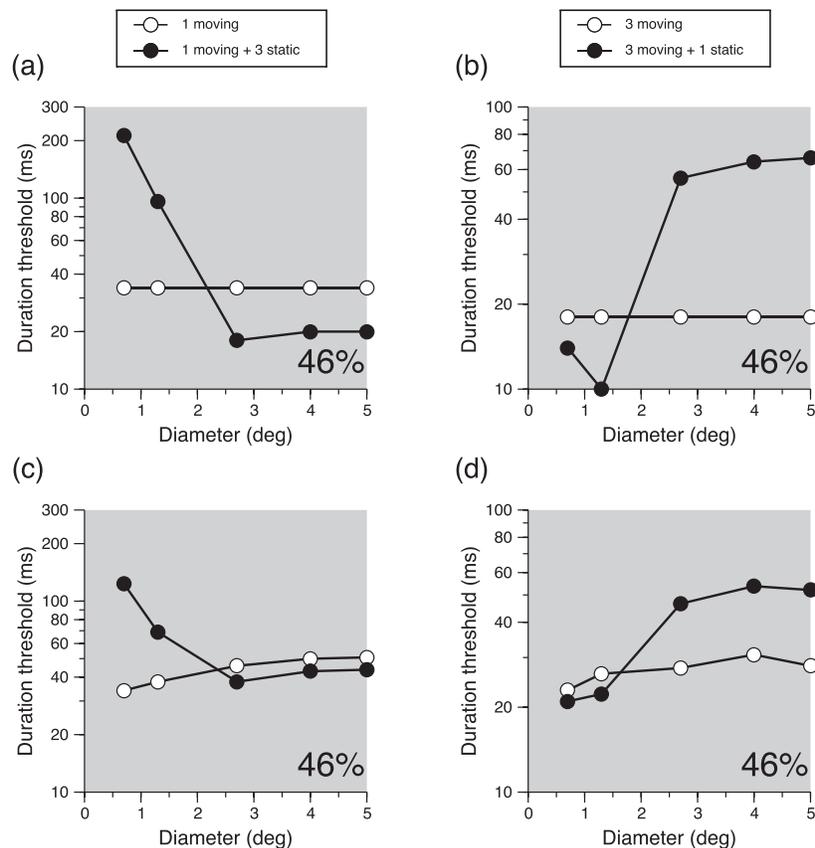


Figure 7. Model simulations of Experiment 2 for high contrast (46%). All panels show the predicted duration thresholds ( $2\sigma_t$ ) for motion-direction discrimination as a function of the Gaussian-window diameter ( $2\sigma_{xy}$ ). Interaction between coarse and fine scales: Panels (a) and (b) show the predictions of the model from Serrano-Pedraza et al. (2007). This model predicted the duration thresholds for a fixed proportion of correct direction discriminations (82%). Interaction between coarse and fine scales and surround suppression: Panels (c) and (d) show the predictions of a simple model that combines linearly the output of the Serrano-Pedraza et al. (2007) model and the empirical duration thresholds for simple stimuli from Figure 6a and b. (a and c) White dots are results for moving Gabor patches of 1 c/deg. Black dots are results for complex stimuli, composed of a moving element of 1 c/deg added to a static element of 3 c/deg. (b and d) White dots are results for moving Gabor patches of 3 c/deg. Black dots are results for complex stimuli, composed of a moving element of 3 c/deg added to a static element of 1 c/deg. Moving patterns always had a fixed speed of  $v = 2^\circ/s$ .

and coarse features is stronger than surround suppression, because the increase in duration threshold is greater.

When the complex stimuli were composed of moving coarse features and static fine features, at low contrast the duration thresholds were similar to those in the case when the moving coarse pattern was presented alone; at high contrast, however, we found a facilitation effect for diameters of the spatial window bigger than  $1.3^\circ$ . This result is novel and has not been reported before.

Serrano-Pedraza et al. (2007) proposed a computational model of motion sensing that implements a subtractive interaction between motion sensors tuned to high and low spatial frequencies. This model could explain errors in motion discrimination when coarse scales were static and fine scales were moving. The same model could also explain the increase in errors with

increasing size and the effect of relative contrast between the scales (Serrano-Pedraza & Derrington, 2010). Here we have used this simple model (see Serrano-Pedraza et al., 2007, appendix A) to explain our results. The output of the original model is a probability of correct direction discrimination for a fixed temporal duration of the stimulus. Here, in order to use the same measure of the thresholds of the experiments, we have fixed the probability of correct response to 0.82 (the probability that is associated with the duration thresholds obtained in the experiments) and we have found the duration of the stimulus that gives that probability.

Figure 7a and b shows the results of simulations using this model, which show approximately the same effect as the main results found here. The simulation results for static coarse scales added to moving fine

scales with 46% contrast (see Figure 7b, black dots) show a similar pattern to that of the empirical results (see Figure 6b). The simulation results when coarse scales were moving and fine scales were static (Figure 7a, black dots) show a similar facilitation to the facilitation found empirically at medium-high sizes (diameters between  $2^\circ$  and  $5^\circ$ ; see Figure 6a). However, the model does not discriminate between 46% and 2.8% contrasts, and it does not have a surround-suppression mechanism implemented, so the duration thresholds for single Gabor patches do not change with contrast or with size (Figure 7a and b, white dots).

To explain all our results, more modeling work is needed. Three main problems are presented: the first is to implement a surround-suppression mechanism; the second is to specify the order in which these two mechanisms (surround suppression and interaction between scales) are working; and the third is the way they are combined (linearly or nonlinearly). To solve these three problems requires more data and more simulations. However, in an attempt to test the hypothesis that the two mechanisms are summed linearly, we have combined the output of the model of Serrano-Pedraza et al. (2007) and the empirical duration threshold for simple stimuli and high contrast taken from Figure 6 (simply adding the duration thresholds and dividing by two). The simulation results are presented in Figure 7c and d. These simulation results do not explain the empirical results completely, suggesting that the interaction between these two mechanisms in the visual system must be more complex than a simple linear summation.

We have shown that a simple model of motion sensing that implements a subtractive interaction between motion sensors tuned to high and low spatial frequencies can account for the facilitation effect; however, there are other results that could explain our facilitation effect. For example, it has been found that static luminance texture increases perceived speed (Nguyen-Tri & Faubert, 2007). These authors found that when a static grating of 2 c/deg was added to a moving grating of 0.5 c/deg, the perceived speed of the low-frequency pattern increased 1.25 times.

We wonder whether this increment in perceived speed could account for the reduction in duration thresholds that we found. Nguyen-Tri and Faubert used a speed of 8°/s, the stimuli were presented in the periphery ( $2.5^\circ$  eccentricity), and the contrast of the moving grating was 10% Michelson contrast; all this makes it difficult to decide, because the experimental conditions and stimulus parameters, particularly the contrast, are not comparable with ours, and we know that contrast makes a big difference. For this reason, we decided to test this increasing-speed hypothesis directly. We performed a control experiment with three subjects (results not shown), replicating Experiment 2

at high contrast (46%) and using simple stimuli condition with a spatial frequency of 1 c/deg but increasing the speed 1.25 times ( $2.5^\circ$ /s). We did not find a facilitation effect like we found for complex stimuli, thus the increasing-speed hypothesis could not explain our results.

In summary, our results show for the first time a direct comparison of two mechanisms in motion perception: surround suppression and interaction between spatial scales. These results show that these mechanisms have different effects on motion discrimination. Although the results obtained with simple stimuli can be explained by the center-surround antagonism displayed by neurons in cortical areas MT and medial superior temporal (MST) (Allman et al., 1985a, 1985b; Tanaka et al., 1986; Born & Tootell, 1992; Eifuku & Wurtz, 1998), as far as we know, there are no physiological results that could explain our results obtained with complex stimuli. We believe that, given the strong suppression found for moving fine features and the facilitation effect found for moving coarse scales, the antagonism between motion sensors tuned to fine and coarse motion sensors must have a neuronal correlate. This poses a challenge for physiologists.

*Keywords: motion discrimination, surround suppression, interaction between motion sensors, motion impairments, inhibition*

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Corresponding author: Ignacio Serrano-Pedraza.

Email: [iserrano@psi.ucm.es](mailto:iserrano@psi.ucm.es).

Address: Faculty of Psychology, Universidad Complutense de Madrid, Madrid, Spain.

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