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Suppressive effects on motion discrimination induced by transient flankers are reduced by perceptual learning

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We investigated spatial suppression of a drifting Gabor target of $0.5\text{ c}/^\circ$ induced by adjacent and iso-oriented stationary Gabors (flankers) whose spatial frequency differed by ± 1 and ± 2 octaves to that of the drifting target. Stimuli (target and flankers) were presented for 33 ms. Results showed greater spatial suppression when the spatial frequency of the stationary but transient flanking Gabors was either equal or 1–2 octaves lower than when it was 1–2 octaves higher than the target's spatial frequency. This asymmetry was evident only for the drifting target, but not for the stationary target. In addition, we investigated whether perceptual learning (PL) reduced the spatial suppression induced by the flankers. We found that PL increased contrast sensitivity for the target, but only when it was reduced by the lateral masking flankers, and its effect did not transfer to an isolated drifting target of equal or higher spatial frequency. These results suggest that PL selectively affects suppressive interactions rather than contrast gain. We suggest that the suppressive effect of low spatial frequency flankers and the lack of suppression with high spatial frequency flankers may reflect two complementary phenomena: camouflage by the transient flankers (i.e., context) and breaking of camouflage by form-motion segmentation. Camouflage may result because both target and flankers activate the motion (magnocellular) system. Breaking of camouflage instead may occur when target and flankers' spatial frequency are more suitable for quasi-independent

activation of the form system (by the flankers) and the motion system (by the target).

Introduction

It is well known that the context can reduce our capability of performing several visual tasks, such as orientation singularity (Casco, Caputo, & Grieco, 2001; Sagi, 1990), texture segmentation (Giora & Casco, 2007; Malik & Perona, 1990), motion discrimination (Alberti, Pavan, Campana, & Casco, 2010; Casco et al., 2001; Casco, Grieco, Giora, & Martinelli, 2006), contrast detection (Maniglia et al., 2011; Polat & Sagi, 1993), and contour binding (Bellacosa Marotti, Pavan, & Casco, 2012; Casco, Campana, Han, & Guzzon, 2009; Casco & Morgan, 1984; Dakin & Baruch, 2009; Robol, Casco, & Dakin, 2012). A texture figure becomes invisible due to the suppression from the surrounding texture (Robol, Grassi & Casco, 2013). Binding elements into contours may be drastically impaired by placing elements in the surround (Bellacosa Marotti et al., 2012; Casco et al., 2009; Dakin & Baruch, 2009; Robol et al., 2012). For example, letter identification is strongly affected by the presence of surrounding letters, a phenomenon known as crowding (Levi, 2008, 2011; Pelli, 2008). Detecting a low-contrast Gabor target can be strongly reduced by high-contrast

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stimuli either surrounding (Petrov, Carandini, & McKee, 2005) or flanking (Polat & Sagi, 1993, 1994a, 1994b) the target, providing that they have the same orientation and spatial frequency of the target. A striking perceptual analog of center-surround neuronal interactions was also demonstrated by Tadin, Lappin, Gilroy, and Blake (2003) in the motion domain. In particular, the authors showed that increasing the size of a high-contrast moving stimulus decreased performance on a direction discrimination task.

Spatial suppression may depend on different mechanisms. It may occur because the surround activates the same filter as the target, thereby increasing its firing rate and reducing the detectability of the target (Carandini, 2004; Loffler, 2008; Petrov et al., 2005; Tadin et al., 2003; Zenger & Sagi, 1996), or it may result from inhibition of the target presented within its classical receptive field by the flanker simultaneously presented outside the target's receptive field (Chen, Kasamatsu, Polat, & Norcia, 2001; Jones, Grieve, Wang, & Sillito, 2001; Knierim & Van Essen, 1992; Nothdurft, Gallant, & van Essen, 1999). Regardless of mask type, suppression is maximal when the mask has the same spatial frequency and the same orientation as the central target (Petrov et al., 2005; Polat & Sagi, 1993, 1994a, 1994b). However, depending on the eccentricity, the type of mask used affects the suppression; surround suppression (Petrov et al., 2005; Petrov & McKee, 2006; Xing & Heeger, 2001) is more effective in the periphery of the visual field, whereas suppression by lateral flankers has been found both in the fovea (Polat & Sagi, 1993, 1994a, 1994b) and in the perifovea (Lev & Polat, 2012; Maniglia et al., 2011; Shani & Sagi, 2005).

Despite the ubiquity of spatial suppression, one can easily experience that directional motion abolishes it. The most compelling example is the breaking of camouflage by motion. Camouflaged animals remain inconspicuous only insofar as they remain static. However, as soon as motion is added, it becomes a powerful cue for figure-ground segregation, allowing detection of moving objects even when their luminance and texture characteristics are matched to the background. Gestalt psychologists (Uttal, Spillmann, Stürzel, & Sekuler, 2000; Wertheimer, 1938) provided the most compelling example of breaking of camouflage by motion. An invisible form defined by randomly arranged dots against a similar dotted background becomes immediately visible as soon as it moves, by virtue of the common fate of its dots, which all move together with a common speed and direction. Psychophysics has demonstrated the role of motion in reducing suppressive effects in contrast detection (Lawton, 2000, 2008), texture segmentation (Alberti et al., 2010; Casco et al., 2001; Casco et al., 2006; Miller & Hurlbert, 1996), contour binding (Ledgeway & Hess,

2002; Watamaniuk, McKee, & Grzywacz, 1995), and biological motion (Dittrich, Troscianko, Lea, & Morgan, 1996; Johansson, 1973).

The ability of motion to reduce contextual suppression raises the theoretical issue of the relationship between the static and motion system (Mather, Pavan, Bellacosa Marotti, Campana, Casco, 2013). The two visual systems processing static and moving stimuli have been classically considered as distinct from the lower to the higher level of central visual processing; the parvocellular system, devoted to processing static form, is more selective to static stimuli of high spatial frequencies, has lower contrast sensitivity, and has sustained responses. On the other hand, the magnocellular system is specialized for motion, has higher contrast sensitivity, is responsive to lower spatial frequencies and higher temporal frequencies, and has transient responses (Derrington & Lennie 1984; Hicks, Lee, & Vidyasagar, 1983; Liu et al., 2006; Maunsell & Newsome, 1987; Schiller & Malpeli, 1987; Shapley, Kaplan, & Soodak, 1981; Ungerleider & Pasternak, 2004). Although there is a considerable overlap in spatial frequency response of the parvocellular and magnocellular systems when using static Gabors, psychophysical and electrophysiological studies indicate a major contribution of the form/static system when spatial frequency is higher than $0.5\text{ c}/^\circ$ and the contrast of the pattern is higher than 5% (Elleberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001; Kulikowski & Tolhurst, 1973; Legge, 1978; Lennie, 1993; Leonova, Pokorny, & Smith, 2003).

The aim of the present study is threefold. First, we ask whether the effectiveness of target motion in reducing spatial suppression induced by flankers depends on their spatial frequency. The moving-target Gabor had a spatial frequency of $0.5\text{ c}/^\circ$ and a temporal frequency of 21 Hz. It should be noted that these parameters are appropriate in stimulating the magnocellular system and, for low contrast stimuli, also prevent the activation of the form system. The stimulus duration was 33 ms. The simplest prediction is that target motion-direction discrimination would not be affected by stationary flankers. However, when stimulus is abrupt and transient, target motion may be masked by the flankers although the transient response is unselective for motion direction (Churan, Richard, & Pack, 2009). This is because a brief stimulus of 33 ms has a very broad temporal frequency spectrum, spreading on both sides of the origin of the temporal frequency axis, so a stimulus moving leftward will also excite detectors tuned to rightward motion, and vice versa (Derrington & Goddard, 1989). Thus, we ask whether transient flankers have different suppressive effects when they have a spatial frequency equal or 1–2 octaves lower than the target with respect to the condition in which the spatial frequency is 1–2 octaves higher. Indeed, on the basis of the hypothesis

of a relative independence between the two systems, we would predict less suppression with high spatial frequency flankers, because the onset transients are particularly effective in the magnocellular processing stream selective for low spatial frequencies (Churan et al., 2009).

In addition, we also asked whether perceptual learning (PL) enhances the effectiveness of the motion system in reducing the spatial suppression induced by the flankers and, if so, whether the reduced spatial suppression depends on the flankers' spatial frequency. This second question has hardly been addressed before. Many studies have proved that PL is a powerful tool to reduce the suppression exerted by the context (Adini, Sagi, & Tsodyks, 2002; Karni & Sagi, 1991; Maniglia et al., 2011; Polat, Ma-Naim, Belkin, & Sagi, 2004). The reduction of suppression has mostly been demonstrated in the static domain with contrast-detection tasks. However, it is unknown whether and how PL improves motion-direction discrimination by reducing spatial suppression. If this is the case, then the inhibition by PL of neural mechanisms that play a critical role in spatial suppression should restore target's motion-direction discrimination. Thus, our hypothesis was that if suppression occurs within the motion pathway, PL should weaken the spatial suppression induced by flankers producing a larger response in the motion system for low spatial frequencies.

Finally, by testing before and after PL the contrast sensitivity for an isolated target and manipulating the spatiotemporal properties of this transfer stimulus, we asked whether PL effectively reduces spatial suppression for the flankers rather than simply increasing the target's contrast gain. Based on the finding that PL of contrast detection with static stimuli may reduce contrast thresholds in addition to a modulation of lateral interactions, it may be expected that PL results in both (a) reduction of spatial suppression and (b) increase of contrast gain for the target (Casco, Guzzon, Moise, Vecchies, Testa, & Pavan, 2014; Maniglia et al., 2011; Polat, 2009; Sagi, 2011).

General methods

Participants

Eight observers (five males and three females), aged 21–26 years, took part in the PL experiment. All participants had normal or corrected-to-normal visual acuity. They sat in a dark room at a distance of 57 cm from the screen. Viewing was binocular. Participants were instructed to fixate at the center of the screen. All participants took part voluntarily and informed oral consent was obtained from all the subjects before the

study was initiated. The study and protocol conformed to the tenets of the Declaration of Helsinki.

Apparatus

Stimuli were displayed on a 22-in. Philips 202P4 CRT monitor with a refresh rate of 85 Hz, and generated using Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1600×1200 pixels. The minimum and maximum luminance of the screen were 0.63 and 112.1 cd/m^2 , respectively, and the mean luminance was 56.8 cd/m^2 . Luminance was measured with a CRS Optical photometer (OP200-E; Cambridge Research System Ltd., Rochester, Kent, UK). A digital-to-analog converter (Bits#, Cambridge Research Systems, Cambridge, UK) was used to increase the dynamic contrast range (12-bit luminance resolution). A 12-bit gamma-corrected lookup table (LUT) was applied so that luminance was a linear function of the digital representation of the image.

Stimuli

Form-motion spatial suppression and PL

Before and after the training sessions we measured contrast thresholds for motion-direction discrimination of a central vertically oriented drifting Gabor target, flanked above and below by vertically oriented stationary high-contrast Gabor patches (0.6 Michelson contrast; i.e., form-motion spatial suppression). This generated a vertical collinear configuration of three Gabor patches. Gabor patches consisted of a sinusoidal carrier enveloped by a stationary Gaussian. The Gabor patches had $\sigma = 1^\circ$. The drifting target Gabor had a spatial frequency of 0.5 $\text{c}/^\circ$ and a temporal frequency of 21 Hz (speed: $42^\circ/\text{s}$); these parameters are appropriate to stimulate the magnocellular system (Derrington & Lennie, 1984). Flankers were located at a fixed distance from the central target (center-to-center distance: 3°). The spatial frequency of the flankers could vary ± 1 and ± 2 octaves with respect to the target's spatial frequency whose spatial frequency was constant at 0.5 $\text{c}/^\circ$. In the PL sessions we used the same stimulus configuration and observers were trained in discriminating the motion direction of the central target (see the General procedure section).

Transfer stimuli: Unflanked drifting gratings

Before and after the training sessions we also measured contrast thresholds for motion-direction discrimination of unflanked drifting Gabor patches. Contrast thresholds for motion-direction discrimination were estimated only for a single vertical Gabor patch

Temporal frequency (Hz)	Spatial frequency (c/°)		
	0.5	4.0	6.0
0.5 Hz	1°/s		
3.0 Hz	6°/s	0.75°/s	
21.0 Hz	42°/s	5.25°/s	3.5°/s

Table 1. Spatial frequencies, temporal frequencies, and speeds (°/s) of the central unflanked drifting Gabor used in the pre- and post-training sessions.

presented at the center of the screen. We used three spatial frequencies (0.5, 4, and 6 c/°) and three temporal frequencies (0.5, 3, and 21 Hz). Table 1 reports the speeds (calculated as the ratio between the temporal and spatial frequency) used in the pre- and post-training sessions for unflanked drifting Gabor patches.

General procedure

Pre- and post-training sessions

Before and after the training sessions we estimated contrast thresholds for motion-direction discrimination of a central drifting Gabor patch with a spatial frequency of 0.5 c/° and a temporal frequency of 21 Hz flanked above and below by two stationary high-contrast Gabors (i.e., form-motion spatial suppression experiment). The spatial frequency of the flankers was varied block-wise. In addition, we also measured contrast thresholds for motion-direction discrimination of drifting unflanked Gabors, manipulating in separate blocks the spatial and temporal frequencies (see Table 1). The spatial phase of the target stimulus was randomized on each trial.

We used a binary choice task (Method of Single Stimuli, MSS; Morgan, Dillenburger, Raphael, & Solomon, 2012) in which the observers were required to discriminate the motion direction of the central target by pressing one of two designated keys on a standard computer keyboard (i.e., “M” key to indicate rightward motion, and “Z” key to indicate leftward motion).

The stimulus duration (i.e., target and flankers) was 33 ms and the intertrial interval was 1 s. We used 33 ms because at this stimulus duration, surround suppression has been shown to be quite strong (Churan, Khawaja, Tsui, & Pack, 2008; Tadin et al., 2003; Tadin & Lappin, 2005). Contrast thresholds for motion-direction discrimination were estimated using two interleaved one-up/three-down staircases (Levitt, 1971), with contrast varying in steps of 0.1 log units. The first staircase started at a contrast level of 0.85 (Michelson contrast), whereas the second staircase started at a contrast level

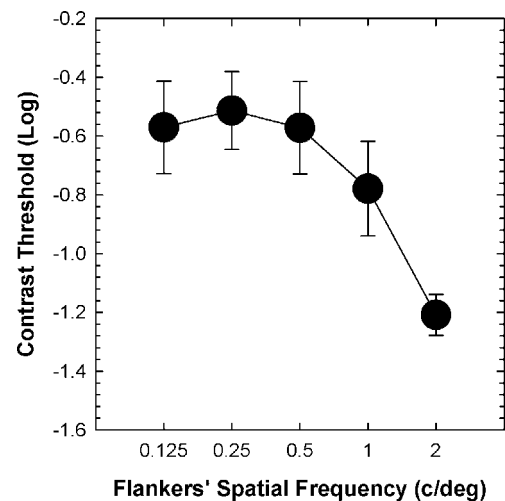


Figure 1. Mean log-contrast thresholds obtained before training for flankers with lower (0.25 and 0.125 c/°), equal (0.5 c/°), and higher (1 and 2 c/°) spatial frequencies than the target's spatial frequency (0.5 c/°). Error bars \pm SEM.

of 0.2. The two staircases were randomized on a trial basis. For example, the first trial could belong to the first staircase, the second trial to the first staircase, the third trial to the second staircase, and so on. The session terminated after either 200 trials or 10 reversals. Contrast thresholds, corresponding to 79% correct responses, were calculated averaging the contrast values corresponding to the last eight reversals and then averaging the two contrast thresholds form the two staircases. No feedback was provided.

PL sessions

A daily session consisted of five blocks. The spatial frequency of the stationary flankers was varied block-wise (spatial frequencies: 0.125, 0.25, 0.5, 1, and 2 c/°), while the target's spatial frequency (i.e., the central Gabor patch) and the target's temporal frequency were constant at 0.5 c/° and 21 Hz, respectively. Each session was approximately 30 min in duration and was administrated four times within the training week. Contrast thresholds for motion-direction discrimination were estimated as described for the pre- and post-training sessions.

Results

Form-motion spatial suppression

Figure 1 shows mean log-contrast thresholds obtained before training with flankers of lower (−1 and −2 octaves), equal, and higher spatial frequency (+1 and

Flankers' spatial frequency	Raw contrast-discrimination thresholds for motion direction						Threshold elevation for motion direction					Raw contrast-detection threshold for static target				
	0.125	0.25	0.50	1.00	2.00	Isolated target	0.125	0.25	0.50	1.00	2.00	0.125	0.250	0.500	1.000	2.000
<i>M</i>	0.390	0.41	0.38	0.27	0.07	0.04	0.830	0.89	0.83	0.62	0.19	0.029	0.034	0.053	0.035	0.027
<i>SD</i>	0.300	0.27	0.27	0.27	0.27	0.02	0.470	0.41	0.48	0.47	0.22	0.005	0.012	0.012	0.009	0.005

Table 2. Mean raw contrast thresholds for motion-direction discrimination, mean threshold elevation for motion-direction discrimination, and mean raw contrast-detection thresholds for a static target. *Note:* Mean contrast thresholds for the isolated target are also reported (individual contrast thresholds for the isolated target were: 0.036 [SD: 0.0147], 0.045 [SD: 0.0086], 0.043 [SD: 0.0095], 0.044 [SD: 0.0403], 0.036 [SD: 0.0091], 0.054 [SD: 0.0122], 0.033 [SD: 0.0134], and 0.032 [SD: 0.0117]). Threshold elevation has been calculated for each subject as $\log_{10}(\text{flanked}/\text{isolated})$; the log ratio between contrast thresholds for motion-direction discrimination of the flanked target (for each flankers' spatial frequency) and the contrast threshold for motion-direction discrimination of the isolated target with spatial frequency of 0.5 $c/^\circ$ and temporal frequency of 21 Hz.

+2 octaves) relative to the target. Raw contrast thresholds are reported in Table 2.

A repeated-measures ANOVA conducted on the log-contrast thresholds revealed a significant effect of the flankers' spatial frequency, $F(4, 28) = 23.85$, $p = 0.0001$. Bonferroni-corrected pairwise comparisons revealed a significant difference between the contrast thresholds obtained with flankers at 0.5 $c/^\circ$ (i.e., at the same spatial frequency of the target; $p = 0.004$), at 0.25 $c/^\circ$ ($p = 0.001$), at 0.125 $c/^\circ$ ($p = 0.001$), and flankers at 2 $c/^\circ$. The difference between flankers of 2 and 1 $c/^\circ$ approached significance ($p = 0.052$). These results suggest that nontranslating flankers of lower and equal spatial frequency to that of the drifting target produce stronger threshold elevation than do flankers of higher spatial frequency. The question is whether this is peculiar for the form-motion configuration used.

Spatial suppression with a static target

With static stimulus configurations, the reduction of spatial suppression by the flankers follows different rules. Static spatial suppression when investigated with a surrounding mask stimulus is known as surround suppression (Petrov et al., 2005). Typically, the largest threshold elevation with surround suppression was found for a mask of the same spatial frequency as the target (1 $c/^\circ$), with threshold elevation decreasing as the mask's spatial frequency differed by ± 1 and ± 2 octaves from the target's spatial frequency. Indeed, Petrov et al. (2005) found that the tuning curve for surround suppression was sharply peaked at a bandwidth of ~ 1.5 octaves for surrounds of both lower and higher spatial frequencies. Meese and Hess (2004) found strong surround suppression when the target had a spatial frequency of 0.47 $c/^\circ$ and that of the mask was 3 times higher. However, with adjacent masking stimuli (i.e., flankers) and static targets, the characteristics of spatial suppression is less clear. Polat and Sagi (1993) showed similar threshold elevation for mask/target

wavelength ratio of 0.5 and 2, but the comparison between the two conditions is not straightforward since the target had a different spatial frequency. Therefore, it is possible that the asymmetry we found with moving targets is not peculiar for motion, but it may occur even with static targets provided that masking is adjacent rather than surrounding. In order to test for this possibility we measured the masking effect of adjacent flankers whose spatial frequency differed by ± 1 and ± 2 octaves from that of a stationary target.

Method

Stimuli were centrally presented and consisted of a vertical stationary Gabor (target) flanked above and below by stationary high-contrast Gabor patches (0.6 Michelson contrast). Flankers were always vertically oriented and located at fixed distance from the central target (center-to-center distance: 3°). The spatial frequency of the flankers was varied across sessions and could have either the same spatial frequency of the target or ± 1 and ± 2 octaves with respect to the target's spatial frequency that was constant at 0.5 $c/^\circ$. In this experiment we used a temporal-2AFC in which the target was presented in only one of two temporal intervals. Each interval was 33 ms with an interinterval delay of 500 ms. Twelve participants took part to the experiment, and they were required to choose which of the two temporal intervals contained the target. Contrast-detection thresholds were estimated using two interleaved one-up/three-down staircases (Levitt, 1971) as described in the General procedure section.

Results

Results are shown in Figure 2. A repeated-measures ANOVA conducted on log-contrast thresholds revealed a significant effect of the flankers' spatial frequency, $F(4, 44) = 6.56$, $p = 0.0001$. Bonferroni-

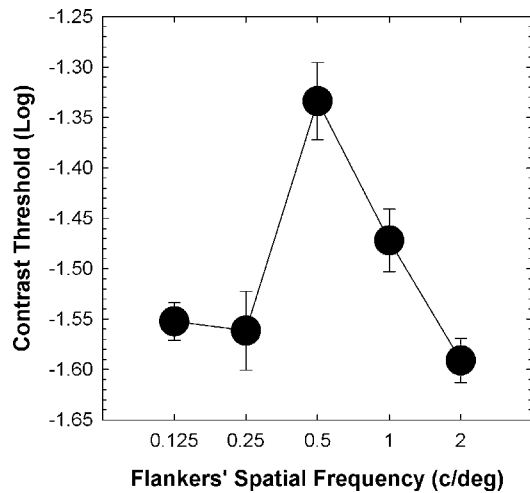


Figure 2. Mean log-contrast thresholds obtained for a centrally presented stationary target as a function of the flankers' spatial frequency (i.e., 0.125, 0.25, 0.5, 1 and 2 c/°). Error bars \pm SEM.

corrected pairwise comparisons revealed a significant difference between the contrast thresholds obtained with flankers of 0.5 c/° and those obtained with flankers of 0.125 ($p = 0.025$), 0.25 ($p = 0.028$), and 2 c/° ($p = 0.017$). The difference between 0.5 and 1 c/° was not significant ($p = 0.11$).

These results indicate that when the flankers' spatial frequency was 1 and 2 octaves higher, the reduction of suppressive effect, relative to the condition with flankers of the same spatial frequency, was similar to what was found with moving targets. Moreover, the contrast-detection threshold for the static target obtained with flankers' spatial frequency 2 octaves higher than the target's spatial frequency was very similar to that obtained with the isolated moving target (i.e., $\log_{10}[0.04] = -1.4$; see Table 2). However, differently from what found with a moving target, a reduction of suppression occurred even when the mask spatial frequency was 1 and 2 octaves lower than the static target. This suggests that the most relevant variable accounting for the higher contrast thresholds obtained with a moving target is the suppression exerted by low spatial frequency flankers rather than the mask type (i.e., flanking vs. surrounding) or the different task (i.e., detection vs. discrimination).

The present results confirm that the asymmetry in spatial suppression, by which motion reduces spatial suppression of flankers of higher but not lower or equal spatial frequency than the target, is peculiar for the motion task.

Perceptual learning

Figure 3 shows the effect of PL on spatial suppression as a function of the flankers' spatial

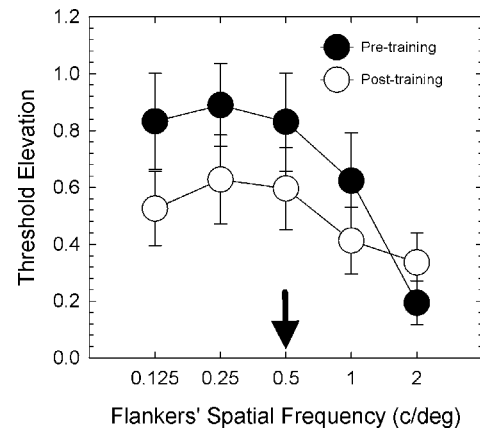


Figure 3. Mean threshold elevation estimated before (pre) and after (post) the perceptual training. Threshold elevation is shown as a function of the flankers' spatial frequency. The black arrow indicates the target's spatial frequency (0.5 c/°). Error bars \pm SEM.

frequency. The figure represents threshold elevation obtained with flankers of the same (0.5 c/°) and either lower or higher spatial frequencies than the target's spatial frequency (0.5 c/°). Contrast thresholds for motion-direction discrimination obtained with flankers of these five spatial frequencies were normalized by the baseline threshold obtained in the condition where the target was presented isolated:

$$\text{Threshold elevation} = \log_{10} \left(\frac{\text{flanked}}{\text{isolated}} \right) \quad (1)$$

A repeated-measures ANOVA conducted on threshold elevation data revealed a significant effect of the PL, $F(1, 7) = 6.4$, $p = 0.039$, and of flankers' spatial frequency, $F(4, 28) = 20.3$, $p = 0.0001$. The interaction between learning sessions (i.e., pre-PL vs. post-PL) and flankers' spatial frequency was also significant, $F(4, 28) = 9.3$, $p = 0.0001$. Bonferroni-corrected pairwise comparisons revealed a significant effect of PL at flankers' spatial frequency of 0.125 c/° ($p = 0.01$), 0.25 c/° ($p = 0.004$), and 0.5 c/° ($p = 0.021$), but not at flankers' spatial frequency of 1 cpd ($p = 0.11$) and 2 cpd ($p = 0.13$). These results clearly indicate that PL selectively reduced spatial suppression induced by the flankers, in the conditions in which suppression was substantial.

Transfer of PL to untrained moving unflanked Gabors

The results relative to the transfer of PL to untrained moving unflanked Gabors are shown in Figure 4. The highest speed condition corresponds to that used in the PL experiment. A repeated-measures ANOVA includ-

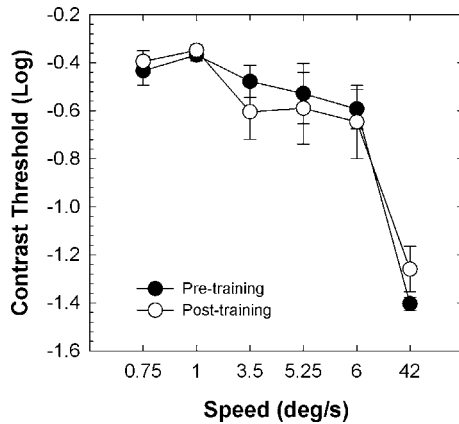


Figure 4. Mean log-contrast thresholds estimated before (pre) and after (post) the training sessions for an unflanked drifting target Gabor presented at the center of the screen at different speeds. The highest speed corresponds to that used in the PL experiment. Speeds were obtained combining different spatial and temporal frequencies (see Table 1). Error bars \pm SEM.

ing PL (before vs. after) and speed of the unflanked Gabor (0.75°/s, 1°/s, 3.5°/s, 5.25°/s, 6°/s, and 42°/s) as main factors, showed a significant effect of the speed, $F(5, 35) = 22.7$, $p = 0.001$. Bonferroni-corrected pairwise comparisons showed that on average the contrast threshold for the stimulus drifting at 42°/s was lower than those estimated with any other speed (6°/s: $p = 0.026$; 5.25°/s: $p = 0.0001$; 1°/s: $p = 0.01$; 0.75°/s: $p = 0.0001$; 3.5°/s: $p = 0.009$). However, the effect of PL was not significant, $F(1, 7) = 0.06$, $p = 0.82$. These results indicate no PL effect for the isolated target having either the same or different combination of spatial and temporal frequency with respect to the flanked target.

These results suggest that the effect of PL did not produce contrast gain but instead it may have reduced inhibitory lateral interactions exerted by the flankers of lower spatial frequency than the target.

Discussion

In the present study we found higher spatial suppression of a drifting Gabor flanked by high-contrast Gabors when the spatial frequency of the flankers was equal or 1–2 octaves lower than the target's spatial frequency (that was constant at 0.5 $c/^\circ$), whereas we found no or strongly reduced masking effects when the flankers' spatial frequency was 1–2 octaves higher than the target. This asymmetry, dependent on flankers' spatial frequency, was specific to the drifting target, since it was not obtained when using a stationary target. Second, we found that PL increased the contrast sensitivity for the target only when it was reduced by flankers' spatial frequencies of

0.125, 0.25 and 0.5 $c/^\circ$. Third, the PL effect did not transfer to an isolated drifting target having either the same or higher spatial frequency than the target and a temporal frequency varying between 0.5 and 21 Hz.

We suggest that the suppressive effect with low spatial frequency flankers and the lack of suppression with high spatial frequency flankers reflect two complementary phenomena: camouflage by the transient context and breaking of camouflage by form-motion segmentation. It should be noted that the breaking of camouflage by form-motion segmentation is different than the breaking of camouflage induced by motion, in which adding directional motion to the target abolishes spatial suppression induced by the static context (Wertheimer, 1938). Indeed, in our transient stimulation the motion system is likely to drive target suppression, and increasing flankers' spatial frequency produces a form-motion segmentation that extinguishes the motion camouflage. We argue that breaking of motion camouflage may occur when the target and flankers' spatial frequency are more suitable for quasi-independent activation of the form system (activated by the flankers) and the motion system (activated by the target). In our transient stimulation is the abrupt onset/offset of the transient flankers (33 ms) to exert the suppressive effect. Indeed, in Fourier space such a transient stimulus is far from static. It contains a lot of energy at \sim 30–60 Hz, predictably generating strong biphasic temporal responses in motion sensors. Although this transient response is unselective for motion direction (Churan et al., 2009), directional information might be contained within oriented stimuli. Presumably, it will be most abundant in directions orthogonal to the orientation of the flankers. Therefore, peripheral flankers producing simultaneous left and right direction responses would interfere with left-right judgments at the target locations. However, this does not explain why the suppression was substantial only with low spatial frequency flankers. One explanation for the nonsymmetrical effect of flankers whose spatial frequency differed by ± 1 and ± 2 octaves from the moving target is that motion-selective cells tend to be low spatial frequency biased. Therefore, although both low and high spatial frequency flankers are transient, suppression tends to be stronger when the suppressive surround has a low spatial frequency content. According to this interpretation, the suppression of the moving target observed in Experiment 1 is likely to be due to the suppressive response of the motion system. Instead, this suppression would not occur when the flankers' spatial frequency is high, despite them being abrupt and highly transient.

Our results present some similarities with previous psychophysical data showing a decrease in performance on a direction discrimination task with increasing

stimulus size (Tadin et al., 2003). Tadin et al. (2003) suggested that the finding is consistent with receptive properties of visual neurons and provide converging evidence that impaired motion-direction discrimination for large stimuli is a perceptual correlate of center-surround antagonism. In our study there are, however, important novelties, such as, first of all, the previously mentioned spatial frequency selectivity of the suppressive effect. Second, in Tadin et al.'s (2003) study, surround suppression is shown to occur providing that the stimulus contrast is high. Indeed, Tadin, Lappin, and Blake (2006) showed that the influence was suppressive with high-contrast targets, whereas with low-contrast targets the influence of the surround motion was facilitatory. Instead, by measuring contrast thresholds for motion-direction discrimination, we were able to show that the direction of motion of the target became discriminable at high contrast. Despite these differences, it appears that with both static and moving surround, surround suppression is strongest when the stimulus is presented very briefly so that the onset of the stimulus coincided with its motion (Churan et al., 2009). Indeed, these authors have shown that when a brief delay was inserted between the stimulus onset and the onset of motion, the surround suppression disappeared. They concluded, in agreement with us, that psychophysical surround suppression is partially linked to the temporal structure of the stimulus, more precisely to a masking effect caused by sudden stimulus onsets. However, our results suggest that spatial suppression depends not only on the temporal structure of the stimulus but also on its spatial frequency content. Indeed, low spatial frequency target suppression is strongly reduced when flankers presumably stimulate channels selective to higher spatial frequencies, whereas the target stimulates low spatial frequency channels. Thus the target may stimulate mainly the motion system, whereas flankers with high spatial frequency, although abrupt and highly transient, may stimulate more the form system. The dissociation between the effect of low and high spatial frequency flankers suggest this interpretation, which seems congruent with the evidence of a considerable overlap in spatial frequency response of parvocellular and magnocellular systems (Ellemberg et al., 2001; Kulikowski & Tolhurst, 1973; Legge, 1978; Lennie, 1993; Leonova et al. 2003). Indeed, static high-contrast Gabors are optimal for the form system when their spatial frequency ≥ 1 $c/^\circ$, but stimulate both the form and motion system when spatial frequency ≤ 0.5 $c/^\circ$ (Lennie, 1993; Leonova et al., 2003). Note that we chose to use high-contrast flankers to reduce the probability that flankers increase the response to the target rather than reducing it (Churan et al., 2008; Meese & Summers, 2007; Tadin et al., 2003; Tadin & Lappin, 2005; Zenger & Sagi, 1996).

The present study reveals, for the first time, the low level nature of underlying neural mechanisms for the camouflage driven by the transient system (Cass, Van der Burg, & Alais, 2011) and breaking of camouflage by form-motion segmentation. The dependence of spatial frequency suggests that the effect of flankers on the moving target may occur at a lower level in the central motion system, possibly in V1 and V2 where neurons are selective for spatial frequency and motion direction (Orban, Kennedy, & Bullier, 1986; Mikami, Newsome, & Wurtz, 1986; Priebe, Lisberger, & Movshon, 2006).

The open question is whether camouflage of the moving target by the static flankers can be accounted by either within or across channel inhibition. This is also an open question for the suppressive effects in the static domain. For example, it has been suggested that lateral masking may result from a combination of mechanisms: contrast integration within the receptive field (Zenger & Sagi, 1996) and broadband inhibition between neighboring cells (in space, orientation, and spatial frequency; Chen et al., 2001; Mizobe et al., 2001). Similarly, surround suppression can result either from within (Carandini, 2004) or cross-channel inhibition, considering that it occurs when mask and test stimuli are very different in spatial frequency and presented to different eyes (Meese, 2004; Meese & Hess 2004). We suggest that a combination of mechanisms may also underlie spatial suppression effects with a moving target. Camouflage may result when target and flankers stimulate similar channels (i.e., those of the magnocellular system). Breaking of camouflage instead may occur when target and flankers stimulate different channels (i.e., those of the magnocellular and parvocellular system, respectively). The breaking of camouflage may suggest a quasi-independent activation of the motion and form systems at a low level of visual processing.

The second result is that PL reduces camouflage. The effect of PL was present at flanker spatial frequencies of 0.125, 0.25, and 0.5 but not at flankers' spatial frequency of 1 and 2 $c/^\circ$. To grasp the effectiveness of this effect, let us compare the effect of PL with flankers 2 octaves lower and higher than the target. Whereas contrast thresholds were reduced by PL from 0.4 to 0.2 in the condition with the lowest flankers' spatial frequency (i.e., 0.125 $c/^\circ$), contrast threshold in the condition with the highest flankers' spatial frequency (i.e., 2 $c/^\circ$) was unaffected by PL (0.07 vs. 0.1). Moreover, in this last condition, contrast thresholds did not differ from those obtained with an unflanked target. These results suggest that PL may selectively reduce the spatial suppression induced by the flankers when their spatial frequency is equal or lower than the target's spatial frequency. This result is relevant because two distinct effects of PL could be hypothesized: increased contrast gain for the target and a

reduction of spatial suppression from the flankers, or a mixture of these two effects (Casco et al., 2014; Maniglia et al., 2011; Polat, 2009; Sagi, 2011). Using static target and flankers, PL results in both reduction of spatial suppression and increase of contrast gain for the target. Indeed, it is well known that PL of contrast detection with a target-to-flankers distance of 2λ transfers to isolated gratings improving contrast sensitivity (Casco et al., 2014; Maniglia et al., 2011; Polat, 2009; Sagi, 2011). The distinction between these two PL effects can be investigated in the motion domain by measuring contrast threshold for motion-direction discrimination (Doshier & Lu, 1998; Lu, Chu, & Doshier, 2006). If PL reflects a contrast-gain mechanism, this would improve contrast sensitivity to the target regardless of whether is flanked or not. Instead if PL produces a flanker exclusion, this would increase in contrast sensitivity for the target only in the presence of the flankers. We found that PL only reduces spatial suppression for the drifting grating, and it has no effect on contrast gain. Indeed, our results suggest that there is no difference in contrast threshold obtained before and after PL with an isolated target and when it is presented amongst high spatial frequency flankers (2 c°).

Keywords: spatial suppression, lateral masking, motion and form systems, perceptual learning, camouflage

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