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No priming for global motion in crowding

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There is psychophysical evidence that low-level priming, e.g., from oriented gratings, as well as high-level semantic priming, survives crowding. We investigated priming for global translational motion in crowded and noncrowded conditions. The results indicated that reliable motion priming occurs in the noncrowded condition, but motion priming does not survive crowding. Crowding persisted despite variations in the direction of the flankers with respect to the prime's direction. Motion priming was still absent under crowding when 85% of the flankers moved in the same direction as the prime. Crowding also persisted despite variations in the speed of the flankers relative to the prime even when the flankers' speed was four times slower than the speed of the prime. However, a priming effect was evident when the prime's spatial location was precued and its distance to the flankers increased, suggesting a release from crowding. These results suggest that transient attention induced by precueing the spatial location of the prime may improve subjects' ability to discriminate its direction. Spatial cueing could act to decrease the integration field, thereby diminishing the influence of nearby distracters. In an additional experiment in which we used fewer flankers, we found a priming effect under conditions in which the interelement distance varied between flankers and prime. Overall, the results suggest that motion priming is strongly affected by crowding, but transient attention can partially retrieve such facilitation.

Introduction

The identification of a target stimulus can be significantly impaired by the presence of nearby stimuli. This phenomenon is known as crowding (D. Levi, 2008). The spatial extent of crowding is usually defined by Bouma's window: Target identification is impaired only within a window, the size of which is defined as half of the target eccentricity (Bouma, 1970; Pelli, 2008).

There are several explanations for crowding. In pooling models, crowding occurs when target and flankers are combined within the same receptive field (Pelli, Palomares, & Majaj, 2004). In the peripheral retina, receptive fields are much larger than in the fovea, and the probability that several features from adjacent stimuli are integrated into the same receptive field becomes higher with increasing eccentricity (Bouma, 1970). Therefore, based on Pelli et al. (2004), crowding is likely to occur at an intermediate level in which the output of single feature detectors is integrated within what they called the "integration fields." According to this bottom-up hypothesis, the integration of visual features occurs preattentively. As a mechanism, it was proposed that crowding occurs through compulsory averaging of target and flanker signals (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). In more complex pooling models, it is suggested

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that the visual system locally represents peripheral stimuli by the joint statistics of responses of neurons sensitive to different positions, spatial frequency, phase, orientation, and scale. Such textural representation is able to predict the jumbling of features in crowding (Balas, Nakano, & Rosenholtz, 2009; Freeman & Simoncelli, 2011).

In substitution models, crowding is thought to occur because features of the flankers (or flankers in their entirety) are confused with features of the target (Ester, Klee, & Awh, 2014; Huckauf & Heller, 2002; Krumhansl & Thomas, 1977). In this case, degraded target perception could arise from a loss of spatial position information or source confusion (Dakin, Bex, Cass, & Watt, 2009; Nandy & Tjan, 2007; Popple & Levi, 2005; Strasburger & Malania, 2013).

There are also top-down explanations for crowding. These theories state that crowding could depend on coarse spatial resolution of attention in the peripheral visual field (Fang & He, 2008; He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001; Kristjánsson, Heimisson, Róbertsson, & Whitney, 2013) or on unfocussed attention (Strasburger, 2005). Yeshurun and Rashal (2010) found that precueing the target location diminishes the effects of crowding and reduces the critical distance for crowding (i.e., the target-to-flankers distance at which the flankers no longer interfere with target identification). Dakin et al. (2009) used an orientation-averaging task in which observers judged the mean orientation of a set of oriented elements either in isolation or crowded by other elements with random orientation. Observers performed also a concomitant attentional task. The results showed that crowding increases the local uncertainty of the orientation of single elements, thus limiting the estimation of local orientation, and distraction by a task at fixation reduced the overall global efficiency, i.e., the orientation information was pooled over a smaller number of elements. These results suggest that attentional and substitution theories are not mutually exclusive.

There is psychophysical evidence suggesting that despite the fact that a crowded target stimulus cannot be discriminated, its information is still processed and is able to guide performance. In the motion domain, for example, a number of studies have shown that high-order motion aftereffects (MAEs) from adaptation to complex motion (e.g., Aghdaee, 2005; Pavan & Greenlee, 2015), second-order motion (Harp, Bressler, & Whitney, 2007), and apparent motion (Rajimehr, Vaziri-Pashkam, Afraz, & Esteky, 2004) persist although reduced in strength. Similarly, other studies, using a priming paradigm with simple oriented stimuli (Faivre & Kouider, 2011a), multifeature crowded objects, such as faces and directional symbols (Faivre & Kouider, 2011b) and semantic stimuli (Peng, Zhang, Chen, & Zhang, 2013; Yeh, He, & Cavanagh, 2012), reported that the crowded prime is encoded, showing a priming effect.

In this study, we investigated the effects of crowding and priming on global motion perception. Motion priming occurs when the processing of a subsequently presented highly visible target is facilitated by a preceding related prime stimulus. Visual priming has been explained in terms of increased saliency of primed features or facilitated deployment of attention to the primed features (Kristjánsson, 2006; Kristjánsson & Nakayama, 2003; Maljkovic & Nakayama, 1994, 1996).

According to the perceptual representation system hypothesis (Tulving & Schacter, 1990) and the sensory memory hypothesis (Magnussen & Greenlee, 1999), visual priming relies on the same brain areas that are responsible for the analysis and representation of a specific visual attribute (Kristjánsson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007). For example, in agreement with this hypothesis, Campana, Cowey, and Walsh (2002, 2006) found that disruption of cortical areas V5/MT had the effect of abolishing priming for motion direction, but it had no effect on priming for spatial position, which is strictly dependent on the functional integrity of the left frontal eye field (Campana, Cowey, Casco, Oudsen, & Walsh, 2007). Thus, using global moving stimuli as prime and probe, it is possible to investigate how facilitation, by means of the priming effect, is deployed at a high-level of motion processing. In addition, neuroimaging and psychophysical studies have shown that crowding is likely to be a multistage process (Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, 2012; Bi, Cai, Zhou, & Fang, 2009; Faivre, Berthet, & Kouider, 2012; Fang & He, 2008; Ikeda, Watanabe, & Cavanagh, 2013; Millin, Arman, Chung, & Tjan, 2013), involving low and high levels of visual analysis.

In a series of experiments, we investigated visual motion priming for globally moving patterns in crowded and noncrowded conditions. In Experiment 1, we attempted to replicate recent findings of Faivre and Kouider (2011a) in the motion domain. Using a priming paradigm in which observers had to perform orientation discrimination on a probe stimulus presented for 0.2 s after the prime, the authors manipulated the prime discriminability and the prime duration. When the prime orientation was not discriminable, they found that increasing its duration (1 s) produced a negative priming effect (i.e., reaction times [RTs] were shorter when prime and probe had different orientations). On the other hand, when the prime orientation was discriminable, the authors found a positive priming effect (i.e., shorter RTs when prime and probe had the same orientation) that was higher for the shorter prime duration (0.2 s). Increasing the prime duration (1 s) led to a decrease of the positive priming effect instead of a reversed effect. In our first experiment, we manipulated the duration of the globally moving prime (0.2, 0.5, 1, and 2 s) in order to assess whether, in the crowded condition, we were able to obtain a shift from positive priming (facilitation) to a negative priming effect (suppression). Surprisingly, our findings showed a complete absence of facilitation or suppression in the crowded condition whereas in the noncrowded condition (i.e., when the prime motion direction was discriminable) we could replicate the findings of Faivre and Kouider (2011a). We then performed a series of experiments aimed at investigating the absence of visual motion priming in the crowded condition. In Experiment 2, we tested whether the direction of the flankers relative to that of the prime modifies its effect. The rationale was that if the motion direction of flankers and prime are pooled and then averaged (in line with what is proposed by pooling models), increasing the number of flankers moving in the same direction to that of the prime should bias the average direction of the whole configuration (made up by flankers and prime) toward the direction of the prime, thus inducing an increase in the priming effect. However, following this manipulation, we found no increase in the priming effect in the crowded condition. This finding suggests that the sensory representation of the moving prime is likely to be degraded or corrupted by adjacent moving flankers, making the motion information of the crowded prime no longer available to the visual system. In Experiment 3, we further confirmed this hypothesis by varying the relative speed of the flankers with respect to the prime speed. The results showed that, regardless of their speed, the flankers maximally interfered with the sensory representation of the prime, inducing a reliable crowding effect even when the flankers were four times slower than the prime. In Experiment 4A and 4B, we investigated the role of attention and spacing (i.e., interelement distance) between flankers and prime. Yeshurun and Rashal (2010) showed that the critical distance was significantly reduced when the interelement spacing was combined with a precue indicating the target's location before it was presented. Using a similar procedure, we found that precueing the prime's location moderately reduces crowding strength and, hence, leads to a small increase of motion priming. Taken together, our findings suggest that motion priming is highly affected by crowding.

General methods

Apparatus

Stimuli were displayed on a 23-in. Samsung T23A750 monitor with a refresh rate of 60 Hz. Stimuli were generated with Matlab PsychToolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1920 × 1080 pixels. Each pixel subtended 1.6 arcmin. The minimum and maximum luminances of the screen were 0.22 and 88.07 cd/m^2, respectively, and the mean luminance was 42.8 cd/m^2. Luminance was measured with a photometer (OP200-E, Cambridge Research System Ltd., Rochester, Kent, UK). A gamma-corrected lookup table was used so that luminance was a linear function of the digital representation of the image. To monitor central fixation, the gaze position of the right eye of the observers was continuously measured using a CRS High-Speed Video Eye-Tracker (Cambridge Research System Ltd., Rochester, Kent, UK; average spatial resolution: 0.125° to 0.25° of visual angle, sampling rate: 250 Hz). Observers sat in a dark room at a distance of 57 cm from the screen. The participant's head was stabilized by asking her or him to rest her or his chin on a chin rest. Participants were instructed to fixate at the center of the screen. Viewing was binocular.

Participants

All participants took part voluntarily, and all received compensation for their time (except for the authors). In addition, all participants gave written informed consent prior to their inclusion in the experiment. Approval from the ethics committee of the University of Regensburg was obtained prior to the start of this study. All participants had normal or corrected-to-normal visual acuity.

Stimuli

Stimuli consisted of globally moving dots (100% coherence) presented in a circular window. The whole circular array was displayed within a Gaussian envelope with a maximum contrast of 0.99 and $\sigma = 1.9°$ (Knapen, Rolfs, & Cavanagh, 2009), subtending a circular aperture of 3° diameter and a density of 14 dots/$^{\circ 2}$. Stimuli with blurred edges are likely to reduce retinotopic effects and are likely to stimulate a high level of motion processing (Ezzati, Golzar, & Afraz, 2008; Knapen et al., 2009). Each moving patch was made up by 50 dots: 50% of the dots were white (88.07 cd/m^2) and 50% black (0.22 cd/m^2) in the center of the envelope, and all dots had a diameter of 0.12°. Dots moved on a homogenous gray background of the same mean luminance (42.8 cd/m^2). The motion sequence was computed offline and stored in the secondary computer memory. In the first frame of the motion sequence, dots were randomly positioned within the circular aperture and were displaced by 0.10° in each subsequent frame, producing a speed of 6.4°/s. Dots could move in one of four cardinal directions: upward, downward, leftward, and rightward.

Local motion signals were strongly minimized by implementing a limited lifetime; that is, after 50 ms, each dot vanished and was replaced by a new dot of the same color at a different randomly selected position within the same sector (M. J. Morgan & Ward, 1980; Newsome & Paré, 1988; Pavan & Greenlee, 2015; Snowden & Milne, 1996, 1997). Dots appeared and disappeared asynchronously on the display, but the perceived motion was continuous. In addition, moving dots that traveled outside the circular aperture were also replaced by a new dot at a different random location within the circular aperture, thus always maintaining a constant density within the circular aperture.

Procedure

Each experiment consisted of two phases: (a) estimation of target eccentricity in the crowded condition and (b) the motion priming experiment.

A: Determination of target eccentricity in the crowded condition

Before each motion-priming experiment, we individually estimated the eccentricity of a target stimulus in the crowded condition. This was done in order to find an eccentricity value for which observers were at chance (0.5 in a two-alternative forced-choice [2AFC] same/different task) in discriminating the motion direction of a target stimulus in the crowded condition (Faivre & Kouider, 2011a).

In the crowded condition, the target was flanked by patches containing moving dots (the patch locations were stationary while the dots within the patches moved). The patches were arranged in a 5 (rows) × 4 (columns) matrix with the target located in correspondence with the third row and second column when the matrix was displayed in the left visual hemifield and in the third row and third column of the matrix when the configuration was displayed in the right visual hemifield (see Figure 1A). Thus the target presented in either the left or right visual hemifield always had the same eccentricity from the central fixation point. In the matrix, the center-to-center distance between moving patches was 3° (note that the interelement distance was systematically varied in Experiment 4A and 4B). The array of patches subtended 15° × 12°. We chose this stimulus configuration on the basis of pilot observations indicating a reliable crowding effect; that is, observers were not able to discriminate the target's motion direction, and the estimated eccentricity values allowed all dots to fall within the display size.

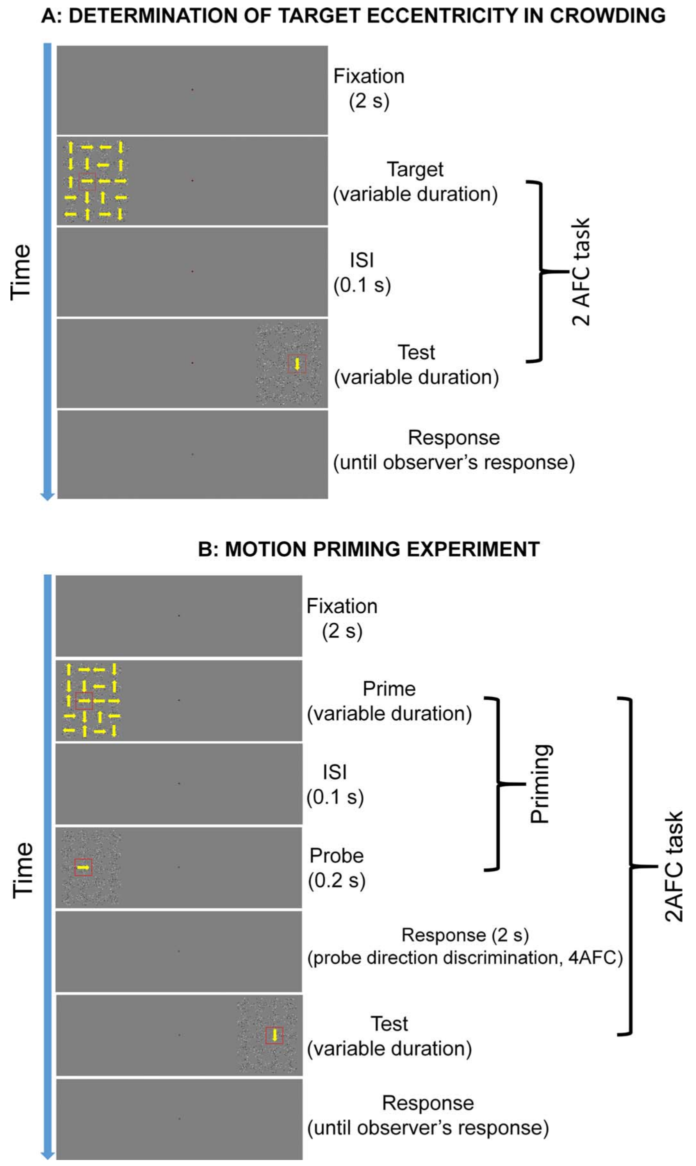

Figure 1. Schematic representation of the general procedures: (A) Experiment for eccentricity estimation and (B) motion priming experiment. The yellow arrows indicate—only for the sake of illustration (not shown in the experiments)—the motion direction of the dot patches. (A) Red frame indicates for sake of illustration the location of the target and test stimuli for the 2AFC task whereas (B) indicates the location of the prime, probe, and test stimuli. (A) The target is crowded by moving flankers and (B) the prime is crowded by moving flankers. The red frame was not shown in the experiments. See text for further details about the procedures.

In all the experiments, the motion direction of the target was randomized and counterbalanced across trials whereas the motion direction of the 19 flankers was randomized on a trial-by-trial basis (note that the motion direction of the flankers was systematically varied in Experiment 2). In each trial, five patches moved upward, five moved downward, five moved leftward, and five moved rightward. Such distribution of directions has been used also in the motion priming experiment to avoid global (remote) priming effects from patterns surrounding the prime because directions average to zero (Harp et al., 2007).

Before the experiment started, the experimenter always instructed the observers as to the location of the moving target. Each session started with the calibration of the eye tracker; subsequently participants heard a 500 Hz tone of 50 ms duration signaling the beginning of the trial. The trial sequence started once the participant's gaze position remained inside a critical square window (area: $2.25^{\circ 2}$) for 2 s. The (virtual) fixation window surrounded a bull's-eye fixation point (red center [diameter: 0.19°] and black surround [diameter: 0.29°]).

After the presentation of the matrix of moving patches containing the target, and following an interinterval delay of 1 s, in which only the fixation point was displayed, we presented another matrix of patches in the opposite visual hemifield. This second matrix contained a test stimulus that was displayed at the same eccentricity as that of the target stimulus but at the mirrored location. The test stimulus was surrounded by stationary patches, and thus, its motion direction was always clearly discriminable. The test stimulus could have the same or different motion direction relative to the target. After the presentation of the two temporal intervals (which duration was systematically varied in Experiment 1), the center of the fixation point turned to green and signaled that observers had to judge whether the target and test were moving in the same direction or in different directions (i.e., 2AFC) by pressing one of two designated keys on a standard computer keyboard (i.e., the left arrow key to indicate same motion directions and the right arrow key to indicate different motion directions).

A test stimulus was employed in order to assess whether the observers were able to discriminate the target's motion direction. The target was always presented in the crowded condition (i.e., with moving flankers) whereas the test stimulus was always presented in the noncrowded condition (i.e., with stationary flankers). In a given trial, the stimulus matrix containing the target could be presented in either the first or second temporal interval. Additionally, the stimulus matrix containing the target could be presented either left or right of the central fixation point. Similarly, also the stimulus matrix containing the test stimulus could be presented in either the first or second temporal interval and either left or right of the central fixation point. So we randomized both presentation interval and visual hemifield. For example, in a given trial, the stimulus matrix containing the test stimulus could appear in the first temporal interval and in the right visual hemifield. Consequently, the stimulus matrix containing the crowded target would be presented in the second temporal interval and in the left visual hemifield. In a subsequent trial, the stimulus matrix containing the target could appear in the first temporal interval and in the left visual hemifield, and the matrix containing the test would be presented in the second temporal interval and in the right visual hemifield (Figure 1A). A simple up–down staircase (Levitt, 1971) was used to estimate the eccentricity for which observers were at chance in the 2AFC task. The starting point of the staircase (i.e., the starting eccentricity) was randomly chosen between 11.8° and 13.3°, and the stimulus matrix was shifted slightly from trial to trial until the threshold value was obtained. The staircase was terminated after either 120 trials or 30 reversals. The eccentricity value for which observers were at chance in the 2AFC task was computed averaging the last 22 reversals. Each observer performed one staircase. The trial sequence for eccentricity estimation is represented in Figure 1A.

B: Motion priming experiment

After having determined the eccentricity value individually for each observer, the the motion priming experiment was performed. Each session started with the calibration of the eye tracker. The trial sequence started once the gaze position of the participant remained inside the critical square window for 2 s. Then the 5×4 matrix containing a prime stimulus was shown (Figure 1B). The prime could appear crowded or noncrowded by flankers. In the case of the noncrowded condition, the flankers were stationary whereas in the crowded condition the dots within the fixed flanker locations moved in different directions and at the same speed as that of the prime (see above). The stimulus matrix containing the prime and the flankers appeared either in the left or right visual hemifield. After the presentation of the prime and after a 0.1 s interstimulus interval, the central part of the fixation turned to green and a probe stimulus was presented for 0.2 s. The probe was displayed in the same spatial location as the prime and was always surrounded by stationary flankers. From the onset of the probe, observers had 2 s to judge its motion direction using one of the four directional arrow keys of the computer keyboard. Then after another interstimulus interval of 2 s from the observer's response, a test stimulus was presented in the opposite visual hemifield to that of the prime and probe stimuli. The test stimulus was always surrounded by stationary patches. Observers had to judge whether the test stimulus was moving in the same or a different direction relative to the prime (i.e., 2AFC task). The test stimulus had the same duration as the prime. After the observer's response, the central part of the fixation point turned to blue, and this signaled the start of the intertrial interval (2 s). The eccentricity of prime, probe, and test stimuli was that estimated in the previous phase (i.e., determination of target eccentricity in the crowded condition). Therefore, in each trial, participants had to perform two tasks: (a) They were asked to judge the absolute direction of the probe stimulus (4AFC) presented 0.1 s after the prime, and (b) they had to judge whether a test stimulus was moving either in the same or a different direction relative to the prime stimulus (i.e., 2AFC task).

The (x, y) position of the right eye was measured continuously during each trial with the eye tracker. During the intertrial interval (2 s), we suspended eye-position recording. Eye-tracking data were analyzed offline, and trials in which fixation strayed from the critical window surrounding the fixation point were discarded from the analysis.

Data analysis

Accuracy on the 2AFC task and the direction discrimination of the probe were analyzed using repeated-measures ANOVA. In addition, for the 2AFC task, we also performed Bonferroni corrected two-tailed, single-sample *t* tests in order to assess whether performance differed from the chance level. With respect to RTs for each observer and condition, outlier RTs were filtered out following the procedure of Lachaud and Renaud (2011). In particular, for each observer, we calculated the median of the RTs, and trials in which RTs were ±2 median of the absolute deviation (MAD) from the median were excluded from the analysis. Estimators of central tendency such as median and MAD are better measures of the central tendency and variability than mean and standard deviation because the former are less influenced by outliers (Lachaud & Renaud, 2011). The RT filtering procedure was applied after removing trials with eye movements that shifted the subject's gaze outside of the fixation window. Subsequently, we used repeated-measures ANOVA to test for main effects and interactions. Pairwise comparisons were performed using the Bonferroni correction. In Experiment 4A and 4B, Bonferroni-corrected two-tailed, single-sample *t* tests were also used to assess whether priming effects significantly differed from zero.

Experiment 1: The effect of prime duration

In Experiment 1, we investigated the effect of the prime duration in crowding with global moving stimuli and whether in the crowded condition the longest prime durations (e.g., 1 and 2 s) induced a negative priming effect (i.e., adaptation) as reported by Faivre and Kouider (2011a). Dependent variables were accuracy and RTs in judging the absolute motion directions of the probe when the prime was presented in the crowded or noncrowded condition. Comparisons of RTs were made when the prime and probe had the same motion direction (match condition) and when they had different motion directions (mismatch condition). We also measured the accuracy in the 2AFC task in which observers compared the motion direction of the prime with that of a test stimulus presented after the probe. Two of the authors (AP and MGG) and six naïve participants took part in the experiment.

Methods

Stimuli and procedure were the same as described in the General methods. We varied the duration of the prime (i.e., 0.2, 0.5, 1, and 2 s) and, consequently, that of the test stimulus while the probe stimulus always had the same duration across all the experiments (i.e., 0.2 s). Each observer performed 384 trials per prime duration (1,536 trials in total). The four prime durations were presented in different experimental sessions, and their order was randomized across participants. Each session was split into eight blocks with 48 trials per block. Because there were four prime durations, the experiment consisted of four sessions. The presentation order of the blocks with respect to target duration within each session was also randomized across participants. The experimental design thus compared the effects of 4 prime durations × 2 crowding conditions (i.e., noncrowded vs. crowded) × 4 prime directions (up, down, left, right). Prime directions were randomized within each block. Each condition was repeated 48 times.

Results

Eccentricity and eye movements

Eccentricity values estimated in Experiment 1 were 15.3° (*SEM*: 0.53°), 17.6° (*SEM*: 0.68°), 19.5° (*SEM*: 0.68°), and 19.6° (*SEM*: 0.49°) for 0.2, 0.5, 1, and 2 s stimulus durations, respectively. We found 0.91% (*SEM*: 0.41%), 1.5% (*SEM*: 0.6%), 2.5% (*SEM*: 0.68%), and 2.64% (*SEM*: 1.24%) of trials with excessive eye movements for 0.2, 0.5, 1, and 2 s prime durations, respectively.

Accuracy for the 2AFC task

A 2AFC task was performed to assess whether observers could discriminate the prime's motion direction in the crowded condition. Figure 2 shows the mean proportion of correct responses for the 2AFC task. A repeated-measures ANOVA including as factors the prime duration and the crowding condition (i.e., noncrowded vs. crowded) revealed a significant effect of the prime duration, $F(3, 21) = 7.72$, $p = 0.001$, partial $\eta^2 = 0.53$, and a significant effect of crowding, $F(1, 7) = 567.63$, $p = 0.0001$, partial $\eta^2 = 0.98$, but no interaction between prime duration and crowding, $F(3, 21) = 0.91$, $p = 0.45$, partial $\eta^2 = 0.12$. In addition, we performed a series of Bonferroni corrected, single-sample t tests relative to chance level to assess whether the proportions of correct responses obtained on the 2AFC task were significantly above chance. For the noncrowded condition, the accuracies were significantly above chance for all the stimulus durations whereas for the crowded condition all the comparisons indicated that the observed frequencies were not significantly different from chance (critical $p = 0.0063$).

It should be noted that Experiment 1 meets the criterion for crowding as defined by Parkes et al. (2001); that is, the flankers affected the direction discrimination performance on the prime stimulus even though observers knew that the prime was always in that specific location (i.e., in correspondence with the third row and second column when the matrix was displayed in the left visual hemifield, and in the third row and third column when the configuration was displayed in the right visual hemifield). The large effect of crowding and the observation that prime direction was not discriminable during presentation with crowding indicate that our manipulation was successful for the prime durations and prime locations employed.

RTs for the 4AFC task

Figure 3A shows the mean RTs obtained in Experiment 1. The amount of trials excluded with the above-described filtering procedure was 7.8%. Therefore, after the exclusion of trials with fixational eye movements (7.55%) and outlier RTs, the analysis was conducted on the remaining 84.6% of trials. Only RTs relative to correct responses with respect to probe directions were analyzed. Data from the four probe directions (up, down, left, and right) were pooled to increase the statistical power. A repeated-measures ANOVA including as factors the prime duration, crowding (i.e., noncrowded vs. crowded), and probe condition (i.e., match vs. mismatch) did not reveal a significant main effect of prime duration, $F(3, 21) = 2.94$, $p = 0.057$, partial $\eta^2 = 0.30$, but did reveal a significant main effect of crowding, $F(1, 7) = 63.07$, $p = 0.0001$, partial $\eta^2 = 0.90$, and a significant main effect of the probe condition (i.e., match vs. mismatch), $F(1, 7) = 38.82$, $p = 0.0001$, partial $\eta^2 = 0.85$. As can be seen in Figure 3A, priming effects (difference between prime probe mismatch vs. match) are only evident for the noncrowded condition. We also found significant interactions: prime duration × probe condition, $F(3, 21) = 7.26$, $p = 0.002$, partial $\eta^2 = 0.51$, and crowding × probe condition, $F(1, 7) = 26.22$, $p = 0.001$, partial $\eta^2 = 0.79$. For the prime duration × probe condition, Bonferroni corrected pairwise comparisons revealed a significant difference between the match and mismatch conditions for all the prime durations tested ($p < 0.05$). This interaction term supports the impression given in Figure 3A that the effects of priming are most pronounced for the short prime durations.

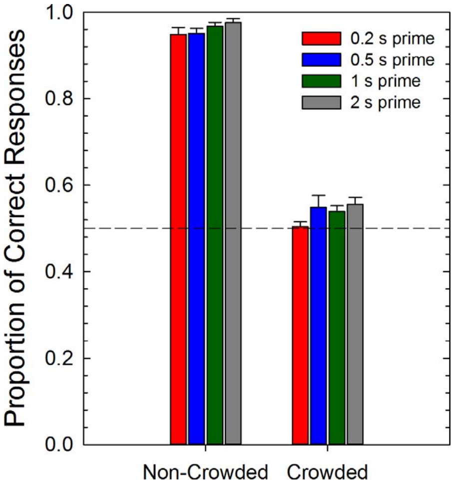

Figure 2. Mean proportion of correct responses obtained for the 2AFC task. The dashed line represents the chance level (0.5). Error bars ± *SEM*.

The three-way interaction prime duration × crowding × probe condition was also significant, $F(3, 21) = 13.88$, $p = 0.0001$, partial $\eta^2 = 0.67$. For the three-way interaction, we performed separate two-way repeated-measures ANOVAs testing the interaction between crowding and probe condition for each prime duration. For all the prime durations, the ANOVA revealed a significant interaction between crowding and probe condition. Bonferroni-corrected pairwise comparisons yielded a significant difference between match and mismatch motion directions only for the noncrowded condition whereas we did not find a significant difference between the match and mismatch motion directions for the crowded condition ($p > 0.05$). The greatest difference in RTs between the match and mismatch motion directions for the noncrowded condition was found for the 0.2-s prime duration, and this difference exponentially declines with increasing prime durations (Figure 3B).

Accuracy for probe direction discrimination

On average, after data filtering (see data analysis section), the proportion of correct responses in judging the motion direction of the probe was >0.95. A repeated-measures ANOVA including as factors the

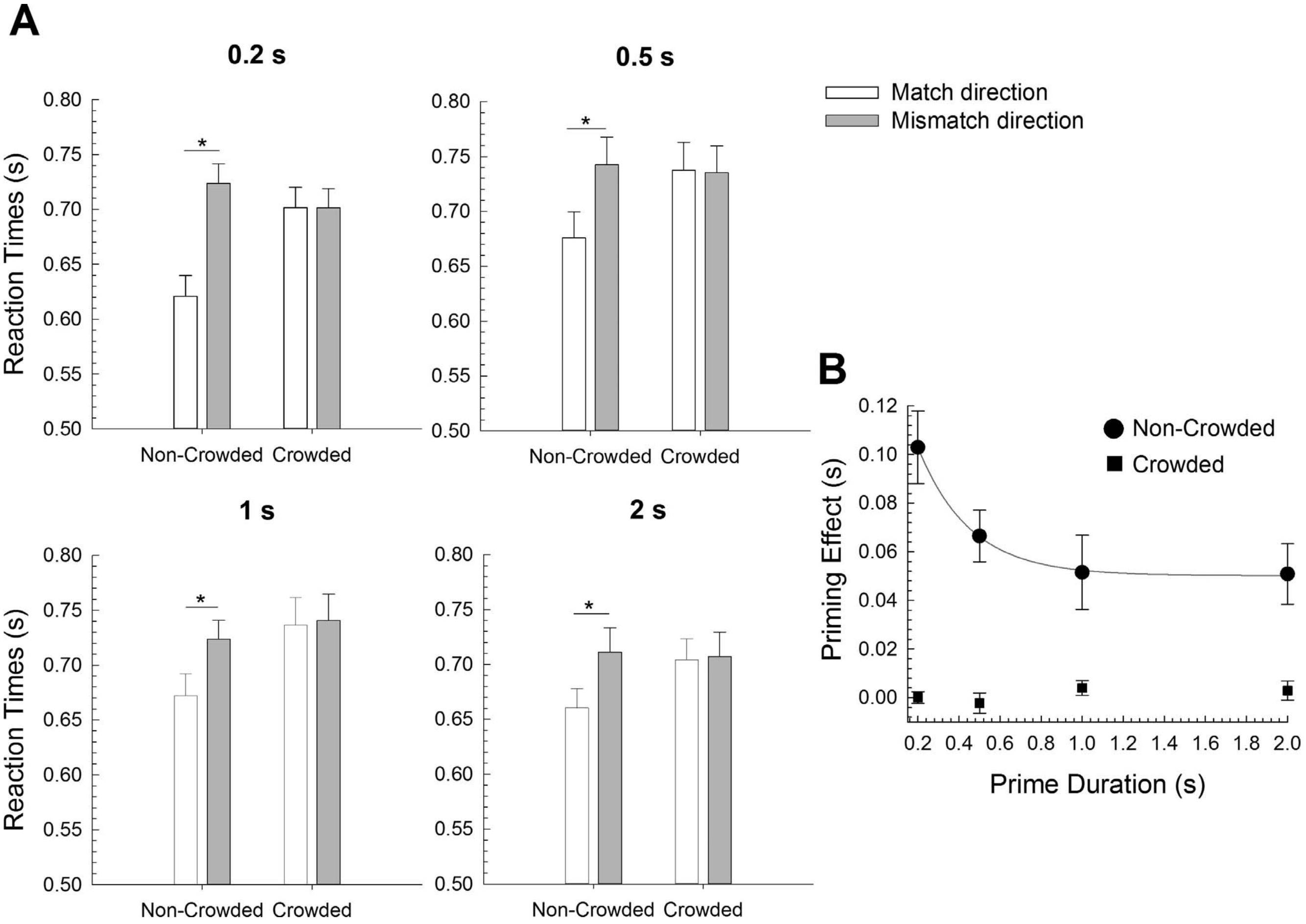

Figure 3. Results of Experiment 1. (A) Mean RTs (in seconds) relative to the prime durations used in Experiment 1 (i.e., 0.2, 0.5, 1, and 2 s). Data are shown for the noncrowded and crowded conditions and when the motion direction of the prime was the same (match condition) or different (mismatch condition) to the motion direction of the probe stimulus. (B) Decay of the priming effect as the prime duration increases. The priming effect was calculated by taking the difference between the RTs estimated in the mismatch and match conditions (i.e., $RT_{mismatch} - RT_{match}$). We fitted a single exponential decay function (dark gray line) on the differences in RTs between the mismatch and the match condition in the noncrowded condition. The exponential function was of the form $y = y_0 + Ae^{-x/t}$, where y_0 is the asymptote (0.05 s, 95% confidence bounds: 0.038, 0.062), A is the amplitude of the function (0.117 s, 95% confidence bounds: 0.028, 0.206), and t is the time decay constant (0.251 s, 95% confidence bounds: 0.012, 0.489), adjusted $R^2 =$ 0.99. Filled squares show the priming effect obtained in the crowded condition. Error bars ± *SEM*.

prime duration, crowding (noncrowded vs. crowded), and probe condition (i.e., match vs. mismatch with respect to prime direction) revealed only a significant interaction between prime duration and probe condition, $F(3, 21) = 5.16$, $p = 0.008$, partial $\eta^2 = 0.42$. Bonferroni-corrected pairwise comparisons reported a significant difference between the proportion of correct responses obtained in the match and mismatch conditions for the 2-s prime duration (i.e., match: 0.95 [*SEM*: 0.01], mismatch: 0.98% [*SEM*: 0.005], $p = 0.002$).

Discussion

The results of Experiment 1 show that priming for global moving stimuli does not survive crowding for any of the durations tested; the relative directions of the prime and probe have no effect on RTs in the crowded condition. These results differ from recent findings reported by Faivre and Kouider (2011a). Using gaze-contingent crowding, the authors assessed how stimulus duration modulates the conscious and unconscious processing of oriented Gabor patches. Results show that in the crowded condition a 0.2-s prime facilitates the processing of a subsequently presented probe stimulus of the same orientation (i.e., positive priming effect). On the other hand, when these authors increased the prime duration to 1 s, an inhibitory effect was found (i.e., adaptation or negative priming effect) with significantly higher RTs in the match condition (i.e., when prime and probe had the same orientation). Additionally, the authors showed that a 1-s prime stimulus cannot induce any facilitatory effect when observers could discriminate its orientation (i.e., in the noncrowded condition). However, in our experiment, 1- and 2-s globally moving prime stimuli in the noncrowded condition still produced a reliable and significant facilitatory effect on a subsequently presented probe stimulus with matching direction (priming effect: 0.05 s) although the magnitude of such facilitation was halved with respect to the facilitation obtained with a 0.2-s prime duration (priming effect: 0.103 s) (Figure 3B). In a series of additional experiments, we investigated under which conditions a priming effect was evident for globally moving stimuli in crowded condition.

Experiment 2: The effect of flankers' motion direction

In Experiment 2, we investigated the absence of priming effect under crowding by varying the motion direction of the flankers. The prime stimulus was always flanked by moving patches (i.e., crowded condition), but we systematically varied the coherence of the entire stimulus configuration. That is, we increased the number of flankers moving in the same direction as that of the prime while the remaining flankers moved in different directions.

According to pooling models, in crowding, the motion direction of flankers and prime are pooled and then averaged. Hence, increasing the number of flankers that move in the same direction as that of the prime should induce an improvement of the performance of the 2AFC task. Accordingly, we should also expect an increase of the priming effect because the motion direction of most of the flankers is the same as that of the prime stimulus; that is, when the motion coherence of the entire configuration is high, the whole matrix should act as a prime.

Also substitution models share the same prediction: With increasing the number of flankers in the same direction as the prime, the probability of picking up motion in the same direction should increase accordingly. On the other hand, if flankers irretrievably degrade the sensory representation of the prime, increasing the number of coherently moving flankers relative to the prime should neither affect the proportion of correct responses in the 2AFC task nor the priming effect, thus replicating the results of Experiment 1 for the crowded condition.

Method

Stimuli and procedure were the same as described in the General methods. The prime duration was 0.2 s; this is because in Experiment 1 such duration produced the largest priming effect in the noncrowded condition. In Experiment 2, we varied the number of patches moving in the same direction as that of the prime. In particular, the percentages of coherently moving patches were 25%, 40%, 55%, 70%, and 85% of the total number of moving patches in the crowded condition (i.e., 20 patches). The prime stimulus was included in the amount of coherently moving patches. The remaining patches moved in different directions.

Observers performed 96 trials per coherence level, giving a total number of 480 trials. The total number of trials was split into 10 blocks (i.e., 48 trials for each block) in which coherence levels were randomized. Eccentricity values were estimated as described in the General methods. One of the authors (MGG) and seven naïve participants took part in the experiment.

Results

Eccentricity and eye movements

The mean eccentricity value was 15.3° (*SEM*: 0.47°). We recorded 0.7% (*SEM*: 0.4%) of fixational eye movements.

Accuracy for the 2AFC task

Figure 4A shows the mean proportion of correct responses for the 2AFC task. A repeated-measures ANOVA did reveal a significant main effect of motion coherence, $F(4, 28) = 3.86$, $p = 0.013$, partial $\eta^2 = 0.35$. Bonferroni-corrected pairwise comparisons revealed only a significant difference between the first level (25%) of motion coherence and the third level (55%) ($p = 0.038$). A Bonferroni-corrected one-sample *t* test with respect to the chance level showed that only the third (55%) and fourth (70%) levels of motion coherency significantly differed from chance ($p = 0.001$ and $p = 0.002$, respectively). Parkes et al. (2001) found that orientation thresholds for a central target (i.e., an oriented Gabor patch) surrounded by similar elements decreased linearly with an increasing number of flankers tilted as the target. The authors described an almost perfect linear relationship between orientation thresholds and number of flankers tilted as the target with a slope of -1 on log–log axes. A slope of -1 (or 1) is only obtained if one variable is an *exact* linear function of the other. Based on Parkes et al., a linear increment of the proportion of correct responses with the number of moving flankers would support the simple pooling or averaging model. On the other hand, any less rapid or nonlinear increment can be used as evidence against pooling. In our case, data are well fit on log–log axes by a line with intercept of -0.53 (*SE*: 0.053) and slope of 0.17 (*SE*: 0.031) (adjusted $R^2 = 0.88$). The estimated slope is significantly different from zero, $F(1, 3) = 31.61$,

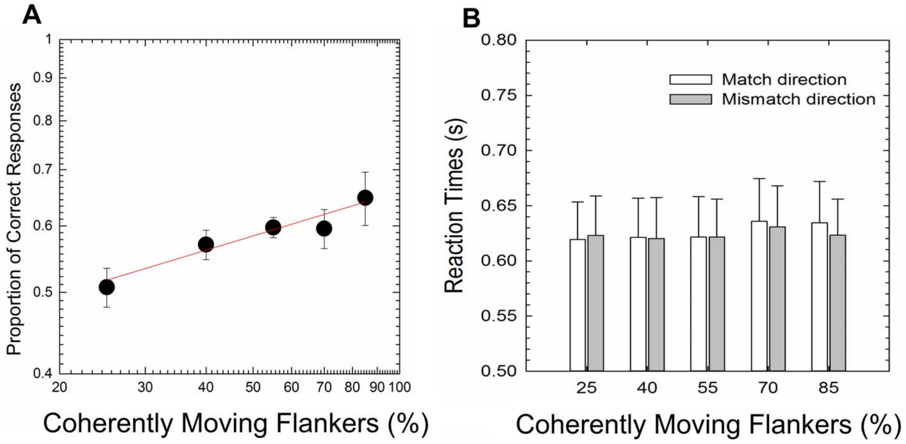

Figure 4. Results of Experiment 2. (A) Mean proportion of correct responses obtained for the 2AFC task. The continuous red line represents the linear fit to the data. (B) Mean RTs (in seconds) for the 4AFC task as a function of the percentage of coherently moving patches in the stimulus matrix. The repeated-measures ANOVA did not reveal any significant main effects or interaction. Error bars ± *SEM*.

$p = 0.011$, but because it was not 1, the averaging model is not supported (Parkes et al., 2001).

RTs for the 4AFC task

Figure 4B shows the mean RTs obtained in Experiment 2 for the 4AFC (probe direction) task. For each observer and for each trial, outlier RTs were filtered out following the procedure described in the General methods (Lachaud & Renaud, 2011). The amount of trials excluded with the filtering procedure was 10%. Therefore, after the exclusion of trials with fixational eye movements (0.7%) and outlier RTs, the analysis was conducted on the remaining 89.3% of the trials. Only RTs relative to correct motion discrimination of the probe stimulus were analyzed. Data from the four motion directions were pooled to increase statistical power. A repeated-measures ANOVA including as factors the coherence levels and probe condition (i.e., match vs. mismatch) did not reveal any significant main effect or interaction: coherence level, $F(4, 28) = 2.20$, $p = 0.092$, partial $\eta^2 = 0.24$; probe condition, $F(1, 7) = 0.49$, $p = 0.51$, partial $\eta^2 = 0.065$; and interaction between motion coherence and probe condition, $F(4, 28) = 0.87$, $p = 0.43$, partial $\eta^2 = 0.11$.

Accuracy for probe direction discrimination

The proportion of correct responses in judging the motion direction of the probe was >0.95. A repeated-measures ANOVA including as factors the motion coherence and probe condition (i.e., match vs. mismatch with prime) did not reveal any significant main effect or interaction: motion coherence, $F(4, 28) = 0.85$, $p = 0.51$, partial $\eta^2 = 0.11$; probe condition, $F(1, 7) = 1.15$, $p = 0.32$, partial $\eta^2 = 0.14$; and interaction motion coherence × probe condition, $F(4, 28) = 2.11$, $p = 0.11$, partial $\eta^2 = 0.23$.

Discussion

The results of Experiment 2 show no evidence that pooling or substitution mechanisms affected the prime stimulus. Indeed, the proportion of correct responses obtained in the 2AFC task indicates only a very small linear increment as a function of the coherence level. Because we increased the number of coherently moving patches relative to the prime, we expected a more rapid linear increment (slope of 1) of the proportion of correct responses. In addition, for high levels of motion coherence of the stimulus matrix, we expected that priming would again be effective on RTs; that is, if the motion signals are averaged (as predicted by pooling models), the entire matrix should behave as a prime stimulus. However, the proportion of correct responses and RTs found does not support an averaging mechanism. Instead, the results suggest that when the prime stimulus is surrounded by other moving distracters, its sensory representation is likely to be corrupted. In addition, although for some coherence levels we obtained a performance on the 2AFC task that was significantly different from chance (i.e., for 55% and 70% coherence levels), this was not sufficient to induce a reliable priming effect.

Experiment 3: The effect of flankers' speed

The results of Experiment 2 suggest that the sensory representation of the prime is likely to be corrupted in the crowded condition, preventing the visual system from estimating its motion direction. In Experiment 3, we measured the effect of flanker speed on the priming effect in the crowded condition. The rationale was that

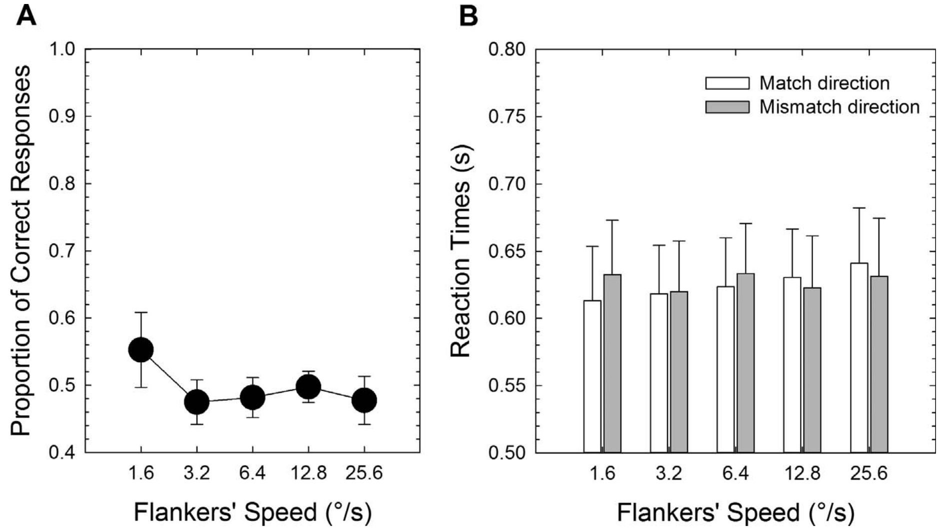

Figure 5. Results of Experiment 3. Mean proportion of correct responses for the 2AFC task. (B) Mean RTs (in seconds) as a function of the flankers' speed for the 4AFC task. The prime and probe speed was 6.4°/s. Error bars ± *SEM*.

decreasing the speed of the flankers relative to the speed of the prime should increase the accuracy in the 2AFC task and restore the priming effect. This is because the motion direction of the prime should pop out (Manassi, Sayim, & Herzog, 2012; Poder, 2007) when the relative speed of the flankers is much slower than that of the prime. Alternatively, if the sensory representation of the prime is completely degraded, manipulating the relative speed of the flankers should produce neither an improvement in the 2AFC task nor a priming effect.

Method

Stimuli and procedure were the same as described in the General methods. The prime duration was 0.2 s. We varied the speed of the flankers relative to that of the prime. In particular, the speed of the flankers was 1.6°/s, 3.2°/s, 6.4°/s, 12.8°/s, and 25.6°/s whereas the speed of the prime was constant at 6.4°/s. Observers performed 96 trials per speed level, yielding a total number of trials of 480. Trials were split into 10 blocks of 48 trials each. The presentation order of the blocks was randomized across subjects. Eccentricity values were estimated only for the condition in which prime and flankers had the same speed (i.e., 6.4°/s). One of the authors (MGG) and five naïve participants took part in the experiment.

Results

Eccentricity and eye movements

The mean eccentricity value was 15.8° (*SEM*: 0.57°). We recorded 0.84% (*SEM*: 0.48%) of fixational eye movements.

Accuracy for the 2AFC task

Figure 5A shows the mean proportion of correct responses for the 2AFC task. Because the Mauchly's test for sphericity was significant ($p = 0.017$), we applied the Greenhouse-Geisser correction for the degrees of freedom. A repeated-measures ANOVA did not reveal a significant effect of the flankers' speed, $F(1.19, 5.97) = 3.04$, $p = 0.13$, partial $\eta^2 = 0.38$. In addition, s Bonferroni-corrected one-sample t test with respect to the chance level (0.5) did not detect any significant effect ($p > 0.05$).

RTs for the 4AFC task

Figure 5B shows the mean RTs obtained in Experiment 3. The amount of trials excluded with the filtering procedure was 9.9%. Therefore, after the exclusion of trials with fixational eye movements (0.84%) and outlier RTs, the analysis was conducted on the remaining 89.3% of the trials. A repeated-measures ANOVA including as factors the flankers' speed and probe condition (i.e., match vs. mismatch) did not indicate the presence of a significant main effect: flankers' speed, $F(4, 20) = 2.49$, $p = 0.076$, partial $\eta^2 = 0.33$, and probe condition, $F(1, 5) = 1.54$, $p = 0.27$, partial $\eta^2 = 0.24$, but we found a marginally significant interaction between flankers' speed and probe condition, $F(4, 20) = 2.83$, $p = 0.052$, partial $\eta^2 = 0.36$. The marginal significance level could imply that we are lacking statistical power for this comparison. However, Bonferroni-corrected pairwise comparisons did not indicate any significant difference between the match and mismatch conditions across all the flankers' speeds tested ($p > 0.05$).

Accuracy for probe direction discrimination

Overall, the proportion of correct responses in judging the absolute motion direction of the probe was >0.93. A repeated-measures ANOVA including as factors the motion coherence and probe condition (i.e., match vs. mismatch) did not reveal any significant main effect or interaction: motion coherence, $F(4, 28) = 0.85$, $p = 0.51$, partial $\eta^2 = 0.11$; probe condition, $F(1, 7) = 1.15$, $p = 0.32$, partial $\eta^2 = 0.14$; and interaction motion coherence × probe condition, $F(4, 28) = 2.11$, $p = 0.11$, partial $\eta^2 = 0.23$.

Discussion

The results show that varying the flankers' speed does not lead to a recovery of prime information (with consequent priming effect). Flankers may disrupt the representation of the prime, reducing the performance on the 2AFC task to chance level and nulling out the priming effect. Overall, our findings suggest that if the prime is surrounded by other moving stimuli, regardless of their direction and speed, it is likely to be degraded, and its motion direction is no longer available to the visual system (He et al., 1996; Nandy & Tjan, 2007; Pelli et al., 2004).

Experiment 4A: The effect of flanker spacing and attention

In Experiment 4A, we investigated whether the absence of motion priming is due to attentional factors. There is psychophysical evidence that precueing the location of a peripheral target crowded by similar flankers improves target discrimination (Felisberti, Solomon, & Morgan, 2005; Huckauf & Heller, 2002; Scolari, Kohnen, Barton, & Awh, 2007; Strasburger, 2005; Yeshurun & Rashal, 2010). Recently, Yeshurun and Rashal (2010), using an orientation-discrimination task in which observers had to discriminate the orientation of a tilted "T" found that precueing the target location diminished crowding and decreased critical distance.

In Experiment 4A, we precued the location of the prime and varied the interelement distance between flankers and prime. The rationale was that if spatial cueing in conjunction with an increment of the interelement distance improves the discrimination of the prime's motion direction, then an improvement in the performance on the 2AFC task is expected, and consequently, a release of the priming effect in the crowded condition is expected.

Methods

Experiment 4A consisted of two parts that were counterbalanced across observers; that is, half of the observers began with the first part of Experiment 4A whereas the other half began with the second part of Experiment 4A, but the same observers performed both parts of Experiment 4A. In the first part, we varied only the interelement distance between flankers and prime. In particular, the distances used were: 3°, 4°, 4.7°, 5.5°, and 6°. Each distance level refers to the center-to-center distance between elements in the stimulus matrix; thus, the first spacing value refers to the condition used in the previous experiments (Figure 1). The maximum interelement distance we could use was 6° (i.e., twice the diameter of each moving patch) in order to avoid that part of the flankers exceeded the screen size and to avoid superimposition between flankers and the central fixation point. The location of the prime stimulus was set at a constant eccentricity across all the experiments and was determined individually for each participant (see General methods). In the second part, we manipulated the interelement distance between elements, but the prime location was also precued by a white oval frame with a diameter of 3°. The cueing stimulus was presented for 0.1 s, and after a stimulus onset asynchrony of 0.2 s in which the display was blank with the exception of the central fixation point, the prime stimulus was presented. These parameters were chosen on the basis of Van der Lubbe and Keuss (2001), who showed that focused attention reduces the effect of lateral interference in multielement arrays. Eccentricity values were also estimated for the second part of the experiment because it was performed on a different day. The prime duration was 0.2 s.

Observers performed 96 trials per interelement distance (i.e., $96 \times 5 = 480$ trials). The total amount of trials was split into 10 blocks (48 trials per block), and the presentation order of the interelement distances was randomized within each block. The conditions tested were 5 interelement distances × 4 prime directions. Data relative to each motion direction were pooled to get more statistical power. This resulted in 48 repetitions for the match condition and 48 repetitions for the mismatch condition. One of the authors (MGG) and seven naïve participants took part in the experiment.

Results

Eccentricity and eye movements

The mean eccentricity value estimated in the first part of Experiment 4A, in which we only varied the interelement distance was 16.1° (*SEM*: 0.263°). In addition, we recorded 0.99% (*SEM*: 0.43%) of fixa-

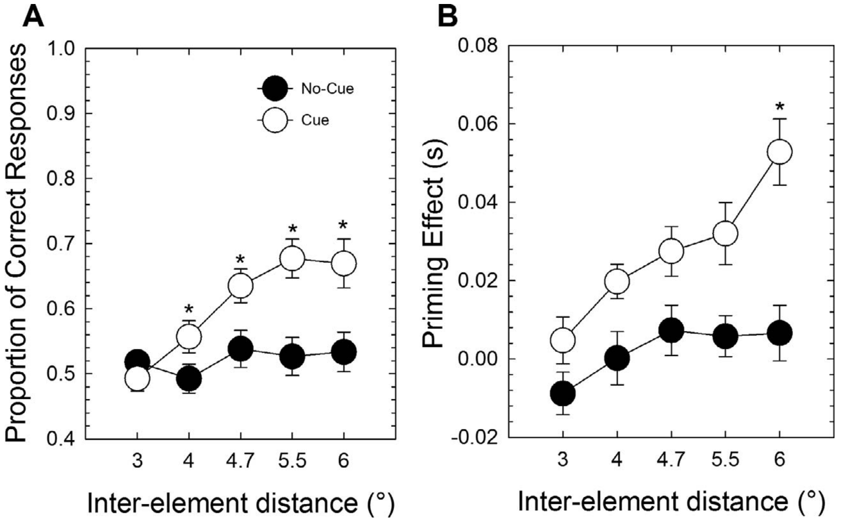

Figure 6. Results of Experiment 4A. (A) Mean proportion of correct responses for the 2AFC task. The asterisks represent a significant difference between the no-cue and cue conditions. (B) Priming effect (in seconds) as a function of the interelement distance (in degrees) for the no-cue and cue conditions for the 4AFC task. The asterisk represents a significant difference between the no-cue and cue conditions at 6° of interelement distance. Error bars ± *SEM*.

tional eye movements. Concerning the second part of Experiment 4A, in which the prime location was also precued, the mean eccentricity value was 16.3° (*SEM*: 0.265°). We removed 0.70% (*SEM*: 0.28%) of trials based on large eye movements.

Accuracy for the 2AFC task

Figure 6A shows the mean proportion of correct responses of the 2AFC task for both spacing and spacing–cueing experiments. We performed a repeated-measures ANOVA including as factors the cue condition (i.e., no cue vs. cue) and the interelement distance. The ANOVA reported a significant effect of the cue, $F(1, 7) = 27.29$, $p = 0.001$, partial $\eta^2 = 0.80$; a significant effect of the interelement distance, $F(4, 28) = 13.27$, $p = 0.0001$, partial $\eta^2 = 0.66$; and a significant interaction between cue and interelement distance, $F(4, 28) = 4.8$, $p = 0.004$, partial $\eta^2 = 0.41$. Bonferroni-corrected pairwise comparisons revealed a significant difference between the cue and the no-cue condition for the spacing levels of 4.0° ($p = 0.02$), 4.7° ($p = 0.048$), 5.5° ($p = 0.006$), and 6° ($p = 0.0001$) (Figure 6A). Additionally, Bonferroni-corrected one-sample *t* tests with respect to the chance level showed that the observers' performance was significantly above chance for the interelement distances of 4.7° ($p = 0.001$), 5.5° ($p = 0.001$), and 6° ($p = 0.003$), but only for the condition in which the prime's location was precued.

RTs for the 4AFC

The amount of trials excluded with the filtering procedure (Lachaud & Renaud, 2011) was 10.1% and 10.9% for the spacing and spacing–cueing experiments, respectively. After the exclusion of trials with fixational eye movements (0.99% and 0.7% for the spacing and spacing–cueing experiments, respectively) and outlier RTs, the analysis was conducted on the remaining 88.9% and 88.4% of the trials, respectively, for the spacing and spacing–cueing experiments.

Figure 6B shows the priming effect measured in the no-cue and cue conditions as a function of the interelement distances. The priming effect was calculated by taking the difference between the RTs estimated in the direction mismatch and match conditions. A repeated-measures ANOVA including as factors the cue condition (i.e., no cue vs. cue) and the interelement distance revealed a significant effect of the cue condition, $F(1, 7) = 21.36$, $p = 0.002$, partial $\eta^2 = 0.75$; a significant effect of the interelement distance, $F(4, 28) = 7.90$, $p = 0.0001$, partial $\eta^2 = 0.53$; and a marginally significant interaction between cue condition and interelement distance, $F(4, 28) = 2.53$, $p = 0.063$, partial $\eta^2 = 0.27$. Although the interaction was not significant, we performed Bonferroni-corrected paired samples *t* tests between the no-cue and cue conditions for each interelement distance value (critical $p = 0.01$). The results showed a significant difference between the no-cue and cue conditions only at 6°, $t(7) = -3.61$, corrected $p = 0.009$, of interelement distance. We also performed a series of one-sample Bonferroni-corrected *t* tests to assess which priming effects were significantly different from zero (critical $p = 0.005$). The one-sample *t* tests reported significant priming effects only for the cue condition and for interelement distances of 4°, $t(7) = 4.49$, $p = 0.003$; 4.7°, $t(7) = 4.33$, p

$= 0.003$; 5.5°, $t(7) = 4.03$, $p = 0.005$; and 6°, $t(7) = 6.27$, $p = 0.0001$.

Accuracy for probe direction discrimination

For the two parts of Experiment 4A, the proportion of correct responses in judging the absolute motion direction of the probe was >0.91. A repeated-measures ANOVA including as factors the cue condition (no cue vs. cue), the interelement distance, and the probe condition (i.e., match vs. mismatch) did not find any significant effect or interaction: cue condition, $F(1, 7) = 0.039$, $p = 0.85$, partial $\eta^2 = 0.006$; interelement distance, $F(4, 28) = 0.46$, $p = 0.76$, partial $\eta^2 = 0.062$; probe condition, $F(1, 7) = 0.053$, $p = 0.83$, partial $\eta^2 = 0.008$; interaction between cue and interelement distance, $F(4, 28) = 0.44$, $p = 0.78$, partial $\eta^2 = 0.059$;interaction between cue and probe condition, $F(1, 7) = 0.12$, $p = 0.74$, partial $\eta^2 = 0.02$; and interaction between interelement distance and probe condition, $F(4, 28) = 0.54$, $p = 0.71$, partial $\eta^2 = 0.07$. The three-way interaction was also not significant, $F(4, 28) = 0.68$, $p = 0.61$, partial $\eta^2 = 0.09$.

Discussion

The results of Experiment 4A showed that (a) cueing the prime's location decreased crowding strength, and (b) the priming effect increased accordingly, but only for the largest spacing value used (i.e., 6°) was the difference between cueing and not cueing significant. However, it should be noted that the overall priming effect is weaker (i.e., 0.053 s) than the priming effect estimated in Experiment 1 (0.103 s) in the noncrowded condition. Hence, cueing attention to the prime's location can modulate the strength of the priming effect although it cannot entirely explain the absence of the priming effect in crowding. Interestingly, increasing the spacing between prime and flankers led neither to a recovery of the priming effect nor to a decrease of the crowding strength. We further investigated this aspect in Experiment 4B.

Experiment 4B: The effect of the number of flankers

In Experiment 4B, we investigated whether the absence of priming is due to a floor effect in crowding. In fact, with the stimulus configuration used so far we could not properly estimate the critical distance in order to obtain a priming effect similar to that reported in Experiment 1 in the noncrowded condition (i.e., 0.103 s). The maximum interelement distance we could use was 6° in order to avoid overlapping of the inner flankers of the matrix stimulus with the fixation point, and to avoid that, the outer flankers exceeded the screen edges. The averaged eccentricity estimated in Experiment 4A was ~16°, and thus, an interelement distance of 6° is still inside Bouma's window (half of the prime eccentricity; Bouma, 1970; Pelli, 2008). Therefore, so many flankers (19) inside Bouma's window could have deteriorated the prime stimulus, thus nulling out any priming effect (i.e., floor effect). For this reason, we conducted an additional experiment using a different stimulus configuration with fewer flankers and varying the motion coherence of the prime rather than its eccentricity. The aim was (a) to assess whether the absence of priming effect is due to a floor effect and (b) to investigate the role of attention with this simpler stimulus configuration.

Method

Stimuli were the same as used in the previous experiments with exception that we used a configuration with seven flankers instead of 19 (Figure 7). The procedure consisted of two phases: (a) motion coherence threshold for the target stimulus in the crowded condition and (b) the motion priming experiment. Two of the authors (AP and MGG) and six naïve participants took part in the experiment.

A: Determination of target's motion coherence thresholds in the crowded condition

The target stimulus was presented at a constant eccentricity of 16°, corresponding to the average eccentricity estimated in Experiment 4A. We manipulated, individually for each observer, the motion coherence of the target stimulus in the crowded conditions in order to estimate the coherence threshold for which the motion discrimination of the target was at chance (0.5) in the crowded condition. The procedure was the same as described in the General methods with the exception that the coherence of the target stimulus (in terms of percentage of coherently moving dots) was manipulated using a simple up–down staircase (Levitt, 1971). Coherently moving dots drifted as described in the stimuli section whereas noise dots had a randomly selected initial direction of displacement and then continued to move linearly in the same direction in successive frames for the duration of their lifetime (i.e., 50 ms). This type of noise has been labeled by Scase, Braddick, and Raymond (1996) as "random-direction" noise. Flankers' motion coherence was always 100%. The starting motion coherence level of the target was 100%. The staircase terminated after 160 trials or 30 reversals. Coherence threshold was esti-

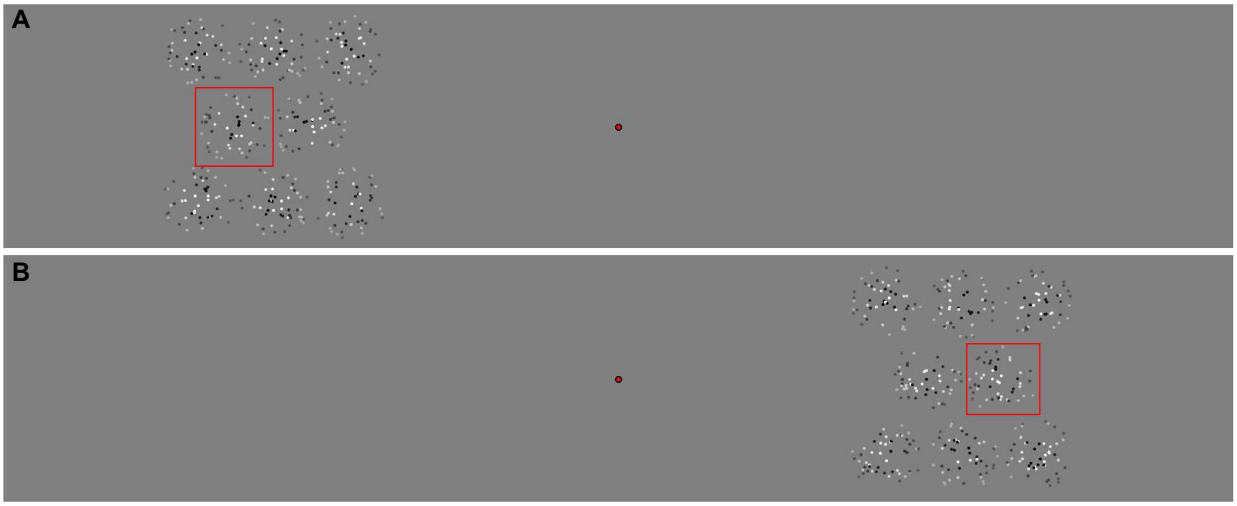

Figure 7. Schematic representation of the stimulus configuration used in Experiment 4B. In this experiment, we presented seven flankers instead of 19. The target location is indicated by the red frame (not shown during the experiment). (A, B) Configurations displayed in the left and right visual hemifields.

mated by averaging the last 22 reversals. In each trial, two patches moved upward, two moved downward, two moved leftward, and two moved rightward. After the presentation of the matrix of moving patches containing the target, in a second temporal interval, we presented another matrix of patches in the opposite visual hemifield. This second matrix contained a test stimulus with the same motion coherence as the target but at the mirrored location. As reported in the General methods, we randomized both temporal presentation interval and visual hemifield. The test stimulus was always surrounded by stationary patches. The test stimulus could have the same or different motion direction relative to the target. After the presentation of the two temporal intervals (0.2 s each), observers had to judge whether the target and test were moving in the same or different directions.

B: Motion priming experiment

The motion priming experiment was the same as in Experiment 4A with the exception that there were fewer flankers (seven vs. 19); the eccentricity was constant at 16°; and the motion coherence of prime, probe, and test stimuli was the same as estimated in the previous coherence threshold experiment (phase A). The prime was always crowded by moving flankers with a motion coherence of 100%. In addition, we used four interelement distances: 3°, 6°, 10°, and 14°. For interelement distances of 10° and 14° flankers fell outside the critical distance. Spacing values were varied within the block. Observers performed three blocks for each part of Experiment 4B (i.e., for the spacing experiment and the spacing–cueing experiment). Each block consisted of 96 trials.

Results

Motion coherence thresholds and eye movements

The mean motion coherence threshold estimated in the first part of Experiment 4B, in which we only varied the interelement distance, was 47.5% (*SEM*: 4%). In addition, we recorded 0.3% (*SEM*: 0.14%) of fixational eye movements. Concerning the second part of Experiment 4B, in which the prime location was also precued, the mean coherence threshold estimated was 56.3% (*SEM*: 6.03%). We removed 0.52% (*SEM*: 0.28%) of trials based on large eye movements.

Accuracy for the 2AFC task

Figure 8A shows the mean proportion of correct responses of the 2AFC task for both spacing and spacing–cueing experiments. A repeated-measures ANOVA including as factors the cue condition (i.e., no cue vs. cue) and the interelement distance revealed a significant effect of the cue condition, $F(1, 7) = 6.81$, $p = 0.035$, partial $\eta^2 = 0.49$; a significant effect of the interelement distance, $F(3, 21) = 59.89$, $p = 0.0001$, partial $\eta^2 = 0.86$; and a significant interaction between cue and interelement distance, $F(3, 21) = 4.91$, $p = 0.01$, partial $\eta^2 = 0.41$. Bonferroni-corrected pairwise comparisons uncovered a significant difference between the cue and the no-cue conditions for the spacing levels of 10° ($p = 0.018$) and 14° ($p = 0.015$). Additionally, Bonferroni-corrected one-sample t tests with respect to the chance level revealed that the observers' performance was significantly above chance for the interelement distances of 10° ($p = 0.005$) and 14° ($p = 0.009$) for the spacing experiment whereas for the spacing–cueing experiment the observers' performance was signifi-

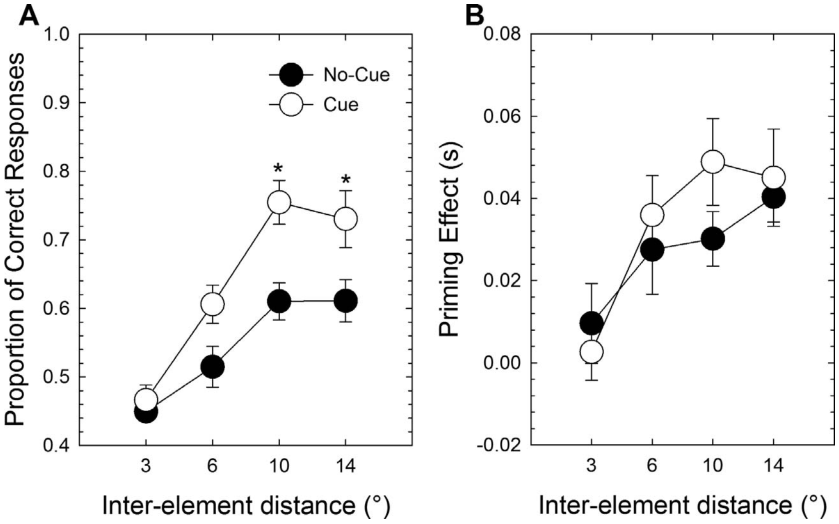

Figure 8. Results of Experiment 4B. (A) Mean proportion of correct responses for the 2AFC task of Experiment 4B. The asterisks represent a significant difference between the no-cue and cue conditions. (B) Priming effect (in seconds) as a function of the interelement distance (in degrees) for the no-cue and cue conditions. Error bars ± *SEM*.

cantly above chance for the interelement distances of 6° ($p = 0.007$), 10° ($p = 0.0001$), and 14° ($p = 0.001$).

RTs for the 4AFC task

The amount of trials excluded with the filtering procedure (Lachaud & Renaud, 2011) was 9.8% and 9.1% for the spacing and spacing–cueing experiments, respectively. After the exclusion of trials with fixational eye movements (0.3% and 0.52% for the spacing and spacing–cueing experiments, respectively) and outlier RTs, the analysis was conducted on the remaining 89.9% and 90.4% of the trials, respectively, for the spacing and spacing–cueing experiments.

Figure 8B shows the priming effect measured in the no-cue and cue conditions as a function of the interelement distances. A repeated-measures ANOVA including as factors the cue condition (i.e., no cue vs. cue) and the interelement distance reported only a significant effect of the interelement distance, $F(3, 21) = 6.52$, $p = 0.003$, partial $\eta^2 = 0.48$. Bonferroni-corrected pairwise comparisons revealed a significant difference between the priming effect obtain at 3° of spacing and that obtained at 6° ($p = 0.011$) and a significant difference between the priming effect at 3° and 10° of spacing ($p = 0.05$).

We also performed a series of one-sample Bonferroni-corrected t tests to assess which priming effects were significantly different from zero (critical $p = 0.0063$). For the spacing experiment, the one-sample t tests pointed to a significant priming effect at 10° and 14° of spacing ($p = 0.003$ and $p = 0.0001$, respectively). For the spacing–cueing experiments, t tests reported a significant priming effect at 10° ($p = 0.002$) of spacing and a marginally significant priming effect for 6° and 14° of spacing ($p = 0.007$).

Accuracy for probe direction discrimination

For the two parts of Experiment 4B, the proportion of correct responses in judging the motion direction of the probe stimulus was >0.93. A repeated-measures ANOVA including as factors the cue condition (no cue vs. cue), the interelement distance, and the probe condition (i.e., match vs. mismatch) did not report any significant effect or interaction. On average, the accuracy obtained in discriminating the probe's motion direction was 0.95 (*SE*: 0.01) in the no-cue condition and 0.98 (*SE*: 0.009) in the cue condition.

Discussion

By decreasing the number of flankers (7 vs. 19), we found that the priming effect was partially retrieved, depending on the distance between prime and flankers. This result further supports the notion that the sensory information relative to the prime stimulus was lost because of crowding, a phenomenon with which target–flankers spacing plays a crucial role. Although it might be argued that the results in Experiment 1 may be due to a floor effect, here we found that the absence of priming effect occurs also with a simpler stimulus configuration. As soon as the prime's motion direction was discriminable (up to 60% accuracy for the spacing-only condition), the priming effect was recovered (0.03 and 0.04 s for 10° and 14° of spacing). However, the effects of crowding were only partially dispersed when the flankers were presented outside Bouma's window, yielding 60% of accuracy. At first glance, this result may seem surprising, but recent studies have shown that flankers outside Bouma's window can still affect crowding strength (see Herzog & Manassi, 2015, for a review). Hence, Bouma's law should be understood more as a "rule of thumb" (Whitney & Levi, 2011) rather than as a fixed, cortical window of interaction (Pelli, 2008). The results of attentional cueing are mixed. Although the cue seems to decrease crowding strength (Figure 8A), it does not seem to increase the priming effect (Figure 8B).

General discussion

We investigated priming for global motion in crowded and noncrowded conditions. In particular, the prime stimulus was surrounded by similarly moving elements (flankers) that could either move in different directions (crowded condition) or be stationary (noncrowded condition). The observer's task was to discriminate the motion direction of a subsequently presented probe stimulus. In addition, observers were required to perform a secondary task in which they had to judge whether a test stimulus (presented after the response to the probe stimulus) was moving either in the same or a different direction as that of the prime (2AFC task). This secondary task was important to assess whether the observers could discriminate the prime's motion direction. Dependent variables were accuracy (for both the direction discrimination of the probe stimulus and the 2AFC same–different task) and RTs in responding to the probe stimulus (4AFC). In Experiment 1, we varied the duration of the prime stimulus from 0.2 to 2 s. This was done to test the dependency of the priming effect in crowding on the stimulus duration and to possibly induce a switch from facilitation to suppression (adaptation). As reported in the Introduction, Faivre and Kouider (2011a), using simple oriented Gabor patches, found that when the orientation of the prime stimulus was not discriminable (i.e., crowded condition) they found a reliable positive priming effect; however, when increasing the prime duration up to 1 s, they found a negative priming effect, indicating a certain degree of adaptation when prime and probe had the same orientation. Moreover, when the prime orientation was discriminable (i.e., noncrowded condition) increasing the prime duration resulted in a reduction of the positive priming effect and not in a negative priming effect. For the first time, we report in the motion domain an important dissociation: Whereas priming for oriented stimuli (Faivre & Kouider, 2011a), multifeature crowded objects, such as faces and directional symbols (Faivre & Kouider, 2011b) as well as semantic stimuli (Peng et al., 2013; Yeh et al., 2012), survives crowding, priming for global motion does not. Our results show that in the crowded condition, no priming effect was present, and this for all prime durations employed. Additionally, for the longer prime durations (e.g., 1 and 2 s) we could not determine any adaptation effect. Similar to what was found by Faivre and Kouider (2011a), in the noncrowded condition, we found the greatest priming effect (i.e., 0.103 s) for the 0.2 s prime duration, and increasing the prime duration, we observed its exponential decay.

In light of this psychophysical evidence, it is not clear why priming for global moving stimuli does not survive crowding. We then performed additional experiments to investigate the spatial and temporal characteristics of priming for global motion in crowding and in order to assess under which conditions the priming effect was retrieved.

In Experiment 2, we investigated whether pooling or substitution models could explain the absence of priming effect in the crowded condition. To test this hypothesis, we varied the percentage of flankers moving in the same direction to that of the prime. The rationale was that if crowding depends on the fact that only the averaged (pooling) or overall (substitution) information is available to the visual system, an array composed of the prime stimulus and a high percentage of flankers that move in the same direction to that of the prime should increase the accuracy in the 2AFC task and thus increase the priming effect.

However, our findings did not support either pooling or substitution models. These results also suggest that (global) motion priming is retinotopic (Campana, Pavan, & Casco, 2008; Yoshimoto, Uchida-Ota, & Takeuchi, 2014) because remote flankers moving in the same direction to that of the prime do not induce any facilitation; instead they may degrade the sensory representation of the prime preventing any further elaboration.

Further experimental evidence that flankers may corrupt the sensory representation of the prime comes from the results of Experiment 3, in which we varied the speed of the flankers relative to that of the prime. In particular, the speed of the prime was always constant at 6.4°/s whereas the speed of the flankers was varied ±1 and ±2 octaves from the prime speed. The rationale was that when the flankers had a lower speed than the prime, the latter should pop out. It was previously shown that pop-out of the target always leads to a decrease of crowding strength (Manassi, Sayim, & Herzog, 2013; Poder, 2007), and hence, a retrieval of the priming effect should occur. However, the results showed no priming effect regardless of the flankers' speed. Previous literature showed that crowding decreases when target and flankers are dissimilar in orientation (Andriessen & Bouma, 1976;

D. M. Levi, Hariharan, & Klein, 2002), spatial frequency (Chung, Levi, & Legge, 2001), shape (Kooi, Toet, Tripathy, & Levi, 1994; Nazir, 1992), contrast polarity (Chung & Mansfield, 2009; Kooi et al., 1994, Sayim, Westheimer, & Herzog, 2008), and color (Kooi et al., 1994; Manassi et al., 2012). Here, we found that speed (along with contrast; Rashal & Yeshurun, 2014) is a remarkable exception. Taken together, the results from Experiments 2 and 3 suggest that, in the case of motion priming, if the prime is flanked by moving elements (regardless of their direction and speed), this is sufficient to disrupt the sensory representation of the prime, thus nulling out the priming effect.

In Experiment 4A, we assessed whether the absence of visual motion priming reported in the previous experiments could be overcome by cueing attention to the target location. In addition, we varied the interelement distance between prime and flankers (i.e., spacing). Yeshurun and Rashal (2010) reported that an attentional cue reduces the critical distance, thus reducing the crowding effect. In particular, the authors reported this effect regardless of the presence or absence of a backward mask and whether the attentional cue was informative or not. More specifically, when the cue was neutral (i.e., when it was presented at the center of the screen) and thus not informative for the target's location, they reported an (exponential) increment of the accuracy in discriminating the orientation of the target (i.e., a tilted "T"). However, when introducing the attentional cue, they also reported a reduction of the critical distance. Our results showed that when introducing the attentional cue while manipulating the interelement distance, there is an improvement of the accuracy in the 2AFC task (up to 70% correct responses). Consistent with that reported by Yeshurun and Rashal, only in this condition and at the largest spacing (6°), we found a significant priming effect although its magnitude was halved with respect to the priming effect obtained in Experiment 1 in the noncrowded condition and with the same prime duration (0.2 s). Thus, the results show a significant attentional increment of accuracy on the 2AFC task, a significant attentional reduction of the crowding strength only for the highest level of spacing, and, consequently, an increase in the priming effect in the condition with the higher accuracy.

The finding that precueing the prime location improves the accuracy is consistent with several previous crowding studies showing that directing attention to the target location leads to better overall performance in crowding (Felisberti et al., 2005; Huckauf & Heller, 2002; Scolari et al., 2007; Strasburger, 2005; Strasburger & Malania, 2013). Such an improvement suggests that attention enhances or restores the processing of the prime at the attended location, possibly restoring the sensory representation of the prime (Poder, 2006, 2007; Scolari et al., 2007). However, previous studies that measured the critical distance while manipulating transient attention (Scolari et al., 2007; Strasburger, 2005; Strasburger & Malania, 2013) did not always find an attention-induced decrement of the critical distance. For example, Scolari et al. (2007) did not find any significant effect of attention on the critical distance whereas Strasburger (2005) found an attention-induced decrement of the critical distance at 1° and 2° of eccentricity but not at 4°. As pointed out by Yeshurun and Rashal (2010), it is possible that the lack of such an attentional effect on the critical distance was due to forward masking between the attentional cue and the target (Huckauf & Heller, 2002; Strasburger, 2005). To this purpose, Yeshurun and Rashal presented a cue near the location of the target, thus reducing a possible interference between the cue and the target and allowing the emergence of a significant attentional effect on the critical distance. However, this seems to apply only when using letters or digits as target stimuli. In our study, we showed that directing attention to the prime location reduced the critical distance although we obtained a significant priming effect only in correspondence of the largest interelement distance (Figure 6B). This is in contrast to what was recently reported by Strasburger and Malania (2013). The authors investigated the quantitative characteristics of flanker confusions in a crowding paradigm and tested whether transient spatial attention reduces the crowding effect by reducing flanker confusions. In particular, they examined the crowding effect for digits at three different eccentricities (2°, 4°, and 6°) and for a range of target-to-flanker distances and attentional cue sizes. The effects of flanker distance confirmed previous findings that errors of both content and position are highest with the shortest interelement distance. However, the authors reported no cue effect on flanker confusions while the cue only affected content information by enhancing target contrast sensitivity regardless of cue size. These different effects of the attentional cue certainly depend on the stimulus configurations used. We argue that in certain paradigms the attentional effects on the critical distance of crowding may be more susceptible to forward masking (Scolari et al., 2007; Strasburger, 2005).

In our study, there could be different explanations concerning the attention-induced reduction of crowding. For example, as reported by Strasburger and Malania (2013), the attentional cue could enhance the prime contrast sensitivity at a far eccentricity, partially rendering the visual motion information of the prime available for subsequent elaboration. Indeed a number of operations are involved in spatial attention, such as gain enhancement, noise reduction, changes in decisional criterion, and overall facilitation of processes

(Carrasco, Penpeci-Talgar, & Eckstein, 2000; Carrasco, Williams, & Yeshurun, 2002; Henderson & MacQuistan, 1993; Luck & Thomas, 1999; Yeshurun & Carrasco, 1999; Yeshurun & Rashal, 2010). Although not all these operations may be involved in the reduction of the critical distance, they may have an effect on the prime by increasing the signal-to-noise ratio. However, if the cue merely reduces noise and increases contrast sensitivity at the prime location, we would expect an improvement of accuracy in the 2AFC task and an increase in the priming effect at the lowest interelement distance (3°); however, this was not the case. It is possible that, in addition to noise reduction and gain enhancement, transient attention may contribute to a reduction in the size of the integration fields at the attended location (Yeshurun & Rashal, 2010). Indeed at the motion integration stage (e.g., motion areas MT and MST), receptive fields are large and can pool information over wide portions of the visual field (up to 25°; Felleman & Kaas, 1984). Thus, transient attention may enhance the spatial resolution at the attended location by facilitating information processing over a small area (Yeshurun & Carrasco, 1998, 1999, 2000). This hypothesis is consistent with physiological studies suggesting that attention contracts the receptive field of MT cells around the attended stimulus (Anton-Erxleben, Stephan, & Treue, 2009). Anton-Erxleben et al. (2009), for example, found that attention reshapes the receptive field profile of MT neurons shifting center and surround toward the attended location. In addition, the size of the receptive fields changes as a function of relative distance to the attentional focus: Attention inside the receptive field has the effect of shrinking it whereas directing attention outside the receptive field expands it. Moreover, the authors reported changes in surround inhibition, which was strengthened just beyond the attended location, and amplitude of the receptive field. These findings suggest that these modulations optimize processing at and near the attentional focus in order to enhance the representation of the attended stimulus while reducing influences of nearby distracters. Thus, the reduction of crowding we found when using the attentional cue may reflect the combination of several attentional mechanisms operating at the stage in which global motion is extracted.

Finally, in Experiment 4B, we investigated whether a floor effect in our crowding task is responsible for the absence of priming. In fact, in the configuration with 19 flankers, all the elements were presented within Bouma's window, thus still interfering with prime perception. For this reason, we repeated the experiment with a configuration of seven flankers instead of 19. The results show that with increasing the target–flankers distance the crowding strength decreased, and as a consequence, motion priming was partially retrieved. In our opinion, the fact that the priming effect is dependent on spacing between prime and flankers is clearly evidence for a crowding mechanism. In addition, in this experiment, the absence of priming cannot be attributed to a floor effect because manipulating the spacing between prime and flankers led to a retrieval of prime information. In Experiment 4B, the role of the attentional cue is not clear. Cueing the prime's spatial location led to a decrease of the crowding strength but no change in the priming effect. This could be due to a ceiling effect of the priming for the specific spacing values tested although further control experiments should be performed to confirm this hypothesis. Still, crowding may be due to difficulties in identifying the prime location. However, location uncertainty cannot entirely explain our crowding effect. First, in Experiment 4A, we precued prime location. If crowding strength was only due to location uncertainty, the effects of crowding should have completely vanished. However, crowding did not completely disappear (as shown in Figure 8). Second, in Experiment 4B, we reduced the number of flankers. Fewer flankers should have made the prime location easier to identify. However, the effects of crowding still remained strong. Therefore Experiment 4A and 4B provides evidence that uncertainty plays a role in crowding, but it cannot entirely explain its strength.

Conclusions

Our results point out, for the first time, an important dissociation between motion priming and motion adaptation. Although motion adaptation and, consequently, the MAE, survives crowding (Aghdaee, 2005; Harp et al., 2007; He et al., 1996; Pavan & Greenlee, 2015; Rajimehr et al., 2004), visual motion priming does not survive crowding regardless of the duration of the prime stimulus. As pointed out previously, attention seems to play a relevant role in determining crowding strength and, as a consequence, in establishing motion priming. The difference between priming and adaptation can be explained by referring to a number of psychophysical studies that show the interdependence of priming and attention (Kristjánsson, Bjarnason, Hjaltason, & Stefánsdóttir, 2009; Kristjánsson et al., 2013; Kristjánsson & Nakayama, 2003; Raymond, O'Donnell, & Tipper, 1998). Kristjánsson et al. (2013), for example, assessed the role of temporal continuity in crowding. In particular, they showed that crowding is considerably diminished when objects remain constant on consecutive visual search trials; that is, the repetition of both the target and distractors on consecutive trials decreases the critical distance between target and distracters. The results suggest that object continuity via between-trial attentional priming (Kristjánsson, 2008; Maljkovic & Nakayama, 1994) enhances the percept of objects that would otherwise be not discriminable due to crowding. On the other hand, in the case of the MAE, the results are contradictory. Indeed although some studies reported that distraction affects the strength of the MAE (Aghdaee & Zandvakili, 2005; Alais & Blake, 1999; Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Chaudhuri, 1990; Kaunitz, Fracasso, & Melcher, 2011; Lankheet & Verstraten, 1995), other studies reported no effect of attention on motion adaptation (M. J. Morgan, 2011, 2012; M. Morgan, 2013; Pavan & Greenlee, 2015; Wohlgemuth, 1911). For example, M. J. Morgan (2012), adapting to complex motion (expanding patterns), did not find an effect of attention on any of the measures of adaptation adopted (i.e., duration and a speed nulling), suggesting that the methods used in the literature to show the effect of distraction (e.g., on the duration of the aftereffect) could be potentially susceptible to bias. This observation could partly explain the dissociation we found between priming and adaptation. Further investigations are necessary to address this issue in order to better understand the dynamics between facilitation and suppression in motion processing.

Keywords: visual motion priming, global motion, crowding, spatial cueing, transient attention

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