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Paradoxical cross-over due to attention to high or low spatial frequencies

Matthias Niemeier [a,b,*], Boge Stojanoski [a], Vaughan W.A. Singh [a], Eddie Chu [a]

[a] Centre for Computational Cognitive Neuroscience, Department of Psychology, University of Toronto at Scarborough, 1265 Military Trail, Toronto MIC 1A4, Canada
[b] Centre for Vision Research, York University, Toronto, Canada

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Abstract

The mechanisms underlying the right hemisphere's dominance for spatial and attentional functions lacks a comprehensively explanation. For example, perceptual biases, as observed in line bisection and related tasks, might be caused by an attentional asymmetry or by perceptual processes such as a specialization of the left and right hemisphere for high and low spatial frequencies (SFs), respectively. Here we used the gratingscales task to measure perceptual bias in SF judgements, and we cued participants' attention either to high or low SFs. Participants showed a leftward bias when comparing the high SF components of the stimulus, and a rightward bias when comparing the low SF components-opposite to what would be expected from a hemispheric lateralization for SFs. Two control experiments used different strategies to manipulate the width of the attentional window. However, we observed no influence on perceptual bias, thus ruling out the possibility that the results in Experiment 1 were due to differences in attentional window size. These data support the idea of an attentional asymmetry underlying perceptual bias. Our results provide novel support for the role of attentional asymmetry in perceptual biases.
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1. Introduction

The right hemisphere is dominant for spatial and attentional functions. This has been concluded from functional imaging and EEG studies (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Coull, Nobre, & Frith, 2001; Fink, Marshall, Weiss, Toni, & Zilles, 2002; Fink, Marshall, Weiss, & Zilles, 2001; Foxe, McCourt, & Javitt, 2003). Yet, data from lesion studies are more compelling. Right-brain damage results in severe disruptions of spatial behaviour such as spatial neglect, a deficit that comprises various difficulties in perceiving and responding to stimuli on the side contralateral to the lesion (Hillis et al., 2005; Karnath, Ferber, & Himmelbach, 2001; Karnath, Himmelbach, & Rorden, 2002; Leibovitch et al., 1998; Mort et al., 2003; Rorden, Fruhmann Berger, & Karnath, 2006; Vallar & Perani, 1986). However, it remains unclear how overt deficits after brain damage relate to underlying functions and dysfunctions.

One example is perceptual biases that are found in some neglect patients (for a different interpretation of this deficit see Ferber & Karnath, 2001). These patients show marked shifts to the ipsilesional right side when bisecting horizontal lines and when assessing pre-bisected lines or related stimuli (e.g., Binder, Marshall, Lazar, Benjamin, & Mohr, 1992; Heilman & Valenstein, 1979; Luh, 1995; Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994; Mattingley et al., 2004; Milner & Harvey, 1995; Nicholls, Bradshaw, & Mattingley, 1999; Schenkenberg, Bradford, & Ajax, 1980).

* Corresponding author. Fax: +1 416 287 7642.
E-mail address: niemeier@utsc.utoronto.ca (M. Niemeier).

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Normal participants, on the other hand, show similar, yet smaller biases mostly to the left side (for a review see Jewell & McCourt, 2000).

Perceptual biases are often assumed to reflect asymmetries in the distribution of attention (Heilman & Van Den Abell, 1980; Kinsbourne, 1970; Mesulam, 1981; Posner, Walker, Friedrich, & Rafal, 1984). Consistent with this "attentional asymmetry account" of perceptual bias are cueing effects. Cueing paradigms ameliorate pathological biases, such as when patients are asked to report or detect stimuli presented on the left side of the line bisection task (Harvey, Milner, & Roberts, 1995; Mennemeier, Vezey, Chatterjee, Rapcsak, & Heilman, 1997; Nichelli, Rinaldi, & Cubelli, 1989; Nicholls & Roberts, 2002; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990; Reuter-Lorenz & Posner, 1990; Riddoch & Humphreys, 1983), when they are verbally cued to the left side (Ishiai, Seki, Koyama, & Okiyama, 1995), or when they observe the experimenter marking the left end of the line (Harvey, Pool, Roberson, & Olk, 2000). Likewise, cueing in normal participants tends to shift biases in the cued direction (e.g., Bultitude & Aimola Davies, 2006; Harvey et al., 1995; McCourt, Garlinghouse, & Reuter-Lorenz, 2005; Nichelli et al., 1989; Reuter-Lorenz et al., 1990).

While these cueing paradigms provide convincing evidence that attention biased through cues influences perceptual bias, the disadvantage is that they introduce biases that might be independent of those observed in *uncued* conditions (McCourt et al., 2005 for a discussion of this matter). In other words, cueing paradigms cannot rule out the possibility that perceptual biases result from perceptual rather than attentional asymmetries.

For example, Monaghan and Shillcock (2004) proposed that perceptual biases might result from hemispheric differences in coarse- and fine-coding of visual stimuli, much in line with previous models which assume that the right hemisphere is dominant for lower spatial frequencies (SFs) and global perception while the left hemisphere is specialized for higher SFs and local perception (e.g., Christman, 1997; Grabowska & Nowicka, 1996; Ivry & Robertson, 1998; Robertson & Lamb, 1991; Sergent, 1982).

In partial support of the "SF account" of perceptual bias, we have recently used a new gratingscales task to show that perceptual bias varies as a function of SFs (Niemeier, Stojanoski, & Greco, 2007). For this task, participants viewed two horizontal bars containing gratings that increased in SF, one from right to left and one from left to right. For example, in Fig. 1A, the upper bar contains a grating that is relatively low in SF on the left side (0.3 cycles per degree, cpd) and relatively high in SF on the right side (1 cpd) with a "central area" of transition between both ends; and the bar at the bottom shows the opposite pattern. We directed participants' attention to the relatively higher SF component in each gratingscales stimulus (1 cpd in Fig. 1A, 2 cpd in Fig. 1B, etc.) by asking, 'which of the two bars has more thinner stripes', and we found that participants preferred bars with high SF components on the left side. That is, when presented with the stimulus in Fig. 1A, participants would rather choose the bar at the bottom even though both bars are mirror-reversed versions of each other, and in Fig. 1B, participants might still tend to choose the bottom bar even though its high SF component is smaller than that of the upper bar and so forth.

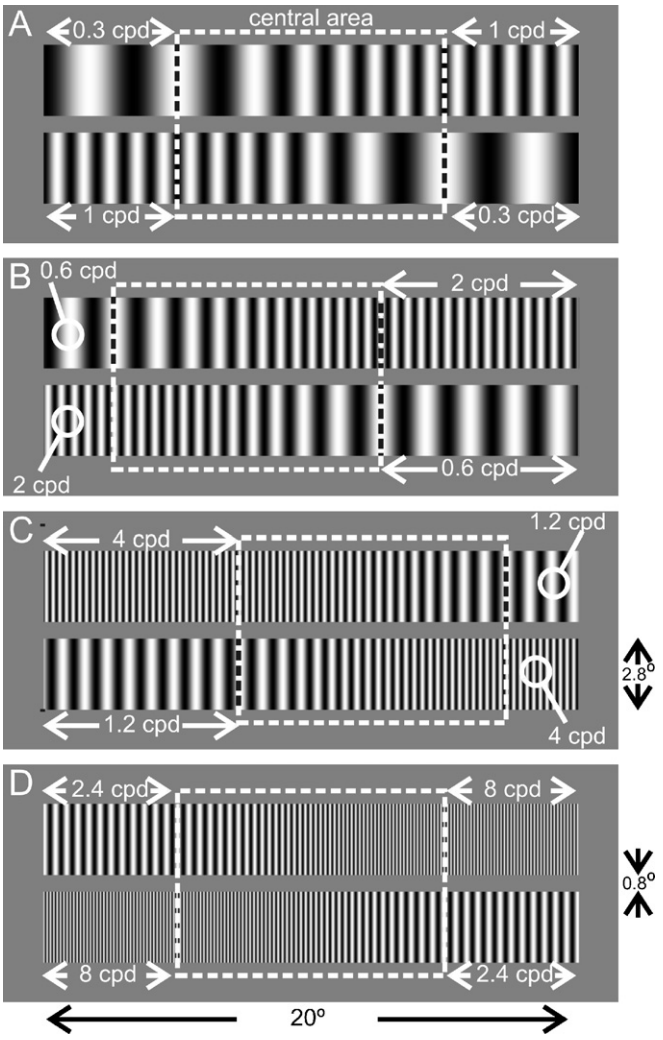

Fig. 1. Experiment 1. Participants viewed the gratingscales task on a grey background and were asked to judge which of the two bars has "more thinner" or "more thicker stripes". Given are examples of (A) a G1 stimulus, (B) a G2 stimulus, (C) a G4 stimulus, and (D) a G8 stimulus.

What is important with respect to the SF account, we found this leftward bias was most pronounced for gratingscales covering an intermediate SF range (0.6–2 cpd, Fig. 1B). In agreement with the SF lateralization models, leftward bias declined with high SF ranges (for example 1.2–4 cpd, Fig. 1C). However, it never declined to the point that bias 'crossed over' to the right side. Cross-over is known to occur in line bisection tasks for very short lines (e.g., Halligan & Marshall, 1988; McCourt & Jewell, 1999; Mennemeier, Rapcsak, Dillon, & Vezey, 1998), but one might expect cross-over for gratingscales with high SF ranges as well, given a left-hemisphere dominance for

high SFs. Also, for low SF ranges (Fig. 1A) we found leftward bias to be reduced instead of increased. Both observations are rather inconsistent with a SF specialization account of perceptual bias, though there might be ways to reconcile them with this hypothesis. The gratingscales task might introduce an unusually strong leftward bias so that any rightward bias disappears or occurs only for very high SFs; and hemispheric lateralization might be somewhat reduced for low compared to intermediate SFs.

Alternatively, leftward bias in the gratingscales task could be explained with the attentional asymmetry account as well. Since attention increases apparent SF (Gobell & Carrasco, 2005; Yeshurun & Carrasco, 1998), a left-biased asymmetry in attention should produce the perceptual bias that we observed.

The aim of the present study was to test the attentional asymmetry account and the SF account of perceptual bias further. To this end we employed the gratingscales task. The task is a valid measure of perceptual bias as it correlates with the greyscales task (Niemeier et al., 2007), an established test of bias in neurological patients (e.g., Mattingley et al., 2004). Participants performed the gratingscales task while their attention was cued in a non-lateralized manner. In Experiment 1 they attended either to the high or to the low SF component of the gratingscales ('Which of the two bars has more thinner/thicker stripes?'). According to the SF account, leftward bias should be stronger when attending to the low than when attending to the high SF component (Christman, Kitterle, & Hellige, 1991). By contrast, according to the attentional asymmetry account, we should expect a paradoxical form of cross-over. Attention biased to the left side should increase apparent SF on that side no matter whether the high or the low SF component is task-relevant. Consequently, participants should show a leftward perceptual bias when attending to high SFs and a rightward bias when attending to low SFs—opposite to the cross-over predicted by the SF account. We observed the latter, in agreement with the attentional asymmetry account. Two additional control experiments used different strategies to manipulate the size of the participants' attentional window. However, we observed no effect on leftward bias, thus, ruling out the possibility that attentional window size had a significant influence on cross-over.

2. Materials and methods

2.1. Participants

One hundred and one undergraduate students gave their informed and written consent prior to their inclusion in the study and obtained a course credit. Twenty-seven of them participated in Experiment 1 (18 females; median age: 19), 34 in Experiment 2 (21 females, median age: 18), and 40 in Experiment 3 (23 females, median age: 18). All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto and therefore have been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants were healthy, had normal or corrected to normal vision, and were right handed as confirmed with the Edinburgh handedness inventory (Oldfield, 1971).

2.2. Apparatus and procedure

Participants sat in front of a 19-inch monitor (Viewsonic E90fb) at a distance of 60 cm. A chin rest was used to keep head movements to a minimum.

We wrote our experiments in Matlab (MathWorks) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). In Experiments 1 and 2 we used the gratingscales task, and in Experiment 3 a simplified version of it. We have recently developed this task to measure perceptual biases based on SF judgments and found that it correlates with other measures of perceptual bias (Niemeier et al., 2007).

Stimulus samples of the gratingscales are given in Fig. 1. Each stimulus consisted of two horizontal bars that were filled with rows of luminance-defined wavelets. SF of the pattern increased from left to right in one bar, half the time in the upper and half the time in the lower bar, and from right to left in the respective other bar. For example in the upper bar in Fig. 1A, SF increased from 0.3 cpd on the left to 1 cpd on the right and vice versa in the lower bar. For convenience we call gratingscales stimuli with this SF range "G1" stimuli. Other SF ranges used in the present study were 0.6–2 cpd ("G2", Fig. 1B), 1.2–4 cpd ("G4", Fig. 1C), and 2.4–8 cpd ("G8", Fig. 1D).

Note that the transition from low to high SF occurred only within a "central area" covering half the width of the two bars within which SF increased following a half-cycle of a cosine function (see Niemeier et al., 2007 for a detailed stimulus description of this "continuous version" of the gratingscales task). Left and right of the central area SF remained constant. This way it was possible to shift the central area to create asymmetrical stimuli that continued to span the same ranges of SFs. For example, in Fig. 1B, the central area is shifted −12.5% leftward relative to stimulus width, and in Fig. 1C, it is shifted +12.5% rightward.

In total there were eight equally spaced degrees of stimulus asymmetry for Experiment 1 from −12.5% (e.g., Fig. 1B) via 0% (e.g., Fig. 1A and D) to +12.5% (e.g., Fig. 1C); and for Experiment 2 we used seven nonlinearly spaced steps (±12.5%, ±5.1%, ±1.6%, and 0%). Each of these stimuli was presented sixteen times, and every time participants were asked to choose the bar with "more thinner" (Experiments 1 and 2) or "more thicker stripes" (Experiment 1).

Based on the participants' responses we calculated probabilities of choosing the bar with the high SF component on the right side as a function of stimulus asymmetry, and we fitted sigmoid psychometric (Weibull) functions to the participants' responses to determine the point at which they had no preference for bars with high SF components on the left or right side. We used this point

of subjective equality (PSE) as our measure of perceptual bias. The other parameter of the Weibull function is its slope which can be used to estimate task difficulty and/or task sensitivity. That is, across different tasks a steep psychometric function will indicate that a task is rather easy as opposed to a difficult one with shallower functions. Similarly, across participants steep psychometric functions reflect that a person performs well or with "high sensitivity" on a given task while flat functions suggest that a participant had difficulties with the task or showed "low sensitivity" (also see Niemeier et al., 2007). Trials were sorted into blocks, two for each condition, and the order of blocks was pseudorandom for the first half and mirror-reversed for the second.

2.2.1. Experiment 1

In different blocks of trials participants either judged which of the two bars "had more thinner stripes" or "more thicker stripes". This way we directed attention either to the high or low SFs of the gratingscales. The second independent variable was SF range. We used gratingscales G1, G2, G4, and G8 (Fig. 1) that were viewed for 150 ms under free viewing conditions, though from behavioural observations we found that participants normally fixate the centre of the monitor.

2.2.2. Experiment 2

The second experiment combined the gratingscales task with a fixation task (Fig. 2) to manipulate the width of the attentional window. Therefore, each trial started with the outline (width: 1 pixel) of a central fixation square (0.3° across). 200 ms to 600 ms later five square-shaped dots appeared for 150 ms. One of them (0.07° across, either black or white) appeared inside the outlined fixation square so that it was difficult to see if not foveated. The other four dots (0.17° across) appeared in the periphery at the corners of an imaginary rectangle (20.3° by 6.4°). They were always of the same colour, either black or white, independent of the dot inside the fixation square. Participants were asked to respond to the dots by pressing a button as quickly as possible. If they responded later than 800 ms or earlier than 100 ms after dot onset the fixation task was repeated. There were two versions. The '*global fixation task*' asked whether the colours of the central and the peripheral dots were the same or different. The '*local fixation task*' asked whether the colour of the central dot was black or white while the peripheral dots could be ignored. Participants retained the respective information in memory to be tested at the end of the trial (in pilot tests we found that testing with an immediate speeded forced choice was too difficult). Even so participants often required repetitions of the fixation task, and one participant was excluded because her average performance was four standard deviations below group average. After the fixation task the screen went blank and then the gratingscales task was presented for 75, 150, or 300 ms, followed by another blank screen. Subsequently, two response screens appeared, one for the gratingscales task and one for the fixation task. Psychometric functions as reported here were modeled based on trials, during which the fixation task was completed successfully, however, additional analyses based on all trials yielded very similar results.

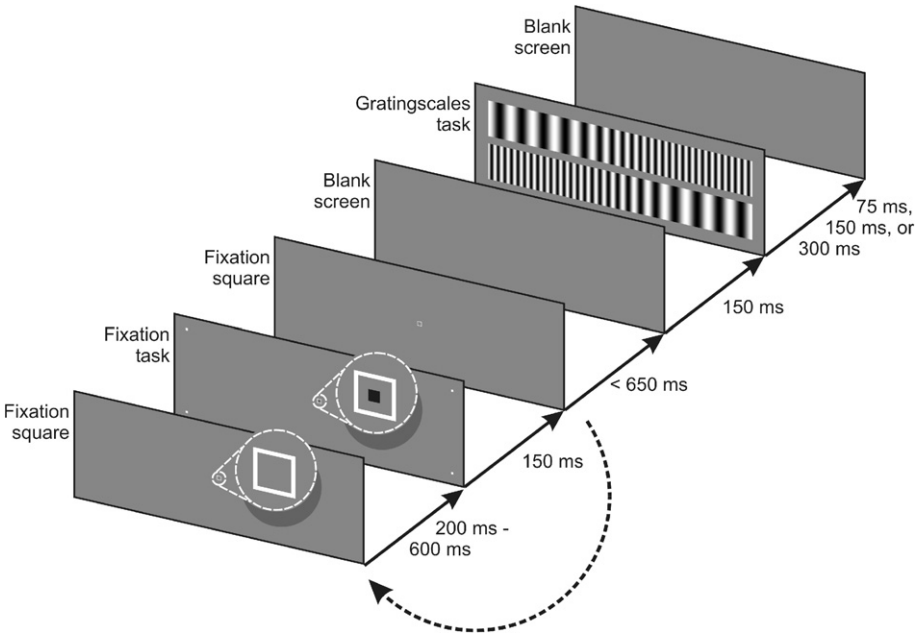

Fig. 2. A schematic representation of a trial sequence in Experiment 2. For the fixation task participants fixated a central fixation square and quickly pressed a button when five small square-shaped spots flashed on the screen. In case of a delayed button press after stimulus onset (>800 ms) the task was repeated (dashed arrow). For the 'local' condition participants were asked to remember the colour of the spot inside the fixation square. For the 'global' condition they were asked to compare the colours of the central and the peripheral spots. The fixation task was followed by the gratingscales task. Afterwards two response screens appeared (not shown here), one for the gratingscales task and one for the fixation task.

2.2.3. Experiment 3

Because the fixation task in Experiment 2 did not have a noticeable effect on perceptual bias, Experiment 3 pursued a different strategy to manipulate the width of the attentional window without an additional fixation task. To this end we simplified the gratingscales task (Fig. 3). Participants were asked to fixate a small white square (0.13° across) in the centre of the screen and then to press a key. Upon key press an array of six elements appeared for 50 ms. Four elements were white gaussian blobs (SD = 1.5°) that served as distracters. The other two elements were luminance-defined sinusoidal gratings enveloped by a two-dimensional gaussian of the same size. The gratings differed from a standard SF of either 1.5 or 3 cpd so that on one side SF was k times higher, and on the other side it was k times lower, with k having one of eight possible values (in natural log steps) between 1 and 1.5. For example, in Fig. 3A, the grating on the left side has a SF of 4.5 cpd (3 cpd × 1.5) and the grating on the right has a SF of 2 cpd (3 cpd/1.5). Participants were asked to indicate which of the two gratings appeared to be higher in SF, and we used Weibull functions to model their responses as a function of Δlog(k) and to obtain PSEs and slopes as perceptual measures just like in Experiments 1 and 2.

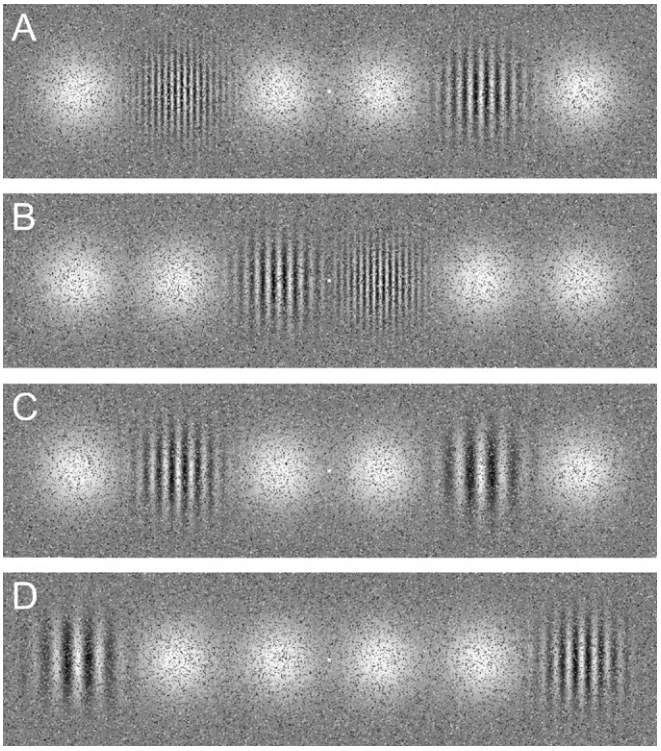

Fig. 3. Sample stimuli used in Experiment 3. Participants were asked to judge which of the two gratings contained "thinner" stripes. Target trials presented gratings at an intermediate eccentricity (A and C) and appeared 50% of the time. The other half of trials were context trials (B and D) to manipulate attentional window size in separate blocks of trials. (A) Target stimulus in the 'narrow' attentional window condition. (B) Context stimulus in the 'narrow' attentional window condition. (C) Target stimulus in the 'wide' attentional window condition. (D) Context stimulus in the 'wide' attentional window condition. The geometrical mean of the SF of each pair of gratings was either 1.5 cpd (A and B) or 3 cpd (C and D).

Of main interest was perception of the "target stimuli" that presented the two gratings 6° left and right of the fixation square (Fig. 3A and C). However to manipulate the width of the attentional window, every block of trials combined target trials with an equal number of context trials that presented the grating pair at a different eccentricity. For the "narrow" condition the context trials presented gratings 2° away from the fixation square (Fig. 3B), and for the "wide" condition the context trials presented gratings at a distance of 10° (Fig. 3D). In pilot tests we tried larger eccentricities, yet even with 11.5° participants had great difficulties with the task.

To avoid that participants adjusted the width of their attentional window for each grating pair separately the stimulus was masked after 50 ms by a random dot pattern, that is, a grey screen with 25% of the pixels set to a random luminance level. Likewise, we set 25% of the pixels of the stimulus to random values to degrade its visibility.

3. Results

Experiment 1 tested whether attention to different SFs influences perceptual bias. The respective PSEs are presented in Fig. 4a. Conducting a two-way ANOVA with factors 'SF-based attention' (to high versus low SFs) and 'stimulus' (G1, G2, G4, and G8) yielded a significant main effect of 'SF-based attention' ($F(1,26) = 23.11$, $p = .000056$, $\eta_p^2 = 0.471$). That is, attending to different SF frequency components of the gratingscales produced very different results. When attending to high SFs (black squares) participants showed a leftward bias. However, when attending to low SFs (white squares) biases crossed over to the right side. Neither the main effect of 'stimulus' nor the interaction were significant (F's $\leqslant 1.41$, p's $\geqslant .247$). Despite this lack of evidence for an influence of absolute SFs, we conducted two one-way ANOVAs for each attentional condition separately. Again, we found no significant effect (F's $\leqslant 2.13$, p's $\geqslant .104$), in contrast to our previous finding of a maximum leftward bias for the G2 gratingscales (Niemeier et al., 2007; but note that the G2 stimulus still yields a trend for maximum leftward bias). A possible explanation might be a contrast effect due to attention switching between high and low SFs.

Another two-factorial ANOVA examined the slopes of the psychometric functions (Fig. 4b) as an estimate of task difficulty. We found a main effect of 'SF-based attention' ($F(1, 26) = 49.30$, $p = .00000019$) and a significant interaction with the 'stimulus' factor ($F(1, 78) = 2.80$, $p = .045$), suggesting that conditions differed in difficulty. Most importantly, the gratingscales task was easier when attending to low rather than high SFs.

Can these differences explain differences in perceptual bias? To look at this we correlated slopes and PSEs for all eight experimental conditions. Correlations between PSEs were mostly significant (23 out of 28 significant on

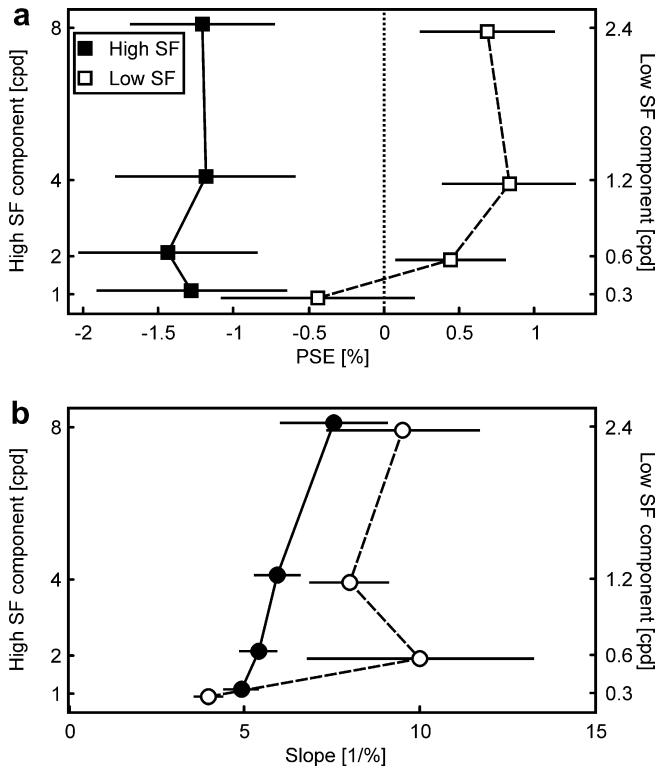

Fig. 4. Results for Experiment 1. (a) Group average of perceptual bias quantified as point of subjective equality of the psychometric functions. (b) Group average of task difficulty (or test sensitivity) quantified as slope of the psychometric functions. Units of the horizontal axis are in percent of bar length. Units of the left vertical axis refer to the high spatial frequency component of the gratingscales, and the right axis refers to the low spatial frequency component. Error bars indicate standard errors. Data points are slightly shifted upward or downward for visibility purposes. PSE, Point of subjective equality; SF, spatial frequency; cpd, cycles per degree.

an uncorrected 5% level, median correlation: 0.529, median p-value: .0046). Likewise we found most correlations between slopes significant (25 out of 28, median absolute correlation: 0.592, median p-value: .0011). In contrast, correlations between PSEs and slopes were small (1 out of 64 significant, median absolute correlation: 0.100, median p-value: .621). Furthermore, we repeated the ANOVA on PSEs including two covariates, average slopes for attending to high SFs and average slopes for attending to low SFs. But again, we observed a main effect of SF-based attention ($F(1,24) = 8.223$, $p = .008$). Therefore, the observed cross-over in perceptual bias cannot be explained with differences in task difficulty. An additional 'SF-based attention' × 'stimulus' interaction ($F(3,72) = 3.445$, $p = .021$) suggests that gratingscales stimuli would have yielded different PSE profiles for the two attentional conditions, had the tasks been equally difficult.

Experiment 2 tested whether the width of the attentional window as manipulated by an additional fixation task influences perceptual bias. We found that neither the PSEs nor the slopes of the psychometric functions reflected such an effect. To examine PSEs (Fig. 5a) we first conducted a two-way ANOVA with the factors 'attentional window'

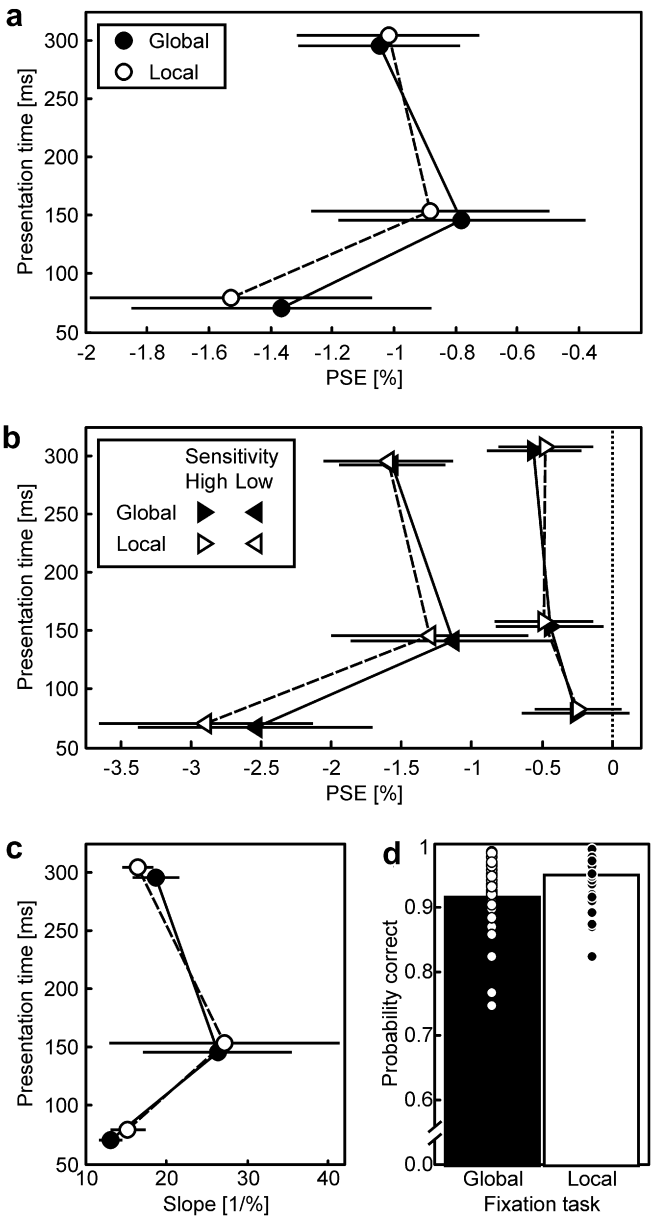

Fig. 5. Results for Experiment 2. (a) Group average of perceptual bias in the gratingscales task. (b) Averages of the same data as in (a) but calculated for two subgroups of task-sensitive and -insensitive performers. (c) Group average of task difficulty in the gratingscales task. (d) Group average and individual data of performance in the fixation task. Error bars indicate standard errors. Data points are slightly shifted upward or downward for visibility purposes. PSE, point of subjective equality.

(local versus global attentional focus) and 'presentation time' (75, 150, and 300 ms). There was no influence of 'attentional window', neither as a main effect ($F(1,32) = .16$, $p = .687$) nor in the form of an interaction with presentation time ($F(2,64) = .12$, $p = .889$). Furthermore, none of the individual t-tests for the three presentation times yielded significant results (t's $\leqslant .56$, p's $\geqslant .579$). Presentation time had no effect either ($F(2,64) = 1.15$, $p = .226$). However, when we used the slopes of the psychometric functions to median-split participants into two subgroups of rather test-sensitive and -insensitive performers

(Fig. 5b) we observed a pattern of leftward biases much like the one we have found previously (Niemeier et al., 2007, Fig. 7B). We confirmed this observation with an ANOVA with a third factor of sensitivity in which we obtained a significant 'presentation time' × 'sensitivity' interaction ($F(2,62) = 3.47$, $p = .037$). However, again there was no influence of the width of the attentional window on perceptual bias. Another two-way ANOVA on slopes found no differences in task difficulty of the gratingscales task across conditions (F's $\leqslant 1.08$, p's $\geqslant .345$, Fig. 5c). By contrast, the global fixation task was performed with less accuracy than the local fixation task ($Z = 4.24$, $p = .000022$, Fig. 5d).

Experiment 3 pursued a different strategy to modify the attentional window. In target trials it presented pairs of gratings at an eccentricity of 6° as the target stimulus combined with context trials that used other eccentricities, either 2° or 10° for a 'narrow' and a 'wide' attentional window condition, respectively. As a first step we conducted a two-way ANOVA with the factors 'attentional window' (narrow vs. wide) and 'SF' of the gratings (geometrical means: 1.5 or 3 cpd). But we found no influence of attentional window size (main effect: $F(1,39) = .01$, $p = .918$; interaction with SF: $F(1,39) = 1.48$, $p = .231$; individual t-tests: $t(39) \leqslant 1.07$, p's $\geqslant .293$). Because there was no influence of SF either ($F(1,39) = .21$, $p = .651$), we joined the data for 1.5 and 3 cpd in an attempt to increase statistical power (white and grey bars in Fig. 6a). However, the influence of the size of the attentional window remained insignificant despite the large number of participants ($t(39) = 1.24$, $p = .223$, $\eta_p^2 = 0.038$). By contrast, attentional window size had a significant influence on task difficulty: Participants showed steeper psychometric functions and performed with significantly higher sensitivity when the target stimulus was presented in a narrow context as opposed to the same stimulus presented in a wide context ($t() = 2.05$, $p = .047$; white and grey bars in Fig. 6b).

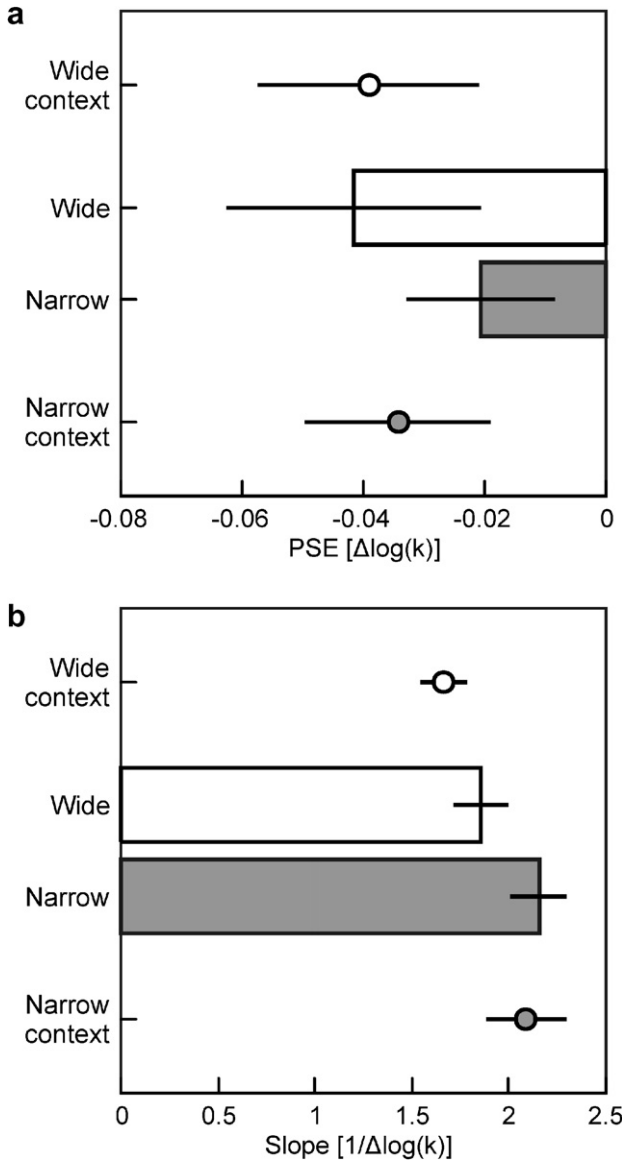

Fig. 6. Results for Experiment 3. (a) Group average of perceptual bias in the simplified gratingscales task. (b) Group averages of task difficulty. Bars represent data for the target stimuli presented at an intermediate eccentricity of 6°. Circles represent data for context stimuli. White symbols, data from 'wide' condition; grey symbols, data from 'narrow' condition; k, multiplication factor to increase and decrease the spatial frequency of the gratings.

4. Discussion

The purpose of the present study was to investigate two explanations of perceptual biases observed in line bisection and similar tasks. Perceptual biases might arise due to an asymmetry in the distribution of spatial attention (Heilman & Van Den Abell, 1980; Kinsbourne, 1970; Mesulam, 1981; Posner et al., 1984) or due to lateralized specializations of the two hemispheres for high and low SFs (Monaghan & Shillcock, 2004). To test these two accounts, we cued our participants' attention either to the high or the low SF components of the gratingscales task, a new test of perceptual bias (Niemeier et al., 2007). When comparing the high SF components, participants showed a bias to the left side, in agreement with our previous findings. Surprisingly however, when comparing the low SF components, bias crossed over to the right side.

This cross-over can be explained with an asymmetry in the spatial distribution of attention (Heilman & Van Den Abell, 1980; Kinsbourne, 1970; Mesulam, 1981; Posner et al., 1984). Attention is known to alter the appearance of visual features. For example, attention increases contrast (Carrasco, Ling, & Read, 2004; Ling & Carrasco, 2006) as well as apparent SF and gap size (Gobell & Carrasco, 2005; Yeshurun & Carrasco, 1998). With respect to the gratingscales task this could mean that participants perceive gratings on the left ends of the two gratingscale bars as higher in SF than those on the right ends. Consequently, when asked about the high SF component of a stimulus participants should prefer bars with the high SF compo-

nent on the left side. But when asked about the low SF component they should prefer the bar with the low SF component on the right end.

Are these potential perceptual consequences of attention due to transient or stimulus-driven mechanisms of attention, or are they due to sustained or voluntary forms of attention? In principle, it is conceivable that there are dissociations between these different types of attention. For example, Niemeier and Karnath (2003) observed that patients with spatial neglect showed two distinct forms of eye movement deficits depending on whether they performed a stimulus-driven or a voluntary visual search task. Relatedly, Ling and Carrasco (2006) reported in part similar, yet not identical influences of transient and sustained attention on a contrast perception task.

Sustained as well as transient influences of attention on perceptual bias have been shown previously (Bultitude & Aimola Davies, 2006; Harvey et al., 1995; Harvey et al., 2000; Ishiai et al., 1995; McCourt et al., 2005; Mennemeier et al., 1997; Nichelli et al., 1989; Nicholls & Roberts, 2002; Reuter-Lorenz & Posner, 1990; Reuter-Lorenz et al., 1990; Riddoch & Humphreys, 1983). However, these studies used cueing paradigms in which attention was directed either to the left or the right side. This bears the risk of introducing additional lateral biases that do not exist under spontaneous, uncued conditions (McCourt et al., 2005). Here we ruled out this possibility by cueing attention in a non-lateralized manner to different features of the test stimuli. Our results triangulate onto the same conclusion. That is, although additional research combining non-lateralized cueing with transient and sustained lateralized cueing will be necessary to further confirm the attentional account, our present data suggest that, paradoxically, perceptual bias might cross over because attention is biased to the left side.

Cross-over of perceptual bias within the same kind of task has been reported for line bisection tasks testing different line lengths (e.g., Halligan & Marshall, 1988; McCourt & Jewell, 1999; Mennemeier et al., 1998; other perceptual biases to the left or the right side are known to occur as a function of test materials, e.g., Lindell, Nicholls, & Castles, 2002; Nicholls, 1994; Okubo & Nicholls, 2006; Yovel, Levy, Grabovecky, & Paller, 2003). Most explanations for cross-over in bisection tasks assume a second mechanism in addition to an attentional asymmetry (e.g., Anderson, 1996; Chatterjee, 1995; Halligan & Marshall, 1988; Mennemeier, Pierce, Chatterjee, Anderson, Jewell, et al., 2005; Mozer, Halligan, & Marshall, 1997; Tegner & Levander, 1991; for a review see Monaghan & Shillcock, 1998). This is not necessary for our data, because here we kept stimulus size constant (shorter gratingscales stimuli might yield the typical cross-over, but this is yet to be tested).

A different account of cross-over, proposed by Monaghan and Shillcock (2004), follows SF lateralization models (Ivry & Robertson, 1998; Robertson & Lamb, 1991; Sergent, 1982). These models assume a specialization for high SFs in the left hemisphere and a specialization for low SFs in the right hemisphere. While SF lateralization models have been successful in explaining a large body of data on visual field differences (e.g., Christman, 1997; Grabowska & Nowicka, 1996), Monaghan and Shillcock (2004) were the first to explore a possible association with asymmetries in line bisection. Using computer simulations they demonstrated that a neural network with one fine- and one coarse-coding hemisphere shows cross-over besides several other known effects of perceptual bias.

However, such a SF account of perceptual bias in bisection tasks would predict the gratingscales task to produce a leftward bias when participants attend to low SFs and a rightward bias for high SFs. There should, at least, be less of a leftward bias for high SFs than for low SFs, that is, if the gratingscales task induced an additional, task-specific bias to the left. These predictions are at odds with the present results. Though we cannot exclude the possibility that future research might reveal that under certain conditions SF-specific activation of the two cortical hemispheres reverses, the SF account in its present form seems to be difficult to reconcile with the perceptual biases as observed here.

Is it possible that the SF account, and not attentional asymmetry, plays a role in perceptual bias but that its influence in Experiment 1 was counteracted due to systematic differences in attentional window size? Because participants in Experiment 1 were free to attend to any part of the gratingscales it is possible that in the high SF condition their attentional window was different from that in the low SF condition. If so, manipulating the size of the attentional window could have a significant influence on perceptual bias. For example, Bedson and Turnbull (2002) found a stronger leftward bias in a detection task that required global attention as opposed to local attention (e.g., Bedson & Turnbull, 2002). Furthermore, in patients with neglect the exploratory deficit changes depending on instructions cueing them either to wide or narrow search areas (Karnath & Niemeier, 2002; Niemeier & Karnath, 2002a; Niemeier & Karnath, 2002b).

To look at a potential influence of attentional window size on perceptual bias, in Experiment 2 we used a fixation task to bias attention towards local or global processing. Additionally, in Experiment 3 we used a simplified version of the gratingscales task, and to manipulate the width of the attentional window, we systematically varied the likelihood of the target stimulus to appear at a certain eccentricity. However, neither in Experiment 2 nor in Experiment 3 did we find any influences of attentional window on perceptual bias.

One might argue that our manipulation of attention was insufficient. For example, in Experiment 2 sensitivity in the gratingscales task, as measured with the slope of the psychometric functions, was essentially identical in both attentional conditions (Fig. 5c) while the global fixation task was significantly more difficult than the local task (Fig. 5d). So, after the global as well as the local fixation

task, attention might have switched back into the same state. However, we have several reasons why we feel that this is unlikely.

Firstly, the fixation task in Experiment 2 was challenging. While average accuracy was higher than 90%, participants often cycled through several attempts to perform the task before continuing with the gratingscales. This suggests, the fixation task required the participants' full local or global attention, respectively.

Could attentional window size have changed, after the fixation task, in anticipation of the size of the gratingscales? Attention shifts relatively slowly in tasks that present stimuli in a rapid sequence (Duncan, Ward, & Shapiro, 1994). Therefore, we might expect a delay in the development of the influence of local and global attention on perceptual bias as a function of presentation time. We did find time-dependent variations in bias depending on task-sensitivity but there was no difference between global and local task conditions, and our data were quite similar to our previous observations obtained without fixation task (Fig. 5b vs. Fig. 7B in Niemeier et al., 2007). However, attentional window size might have switched on the afterimage of the gratingscales.

Such switches in attentional window size are implausible for Experiment 3. Window size could not have changed before stimuli appeared because the eccentricity of the gratings was unknown, and switches on the afterimages are unlikely because of the mask. What is more, we did observe an influence of attentional window size on task difficulty: Participants were less accurate in the wide than in the narrow attentional window condition. At the same time we found no significant influence on perceptual bias even though we tested a large number of participants.

This does not rule out the possibility that perceptual bias would have increased had we presented context trials at eccentricities greater than 10° so as to open the attentional window further (although, our pilot data suggest that with larger eccentricities the task soon becomes prohibitively more difficult). However, the gratingscales stimuli are $\pm 10°$ wide and therefore there is no reason to believe that in any of the conditions in Experiment 1 the attentional window was much larger than that. Likewise, the onset of the gratingscales in Experiments 2 and 3 might have reflexively forced the attentional window open. But then this should have happened in Experiment 1 as well. Therefore, it appears difficult to explain the cross-over in Experiment 1 with systematic differences in attentional window size. Consequently, it seems unlikely that window size counteracted any influence of lateralized SF processing.

On the other hand, it is possible that lateralized SF processing was counteracted by attentional asymmetry. Spatial frequency perception has been associated with a similarly lateralized organization of global and local processing modes (e.g., Grabowska & Nowicka, 1996; Ivry & Robertson, 1998; Sergent, 1982) typically tested in recognition tasks of hierarchical figures such as letters consisting of smaller letters (Navon, 1977). Since the fixation task in Experiment 2 required global and local detection one might conclude that our data argue against an involvement of global and local processing in perceptual bias as observed in the gratingscales task. However, lateralized global and local processing depends on multiple factors (Yovel, Levy, & Yovel, 2001), and the connection between global and local modes and SF processing are complex (Hübner, 1997). Therefore, further research would be required to rule out any involvement of the SF account in perceptual bias. Still, our data suggest that the SF account plays a comparatively small role in perceptual bias as measured with the gratingscales task.

Could other accounts explain our data? Pathological perceptual biases have been proposed to result from distortions of size perception (e.g., Milner & Harvey, 1995), and sometimes neurological patients exhibit dysmetropsia (e.g., Frassinetti, Nichelli, & di Pellegrino, 1999). Therefore, could our data reflect a subclinical micropsia for the left visual field? This would yield the same leftward and rightward biases in the gratingscales task as we observed. But it would also predict a rightward bias in other bisection tasks. However, we found that leftward bias in the high SF condition of the gratingscales task is positively correlated with leftward bias in the greyscales task (Niemeier et al., 2007) which would suggest that dysmetropsia reverses with larger sizes. This appears to be unlikely. Though Mennemeier, Pierce, Chatterjee, Anderson, Jewell, et al. (2005) have proposed that long and short lines are misperceived in magnitude in different ways, they assumed that short lines are overestimated and long lines are underestimated.

In conclusion, in the present study we have used non-lateralized cueing paradigms in combination with the gratingscales task to demonstrate a new form of cross-over. Our data offer novel support for the attentional asymmetry account of perceptual bias. Further research will be necessary to investigate interactions between lateralized and non-lateralized cueing of transient and sustained attention. Our data argue for a weak or even no connection between perceptual bias and a hemispheric asymmetry for SFs. Given that SF asymmetries are associated with a large body of data on visual field differences the lack of a connection with perceptual bias is somewhat unexpected and deserves further investigation. Future research will also be necessary to investigate in greater detail as to how the two phenomena differ. This will serve to create a more comprehensive understanding of the attentional and spatial functions of the right hemisphere.

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