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Research report

Spatial frequency-specific effects on the attentional bias: Evidence for two attentional systems

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ABSTRACT

Using a gratingscales task as a sensitive measure of the attentional bias, we have recently observed a new form of frequency-specific cross-over; people showed left-biased preferences when comparing the high spatial frequency (HiSF) components of the task and rightward biases when comparing low spatial frequencies (LoSFs). Here we investigated which mechanisms underlie the cross-over. (1) We found that leftward and rightward biases were positively correlated, suggesting that the same set of mechanisms are involved in both versions of the task. (2) When we cued attention to the left or right side we found transient effects on gratingscales biases that were symmetrical for the LoSF condition but asymmetrical for the HiSF condition. This indicates that the HiSF condition itself biased stimulus-driven attention more to the left side than the LoSF condition. (3) When we lowered the contrast of the HiSF or the LoSF stimulus components, specifically the latter case made HiSF and LoSF conditions more different. This suggests that HiSF and LoSF conditions differ because HiSF components are more salient and more likely stir stimulus-driven attention. Our data are consistent with the idea that the attentional bias results from right-dominant control mechanisms of stimulus-driven attention potentially interacting with voluntary control mechanisms.

1. Introduction

Somewhat paradoxically, right-brain dominant functions of attention and spatial awareness are most prominently studied in their absence, that is, patients with right-brain damage, more so than patients with left-brain damage, show abnormal difficulties in perceiving and responding to stimuli on the left side. These difficulties are called spatial neglect, and it has been proposed to be associated with several lesion sites: the inferior parietal cortex (Mort et al., 2003; Vallar and Perani, 1986), the superior temporal cortex (Karnath et al., 2001; Rorden et al., 2006) as well as frontal (Damasio et al., 1980; Husain and Kennard, 1996) and subcortical regions (Doricchi et al., 2008; Karnath et al., 2002; Leibovitch et al., 1998). Interestingly, some of these lesion sites appear to be equivalent to brain areas that constitute cortical networks involved in attentional functions (Corbetta and Shulman, 2002). However, the mechanisms underlying neglect remain poorly understood in that it is still unclear which right-dominant neurocognitive functions are disrupted in neglect patients.

To draw the connection to the intact brain, it is helpful to investigate behavioural asymmetries indicating right-brain

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dominance in healthy people that potentially mirror the asymmetries observed in patients. For example, the line-bisection task and similar perceptual judgment tasks (Binder et al., 1992; Heilman and Valenstein, 1979; Luh, 1995; Mattingley et al., 1994, 2004; Milner and Harvey, 1995; Nicholls et al., 1999; Schenkenberg et al., 1980) have been used to measure ipsilesional, rightward biases of attention observed in some patients (though not all: e.g., Binder et al., 1992; Ferber and Karnath, 2001; Halligan and Marshall, 1992; McGlinchey-Berroth et al., 1996), but they also reveal smaller, leftward asymmetries in normal participants consistent with a right-brain dominance (reviewed in Jewell and McCourt, 2000).

We recently proposed a novel measure of attentional bias, called the gratingscales task (Niemeier et al., 2007, 2008a) that was originally inspired by the greyscales task (Mattingley et al., 1994). The gratingscales task is correlated with other neglect tests measuring attentional bias (Niemeier et al., 2007). It presents two rectangular gratingscales containing wavelets that gradually increase in spatial frequency from left to right in one rectangle and from right to left in the other rectangle (Fig. 1). When we asked participants to select the gratingscale that contains “more of the thinner stripes” (high spatial frequency or ‘HiSF’ condition) they showed a preference for the gratingscale that carried HiSF wavelets on the left side, and the bias increased when we added pixel noise (Niemeier et al., 2008b). Surprisingly however, when we reversed the question, asking “which bar has more of the thicker stripes” (low spatial frequency or ‘LoSF’ condition), leftward bias disappeared (Niemeier et al., 2008a). Instead, participants showed a bias to the right side.

Superficially, this cross-over resembles other forms of cross-over which occur for the line-bisection task performed on long versus short lines (Halligan and Marshall, 1988; McCourt and Jewell, 1999; Mennemeier et al., 2005; Rueckert et al., 2002). Nevertheless, there is an important difference in that the frequency-specific cross-over occurs for stimuli with identical length and only based on differences in instructions. Given this, cross-over as observed in the gratingscales task is likely to be different from cross-over observed in the line-bisection task.

How can the frequency-specific cross-over effect be explained? In principle four nested possibilities exist, involving a single mechanism (model 1) or more than one mechanism (model 2A, and two versions of model 2B).

1.1. *Model 1: one mechanism model*

Which single mechanism could explain frequency-specific cross-over? One example might be a peculiar effect of attention on perception. That is, attention cued to a certain location can result in spatial frequencies in that area to be perceived as higher than they really are (Gobell and Carrasco, 2005). We have previously speculated (Niemeier et al., 2008a) that this effect might apply to the gratingscales task: attention naturally biased to the left side of the gratingscales stimulus might let gratings on the left appear higher in spatial frequency and, thus, ‘stripes’ on the left to be thinner and more frequent than ‘stripes’ on the right. If so, the HiSF and the LoSF conditions of the task should yield opposite results. In the HiSF condition, people should be more inclined to choose the gratingscale with the HiSF grating on the left side. But in the LoSF condition, they should be more inclined to choose the gratingscale with the LoSF grating on the right side. As a consequence, biases should be negatively correlated: someone with a strong attentional bias to the left side should show a strong leftward bias in the HiSF condition as well as a strong rightward bias in the LoSF condition. But someone with a weak attentional bias should show a weak leftward bias for HiSF and a weak rightward bias for LoSF.

The same relationship between HiSF and LoSF biases would be expected for any other kind of single mechanism that is responsible for the frequency-specific cross-over. For example, people might be asymmetrical in how they perceive spatial frequencies. Regardless of attention, they might perceive frequencies in the left visual field as higher than frequencies in the right visual field. Several other possibilities might exist, yet what all these versions of the ‘one mechanism model’ have in common is that the same biasing mechanism should play a role in both versions of the gratingscales task, but should have opposite consequences as to how participants respond. That is, they all predict HiSF and LoSF biases to be negatively correlated, otherwise more than one mechanism must be involved in the frequency-specific cross-over.

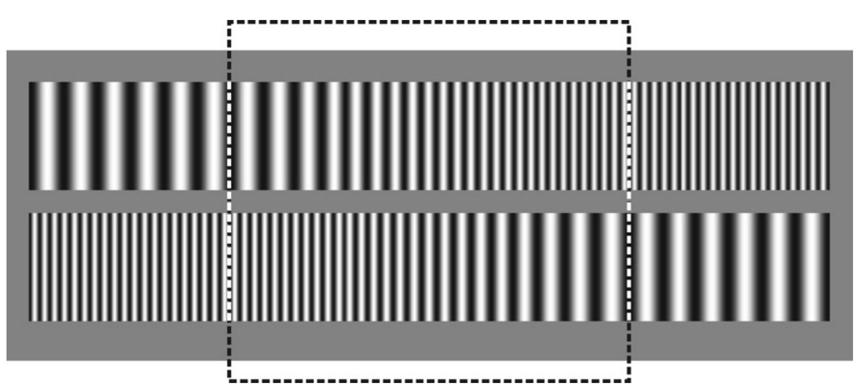

Fig. 1 – Gratingscales stimulus. Participants were asked to indicate which rectangle contained “more of the thinner lines” in the HiSF condition and which had “more of the thicker lines” in the LoSF condition. Dashed rectangle superimposed onto the stimulus indicates the central area in which the gratingscales increased/decreased in spatial frequency (frequency changed as a function of a half-cycle of a cosine wave, see Niemeier et al., 2007).

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1.2. Model 2A: different mechanisms model

If frequency-specific cross-over involves more than one mechanism, we need to consider two nested possibilities. The first we will call 'different mechanisms model', and the second 'same mechanisms model'. According to the 'different mechanisms model' there is essentially no overlap: one mechanism A would cause leftward bias in the HiSF condition, and another mechanism B would cause rightward bias in the LoSF condition (or mechanisms A and B each could represent entire sets of mechanisms).

Here we will not expand on what the different mechanisms might be, except we can rule out one version of the 'different mechanisms model'. That is, Sergent's model of a hemispheric specialization for spatial frequencies (Sergent, 1982) argues that one mechanism residing in the left hemisphere is specialized for high spatial frequencies, and another mechanism in the right hemisphere is specialized for LoSFs, at least in certain tasks. Applied to the gratingscales task this would mean attention to high frequencies should result in a rightward bias and attention to LoSFs should result in a leftward bias (Monaghan and Shillcock, 2004). But that is opposite to the cross-over that we observed (Niemeier et al., 2008a). Nonetheless, frequency-specific cross-over might result from some other version of the 'different mechanisms model'. Whatever the nature of those mechanisms, they should result in uncorrelated leftward and rightward biases.

1.3. Model 2B: same mechanisms model

In contrast, positively correlated leftward and rightward biases would indicate that the HiSF and LoSF conditions involve the same set of two or more mechanisms. Some of these mechanisms in isolation would cause biases to the right side, others would cause biases to the left side, and together they would amount to either a leftward or a rightward bias depending on which mechanism is more prominent. For example, left-biasing mechanisms might be stronger in the HiSF condition. We will call this the 'same mechanisms model'. Or the LoSF condition might yield stronger right-biasing mechanisms. This we will call the 'alternative same mechanisms model'.

To test which of the models best explains frequency-specific cross-over, we conducted three experiments. Experiment 1 looked at the correlational structure of the gratingscales task. We found biases to be positively correlated, in support of the 'same mechanisms model' or the 'alternative same mechanisms model'. To distinguish between these two model versions, Experiment 2 tested how attentional cues influence gratingscales biases. We found that in the HiSF condition cues on the right side moved biases to the right but biases on the left had little influence much like what has been reported for the line-bisection task (e.g., McCourt et al., 2005). However, cueing in the LoSF condition had symmetric effects, shifting biases in the direction of the cue. This supports the idea of a leftward biasing attentional mechanism that is stronger in the HiSF condition, consistent with the first version of the 'same mechanisms model'. Finally, Experiment 3 investigated why people respond differently to cues depending on spatial frequency. We considered two potential frequency-dependent anisometries. First, higher spatial frequencies might be more salient than lower frequencies so that specifically the HiSF condition activates neural control circuits for stimulus-driven attention in the right hemisphere (Corbetta and Shulman, 2002). Second, lower spatial frequencies might inhibit higher frequencies more than the other way round (Betts et al., 2009) so that it is harder to process high spatial frequencies in the HiSF condition than LoSFs in the LoSF condition, and this might bias attention to the left side. To pit the two possibilities against each other, we lowered the contrast of the high and/or the LoSF components of the gratingscales in order to manipulate salience or inhibitory effects. Our results are rather consistent with the salience hypothesis.

2. Methods

2.1. Subjects

Fifty undergraduate students (36 females, median age: 18) participated in Experiment 1, 34 students (21 females, median age: 19) participated in Experiment 2, and 30 students (18 females, median age: 20) participated in Experiment 3. All had normal or corrected-to-normal vision, were healthy and right-handed as confirmed with the Edinburgh handedness inventory (Oldfield, 1971). All gave their written and informed consent to participate in the present study. All procedures were approved by the Human Participants Review Subcommittee of the University of Toronto and therefore have been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Apparatus and procedure

Participants sat in front of a CRT monitor (19″, 100 Hz refresh rate, Viewsonic E90fb) at a distance of 60 cm. A chin rest was used to keep head movements to a minimum. Participants were free to move their eyes, though from behavioural observations we found that participants normally fixate the centre of the monitor.

All experiments were programmed in Matlab together with the Pschophysical Toolbox (Brainard, 1997; Pelli, 1997) using the gratingscales task to quantify attentional bias (Fig. 1). The task is a sensitive measure of attentional bias that is correlated with other measures of attentional bias (Niemeier et al., 2007).

For the task, two horizontal rectangles were presented on a grey background. Each rectangle was filled with luminance-defined gratings that increased in spatial frequency from the left to the right side in one bar and vice versa in the other bar (relative position of the two bars was counterbalanced across trials). More specifically, spatial frequency increased smoothly, in a central area of each rectangle (see dashed rectangle superimposed onto the gratingscales stimulus in Fig. 1), and this area shifted randomly in 11 steps, from trial to trial, between ±12.5% relative to the length of the rectangles. Gratings on the sides of the central area of the rectangles remained constant in spatial frequency. This way, all gratingscales stimuli covered the same range of spatial frequencies (for more details see Niemeier et al., 2007). Frequency ranges were .6–2 cycles per degree (cpd, called 'G2 stimulus') for Experiment 1 and Experiment 3, and 1.2–4 cpd ('G4 stimulus') for Experiment 2.

For each stimulus, participants pressed the arrow-up or arrow-down key on the number pad of the keyboard to choose the rectangle that appeared to contain more of the target feature, that is, the one with "more of the thinner stripes" in the HiSF condition or the one with "more of the thicker stripes" in the LoSF condition. Based on each participant's responses we quantified the probability of choosing the rectangle containing the target feature on the left side as a function of stimulus asymmetry. For example, if in Fig. 1 the central area in the two gratingscales was shifted 12.5% to the left side the upper rectangle would contain substantially "more of the thinner stripes" and so most participants would be very unlikely to choose the lower rectangle as the one to contain "more of the thinner stripes" ($p = 0$). But they would choose the lower rectangle almost all the time ($p = 1$) if the central area was shifted 12.5% to the right side, and in between there would be a monotonic, sigmoid transition between $p = 0$ and $p = 1$. This sigmoid or psychometric function is well described by several parametric functions. Here we used Weibull functions of the following form:

$$p(\text{response} = \text{left} = 1 - \exp(-10m(x - k))),$$

where p is the probability of choosing the rectangle with the target feature on the left and x is the asymmetry of the stimulus; m and k are free parameters that we determined with a conventional data fitting method (Gauss–Newton) so that p best described the actual data of the participant. Finally, based on the fitted curve we could determine two psychologically relevant parameters. The first is the degree of asymmetry that yields a probability of .5 reflecting that the two gratingscales appear (to a given participant) to be symmetrical. Note that this point of subjective equality usually does not coincide with the point at which the gratingscales are physically symmetrical. For instance, in Fig. 1 the two gratingscales are mirror-symmetric, and yet most people would tend to see the lower rectangle to carry "more of the thinner stripes" in the HiSF condition, and in the LoSF condition they would tend to see the same rectangle to carry "more of the thicker stripes", reflecting leftward and rightward biases respectively (Niemeier et al., 2008a). In the present study we took these biases to be our main dependent variable.

The second psychologically relevant parameter (and second dependent variable examined in Experiment 1) is the slope of the psychometric function, reflecting task difficulty. That is, a shallow slope would indicate that a participant has difficulties with the gratingscales task, and a steep slope would reflect that the gratingscales task is easy. Though we had no particular predictions about slope/task difficulty we studied it to confirm that differences in slope did not simply explain differences in bias (Niemeier et al., 2008a).

2.2.1. *Experiment 1: presentation times*

The main aim of the experiment was to investigate whether biases observed in the HiSF and the LoSF conditions are positively, negatively or not correlated. Also, we looked at these correlations for different presentation times (75, 150, 300 msec) for exploratory reasons because we have previously found that presentation times have differential effects on subgroups of participants (Niemeier et al., 2007), so correlations might change with presentation time. Each of the resulting six experimental conditions (2 instructions × 3 presentation times) were tested in different blocks (a total of 2 blocks per condition, 88 trials per block) such that block order was counterbalanced while we had to change instructions as little as possible. Generally, the order was A1/A2/A3/B3/B2/B1/B1/B2/B3/A3/A2/A1, where numbers could represent any of the three presentation times, and letters A and B could mean 'HiSF' and 'LoSF', respectively, or vice versa. We chose the 'G2' gratingscales because we have previously found that participants have more leftward bias than with other frequency ranges (Niemeier et al., 2007).

2.2.2. *Experiment 2: attentional cueing*

Experiment 1 yielded positive correlations between HiSF and LoSF biases, contrary to what we had expected. Therefore, in the second experiment we chose the 'G4' gratingscales because we have found that differences between HiSF and LoSF biases are most pronounced (Niemeier et al., 2008a).

To study the effect of attentional cues on the gratingscales task we first presented a white fixation square (.13°) containing a black dot (.07°) in the centre of the screen. Participants fixated it and pressed a button. Next, one or two white circular cues (.13° across; 100 msec duration) appeared on the left, right, or on both sides so that their outer edges were 20° away from the fixation square. Participants were informed that the cues were irrelevant for the gratingscales task. Then only the fixation square remained until the gratingscales appeared briefly (75 msec duration), 150, 200, or 300 msec after cue onset.

These stimulus onset asynchronies (SOAs) as well as the three cue locations were chosen randomly within 12 blocks of 168 trials each. The third independent variable, Instructions (HiSF *vs* LoSF), changed after blocks 3 and 9, resulting in the following order of blocks: A/A/A/B/B/B/B/B/B/A/A/A where A and B could mean HiSF or LoSF, respectively or vice versa.

2.2.3. *Experiment 3: contrast modulations*

To investigate why attention is more leftward biased in the HiSF condition than in the LoSF condition, we manipulated stimulus contrast in four conditions. As reference, the first condition showed the gratingscales with 100% contrast and the second showed stimuli with 25% contrast. In the third condition, contrast was 100% on the HiSF components of the gratingscales and linearly declined to 25% on the LoSF components. The fourth condition reversed the contrast gradient: LoSF components had high contrast and HiSF components had low contrast.

All contrast conditions were presented in random order in blocks of 80 trials, and there were four blocks for the HiSF condition and four for the LoSF condition, conducted in a counterbalanced order: A/A/B/B/B/B/A/A or vice versa.

3. Results

We conducted Experiment 1 to look at the correlational relationship between HiSF and LoSF biases for different presentation times. But first we calculated two repeated measures ANOVAs to confirm previous observations. The first ANOVA included Instructions (HiSF *vs* LoSF) and Presentation time (75, 150, and 300 msec) as factors and tested bias (the point of subjective equality of the psychometric functions, see Section 2.2) as the dependent variable. We found only Instructions to have a significant influence [$F(1,49) = 42.64$, $p < .0001$]. That is, participants showed a leftward bias in the HiSF condition, and a rightward bias in the LoSF condition (Fig. 2A), consistent with our previous study (Niemeier et al., 2008a). Presentation time and the interaction were not significant ($p = .07$ and $p = .411$, respectively).

The second ANOVA had the same factors but tested task difficulty (i.e., the slope of the psychometric functions, see Section 2.2) as the dependent variable. We found no effect to reach significance ($ps > .11$). Therefore, task difficulty cannot explain differences in bias in the HiSF and LoSF conditions. This too is consistent with our previous data (Niemeier et al., 2008a). For this reason and to simplify matters, subsequent sections of the Results will focus on bias as the dependent variable that is relevant to test our model predictions.

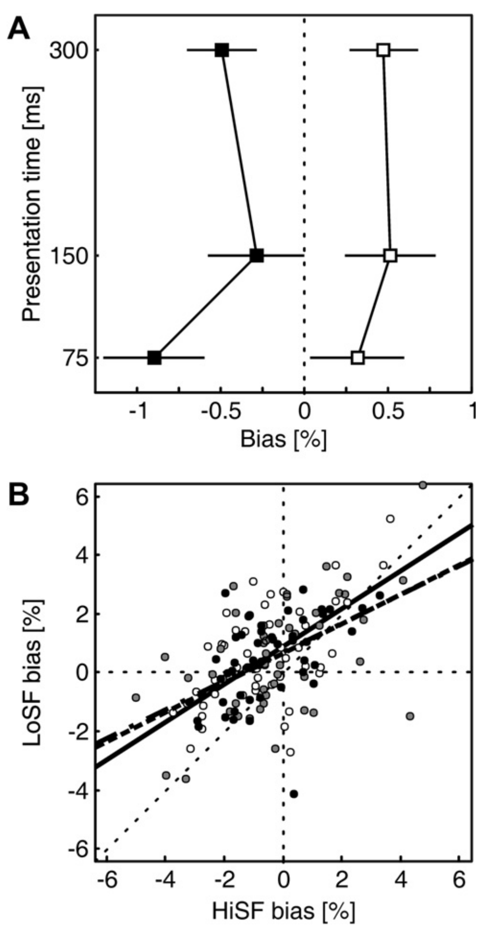

Fig. 2 – Biases measured in Experiment 1. (A) Group averages of the point of subjective equality of the psychometric functions (horizontal axis) are plotted as a function of presentation time (vertical axis). Full squares: HiSF, open squares: LoSF. Error bars indicate standard errors. (B) Scatterplot of biases for the HiSF and LoSF conditions. White, grey and black dots: 75, 150, and 300 msec presentation time, respectively.

The model predictions differ in terms of how HiSF and LoSF biases should be correlated. To look at this we plotted LoSF biases of individual participants as a function of their HiSF biases for the 3 presentation times separately (see the differently coloured circles in Fig. 2B). Regardless of presentation time we found that HiSF biases correlated positively with LoSF biases (75 msec: $r = .698$, $p < .0001$; 150 msec: $r = .540$, $p < .0001$; 300 msec: $r = .494$, $p = .0003$; Fig. 2b), and the correlations were comparable to correlations among HiSF (75/150 msec: $r = .579$, 75/300 msec: $r = .575$, 150/300 msec: $r = .602$) and LoSF biases (75/150 msec: $r = .757$, 75/300 msec: $r = .495$, 150/300 msec: $r = .642$). This argues against the ‘one mechanism model’ (model 1) and the ‘different mechanisms model’ (model 2A) predicting negative and zero correlations, respectively. Instead the data support the ‘same mechanisms model’ (model 2B) that assumes that HiSF biases and LoSF biases result from the same set of multiple mechanisms some of which in isolation would contribute to leftward biases while others would cause rightward biases.

So then the next question arises: how do these mechanisms amount to overt leftward biases in the HiSF condition and rightward biases in the LoSF condition? As one possibility, overt rightward biases could result from certain default mechanisms and these mechanisms could be equally involved in the HiSF and the LoSF condition, whereas other mechanisms would be more dominant in the HiSF condition thus resulting in a net bias to the left side in that condition (“same mechanisms model”). Or the opposite could be true: leftward biases could be due to default mechanisms that are the same in the HiSF and the LoSF condition, whereas other, right-biasing mechanisms would be more dominant in the LoSF condition (“alternative same mechanisms model”).

To distinguish between these two possibilities and to see whether any mechanisms underlying the HiSF and the LoSF conditions are associated with attention, in Experiment 2 we presented attentional cues. Similar cues have been shown to affect biases in line-bisection tasks such that cueing attention to the left influences biases less than cueing to the right (e.g., McCourt et al., 2005), consistent with the idea that attention is already biased to the left.

This asymmetry is what we observed in the HiSF condition. In summary, cues on the right side biased people’s responses more in that direction than bilateral cues, especially for the short SOA of 150 msec (as expected for stimulus-driven cueing effects), but cues on the left side did not have this effect (Fig. 3A, Table 1). However, cueing effects in the LoSF condition were symmetrical. No matter whether the cue appeared on the left or the right side, people’s responses shifted in the same direction (Fig. 3B, Table 1). This effect was more pronounced for the short SOA of 150 msec than later and it was rather symmetrical.

We confirmed these observations with a series of tests. A three-way ANOVA with factors Instructions (HiSF *vs* LoSF), Cue location (left *vs* right), and SOA (150, 200, 300 msec) tested cueing effects on biases (biases after cues on the left or right relative to biases after bilateral cues). It yielded an effect of Cue location [$F(1,33) = 20.40$, $p = .0001$], and a three-way interaction [$F(2,66) = 5.84$, $p = .005$; other effects: $p > .096$].

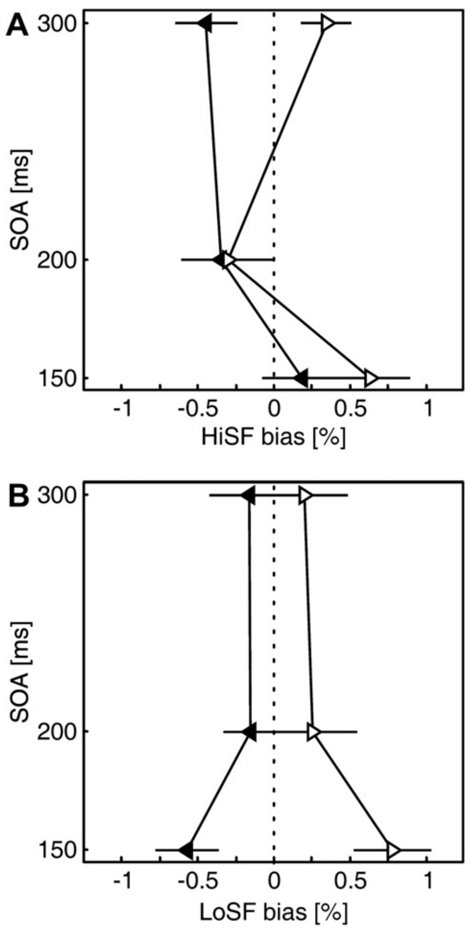

Fig. 3 – Cueing effects observed in Experiment 2. (A) Group averages for the HiSF condition. (B) Group averages for the LoSF condition. SOA, stimulus onset asynchrony. Error bars indicate standard errors.

Next, we conducted a two-way ANOVA for each level of the Instructions separately. The ANOVA for the HiSF conditions showed an effect of Cue location [$F(2,33) = 13.88$, $p = .0007$, significant after Holm correction]. The factor SOA and the interaction showed trends [$F(2,66) = 3.11$, $p = .051$; $F(2,66) = 3.09$, $p = .052$]. Follow-up *t*-tests looked at SOAs individually. For an SOA of 150 msec we found that left-cue and right-cue effects differed significantly [$t(33) = 2.44$, $p = .020$], and only the right-cue effect was different from zero [$t(33) = 2.39$, $p = .023$], but not the left-cue effect [$t(33) = .71$, $p = .484$]. For an SOA of 200 msec these early asymmetric cueing effects disappeared [$t(33) = .19$, $p = .853$]. However, for an SOA of 300 msec the difference in effect between left- and right-sided cues reappeared [$t(33) = 3.76$, $p = .0008$; see Section 4 for an interpretation of the effect].

Next, the ANOVA for the LoSF conditions revealed an influence of Cue location [$F(2,33) = 11.26$, $p = .002$] and an interaction with SOAs [$F(2,66) = 4.20$, $p = .019$]. Follow-up *t*-tests for an SOA of 150 msec found an early cueing effect (cues on the left *vs* right: $t(33) = 5.04$, $p < .0001$) with left-cue effects as well as right-cue effects being different from zero [left: $t(33) = 2.72$, $p = .010$; right: $t(33) = 3.07$, $p = .004$]. No later effects were observed ($p > .230$).

These results confirm that cueing effects in the LoSF condition were symmetrical, in contrast to the HiSF condition. However, it is possible that symmetries and asymmetries were simply due to the fact that we tested biases relative to different bilateral cueing conditions. To rule out this possibility, we looked at uncorrected biases after an SOA of 150 msec (HiSF left-cue: −.64%, HiSF right-cue: −.19%, LoSF left-cue: −.78%, LoSF right-cue: .57%, see Table 1) relative to biases after an SOA of 200 msec as baseline condition (HiSF: average of −.61% and −.57%, LoSF: average of −.30% and .11%, Table 1). As before, we found asymmetric cueing effects for the HiSF condition: there was no effect after left-sided cues [$t(33) = .24$, $p = .405$] but there was a significant effect after right-sided cues [$t(33) = 1.99$, $p = .0275$]. In contrast, for the LoSF condition cues on either side yielded differences [left: $t(33) = 3.27$, $p = .002$; right: $t(33) = 2.96$, $p = .003$; all tests were one-tailed and evaluated using Holm's criterion].

What is the reason for this frequency-dependent difference in cueing effects? In Experiment 3 we investigated two possible explanations, the first that the task-relevant components of the gratingscales ("thin stripes" in HiSF and "thick stripes" in LoSF) might differ in salience, and the second that the task-irrelevant components might differ in the degree to which they inhibit perception of the task-relevant components. To test these possibilities we manipulated the contrast of the gratingscales. If reducing the contrast of the "thick stripes" increased the difference between biases in the HiSF and LoSF condition this would indicate that leftward bias (or the lack thereof) is due to higher spatial frequencies being

Table 1 Experimental effects in Experiment 2.

		Bias						Cueing effect			
		HiSF			LoSF			HiSF		LoSF	
		Left	Both	Right	Left	Both	Right	Left	Right	Left	Right
150 msec	Avg	−.64	−.82	−.19	−.78	−.21	.57	.19	.63	−.57	.78
	SD	2.28	2.10	2.23	1.62	1.63	2.00	1.53	1.55	1.22	1.48
200 msec	Avg	−.61	−.27	−.57	−.30	−.15	.11	−.34	−.30	−.15	.26
	SD	2.01	2.13	1.80	1.56	1.29	2.20	1.53	1.76	1.03	1.73
300 msec	Avg	−.90	−.45	−.11	−.42	−.26	−.06	−.44	.34	−.16	.20
	SD	2.00	1.82	1.94	1.46	1.75	2.24	1.19	.98	1.54	1.67

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more salient than lower ones. If however reduced contrast of the "thin stripes" increased the differences in biases this would indicate that the difference between the HiSF and the LoSF condition is mainly due to stronger inhibition of lower spatial frequencies.

As shown in Fig. 4A, HiSF conditions were consistently more left-biased than LoSF conditions, and there appeared to be a larger difference between HiSF and LoSF biases when contrast of the "thick stripes" of the gratingscales was low (Fig. 4B). However, when we conducted a two-way ANOVA (Instructions: HiSF *vs* LoSF; Contrast condition: high contrast/low contrast/low contrast on LoSFs/low contrast on high spatial frequencies) we only found a main effect of Instructions [$F(1,29) = 12.06$, $p = .002$; other effects: $p > .168$]. Regardless of the non-significant interaction, we conducted two additional, pre-planned tests to examine our model predictions. The first test compared differences in the 'low contrast on LoSF' condition with average differences in the other conditions and yielded a significant result (one-tailed: $t(29) = 2.25$, $p = .016$) in support of the salience model. However, the inhibition model was not supported: differences in the 'low contrast on HiSF' condition were the same as average differences in the other conditions [one-tailed: $t(29) = .34$, $p = 1.00$ because the sign was opposite to what expected].

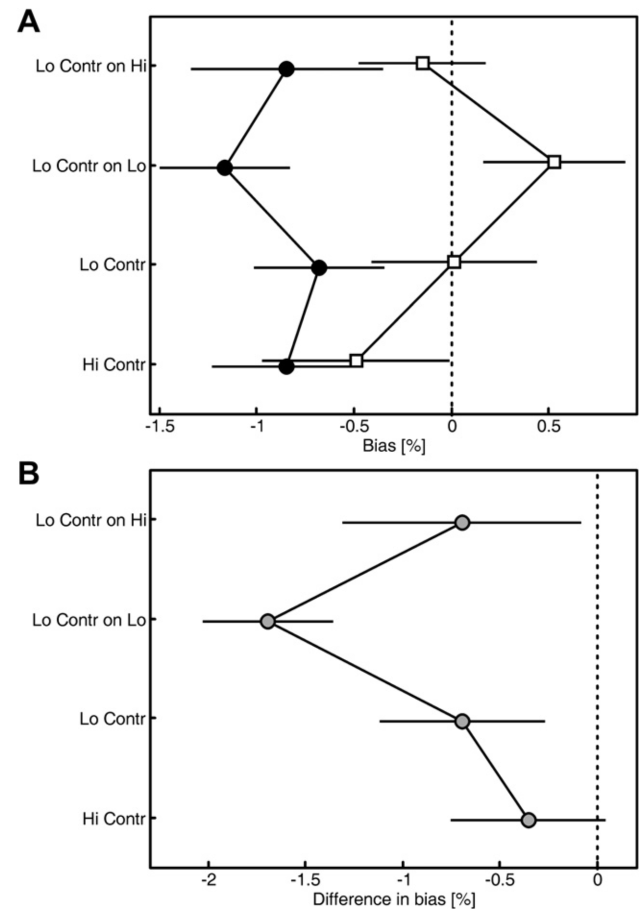

Fig. 4 – Results Experiment 3. (A) Biases for the HiSF condition (filled circles) and the LoSF condition (open circles). (B) Differences in bias for the HiSF versus LoSF condition. Lo Contr on Hi, contrast decreased linearly from 100% down to 25% from the LoSF to the HiSF portions of the gratingscales; Lo Contr on Lo, contrast decreased linearly from 100% down to 25% contrast from the HiSF to the LoSF portions of the gratingscales; Lo Contr, gratingscales displayed at 25% contrast; Hi Contr, gratingscales displayed at 100% contrasts. Error bars indicate standard errors.

4. Discussion

In the present study we investigated which mechanisms underlie the attentional bias using the gratingscales task. Interestingly, people performing this task show a leftward bias when looking for the higher spatial frequency component ("thinner stripes": HiSF condition) of the stimulus, but show a rightward bias when looking for its LoSF component ("thicker stripes": LoSF condition; Niemeier et al., 2008a).

We recently speculated that this cross-over might be due to a single attentional bias to the left side that causes gratings on the left to appear higher in spatial frequency than they really are (Gobell and Carrasco, 2005). Consequently, people should be more inclined to choose the gratingscale with the HiSF grating on the left side when looking for "thinner stripes", and they should choose the same gratingscale when looking for "thicker stripes". However, this 'one mechanism model' would predict negative correlations between leftward and rightward biases. Instead we found positive correlations.

Positive correlations also rule out the 'different mechanisms model' which proposes that leftward and rightward biases result from independent mechanisms and therefore should not be correlated. Instead, the 'same mechanisms model' assumes that there is substantial overlap in mechanisms that cause biases to the left and the right side in the HiSF and the LoSF conditions, respectively. Further, the model assumes that some of the mechanisms are stronger in the one than the other condition. Either the HiSF condition is associated with stronger leftward biasing mechanisms, or the LoSF condition is associated with stronger rightward biasing mechanisms.

Using an attentional cueing paradigm in Experiment 2 we found support for the former possibility. That is, for the HiSF condition cues with brief SOAs were only effective if they appeared on the right side. On the left side they had no effect compared to the control condition. This is consistent with the idea that attention is already biased to the left side. In contrast, the LoSF condition showed symmetrical cueing effects, suggesting that attentional asymmetries have little influence in this condition. Thus the rightward bias observed in the LoSF condition seems to result from mechanisms that have little to do with attention. In addition, Experiment 2 further disconfirms the 'one mechanism model'. The model would predict strangely crossed cueing effects for the LoSF condition, cues on the right side would cause biases to shift to the left side because shifting attention to the right side should have increased apparent spatial frequency on that side which in turn should have made stripes there look "thinner" and stripes on the left look "thicker".

However, one might wonder whether our interpretation of the cueing effects is correct. One concern could be that cueing effects in the HiSF condition might be asymmetric because of a ceiling effect that prevents leftward biases to shift further to the left side. This is unlikely because all biases are quite modest (e.g., Figs. 2A and 4A), and we have previously shown (Niemeier et al., 2008b) that in principle leftward biases can be substantially larger than those observed here.

A second concern might be that attention is not only altered by the cues but also by the gratingscales stimulus itself. That is, when gratingscales appear on the screen they might re-centre attention thus making it difficult to interpret cueing effects. However, as we will argue based on previous research and on the control measures in the present study re-centring cannot explain our results. Previous research in our lab has shown that directing people's attention to the centre versus the periphery of the gratingscales stimulus has no effect on biases (Niemeier et al., 2008a). Also, the cueing effects in the HiSF condition are similar to previously reported cueing effects on the line-bisection task (Bultitude and Aimola Davies, 2006; Harvey et al., 1995, 2000; Ishiai et al., 1995; McCourt et al., 2005; Mennemeier et al., 1997; Nichelli et al., 1989; Nicholls and Roberts, 2002; Reuter-Lorenz et al., 1990; Reuter-Lorenz and Posner, 1990; Riddoch and Humphreys, 1983). Crucially, cueing affected line-bisection biases no matter whether people were cued before task onset (e.g., McCourt et al., 2005) or with the line-bisection task already present (e.g., Harvey et al., 1995), that is, when no stimulus onset could have re-centred attention. Even if in the present study re-centring had played a small, so-far-overlooked role, our data analysis should have filtered it out in two ways. The first is that we analyzed effects of unilateral cues minus effects of bilateral cues, so the re-orienting effect should have cancelled out. Secondly, any leftover of the effect should have occurred in the HiSF as well as the LoSF condition and therefore cannot explain the substantial difference in cueing between the HiSF and the LoSF condition.

Why do people show distinct patterns of cueing effects when they pay attention to the high versus LoSF component of the gratingscales? Here we considered two possibilities. Either the gratingscales component that is relevant for the respective task is processed differently. Specifically, the HiSF component might be more salient, and this way the HiSF condition might be more likely to activate attention-related mechanisms in the right hemisphere. Or the respective gratingscales component that is task-irrelevant is differently distracting. For example, under certain high contrast conditions LoSFs exert greater centre-surround suppression than high spatial frequencies (Betts et al., 2009). It is possible that in the case of the gratingscales task this frequency-specific suppression results in greater perceptual effort when people look for "thinner stripes" rather than "thicker stripes" and that the effort biases attention to the left side.

To test the two possibilities, in Experiment 3 we manipulated the contrast of the gratingscales. We found more pronounced differences between the HiSF and LoSF conditions when the LoSF components of the gratingscales were reduced in contrast compared to the HiSF component having reduced contrast. This rather supports the idea that looking for "thinner" is different from looking for "thicker stripes" because higher spatial frequencies are more salient.

What causes the difference in salience? Differences might arise from properties of early visual areas. For example, contrast sensitivity at a retinal eccentricity of 14° peaks for spatial frequencies of 2–3 cpd (Rovamo et al., 1978), while leftward bias in the gratingscales task peaks for the 'G2' stimulus, so when people compare frequency components of 2 cpd at a roughly similar eccentricity of about 10° away from the centre of the stimulus (Niemeier et al., 2007). But even if this is more than a coincidence, it can only be part of the explanation because gratingscales components with the same spatial frequency result in leftward as well as rightward biases depending on whether they constitute the relative high or LoSF component of the gratingscales, an effect that we found to be quite large (Niemeier et al., 2008a). Therefore, additional mechanisms sensitive to relative frequencies must contribute to the difference in salience and require further investigation.

Moreover, salience differences might be only part of the reason for the difference in cueing effects. Experiment 3 suggests that salience is the more dominant influence compared to suppression but it does not rule out that both play a role. A combination of both might explain why our effects were relatively weak, and of course it is also possible that there are other causes of frequency-specific differences that we did not consider here.

Either way, the present results in Experiment 2 suggest that the leftward biases observed in the gratingscales task are due to an asymmetry in the spatial distribution of attention. The reference frame in which the asymmetry occurs might be eye-head-, body-, or object-centred, or it might be a combination of several reference frames (e.g., Niemeier and Karnath, 2002; Karnath and Niemeier, 2002). For now we cannot tell them apart because participants' head and body were aligned with the monitor and the gratingscales. This was also mostly true for the eyes because based on behavioural observations participants usually fixated the centre of screen (perhaps with one exception that in Experiment 2 cues with long SOAs might have triggered eye movements, also see below). Also, there was not enough time to move the eyes while the gratingscales were presented. Furthermore, HiSF and LoSF biases obtained with and without fixation point (Experiment 2 as opposed to Experiments 1 and 3) showed essentially the same differences in bias.

Leftward biases observed here were similar to those shown for the line-bisection task, and given that the line-bisection task involves the right hemisphere more than the left (Fink et al., 2001, 2002; Foxe et al., 2003) it is conceivable that leftward bias in the gratingscales task too indicates the right hemisphere to be more involved than the left hemisphere. What is more, the asymmetric transient cueing effects in Experiment 2 and the contrast effects in Experiment 3 together seem to suggest that HiSF leftward biases observed in the gratingscales task reflect asymmetries in the distribution of stimulus-driven aspects of attention. This is particularly interesting because it appears to agree well with Corbetta and Shulman's (2002) model of attention comprising two attentional systems. One of these systems is the ventral attentional network that is associated with stimulus-driven control of attention and that resides in parieto-temporal and inferior frontal areas, rather in the right than the left hemisphere. Corbetta and Shulman (2002) argued that brain lesions causing a functional breakdown of the ventral attentional network might be at the core of spatial neglect. Using a task derived from neglect tests, our data seem to confirm the significance of stimulus-driven aspects of the right-brain dominance associated with neglect.

The other attentional system proposed in Corbetta and Shulman's (2002) model, the dorsal attentional network, is associated with voluntary control of attention and resides in dorsal fronto-parietal areas in both hemispheres. It might also be involved in neglect through interactions with the ventral attentional network. Consistent with this idea, we have previously found that patients with neglect show different kinds of eye movement deficits depending on whether they move their eyes in a stimulus-driven fashion by tracking a target that jumps across a random stimulus array or whether they move their eyes voluntarily to search for targets within the array (Niemeier and Karnath, 2003).

Voluntary control might also have played a role in our present data: we found that for the LoSF condition cueing effects disappeared for SOAs of 200 msec, as expected for the transient nature of stimulus-driven attention. However, for the HiSF condition cueing effects re-appeared for SOAs of 300 msec, suggesting that the HiSF condition involved slower, potentially voluntary attentional mechanisms associated with the dorsal attentional network.

While this interpretation is speculative and requires further investigation, three alternative explanations would be either incomplete or unlikely: eye movements are an incomplete explanation. Though we cannot rule out that eye movements occurred after an SOA of 300 msec and that they altered biases in some way, it remains unclear why there were no late cueing effects in the LoSF condition. What is more it is unlikely that this late difference between HiSF and LoSF (whether or not eye movements were involved) was due to differences in the earlier, transient mechanisms, because the late cueing effects in the HiSF condition were symmetrical whereas early effects in the HiSF condition were asymmetrical. Finally, the symmetry of the late effect and the fact that it was in the same direction as the early effect also makes it unlikely that the late cueing effects reflect inhibition of return.

In conclusion, in the present study we found evidence that the leftward and rightward biases in the gratingscales task largely involve the same set of two or more mechanisms. At least one of these mechanisms is a form of left-biasing, stimulus-driven attention that is more prominent in the HiSF condition than the LoSF condition. As such it might reflect activity in the right-dominant ventral attentional network proposed by Corbetta and Shulman (2002). Furthermore, a late cueing effect in the HiSF condition could indicate activation of voluntary attentional processes. While these speculations require further experimental confirmation, our present data indicate that the contrast between the two gratingscales conditions might be ideal to identify brain processes that, when disrupted, give rise to certain kinds of spatial neglect.

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