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Influences of time and spatial frequency on the perceptual bias: Evidence for competition between hemispheres

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Abstract

Perceptual biases for various visual features, such as size, luminance and numerosity, have been implicated with a right-hemisphere dominance in spatial and attentional functions and/or an asymmetrical competition between the two hemispheres. However, the mechanisms underlying these biases are poorly understood. For example, it has been largely ignored that processing of those features is closely interconnected with spatial frequency filters. To probe the influence of spatial frequencies on perceptual biases, here we used a new gratingscales task in neurologically healthy participants. We found that perceptual bias was strongly influenced within a bandwidth of spatial frequencies and that this bias correlated with a bias for luminance depending on presentation time. Furthermore, our participants, divided into two subgroups of perceptually "sensitive" and "insensitive" performers, showed considerably different, presentation time-dependent patterns of perceptual bias. While both groups were biased to the left, insensitive performers more than sensitive performers, these biases varied in a mirror-symmetric manner such that one group showed peaks of bias at times when the other group showed minima and vice versa. Our data suggest that perceptual bias results from an interhemispheric competition within a right-dominant system responsive to spatial frequencies, luminance and perhaps other magnitudes including abstract ones.
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1. Introduction

The right hemisphere is dominant in various visuo-spatial tasks and those involving spatial attention and alertness (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Coull, Nobre, & Frith, 2001; Fink, Marshall, Weiss, & Zilles, 2001; Fink, Marshall, Weiss, Toni, & Zilles, 2002; Foxe, McCourt, & Javitt, 2003; Heilman & Van Den Abell, 1980; Mesulam, 1981; Sturm et al., 1999). Further, lesions of the right hemisphere lead to severe disruptions of behaviour in space (e.g., Hillis et al., 2005; Karnath, Ferber, & Himmelbach, 2001; Karnath, Himmelbach, & Rorden, 2002; Karnath, Himmelbach, & Kuker, 2003; Leibovitch et al., 1998; Mort et al., 2003; Rorden, Berger, & Karnath, 2006; Vallar & Perani, 1986). One such disruption is spatial neglect, a syndrome that renders patients severely impaired in reporting or responding to stimuli on the contralesional side.

A classic strategy to measure the disturbed right-hemisphere dominance in spatial neglect is the line bisection task in which patients have been reported to show pathological rightward biases in their size judgments (e.g., Binder, Marshall, Lazar, Benjamin, & Mohr, 1992; Heilman & Valenstein, 1979; Milner & Harvey, 1995; Schenkenberg, Bradford, & Ajax, 1980). Similar misperceptions occur with non-spatial visual features, such as luminance (Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994; Mattingley et al., 2004), numerosity (Luh, 1995; Nicholls, Bradshaw, & Mattingley, 1999) or even numbers (Zorzi, Priftis, & Umilta, 2002). Furthermore, in neurologically healthy individuals smaller yet consistent biases to the left side can be observed (see Jewell & McCourt, 2000, for a review), a finding that is also consistent with a right-hemisphere dominance.

However, it remains unclear what these perceptual biases actually reflect. Line bisection tasks seem to involve areas within the posterior parietal cortex (Fink et al., 2001, 2002) similar to those that are activated by various attentionally demanding tasks (Nobre, Coull, Walsh, & Frith, 2003; Wojciulik & Kanwisher,

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1999), and transcranial magnetic stimulation in the right posterior parietal cortex disrupts line bisection as well as visual search functions (Ellison, Schindler, Pattison, & Milner, 2004; Rosenthal et al., 2006). However, brain lesions associated with pathological biases are different from those resulting in deficits in other standard neglect tests (Binder et al., 1992; Ferber & Karnath, 2001a; Hillis et al., 2005; Rorden et al., 2006), and scores in the two groups of tests only poorly correlate (Binder et al., 1992; Ferber & Karnath, 2001b; Halligan & Marshall, 1992; McGlinchey-Berroth et al., 1996). There even is little correlation between different types of perceptual biases (e.g., Luh, 1995; Mattingley et al., 1994; Nicholls et al., 1999).

Which mechanisms underlie biases in perceptual judgments? One central aspect of perceptual biases, in particular in line bisection tasks, has been largely ignored: size perception is closely related with spatial frequency perception. The close link between size and spatial frequencies becomes obvious in visual distortions of size perception such as the Müller-Lyer illusion that results from low-frequency filtering and disappears when the brain's low spatial frequency filters are desensitized through adaptation to low spatial frequency gratings (Carrasco, Figueroa, & Willen, 1986). Such gratings can also affect size perception when used as masks (Gelb & Wilson, 1983). Moreover, learning to discriminate spatial frequencies transfers to better discrimination of bar widths and vice versa (Meinhardt & Grabbe, 2002).

Given the connection between size and spatial frequency and a right-hemisphere dominance in spatial tasks one could conclude that biases in size perception (and perhaps biases for other visual features as well) depend on spatial frequencies. The first aim of our study was to test this hypothesis. A second aim was to explore the mathematical relationship between frequencies and biases.

A monotonic relationship could be expected from models such as Sergent's (1982) hypothesis that in certain tasks the right hemisphere is dominant for lower spatial frequencies and global perception while the left hemisphere is specialized for higher frequencies and local analysis (see Christman, 1997; Grabowska & Nowicka, 1996; Robertson & Lamb, 1991 for reviews). Ivry and Robertson (1998) have expanded this idea in a neural network model that uses task-sensitive second-stage frequency filters combined with attentional weights different for the two hemispheres. In simulations the model could explain various effects of hemisphere asymmetries. Asymmetries in line bisection tasks have been examined in computer simulations of another model that implemented one fine-coding and one coarse-coding hemisphere (Monaghan & Shillcock, 2004). The model explained a number of line bisection findings, most interestingly here, the 'cross-over effect' (e.g., Halligan & Marshall, 1988; McCourt & Jewell, 1999). That is, for very short lines the model's bisection biases switched to the opposite side, perhaps because in the power spectrum of shorter lines higher frequencies have a stronger relative weight compared to the spectrum of longer lines.

As another possibility, biases in spatial frequency perception could result from a bias in spatial attention. Because attention modulates apparent spatial frequency, size and luminance perception (Carrasco, Ling, & Read, 2004; Gobell & Carrasco, 2005; Yeshurun & Carrasco, 1998), it is conceivable that a normal or pathological bias in spatial attention would turn up spatial resolution and/or contrast gain (Lee, Itti, Koch, & Braun, 1999) in a particular part of the visual field and thus would create biases in size and luminance perception as well as in spatial frequency perception. So then, spatial frequency judgments should yield perceptual biases consistently to one side and no cross-over.

Here we studied the influence of spatial frequencies on perceptual biases in neurologically healthy individuals using a new task called "gratingscales" that we derived from Mattingley et al. (1994) greyscale task. We chose a similar paradigm because it is well suited for testing different types of visual features. Furthermore the greyscales task is known to be very sensitive to biases (Mattingley et al., 2004), and it disentangles perceptual biases from response biases.

2. Methods

2.1. Subjects

One hundred and fifty-seven undergraduate students gave their informed and written consent prior to their inclusion in the study and obtained a course credit. All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto and have therefore 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) that measures a laterality quotient running from −100 (left lateralized) to +100 (right lateralized).

2.2. Apparatus and procedure

Participants sat in front of a 19 in. monitor (Viewsonic E90fb) at a distance of about 60 cm. A chin rest was used to keep head movements to a minimum. All tests were performed under free viewing conditions.

We wrote our experiments in Matlab (MathWorks) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). There were two types of tests. The first was a modified version of Mattingley et al.'s (1994) greyscales task (Fig. 1). The second was the new gratingscales task (Fig. 2).

2.2.1. Greyscales

Similar to Mattingley et al. (1994) we presented a pair of horizontal bars (Fig. 1A). Trial by trial either the upper or lower bar was black on its left side and gradually changed to white on its right while the other bar changed luminance in the opposite direction. Each time participants judged which of them "on average was darker" (reporting the "brighter" bar yields similar results; Nicholls et al., 1999).

Unlike the original greyscales that changed luminance linearly, we chose half-cycles of sine functions spanning 80% of the bars roughly in their centres (marked by the grey rectangles underlying Fig. 1B and C). The remaining 20% on the left and/or right sides stayed consistently black or white.

This way we could displace the sine waves, in both bars concurrently, across trials to expand the dark region in one bar at the expense of its bright region and vice versa in the other bar without changing the contrast of the bars' left and right edges with respect to the background. For example in Fig. 1C the central area is shifted −10% leftward relative to the length of the bar so that the black region in the upper bar is reduced to a minimum while it is maximally increased in the lower bar.

From these asymmetrical stimuli and the participants' luminance judgments we obtained psychometric functions (see Section 2.2.3 below).

2.2.2. Gratingscales

To direct attention explicitly to spatial frequencies we designed a new "gratingscales task". Stimulus samples of the gratingscales are given in Fig. 2. Like

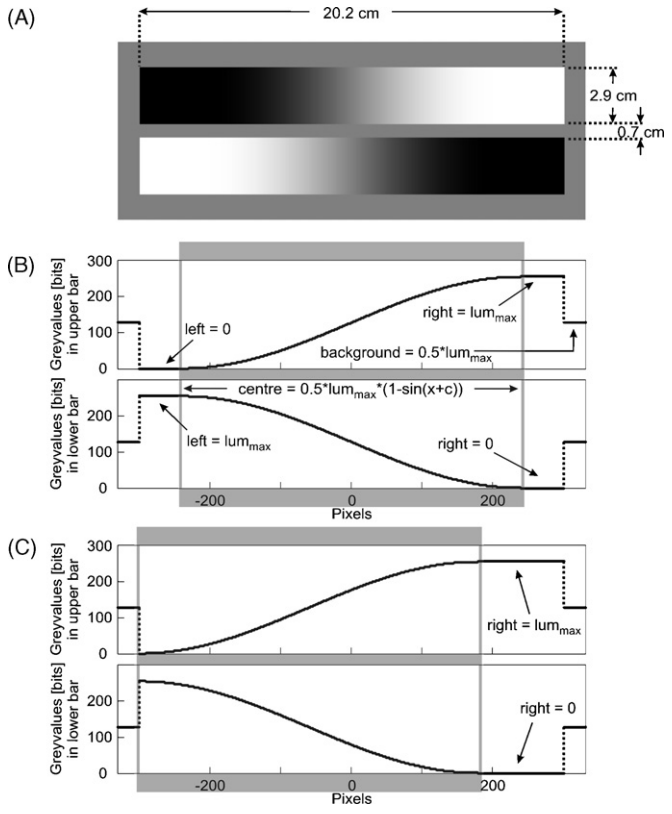


Fig. 1. Greyscales task. Participants are asked to judge which of the two bars on average is darker. (A) Example for a stimulus. (B and C) Luminance distribution of the greyscale bars. The grey rectangles underlying the graphs mark the central area of the bars in which luminance changes as a sine function of horizontal pixels. (B) Luminance distribution of the stimulus in (A). The distribution in the two bars is mirror-symmetrical. (C) Asymmetrical luminance distribution. The central area in both bars is shifted −10% to the left. lum_{max}, maximum luminance.

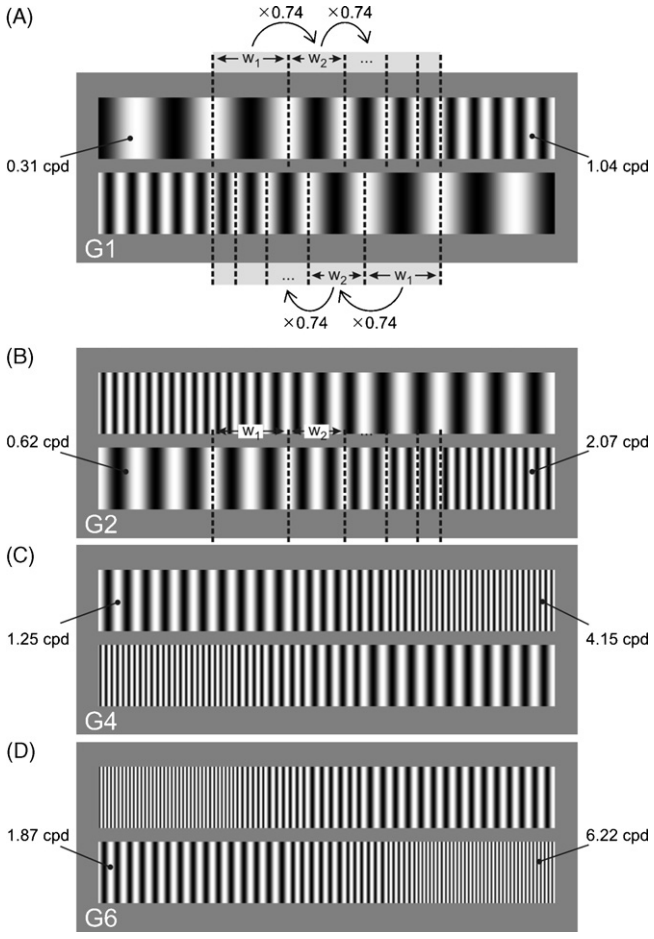


Fig. 2. Gratingscales task. Participants are asked to judge which of the two bars has "more thinner stripes". (A) Example of a grating 1 ("G1") with spatial frequencies of 0.31 cycles per degree (cpd) to 1.04 cpd. Spatial frequency increases wavelet by wavelet (w1, w2, etc.) by a factor of about 1/0.74. (B) Example of a G2 grating with spatial frequencies of 0.62–2.07 cpd. Each wavelet runs through two cycles of a sine wave. (C) Example of a G4 grating with spatial frequencies from 1.25 cpd to 4.15 cpd. (D) Example of a G6 grating (1.87–6.22 cpd).

the greyscales task each stimulus consisted of two horizontal bars. However, the new bars were filled with rows of luminance-defined wavelets. Spatial frequency of the wavelets increased within a central area (marked by the grey rectangle underlying Fig. 2A) from left to right in one bar and from right to left in the other bar. Participants judged which of the two bars "had more thinner stripes".

For "grating 1" or G1 (Fig. 2A) each wavelet of the central area ran through one cycle of a sine wave. Wavelet w1 had 0.31 cycles per degree (cpd), w2 0.42 cpd and so forth until w5 with 1.04 cpd. The margins left and right of the central area had constant spatial frequencies. For gratingscales with higher spatial frequencies (Fig. 2B–D) we inserted wavelets with more cycles so that spatial frequencies were two, four or six times higher (e.g., w1 in Fig. 2A versus B).

For control Experiment 1C we also used a continuous version of the gratingscales. Here spatial frequency increased not in steps but as half a cycle of a cosine function within the central area. To achieve this, pixel luminance was calculated as follows:

$$\text{luminance} = \cos(h(x))$$

Here h is a spline function of horizontal pixel position x with three segments, that is, the central area and two segments on the sides. The latter two are linear functions with a slope of the first and the second frequency, respectively ($h_1 = f_1 \times x_1$; $h_3 = f_2 \times x_3 + a$). The second segment, the central area with borders t_1 and t_2, is the integral of a cosine:

$$h_2 = \int \frac{f_2 + f_1}{2} - \frac{f_2 - f_1}{2} \cos\left(\pi \frac{x_2 - t_1}{t_2 - t_1}\right) \mathrm{d}x_2$$

As for the greyscales we mapped psychometric functions by displacing the central areas to expand regions of high and low spatial frequency either on the right or the left side. Although these displacements caused the contrast of the left and right edges of the bars to change, the changes were ambiguous with respect to the direction of the displacement. The central areas spanned only 50% of the entire bar (as opposed to 80% for the greyscales) so even with maximum displacements spatial frequency on the bar ends always had at least 1.5 cycles which is important for spatial frequency perception (Wilson & Gelb, 1984).

2.2.3. Data analysis

We chose a psychophysical approach to estimate two measures of test performance. One is an estimate of the commonly studied perceptual bias, which is equivalent to the systematic errors in the perceptions of a participant. The second measure, sensitivity, is seldom looked at. It relates to the degree of unsystematic errors or the variability in the participant's perceptions and therefore reflects how difficult the task is for the participant. Both measures, bias and sensitivity, can be derived from psychometric functions (see below).

To obtain psychometric functions we presented stimuli that varied in symmetry. That is, the central areas in which the greyscales' luminance, or the gratingscales' spatial frequency, changed was displaced. For example, the central area of the greyscales in Fig. 1C is shifted −10% leftward, in another greyscales stimulus the central area was shifted +10% rightward, and in total there were 11

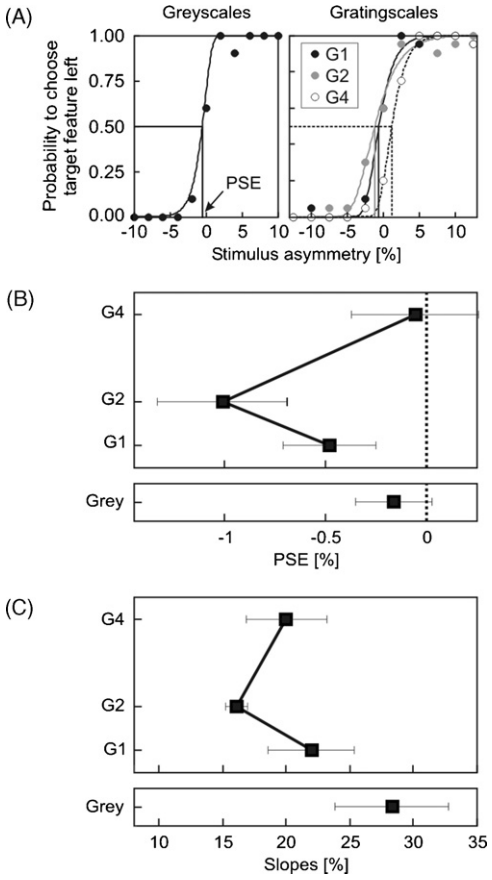


Fig. 3. Experiment 1. Perceptual bias and task difficulty are quantified with the points of subjective equality (PSEs) and the slopes of the psychometric functions, respectively. Presentation time was 1500 ms. Units are in percent of bar length. (A) Psychometric functions of one participant for the greyscales task (left) and the three gratingscales tasks (right). (B) Group average of perceptual bias in the four tasks. (C) Group average of task difficulty. Error bars indicate standard errors.

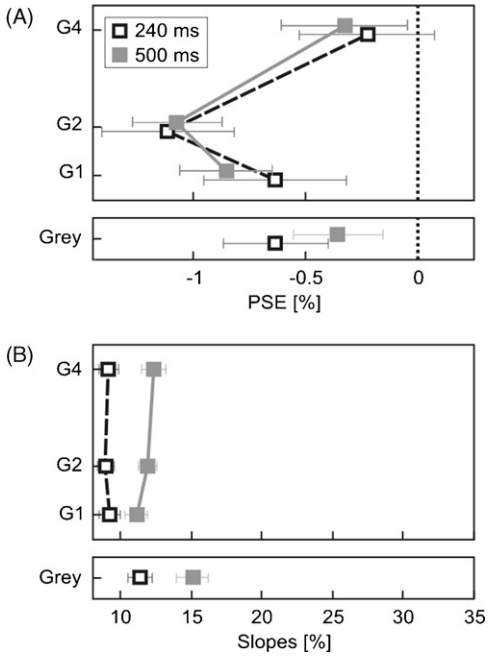


Fig. 4. Experiment 1B. (A) Group average of perceptual bias in the four tasks (greyscales and gratingscales G1, G2 and G4). (B) Group average of task difficulty. Grey curves, 500 ms presentation time; dashed curves, 240 ms presentation time. The curves are slightly offset relative to each other for reasons of visibility.

greyscales stimuli between ±10%. Likewise for the gratingscales task we used 11 stimuli with asymmetries ranging from −12.5% to +12.5%.

Participants viewed each stimulus 20 times, and each time they were asked to choose either the upper or lower bar thereby indicating whether they saw the bar with the target feature "black" or "high spatial frequency" on the left as more prominent (counted as "1") or the bar with the target feature on the right (counted as "0"). We then plotted the average probability of choosing the target feature on the left as a function of asymmetry (e.g., the circles in Fig. 3A represent averages for one participant). These functions have a sigmoid shape and can be described by so called "Weibull" functions:

$$P(\text{response} = \text{"left"}) = 1 - \exp(-10^{m(x-k)}).$$

Here P is the probability of choosing the bar 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 optimally fitted the actual data (e.g., curves in Fig. 3A).

Given this we could calculate bias and sensitivity. The former is identical with the "point of subjective equality" (PSE) of the psychometric function where the stimulus is perceived as symmetrical, so the point where the function reaches 0.5 probability. For example, in Fig. 3A the participant's PSE for greyscales was about −0.52%.

Sensitivity is reflected in the slope of the psychometric function. A relatively steep slope means that with small changes in symmetry the participant's average responses quickly switch from consistently "0" to consistently "1". In other words, the participant notices even small changes; we can say s/he shows "high perceptual sensitivity" for stimulus asymmetry. In contrast, a relatively flat curve indicates that a participant has more difficulties with the task. So only with large changes in symmetry the participant's responses will switch from consistently "0" to consistently "1". For example, the psychometric functions in the right panel of Fig. 3A are somewhat flatter than the function in the left panel indicating that the participant had more difficulties with the gratingscales than the greyscales. As we will demonstrate teasing apart bias and sensitivity reveals important information about perceptual biases that would go unnoticed otherwise.

2.2.4. Overview on experiments

In the first experiment 20 participants were tested (10 females, median age 19, laterality 97.8, S.D. 6.6). We compared the greyscales task ("grey") with gratings G1, G2 and G4 from the gratingscales task. Trials for each condition were split into two blocks each and were presented in a pseudo-randomly chosen sequence that counterbalanced order within participants. Participants viewed the stimuli for 1500 ms and then the screen turned grey. This made it impossible to compare the gratings simply by counting the stripes because counting takes 250–350 ms per item (Trick & Pylyshyn, 1994), too long for the 24 or more "stripes" of the gratingscales. There was unlimited time to respond with a keyboard press.

Experiment 1B repeated the procedure of the first with viewing times 500 ms and 240 ms. Thirty-eight participants were tested (26 females, median age 19.5, laterality 94.9, S.D. 10.1), two of which performed only the 240 ms condition and four only the 500 ms condition. We included these data in the separate analyses and in the graphs in Fig. 4 because they showed no noticeable difference. Participant performed pseudo-random counterbalanced orders of blocks of trials.

Experiment 1C served as an additional control. Thirty participants (15 females, median age 24, laterality 92.1, S.D. 14.8) viewed the continuous version of gratingscales G1, G2 and G4 at 240 ms and 500 ms presentation time.

Experiment 2 also focused on the gratingscales. We tested 31 participants (16 females, median age 19, laterality 97.3, S.D. 6.9) with gratingscales G2, G4 and G6 and with presentation times 1500 ms and 400 ms.

Experiment 3 examined influences of presentation time. Thirty-eight participants (26 females, median age 18, laterality 95.7, S.D. 10.3) were tested with gratingscales G2 and G6 and viewing times 75 ms, 150 ms, 300 ms and 600 ms.

3. Results

3.1. Experiment 1: influences of spatial frequency on perceptual bias

The principal aim of Experiment 1 was to explore a possible influence of spatial frequency on perceptual bias. Fig. 3A plots the psychometric functions of one participant for the greyscales task (left panel) and the three different gratings of the gratingscales task (right panel). The PSEs are marked by the intersection of the horizontal 0.5 line. Negative values indicate a leftward bias, that is, the target feature in the two bars (either black or high spatial frequency) was perceived as equal when the one on the left was actually smaller than the one on the right. Positive PSEs indicate a rightward bias.

Group averages of PSE showed a maximum leftward bias for gratingscales G2 (Fig. 3B). Consistently, a one-way ANOVA found significant differences between stimulus types ($F(3, 57) = 4.81$, $p = 0.005$) which was due to the stronger leftward bias for G2 compared to G4 ($t(19) = 3.18$, $p = 0.005$) and similar trends compared to greyscales and G1 (t's$(19) \geq 2.65$, p's ≤ 0.016, not significant after Holm's correction). These data suggest that spatial frequency has a substantial impact on perceptual bias, perhaps in a non-monotonic fashion.

Average slopes had a similar profile (Fig. 3C), and an ANOVA found a significant task effect ($F(3, 57) = 4.69$, $p = 0.005$) due to somewhat more sensitive performance during the greyscales than G2 and G4 (t's$(19) \geq 2.27$, p's ≤ 0.035, not significant after Holm). Given the similarity, was leftward bias in the gratingscales a mere result of tasks sensitivity or difficulty? If so, slopes and PSEs should be positively correlated. But they were not; there was a trend towards negative correlations.

Lastly, to better understand the mechanisms underlying the new gratingscales task we explored the correlational structure of our data. We found biases in the gratingscales correlated only weakly with biases in the greyscales (Table A1). Also, a principal component analysis extracted only one factor with an eigenvalue larger than 1 but when forced to extract two factors the varimax-rotated solution found greyscales and gratingscales to load differentially on the two components (Fig. B1). One possible reason is that correlations were corrupted by poor reliability, though this is unlikely because there were significant correlations among the three types of gratingscales (Table A1).

Another explanation for the relative independence of greyscales and gratingscales is that participants carried out the tasks with different strategies. In particular, without a time limit the gratingscales task – but not the greyscales task – could be solved simply by counting the stripes in the two bars. Our presentation time of 1.5 s made that extremely unlikely. Nevertheless, it is possible that some participants tried to count stripes – perhaps at least in the gratings with fewer stripes (G1 and G2) and perhaps beginning from the left end – and thereby showed a stronger leftward bias depending on the kind of gratingscales.

3.2. Experiment 1B: possible influences of scanning strategies

Experiment 1B tested whether the non-monotonic relationship between spatial frequencies and leftward bias in Experiment 1 was merely caused by counting strategies. If so, presentation time should have a strong influence on PSEs, but Fig. 4A shows that there was no such influence (also note the overlap with the PSEs in Fig. 3B). Consistently, a 4×2 ANOVA revealed an effect of "stimulus type" ($F(3, 93) = 5.37$, $p = 0.002$) but no influence of "presentation time" (main effect: $F(1, 31) = 0.059$, $p = 0.809$; interaction: $F(3, 93) = 1.34$, $p = 0.265$), and in simple comparisons only the greyscales bias showed a marginal effect ($t(31) = 2.40$, $p = 0.023$, not significant after Holm). Thus, we were unable to confirm the hypothesis that leftward bias in gratingscales results from counting.

Presentation time did affect task difficulty (Fig. 4B): a 4×2 ANOVA on slopes found presentation time to significantly reduce task difficulty ($F(1, 31) = 20.06$, $p < 0.0005$, also compare Figs. 4B and 3C). Furthermore, stimulus type had an effect ($F(3, 93) = 7.33$, $p < 0.0005$) due to greyscales being performed with higher sensitivity than the gratingscales (t's$(37) \geq 2.91$, p's ≤ 0.006) while there was no difference between any two gratingscales (t's$(37) \leq 0.89$, p's ≥ 0.382).

Despite the differences in difficulty, almost all biases in the greyscales and the gratingscales were significantly correlated – unlike those in Experiment 1 (Table A2). Also, a principal component analysis with varimax rotation found only a small separation between greyscales and gratingscales in factor space (Fig. B1). Together these results suggest that greyscales and gratingscales measure similar mechanisms of perceptual bias, perhaps specifically for certain presentation times.

3.3. Experiment 1C: continuous gratingscales

To rule out artefacts due to the stepwise increases in the gratingscales stimuli we used a continuous version of the stimulus. We observed similar influences of spatial frequency on leftward bias ($F(2, 58) = 6.92$, $p = 0.002$, Fig. 5A) with G2 yielding a stronger bias than the other stimuli (G2 versus G4: $F(1, 29) = 12.22$, $p = 0.002$; G2 versus G1: $F(1, 29) = 4.87$, $p = 0.035$, not significant after Holm; G1 versus G4: $F(1, 29) = 2.97$, $p = 0.096$). But there was no significant effect of time nor of interaction (F's ≤ 1.22, p's ≥ 0.278). Likewise, slopes did not yield any significant results ('stimulus' effect: $F(2, 58) = 0.11$, $p = 0.897$; 'time' effect: $F(1, 29) = 0.55$, $p = 0.466$; interaction: $F(2, 58) = 2.06$, $p = 0.136$).

3.4. Experiment 2: higher spatial frequencies

Gratingscales in the first group of experiments produced biases that varied with spatial frequency, but even the G4 stimulus failed to show rightward biases which might be expected according to Sergent's hypothesis of lateralized spatial frequency processing (Monaghan & Shillcock, 2004; Sergent, 1982). To further examine this idea, the second experiment tested gratingscales G6, which carried the highest spatial frequencies

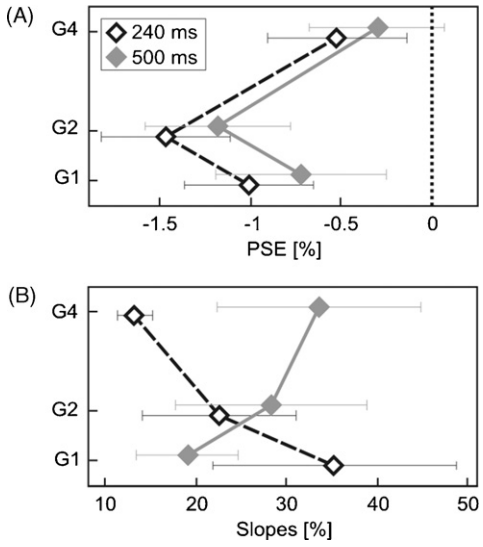


Fig. 5. Experiment 1C. (A) Group average of perceptual bias in the continuous version of the gratingscales task. (B) Group average of task difficulty. Grey curves, 500 ms presentation time; dashed curves, 240 ms presentation time.

that were possible given the resolution of our monitor. G2 and G4 served as comparison stimuli, and we tested two presentation times.

But again all biases pointed leftward (Fig. 6A). A 3×2 ANOVA found a significant effect of "stimulus type" ($F(2, 60) = 7.04$, $p = 0.002$) that again resulted from a stronger leftward bias for G2 (main effect "stimulus type" in post hoc 2×2 ANOVAs: F's$(1, 30) \geq 6.19$, p's ≤ 0.019, significant after Holm). For higher spatial frequencies leftward bias shrank to some small value with no noticeable change from G4 to G6 ($F(1, 30) = 0.34$, $p = 0.566$). At no point did we observe biases to switch from left to right.

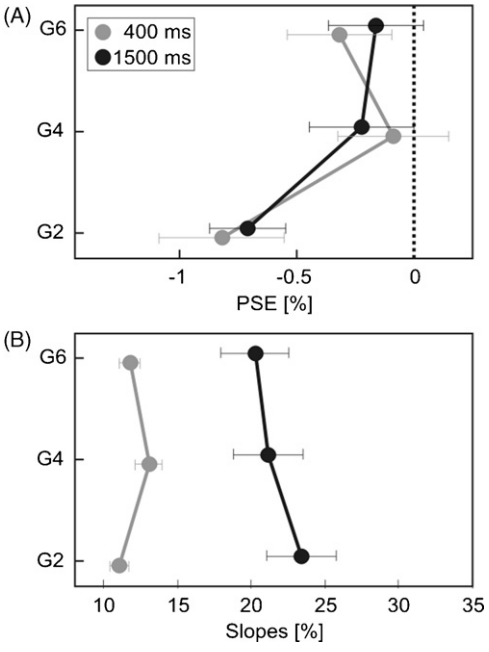


Fig. 6. Experiment 2. (A) Group average of perceptual bias in the three tasks. (B) Group average of task difficulty. Black curves, 1500 ms presentation time; grey curves, 400 ms presentation time.

Also similar to before, there was no effect or interaction involving "presentation time". Further, a second 3×2 ANOVA demonstrated a decline in task difficulty with presentation time ($F(1, 30) = 40.84$, $p < 0.0005$) (Fig. 6B) but no other effect. Finally, we found high correlations between almost all gratingscales types and presentation times (Table A3), and in a principal component analysis the tasks showed a continuum of loadings on the first two components (Fig. B1).

3.5. Experiment 3: influences of presentation time

As an alternative to lateralized frequency processing, the relationship between perceptual bias and spatial frequencies could reflect biased spatial attention that modulates apparent spatial frequency (Gobell & Carrasco, 2005). However, spatial attention is time-sensitive (Chambers, Payne, Stokes, & Mattingley, 2004) which might be at odds with our finding that presentation time had no influence on biases. Still, time affected task difficulty and perhaps correlations between greyscales and gratingscales (Experiment 1 versus 1B). To search for less straightforward timing effects on bias, our third experiment examined time more systematically. We presented gratingscales G2 and G6 for 75 ms, 150 ms, 300 ms and 600 ms, respectively.

First we analyzed data as before. Fig. 7E follows the previous pattern to graph PSEs as a function of gratingscales type. A more comprehensive way to organize the data in Fig. 7A plots PSEs as a function of presentation time. Gratingscales G2 once more yielded the strongest leftward bias (2×4 ANOVA, main effect "stimulus type": $F(1, 37) = 5.65$, $p = 0.023$). But, again there was no influence of "presentation time" (main effect of timing: $F(3, 111) = 1.01$, $p = 0.390$; interaction: $F(3, 111) = 0.08$, $p = 0.969$). As before, correlations were high (Table A4), and in the principal component analysis the tasks showed a relative separation of the G2 and G6 tasks consistent with what should be expected from Experiment 2 with the G4 tasks missing (Fig. B1). Furthermore, a 2×4 ANOVA on slopes found task difficulty to be significantly affected by presentation time ($F(3, 111) = 46.87$, $p < 0.0005$) while no other effect proved significant (F's ≤ 0.75, $p \geq 0.524$).

We then split the group of participants into subgroups according to task difficulty: we calculated individual slope averages for each gratingscales separately and then determined group medians. Participants with average slopes higher than the median were called "sensitive performers" and participants below the median were called "insensitive performers".

Fig. 7B presents the PSEs for G2. Insensitive performers showed more pronounced leftward bias than sensitive performers and the profiles of leftward bias were roughly symmetrical (Fig. 7B). Accordingly, a 2×4 ANOVA found a significant effect of "sensitivity level" ($F(1, 36) = 8.56$, $p = 0.006$) and a significant interaction with "presentation time" ($F(3, 108) = 3.76$, $p = 0.013$; after Greenhouse-Geisser correction to rule out the possibility of spurious effects: $F(2.9, 104.2) = 3.76$, $p = 0.014$). The main effect of "presentation time" was insignificant ($F(3, 108) = 0.63$, $p = 0.595$). We also found no effects for the G6 task (F's ≤ 0.84, $p \geq 0.511$, Fig. 7C).

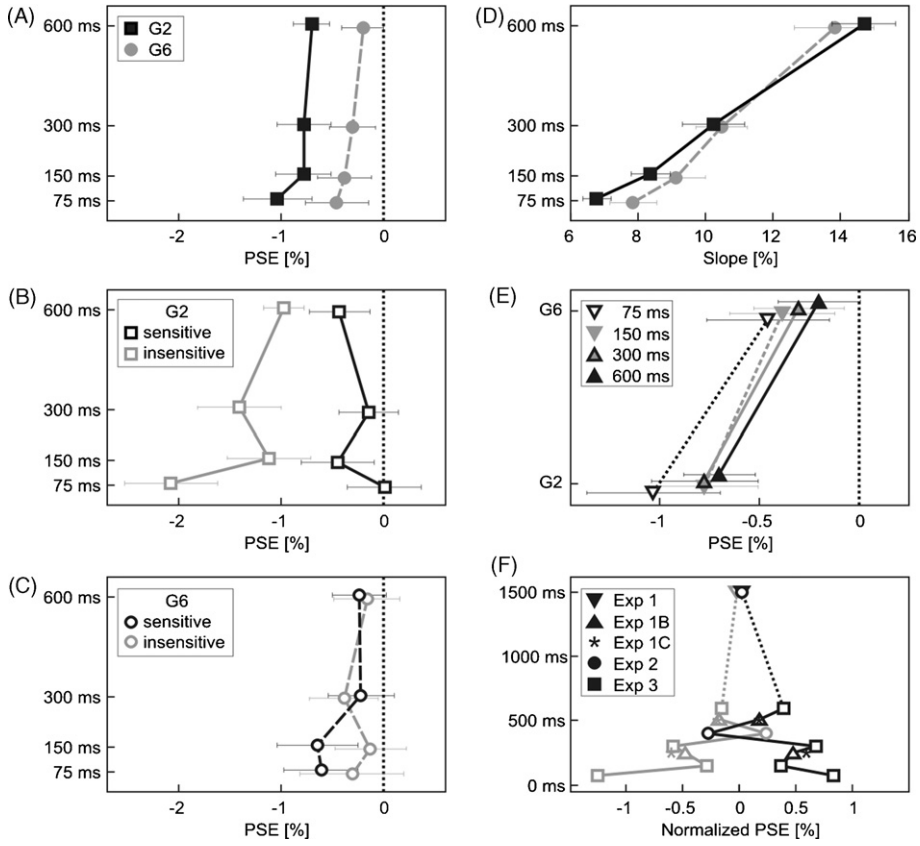


Fig. 7. Experiment 3. (A) Average perceptual biases are plotted as a function of presentation time (also see (E)). Black curve, G2 gratingscale; grey curve, G6 gratingscale. (B) The data for the G2 grating are presented for sensitive (black curve) and insensitive (grey curve) performers separately. (C) Sensitive and insensitive performers in the G6 task (black and grey curve, respectively). (D) Average task difficulty in the G2 and G6 task. (E) Repetition of the data in (A), however, plotted according to the conventions of the previous experiments in Figs. 3–5. (F) Summary across all experiments. Perceptual biases are presented for sensitive and insensitive performers separately. The data are normalized to account for experiment specific differences.

Did similar symmetry effects occur with the G2 task in the previous experiments as well? For a re-analysis we median-split the respective groups of participants into sensitive and insensitive performers, and we subtracted average leftward biases for each experiment separately to account for study-specific differences such as possible task interactions or variations in medians. As shown in Fig. 7F we found a good agreement of most data points with mostly consistently stronger leftward biases for insensitive performers except for the 400 ms presentation time in Experiment 2.

4. Discussion

Current research suggests that perceptual biases are associated with a right-hemisphere dominance in spatial and attentional functions (Corbetta et al., 2000; Coull et al., 2001; Fink et al., 2001, 2002; Foxe et al., 2003; Heilman & Van Den Abell, 1980; Mesulam, 1981). Here we used a new gratingscales task to explore the influences of spatial frequencies on such biases in neurologically healthy participants. We found that perceptual biases depended on spatial frequencies in a non-monotonic fashion. Gratingscales with intermediate spatial frequencies yielded the strongest leftward bias, and biases were reduced for gratingscales with lower or higher spatial frequencies.

These results cannot be explained with a strategy of counting the stripes because the biases proved robust across various presentation times. For the same reason it appears unlikely that the differences in bias were due to eye movements.

Our results disagree with the hypothesis that in a range of tasks low spatial frequencies involve the right hemisphere more than the left (e.g., Christman, 1997; Grabowska & Nowicka, 1996; Ivry & Robertson, 1998; Robertson & Lamb, 1991; Sergent, 1982). Accordingly, leftward biases should be strongest for low spatial frequencies, and high spatial frequencies should induce a bias to the right because they activate the left hemisphere more than the right (Monaghan & Shillcock, 2004). However, we did not observe such low- and high-pass effects. The leftward bias was maximal within a bandwidth of intermediate spatial frequencies and we never observed rightward biases.

It might be argued that rightward biases did not occur because all gratingscales contained low spatial frequencies. However, our instructions directed attention to the high frequency component of the stimuli. This should induce right visual field advantages even if low spatial frequencies are present (Kitterle et al., 1992). What is more, we asked for the relatively higher spatial frequencies of the gratingscales which should further add to a rightward bias (Christman, Kitterle, & Hellige, 1991).

Of course rightward biases might eventually show up for spatial frequencies higher than the tested ones. Or the gratingscales could involve additional biased mechanisms that shift all frequency-sensitive biases to the left. But we also found leftward bias to peak at the G2 stimulus while for lower spatial frequencies, G1 and the greyscales, the bias grew smaller again. These results would not be expected based on a usual model of lateralized spatial frequency processing, though revisions of the model, perhaps regarding response properties of visual neurons, might resolve the discrepancy.

For example, interestingly our data resemble contrast sensitivity functions. For 14° eccentricity, which is close to the average location of the high frequency component of the gratingscales, sensitivity is maximal at about two to three cpd (Rovamo, Virsu, & Nasanen, 1978). This might be a coincidence, but there are also two other explanations. One is that the G2 stimulus might have yielded more bias due to more apparent contrast. This is unlikely because our stimuli had high contrast and because contrast sensitivity would change with presentation time, yet time did not change biases. Furthermore, leftward bias is known to increase, not decrease, with lower contrast (Bradshaw, Nathan, Nettleton, Wilson, & Pierson, 1987; McCourt & Jewell, 1999).

Another explanation for the resemblance might be related to the fact that contrast sensitivity reflects the response properties of a neural population with receptive fields at a given eccentricity. This population could be slightly larger for the left than for the right visual field, hence the peak for the G2 gratingscales. However, previous research found no visual field differences in sensitivity (e.g., Kitterle, Christman, & Hellige, 1990). Further studies are necessary to clarify whether small differences become obvious in sensitivity tests that involve interhemispheric competition.

An alternative (not necessarily mutually exclusive) interpretation of the present results is that perceptual bias was due to participants distributing their attention asymmetrically (e.g., Milner, Brechmann, & Pagliarini, 1992). Since attention is known to alter perception – for example it increases apparent luminance contrast (Carrasco et al., 2004) and it changes apparent size and spatial frequency (Gobell & Carrasco, 2005; Tsal & Shalev, 1996; Yeshurun & Carrassco, 1998) – a bias in attention should also cause a perceptual bias.

If perceptual biases were governed by attention it should have a general effect. Indeed, perceptual biases occur in a variety of tasks involving perceptual judgments of size, luminance and numerosity. However, general effects should also yield correlations between these biases. This is at odds with previous studies that reported poor correlations suggesting that biases reflect task-specific mechanisms (Luh, 1995; Mattingley et al., 1994; Nicholls et al., 1999). How can this inconsistency be resolved?

We note that with short presentation times (240 ms or 500 ms) gratingscales and greyscales did correlate, but correlations were weak when stimuli appeared for longer (1.5 s). So it is conceivable that correlations between greyscales and gratingscales depend on presentation time. The two tasks might involve overlapping early neural mechanisms but dissimilar ones or temporally more variable processing at later stages. It therefore would be interesting to revisit previous reports of poorly correlated biases because those were obtained under free viewing conditions with no time limits which is about equivalent to – or even shorter than – our 1.5 s presentation time. Correlations would probably rise with shorter presentations.

In our study presentation time modified not only correlations but also task difficulty. Thus, one might expect that presentation time affects leftward bias as well. Quite strikingly, however, the total group average of perceptual bias remained constant across various times. In contrast, we found that subgroups of sensitive and insensitive test performers showed considerably different, time-dependent patterns—at least in the G2 task, the gratingscales that yielded the strongest leftward bias. Insensitive performers had stronger leftward biases than sensitive performers, and bias varied in a mirror-symmetric manner: insensitive performers exhibited peaks of bias at times when sensitive participants showed minima and vice versa. So, it seems that we never found a main effect of presentation time across the entire group of participants because of this balanced symmetry.

We believe that this balance is quite remarkable as there is no a priori reason to assume that biases should be time-invariant across an entire group of unselected participants.

Could the pattern in our data simply be due to task proficiency? Obviously, a leftward bias that is too strong should lead to poor performance in a task that requires comparing the left and right side of a stimulus. Or insensitive performers could be more biased because their brains are more asymmetrical which for some reason might be a disadvantage for this particular task. Either way, proficiency itself cannot explain the mirror-symmetric pattern of perceptual bias that we observed.

Is it possible that participants fixated systematically on different parts of the display and in this way caused the observed pattern in our data? From unsystematic observations we found that participants tended to fixate the centre of the display. But for example, McCourt and Jewell (1999) have shown that line bisection biases change with small deviations in the retinal position of the stimulus (note though, that this result confounds effects of retinal position with those of stimulus position relative to the monitor). So perhaps insensitive performers fixated further to the right than sensitive performers, thus causing a stronger leftward bias. However, the fact that insensitive performers by definition had psychometric functions with smaller slopes is inconsistent with McCourt and Jewell's (1999) finding that retinal positions did not affect slopes. More importantly, it is difficult to imagine that our participants would have distributed their fixations in a way that would have coincided with the complex pattern of time-dependent symmetry of leftward bias that we observed. Therefore, like any other study using free viewing we cannot rule out effects of eye position, but there seems to be no reason why eye movement patterns could have had a systematic influence on our results. Likewise, it is implausible that diverging high-level cognitive strategies, such as decision-making, or low-level visual adaptation to the gratings would explain these results.

Instead, our data suggest the following set of mechanisms: firstly, they support the notion of a right hemisphere dominance for spatial and attentional tasks (Corbetta et al., 2000; Foxe et al.,

2003; Heilman & Van Den Abell, 1980; Wojciulik & Kanwisher, 1999). This could also entail functions that are regarded as non-attentional, for example, slight miscalibrations in perceptual judgments between the two visual half-fields. Greatly exaggerated miscalibrations can occur after extra-striate lesions involving cortical areas in the ventral stream and area V4 (Frassinetti, Nichelli, & di Pellegrino, 1999; Schiller & Lee, 1991). However, at present it is unclear whether ventral mechanisms rely on spatial frequency processing in the same way as dorsal areas do (Fiser, Subramaniam, & Biederman, 2001), and it is doubtful to which degree these mechanisms are actually independent of attention since V4 is a key region to convey spatial attention (e.g., Moore & Armstrong, 2003).

Secondly, the correlations between greyscales and gratingscales that we observed in Experiment 1B imply a neural structure involved in representing spatial frequencies as well as luminance, and likely other features such as size and numerosity. Intriguingly, such a representation may even be suitable for representing more abstract forms of magnitudes (Pinel, Piazza, Le Bihan, & Dehaene, 2004; Walsh, 2003; Zorzi et al., 2002; but see Shuman & Kanwisher, 2004).

Thirdly, the symmetry in perceptual bias, that is, the negative correlation of bias in sensitive versus insensitive participants suggests that participants use neural processes with similar presentation time dependency so that at certain times either the right hemisphere dominates or the left hemisphere gains relative control. Importantly, across the different presentation times and groups of participants either the one or the other process seems to dominate but not both at the same time. The simplest explanation for such an effect is that perceptual bias is governed by competition in the recursive form of a push-pull mechanism where one hemisphere inhibits the other and vice versa. This agrees with previous ideas of interhemispheric competition in spatial and attentional tasks (e.g., Fecteau, Enns, & Kingstone, 2000; Hilgetag, Theoret, & Pascual-Leone, 2001; Kinsbourne, 1970; Pollmann, 1996). Our findings are also remarkable because competition is a central feature of attention (e.g., Desimone & Duncan, 1995; Kastner, De Weerd, Desimone, & Ungerleider, 1998), perhaps consistent with the idea that perceptual biases actually reflect an attentional bias (Milner et al., 1992).

Fourthly, competition and right-hemisphere dominance are likely represented within the same structure because stronger perceptual biases in insensitive performers coincided with their opposing time course relative to sensitive performers. Two independent structures that together add up to leftward bias would be more difficult to reconcile with these data.

At present there is no model of line bisection that we are aware of that accommodates all of our observations. However, several quantitative approaches explain some aspects and a future model may build on them: Anderson (1996) proposed a bilateral, right-dominant system that assigns salience to a visual input. A neural implementation of his model could resemble the basis function model proposed by Pouget and Sejnowski's (1997). Ivry and Robertson's (1998) model focuses on the contributions of spatial and temporal frequency processing to perceptual analysis. However, neither of these models incorporates interhemispheric competition. Monaghan and Shillcock's (2004) model is a three-layer feedforward network that achieves interhemispheric competition through projections from its hidden layer to its output. But the model is not recursive and so it cannot establish a push-pull mechanism. Mozer, Halligan, and Marshall (1997) model on the other hand has a recursive attentional mechanism but it is not specifying a left and right hemisphere. A more explicitly bilateral implementation of a recursive interhemispheric competition between two spatial representations has been proposed by Hilgetag, Kotter, and Young (1999), though this model was designed to simulate subcortical structures involved in orienting. Lastly, none of these models regard the influence of attention on perceptual processing or on sensitivity to spatial frequencies. Therefore, incorporating a non-spatial model of attentional effects on perception may be of interest (Lee et al., 1999).

This structure is likely to be implemented in parietal and occipital areas (Fink et al., 2001, 2002). A recent ERP study on line bisection suggests a time-dependency of perceptual bias in the occipito-temporal cortex and a dorsal region in the right hemisphere (Foxe et al., 2003). Specific time-dependent patterns can also be found in attentional detection tasks (Chambers et al., 2004). These results could be consistent with neural competition; however, further research will be required for more direct evidence. For instance, it will be interesting to explore which pattern of brain activity reflects our finding that bias depends on task difficulty. A second question concerns the time dependency of our data. This could relate to a similar time course of neural functions, but it is also possible that with manipulating presentation time we highlighted competitive processes sensitive to certain temporal frequencies.

In conclusion, in the present study we used a new test to examine the effects of time and spatial frequency on perceptual bias in neurologically healthy participants. Our data suggest that perceptual bias is governed by interhemispheric competition within a right-dominant system sensitive to a bandwidth of rather lower spatial frequencies. The fact that participants were more biased when performing our G2 gratingscales task could indicate that attention changes appearance most prominently in certain ranges of spatial frequency, presumably around 2 cpd, or that spatial attention involves neural mechanisms that are particularly tuned to these spatial frequencies, in keeping with mechanisms underlying contrast sensitivity functions. Furthermore, the correlations between perceptual judgments regarding spatial frequencies or luminance could be indicative of a system that partakes in a crossmodal representation of magnitudes, perhaps including abstract ones. We are presently conducting studies to further explore these intriguing possibilities.

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Appendix A

Table A1
Correlation matrix of leftward bias in Experiment 1

	G1	G2	G4
Grey	.343 (.139)	.343 (.139)	.331 (.155)
G1	--	.785 (<.0005)	.549 (.012)
G2		--	.557 (.011)
G4			--

Table A2
Correlation matrix of leftward bias in Experiment 1B

	Grey	G1	G2	G4
Grey	--	.410 (.018)	.290 (.101)	.467 (.006)
G1	**.538 (.001)**	--	.682 (<.0005)	.653 (<.0005)
G2	**.409 (.012)**	**.597 (<.0005)**	--	.492 (.004)
G4	**.468 (.003)**	**.592 (<.0005)**	**.660 (<.0005)**	--

White cells, 240 ms presentation time; grey cells, 500 ms presentation time.

Table A3
Correlation matrix of leftward bias in Experiment 2

	G2	G4	G6
G2	--	. 534 (.002)	.299 (.103)
G4	**. 682 (<.0005)**	--	.667 (<.0005)
G6	**. 463 (.009)**	**. 597 (<.0005)**	--

White cells, 400 ms presentation time; grey cells, 1500 ms presentation time.

Table A4
Correlation matrix of leftward bias in Experiment 3

	75 ms	150 ms	300 ms	600 ms
75 ms	--	.632 (<.0005)	.593 (<.0005)	.460 (.004)
150 ms	**.658 (<.0005)**	--	.542 (<.0005)	.453 (.004)
300 ms	**.485 (.002)**	**.718 (<.0005)**	--	.467 (.003)
600 ms	**.344 (.035)**	**.630 (<.0005)**	**.673 (<.0005)**	--

White cells, G2 grating; grey cells, G6 grating.

Appendix B

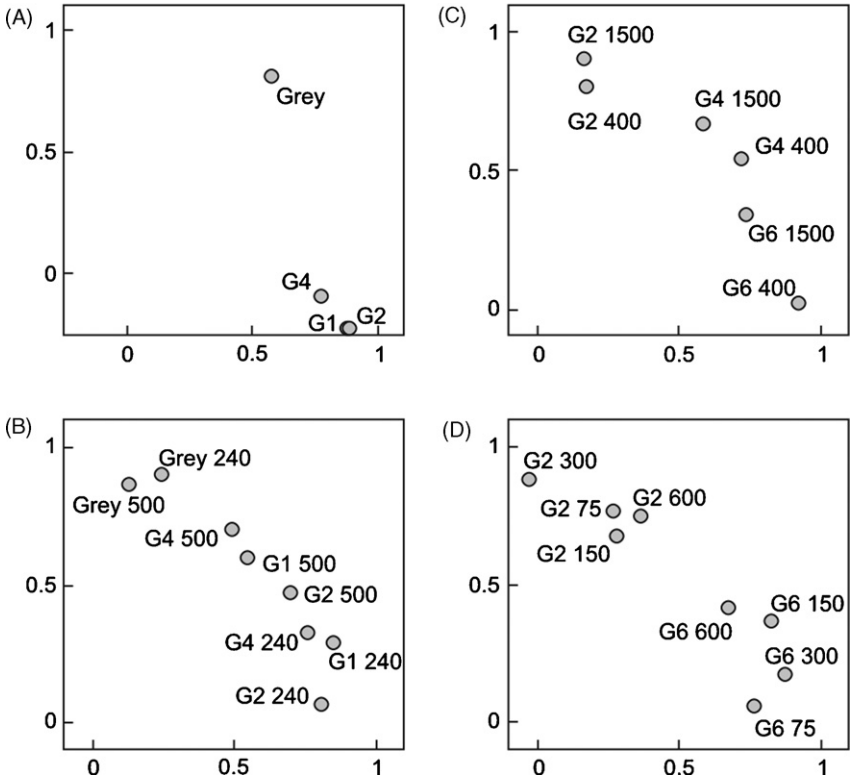


Fig. B1. Results from principal component analyses after varimax rotation. Data for the first two factors are plotted. No experiment had more than two factors with eigenvalues >1, for Experiments 1 and 2 extraction of the second factor was forced for comparison purposes. (A–D) Experiment 1, 1B, 2 and 3, respectively.

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