Exp Brain Res (2008) 187:535–549
DOI 10.1007/s00221-008-1322-z

RESEARCH ARTICLE

Attention and contrast differently affect contextual integration in an orientation discrimination task

M. J. Roberts · A. Thiele

Received: 23 November 2007 / Accepted: 11 February 2008 / Published online: 28 February 2008

Abstract Attention is often regarded as a mechanism by which attended objects become perceptually more salient, akin to increasing their contrast. We demonstrate that attention is better described as a mechanism by which task relevant information impacts on ongoing processing, while excluding task irrelevant information. We asked subjects to judge the orientation of a target relative to a reference, in a single and dual task setting. The target orientation percept was systematically influenced by the presentation of prior spatio-temporal context. We found that the sign of the context influence depended on target contrast, but its strength depended on the level of attention devoted to the task. Thus the effects of attention and contrast were fundamentally different; contrast influenced the sign of contextual interactions, while attention suppressed these interactions irrespective of their sign.

Keywords Primary visual cortex · Orientation tuning · Contextual influences · Bayesian inference

M. J. Roberts · A. Thiele (✉)
Department of Psychology, Institute of Neuroscience,
Henry Wellcome Building for Neuroecology,
University of Newcastle upon Tyne,
Newcastle upon Tyne NE2 4HH, UK
e-mail: alex.thiele@ncl.ac.uk

Present Address:
M. J. Roberts
F.C. Donders Centre for Cognitive Neuroimaging,
P.O. Box 9101, 6500 HB Nijmegen, The Netherlands

M. J. Roberts
Neurocognition Group, Psychology Department,
University of Maastricht, P.O. Box 616,
6200 MD Maastricht, The Netherlands

Introduction

Local context influences the ability to detect or discriminate visual targets (Ito et al. 1998; Ito and Gilbert 1999; Zenger et al. 2000; Freeman et al. 2001; Albright and Stoner 2002; Schwartz et al. 2007; Thiele 2007). Certain contextual configurations result in pop-out which enhance stimulus detection (Nothdurft 1993; Wang et al. 1994; Braun and Julesz 1998), while others result in crowding and impair stimulus detection (Pelli et al. 2004). Neural correlates of these perceptual phenomena have been found in sensory visual areas, where responses to a stimulus in the classical receptive field (CRF) are facilitated or suppressed by stimuli presented in the non-classical receptive field (nCRF) (Knierim and van Essen 1992; Polat et al. 1998; Jones et al. 2002; Schwabe et al. 2006; Ichida et al. 2007). Whether context facilitates or suppresses responses depends on a variety of factors, including luminance contrast of the target. At high target contrast, contextual effects are generally suppressive (Knierim and van Essen 1992; Levitt and Lund 1997; Polat et al. 1998; Williams et al. 2003; Schwabe et al. 2006; Ichida et al. 2007), while facilitation occurs for low target contrasts (Kapadia et al. 1995, 2000; Polat et al. 1998; Ito and Gilbert 1999; Freeman et al. 2001, 2004; Mizobe et al. 2001; Schwabe et al. 2006; Ichida et al. 2007). There is considerable overlap between the effects of simultaneously presented spatial context and of sequentially presented temporal context. Despite this overlap, spatial and temporal context have typically been treated separately (see Schwartz et al. (2007) for review). In this study we investigate the effects of combined spatial and temporal context.

Attention equally affects the strength of contextual influences, contrast sensitivity, and detection rates. Attending to low luminance contrast stimuli increases their apparent contrast (Carrasco et al. 2004), and boosts neuronal responses to match responses elicited by higher contrast stimuli (Reynolds et al. 2000; Martinez-Trujillo and Treue 2002; Williford and Maunsell 2006). Thus attending to a stimulus has been suggested to be equivalent to increasing its luminance contrast (Carrasco et al. 2004; Huang and Dobkins 2005). The similarity between increasing contrast and attending to a stimulus has resulted in the "contrast gain model" of attention (Reynolds et al. 2000). The effect of attention on contextual influences is more contentious, as attention can increase (Freeman et al. 2001, 2003; Tzvetanov et al. 2006), as well as reduce contextual influences (Ito et al. 1998; Zenger et al. 2000). Within the context of the contrast gain model of attention, it is possible that attentional modulation of contextual influence could be an indirect effect of enhanced apparent contrast. Alternatively, theoretical (Yu and Dayan 2005) and neurophysiological (Roberts et al. 2007) studies suggest that attention has a direct role in modulation of contextual influence, which is independent of its effect on contrast perception.

To investigate these issues, we tested how context affects orientation perception at different levels of target contrast and different levels of attention (single vs. dual task condition). We exploited the fact that the perception of oriented lines is systematically shifted when surrounded by other oriented lines. In the classic "tilt illusion" the orientation of a target is perceived to be shifted away from that of an oriented surround (Wenderoth and Johnstone 1988; Westheimer 1990; Wenderoth and Smith 1999; Kapadia et al. 2000; Schwartz et al. 2007), thus context causes a repulsion of the perceived target orientation. Our experimental design reveals a dual nature of contextual influences at high vs. low target contrast. At high contrast the percept of target bar orientation was systematically shifted away from the orientation of context bars, in line with the "tilt illusion", while at low contrast context bars had an attractor effect, reflecting the dual nature of contextual effects in V1 (Polat and Norcia 1996; Polat et al. 1998; Mizobe et al. 2001; Schwabe et al. 2006). Both effects, repulsion and attraction, were reduced in the full attention condition relative to a divided (low) attention condition. Thus, contrast determines the sign of contextual influences while attention suppresses contextual influences independent of the sign. Attention is thus not equivalent to increasing the target contrast.

Methods

Our stimulus was a series of five short bars presented sequentially at adjacent locations diagonally (45°) across a uniform gray background (13.6 cd/m^2). The orientation of the first four bars in this apparent motion sequence were identical, thereby producing a strong orientated spatial and temporal context relative to the final bar, the orientation of which varied on a trial-by-trial basis (Fig. 1a). In high contrast experiments the size and luminance of each bar was identical (0.8° by 0.07°, 139.6 cd/m^2, 82% Michelson contrast). In medium contrast experiments the contrast the fifth bar (target) was reduced to 10% (16.6 cd/m^2) and in "low contrast" experiments it was reduced to 3.6% (15.0 cd/m^2). Pilot experiments showed that this was the lowest contrast (available on our eight bit graphics board) at which subjects could detect the presentation of the final bar in more than 90% of trials in a 2AFC target-present/target absent task. Bars 1–4 (context bars) were presented for 160 ms. Bar 5 (target) was presented for 80 ms. Thus the average speed of the stimulus was 5°/s. The target was located 1.1° from the fixation spot diagonally to the upper left of the fixation spot. The orientation of the target varied from trial to trial between nine possible orientations relative to the context bars (Fig. 1, Table 1). The exact values used varied between subjects (Table 1). A sixth bar (reference), of identical size and luminance to the context bars (i.e., 0.8° by 0.07°, at 139.6 cd/m^2), was presented simultaneously with the target bar. The orientation of the reference bar varied from trial to trial between seven possible orientations relative to the target bar (Fig. 1, Table 1). Again the exact values used varied between subjects (Table 1). The reference was presented 1.1° diagonally to the lower right of the fixation spot, but it was additionally randomly displaced from this location by 0.4° (i.e., by half its length) along the 45° diagonal on a trial-by-trial basis. This was done to prevent subjects using the separation between the ends of the target and reference to solve the task without explicitly responding to the stimulus orientation (i.e., making proximity judgments rather than orientation judgments). The number of reference bars relative to each target bar resulted in 63 possible combinations (conditions) of target and reference orientation, which were presented in pseudo-random order in both the single and dual task conditions (Fig. 1b). Each condition was presented 20 times giving a total of 1,260 trials for both the single and the dual task condition. Inter-trial interval was set to 550 ms. In the low contrast experiments an additional 140 trials were included in which the target was not presented, to test whether subjects were able to perceive the low contrast target. Five subjects (four at high contrast, one at low contrast) out of the total of 21 subjects participated in a shorter version of the experiment in which each condition was presented 10 times. There were no differences in the patterns of the responses between subjects who participated in the longer or shorter experiment.

The subjects were required to report whether the target orientation was clockwise or counter-clockwise from the

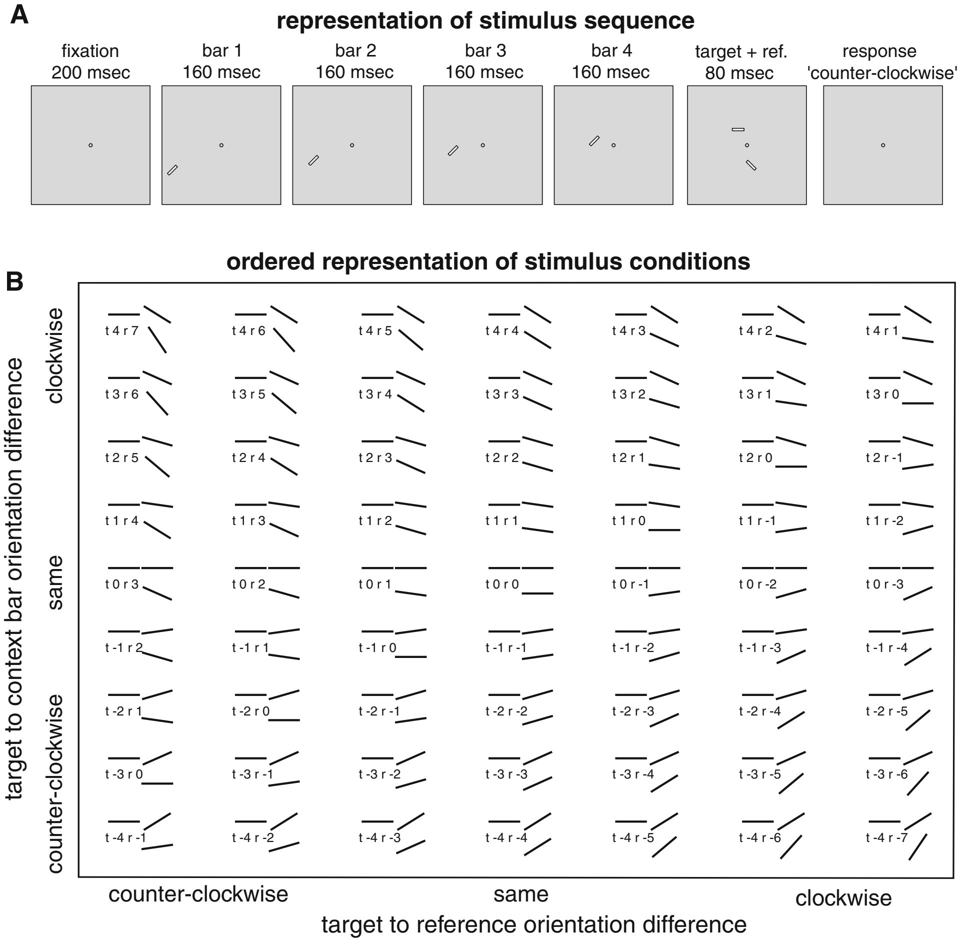

Fig. 1 **a** Representation of stimulus sequence. The colored circle relevant for the dual task condition is omitted for simplicity. The presentation time of each frame is given above each panel. **b** Ordered representation of stimulus conditions. Each combination of target and reference orientation is represented as a triplet of lines. The horizontal line on the left represents the final context bar, the line adjacent to it represents the target. The reference is represented below the target. The orientation difference between target and reference changes across columns. Columns to the left show conditions where the target was counter-clockwise to the reference. Columns to the right show conditions where the target was clockwise to the reference. The central column shows conditions where the target and reference had the same orientation. The orientation difference between the target and the context bars changes across rows. Upper rows show conditions where the target was clockwise to the context bar, lower rows show conditions where the target was counter-clockwise to the context bars. The central row shows conditions where the target had the same orientation as the context bars. The full raw data set shown in Fig. 3 is shown according to these stimulus conditions. Next to each triplet of lines the relative orientation difference between the target and context bars is given by the value "*t*". The relative orientation difference between the reference and context bars is given by the value "*r*". The values given here are generic for all experiments, the exact values are given in Table 1. For data transformation, data were combined from conditions of equal value of *t* and *r* but opposite sign, for example the condition at the top left ($t = 4$, $r = 7$) is a mirror image match for the condition at the bottom right ($t = -4$, $r = -7$). Responses along the central row were not combined

reference or whether they appeared the same [three alternative forced choice (AFC)]. Responses were made on a keyboard using keys "J", "K" and "L" for "counter-clockwise", "same", and "clockwise" responses, respectively. In the low contrast experiments subjects could also indicate that the target was not presented by pressing "O" (4AFC).

In the dual task attention was withdrawn from the orientation task and directed to an additional color counting task: Superimposed on the central fixation point was a colour-filled circle. This was presented in both the single and dual task, but was irrelevant to the former. The color of the circle changed randomly four times during each trial between seven possible colors (red, green, blue, magenta, grey, dark yellow and bright yellow). Each color was presented for 78 ms with a 109 ms interval between presentations. The first color was presented 109 ms after the presentation of the first bar. The last color was extinguished 27 ms after the reference and target were extinguished. Thus, in the dual task condition, subjects were asked to

Table 1 Range of target-to-reference and target-to-context bar orientation differences

Exp. #	Target to reference orientation difference	Target to context orientation difference	Number of subjects
1	−3 −2 −1 0 1 2 3	−4 −3 −2 −1 0 1 2 3 4	3 high contrast
2	−6 −4 −2 0 2 4 6	−8 −6 −4 −2 0 2 4 6 8	3 high contrast
3	−3 −2 −1 0 1 2 3	−12 −9 −6 −3 0 3 6 9 12	2 high contrast 1 low contrast
4	−6 −4 −2 0 2 4 6	−12 −9 −6 −3 0 3 6 9 12	5 high contrast 4 mid contrast 6 low contrast 2 no context bars

Our experimental design was based around nine different target orientations relative to the context bar orientation. For each target orientation we presented seven reference orientations. The exact values of the target-to-context bar orientation differences and the target-to-reference orientation differences varied between experiments. The table gives these values for each of the four settings and gives the numbers of subjects measured in each contrast condition using each setting

report the number of times the circle had been either red or green during the trial (which could be between one and four times) using the numbered keys on the keyboard, in addition to performing the orientation task (subjects were instructed to give priority to the former). The function of the color counting task was to divert attention from the bar stimulus. The single and dual task conditions were divided into separate sessions which were separated by at least one day.

Stimuli were displayed on a 20-in. analogue CRT monitor (75 Hz, 1,600 × 1,200 pixels) positioned 1.4 m from the subject. Stimuli were presented and responses recorded under the control of Remote Cortex 5.95 (Laboratory of Neuropsychology, National Institute of Mental Health, Bethesda). In all experiments subjects were trained at the start of the first session (15–20 min practice session). During sessions subjects sat in a dark, or dimly lit, quiet room and were able to take breaks when they wished. To avoid order and learning effects we ensured that for each target bar contrast level (i.e., high, medium, low) ~half of the subjects performed the single task first, while the remaining performed the dual task first. For some subjects sessions were split into two halves to be completed on separate days. Six subjects (no members of our research group) were paid for their participation (£5/h). Sessions typically lasted 1–2 h. All subjects (other than the authors) were naïve with respect to the hypotheses investigated.

No context bars control experiment

To test whether changes in the perceived orientation of the target were due to the presentation of the context bars, and not some other factor, we ran a control experiment in which no context bars were presented, while all other aspects of the stimulus and of the subject's task remained the same. The target was presented at high contrast. Each combination of target and reference orientation (total 63) was presented ten times, interleaved in a pseudo-random order in one session. Two subjects participated in this control (MR and EA). Both subjects had previously participated in the experiments (including high contrast pilot sessions) and shown typical effects of repulsion and attraction, respectively.

Data analysis

We first examined proportions of "target clockwise to reference", "target same as reference" and "target counter-clockwise to reference" responses from each combination of target and reference orientation. We represented these proportions as triplets of bars where the height of the bar represented the proportion of responses. We arranged these triplets into columns (see Fig. 3a where seven columns are shown for each task) representing conditions of equal orientation difference between target and reference and rows representing conditions of equal orientation difference between target and context bar (i.e., each triplet column in Fig. 3a corresponds to the stimulus column from Fig. 1b). If the only factor influencing responses was the orientation of the target relative to the reference then "counter-clockwise" responses should be dominant in columns where the target was indeed "counter-clockwise" to the reference (columns to the left of the centre), while "clockwise" responses should be dominant in columns where the target was "clockwise" to the reference (columns to the right of the centre). "Same" responses should dominate in the central column, where target and reference had the same orientation.

Data transformation

From Fig. 1b it is obvious that each condition has a mirror image partner condition (the central condition is an exception). To find the corresponding mirror image it is necessary to first reflect all conditions along the central column and then along the central row. These mirror image pairs are identical when the absolute angular distance of the "target-to-context" and of the "reference-to-context" is considered. Data from the corresponding mirror pairs can thus be combined, also in a mirror image manner, i.e., the proportion of "clockwise" responses can be combined with the proportion of "counter-clockwise" responses (and vice versa). Following this merger, it is necessary to replace the nomenclature "clockwise", "same", and "counter-clockwise", with a nomenclature that describes how close the percept of the target bar orientation was to the context bar orientation and how close the percept of the reference bar orientation was to the context bar orientation. Such a data reduction has three advantages: first, it increases the sampling at fixed orientation differences, second, it removes any bias the subject may have had for "clockwise" or "counter-clockwise" responses, and third it allows a description of the data in the more meaningful reference frame of the orientation difference between the target and the context bar orientation in one dimension, and the angular distance between the target and reference in a second dimension.

Why is the *"transformed"* framework more meaningful? It provides insight how the context bar influenced perception. This is illustrated in Fig. 2. In Fig. 2a the target is physically counter-clockwise to the reference, while in Fig. 2d it is physically clockwise to the reference. A correct response for Fig. 2a would thus have been "counter-clockwise", while it would have been "clockwise" for Fig. 2d. Both of these responses would also have indicated that the perceived orientation difference between the target and the context bar was *smaller* than the orientation difference between the reference and context bar orientation. Such perceptual reports will be abbreviated as T-C<R-C for the remainder of the text. Conversely, if the subjects instead had responded "clockwise" for Fig. 2a and "counter-clockwise" for Fig. 2d (both responses would be wrong), it would indicate that the perceived orientation difference between the target and the context bar was *larger* than the orientation differences between reference and context bar orientation (this percept is illustrated by the dashed bars in Fig. 2a, d). Such perceptual reports will be

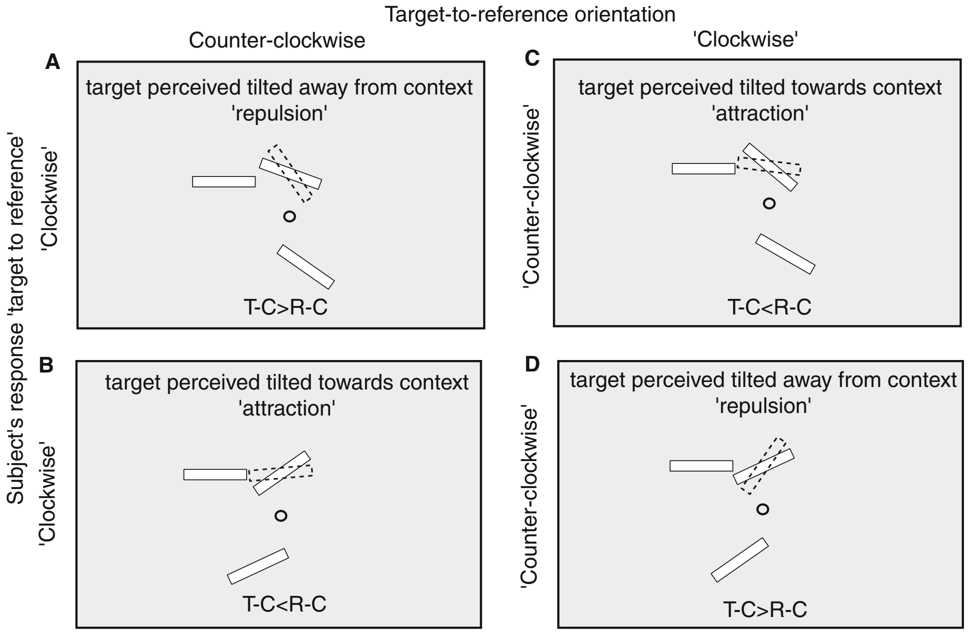

Fig. 2 Illustration of possible shifts in perceived orientation. In each subplot the context-bar, target and reference are shown in white, in the same format as in Fig. 1b. The perceived target orientation is shown as a dashed bar. The left column shows examples where the target was physically counter-clockwise to the reference, while the subjects perceived it to be clockwise. The right column shows examples where the target was physically clockwise to the reference, while the subjects perceived it to be "counter-clockwise" to the reference. The top row shows cases where the target was clockwise to the context bar, the bottom row shows cases where the target was counter-clockwise to the context bar. In **a** and **d** the tilt of the target orientation relative to the context orientation was perceived to be larger than the tilt of the reference orientation relative to the context orientation (although the opposite was true on the screen). This percept can be described as T-C>R-C, and the influence of the context would be described as "repulsive". Conversely, in **b** and **c** the tilt of the target orientation relative to the context orientation was perceived to be smaller than the tilt of the reference orientation relative to the context orientation (although the opposite was true on the screen), and the percept can be described as T-C<R-C. Here the influence of the context would be described as an "attractor" effect

abbreviated as T-C>R-C for the remainder of the text. Figure 2a, d additionally demonstrates what we consider a “repulsive” influence of the context. In this sketch the presence of the context bars results in a percept where the target orientation was perceived to be more tilted away from the context bar than it really was (dashed bar in comparison to underlying white bar). Figure 2b, c shows an example constellation where the presences of the context bar resulted in an “attractor” effect, i.e., the target was perceived to be tilted closer towards the context than it really was.

After converting the original responses into responses that reflected the percept of the target and reference orientation relative to the context orientation (as described above) we arranged the triplets of proportions of “T-C>R-C”, “same” and “T-C<R-C” responses in columns representing conditions of equal orientation difference between target and reference and rows representing conditions of equal absolute orientation difference between target and context bar (see Fig. 3b for an example).

Fitted surface

To give a simple and quantifiable description of the data we took the difference between proportions of “T-C<R-C” and “T-C>R-C” responses. The result could be between -1 and +1. Values around -1 indicated a high proportion of “T-C<R-C” while values around +1 indicated a high proportion of “T-C>R-C”. Values around 0 indicated either a high proportion of “same” response or an equal proportion of “T-C<R-C” and “T-C>R-C”. We arranged these difference values into a matrix, where columns of values relate to conditions of equal orientation difference between target and reference. Rows in the matrix relate to conditions of equal orientation difference between target and context. To quantify the data we fitted a 3D surface model that was described by a sigmoidal function along the target-to-reference axis, and a tilted straight line along the target-to-context bar axis. The form of this surface was:

$$P(X,Y) = R_{\max} * \left(\frac{(X - (g * Y))}{i^n + (X - (g * Y))^n} \right) + R_{\min} \qquad (1.1)$$

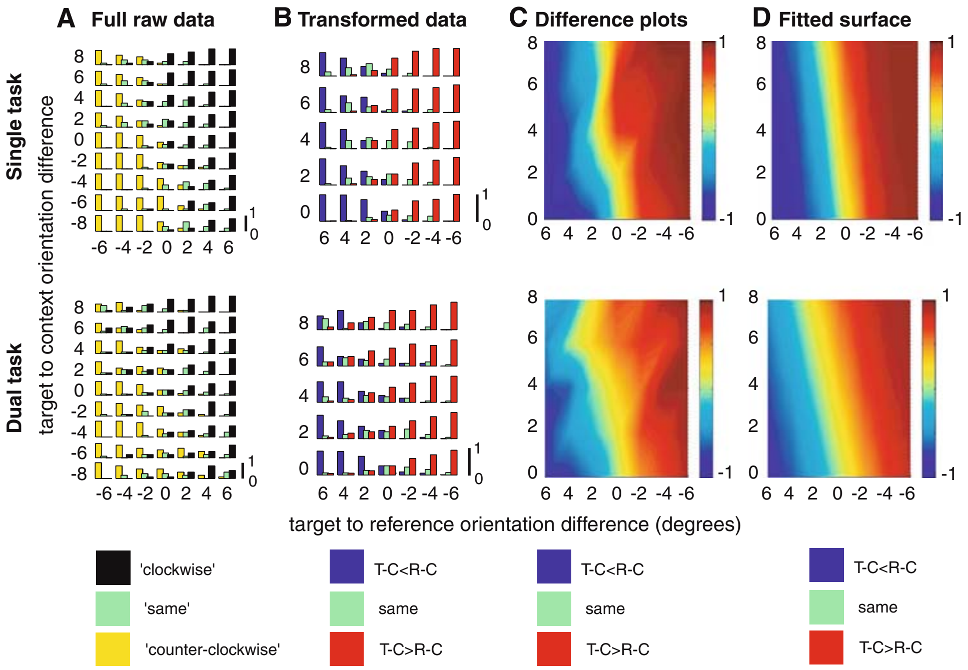

Fig. 3 Example subject (AT) from the high contrast condition. Data from the single task are shown along the top row, data from the dual task are shown along the bottom. **a** Full raw data: proportions of “clockwise” (*black bars*), “same” (*green*) and “counter-clockwise” (*yellow*) responses in each condition. Rows show data from conditions of equal target-to-context orientation differences, columns show conditions of equal target-to-reference orientation differences. **b** Transformed data: opposite responses have been combined from conditions of equal but opposite target-to-reference and target-to-context orientation differences. Responses are transformed to show proportions of trials in which the perceived target-to-reference orientation difference was larger or smaller than the target-to-context orientation difference (T-C<R-C or T-C>R-C, *blue and red bars*, respectively). *Green bars* show proportion of “same” responses. *Rows of bars* show data from conditions of equal target-to-context orientation differences, columns show conditions of equal target-to-reference orientation differences. **c** Difference plots: *colored surface* shows the difference between T-C<R-C and T-C>R-C responses. *Blue indicates* a high proportion of T-C<R-C responses, *red* a high proportion of T-C>R-C responses. *Green/yellow* shows either an equal proportion of T-C<R-C and T-C>R-C responses or a high proportion of “same” responses. **d** Fitted surface: the difference plots were fitted with a 3D surface from a sigmoidal function along the target-to-reference axis and a sloping straight line along the target-to-context bar axis

where the "X" dimension is the orientation difference between target and reference and the "Y" dimension is the orientation difference between the target and context bar. $R_{\max}$ and $R_{\min}$ are scaling factors determining the upper and lower range of the surface. The inflection point of the surface is determined by the parameter "i" this relates to a bias the subject may have for reporting either "T-C<R-C" or "T-C>R-C", and so is essentially a third scaling factor. The parameter "n" determines the slope of the sigmoid (i.e., the slope along the target-to-reference dimension) and so relates to the reliability of the subject's responses. The parameter "g" determines the gradient of the straight line component (i.e., along the target-to-context bar dimension) and so measures the strength of the contextual influence. Thus the parameters which are most relevant to the subjects' performance are "n" and "g", since "n" indicates the reliability of the subjects' target-to-reference judgments and "g" indicates the extent of the shift in perceived orientation as a function of the context-to-target orientation difference. We adjusted these five parameters ($R_{\max}$, $R_{\min}$, i, n and g) to fit the surface to the matrix of difference values by minimizing the summed squared error. We assessed the goodness of fit by calculating the percentage of variance accounted for by the model.

To assess the importance of the straight line component (i.e., the importance of contextual influence) we fitted the data with a model where the parameter "g" was fixed to 0. Not surprisingly this model gave poorer fits than the full model since it has fewer free parameters. To compare the goodness of fit of the two models we normalized the percentage-variance-accounted-for by the number of fitting parameters. The difference in normalized-percentage-variance-accounted-for gave an indication of the additional explanatory power gained by considering systematic contextual influences on the subjects' responses.

We have used a number of different fitting models to quantify the data (e.g., linear 2D regression, fitting rows in the difference matrix individually with sigmoidal functions and finding a regression along the zero points of each fit). All fitting routines gave essentially identical results regarding the effect of attention on contextual modulation.

Results

Subjects were required to report the orientation of a target bar in relation to a reference bar that was displayed simultaneously with the target bar, opposite from the fixation spot (Fig. 1, and see "Methods" for details). The target appeared as the 5th bar in the sequence of apparent motion stimuli which served as the context stimulus. Subjects reported whether the orientation of the target was counter-clockwise, same, or clockwise relative to the reference bar. We manipulated the subject's attention between two conditions. In one condition subjects could fully attend to the orientation discrimination task (single task condition). In a second condition subjects were required to additionally perform a demanding color-counting task (centrally on the screen). In the dual task, subjects first reported the number of colors (their main task), and then indicated their perception of the target orientation relative to the reference orientation. We collected data from three target contrast conditions; high target contrast (82%), medium target contrast (10%) and low target contrast (<4%). We found that the influence of the context on the perceived orientation was dependent on the level of attention subjects could devote to the orientation discrimination, the contrast of the target bar, and the orientation difference between the target and context bars. We will first describe the effects from the single task condition where subjects could fully attend to the orientation discrimination. This will be followed by a description of the dual task data, where voluntary attention was focused on the color counting task.

Single task

High contrast experiments

When the target had high luminance contrast subjects perceived it to be tilted further from the context bar orientation than was the case. Thus, the presence of the context bars had a repulsive effect on the perceived target orientation. This is demonstrated in Fig. 3 were a high proportion of "clockwise" responses occurred although the target was counter-clockwise to the reference *but clockwise to the context bars*, and a high proportion of "counter-clockwise" responses occurred although the target was clockwise to the reference *but counter-clockwise to the context bars*. We transformed the data by combining opposite responses (clockwise and counter-clockwise responses) from conditions of equal but opposite target-to-context and target-to-reference orientation differences (see "Methods"). This transformation allowed the subject's "clockwise" and "counter-clockwise" responses to be interpreted in the more meaningful framework of the absolute orientation difference between target and context bar, and between reference and context bar. In other words, we transformed the data such that we had a framework that describes whether the subject perceived either the target or the reference as being more similar to the context bar orientation. Specifically, we determined whether the absolute target-to-context bar orientation difference (T-C) was perceived to be larger or smaller than the reference-to-context orientation difference (R-C), i.e., T-C>R-C and T-C<R-C responses, respectively. If subjects indicated

a larger proportion of “T-C>R-C” responses, when in fact the physical display for these trials corresponded to T-C<R-C, then the condition of contextual repulsion was fulfilled (see also Fig. 2). If, however, subjects indicated a larger proportion of “T-C<R-C” responses, when in fact the physical display for these trials corresponded to T-C>R-C, then the condition of contextual attraction was fulfilled.

At high luminance contrast we found high proportions of “T-C>R-C” responses although in reality the orientation difference was T-C<R-C. The proportion of these misjudgments indicated the strength of the repulsion effect induced by the context bars. The strength of repulsion was dependent on two factors: the orientation difference between the target and context bars, and the allocation of voluntary attention. The repulsion effect was largest in conditions where there was a large orientation difference between the target and context bars, and in conditions of reduced attention (see below).

To quantify these effects we took the difference between proportions of “T-C>R-C” and “T-C<R-C” responses and fitted this matrix with a 3-dimensional curved surface as described in Methods. This surface gave good fits to the data, evident by a relatively high percentage of variance accounted for (median = 90.07%, 25th percentile 86.62%, 75th 92.84%). Of the five fitting parameters, two are relevant to the performance of the subject, the remaining three being essentially scaling factors. The slope of the sigmoidal function is related to the reliability of the subjects’ responses, where high slopes reflect reliable responses. The gradient of the straight line component demonstrates the influence of the context bars. It represents the amount by which the subject’s perception was shifted as a function of the angular difference between the target and context bars (perceived orientation change [in degrees] per degree of angular difference between target and context), the sign indicates whether context resulted in an attractor (positive values) or repulsion (negative values) effect. The median gradient in the high contrast experiments was −0.24 (25th percentile = −0.13, 75th percentile −0.33), thus for each degree of difference between the target and context bar orientation, the subject’s perception of the target was shifted away (repelled) from the context bars by 0.24°.

Medium contrast experiments

Data from these experiments were essentially identical to those from high contrast experiments. We found a high proportion of “clockwise” responses although the target was counter-clockwise to the reference *but clockwise to the context bars*, and a high proportion of “counter-clockwise” responses occurred although the target was clockwise to the reference *but counter-clockwise to the context bars*. After data transformation we found high proportions of “T-C>R-C” responses even when in reality the orientation difference was T-C<R-C. This is indicative of a repulsion of perceived target orientation away from the context bar orientation. We quantified the strength of the effect by fitting the 3D surface to the matrix of difference values between T-C<R-C and T-C>R-C. The median gradient of the straight line component (indicating the strength of the repulsion effect) was −0.3 (25th percentile = −0.25 75th = −0.36), thus for each degree of difference between target and context bars the perceived target orientation was shifted away from the context bar orientation by 0.3°. There was no significant difference between gradient values in the high and medium contrast experiments (two-sample *t*-test $P = 0.43$ CI = −0.26, 0.12).

Low contrast experiments

In these experiments the pattern of responses was opposite to that found in the high and medium contrast experiments. We found high proportions of “counter-clockwise” responses when the target was presented clockwise from the reference *and clockwise to the context bars*. There were also high proportions of “clockwise” responses when the target was presented counter-clockwise from the reference *and counter-clockwise from the context bars* (Fig. 4). After data transformation this pattern resulted in high proportions

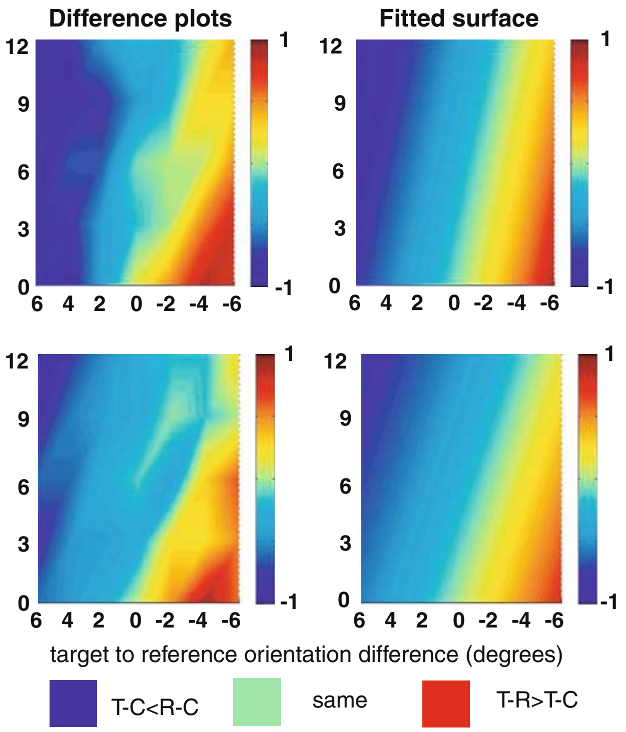

Fig. 4 Example subject (EA) from the low contrast condition. The leftward spread of *blue/green colors* in surface plots demonstrates the attractor effect of the context bars. Data are shown in the same format as in Fig. 3c, d

of T-C<R-C in conditions where the physical display was T-C>R-C. The pattern indicates that the subjects perceived the target to be oriented closer to the orientation of the context bars than it really was. Thus, lowering the luminance contrast of the target to <4% reversed the repulsion effect seen in the high (82%) and medium (10%) contrast experiments, and caused the orientation of the context bars to have an attractor effect on the perceived orientation of the target. We tested whether subjects reliably perceived the target by including an additional 10% of trials in which the target was not presented. On these trials the subjects should report that the target was not presented. Subjects correctly identified that the target was not presented on 72% (median) of trials in which the target was not presented (25th percentile = 39%, 75th percentile = 94%, chance performance = 10%). Subjects correctly identified the presence of the target (by making a "clockwise", "counter-clockwise" or "same" response) on 96.5% of trials in which the target was presented (25th percentile 85.5%, 75th percentile 99.0%). Thus subjects reliably perceived the absence and presence of the target.

We took the difference between proportions of "T-C>R-C" and "T-C<R-C" responses and fitted the resulting data with a 3-dimensional surface (Fig. 4). In the single task, the median gradient of the straight line component (along the target-to-context bar dimension) was 0.21 (25th percentile 0.03, 75th 0.28), thus for each degree of angular difference between the target and context bars the perceived target orientation was shifted towards the context bar orientation by 0.21°.

Dual task data

The effect of the context bars was stronger in the dual task (reduced attention) than in the single task (full attention), irrespective of whether context bars caused repulsion or attraction of the perceived target orientation. This was true for 19 out of 21 subjects (20 out of 24 data points, two subjects participated in both high and low contrast experiments). Of the remaining three subjects, subject DH participating in the high contrast experiment showed no change in the repulsion effect between task conditions, subject CP participating in the medium contrast experiment showed a reduction in the strength of the effect in the dual task, and subject YL participating in both the high and low contrast experiments also showed a reduction in the size of the effect in the dual task. Thus, devoting full attention to the orientation discrimination task reduced the contextual influences, independent of the nature of this influence for the majority of subjects (high contrast target $n = 11/13$, mid contrast target $n = 3/4$, low contrast target $n = 6/7$).

To quantify the effect of attention on contextual modulation we examined the gradient of the shifting parameter "g" which we obtained from the 3D surface fits. In the high contrast experiments the median gradient was −0.24 in the single task (25th percentile = −0.13, 75th percentile −0.33) and −0.37 in the dual task (25th percentile = −0.27, 75th −0.51). In the medium contrast data the median gradient was −0.3 in the single task (25th percentile = −0.25, 75th −36) and −0.8 in the dual task (25th percentile = −0.52, 75th −1.24). In the low contrast experiments the median gradient in the single task was 0.21 (25th percentile 0.03, 75th 0.28), and 0.41 in the dual task (25th percentile 0.28, 75th 0.49). Thus the effect of directing full attention was to reduce the shift of perceived orientation (be it repulsion or attraction) by more than 0.1° per degree of angular difference between the target and context bars (median change high contrast = 0.13, medium contrast = 0.5, low contrast 0.15, 25th percentile high contrast = 0.09, mid contrast = 0.2, low contrast = 0.09, 75th percentile high contrast = 0.37, mid contrast = 0.95, low contrast = 0.31). This means that the effect of the context bars in the full attention condition was reduced by almost 50% (median percentage change = 48%, 25th percentile = 28%, 75th percentile = 87%).

Figure 5 shows a comparison between the single and dual task of the two fitting parameters relevant to the subject's performance (the slope of the sigmoidal function, and the gradient of the straight line component). Significance was tested for each contrast condition separately, and for the all contrasts combined using a signed rank test (SRT). For the combined data we used the absolute values of the fitting parameters to account for the fact that an increase in repulsion effect (high/medium contrast experiments) was associated with the gradient of the straight line becoming more negative in the dual task, while an increase in the attractor effect (low contrast experiments) was associated with a more positive gradient in the dual task. In line with the previous description of the data, the dual task was associated with an increase in the gradient of the straight line component which was significant for the high (values in Table 2, $P = 0.005$, SRT) and low (values in Table 2, $P = 0.031$, SRT) contrast data separately but was not significant for the medium contrast data (values Table 2, $P = 0.25$ SRT) possibly due to the small sample size ($n = 4$). The change in gradient was highly significant for the absolute values when the data from all contrast levels were combined (values in Table 2, $P = 0.00014$, SRT). There was a trend for a reduction in the slope of the sigmoidal function between the single and dual task. This trend was significant for the high contrast data (values in Table 2, $P = 0.033$), but did not reach significance either for the combined data (values Table 2, $P = 0.077$, SRT), or for any other individual contrast level (values in Table 2, medium $P = 0.13$, low $P = 0.94$ SRT). There was no trend for a change in any of the three scaling factors

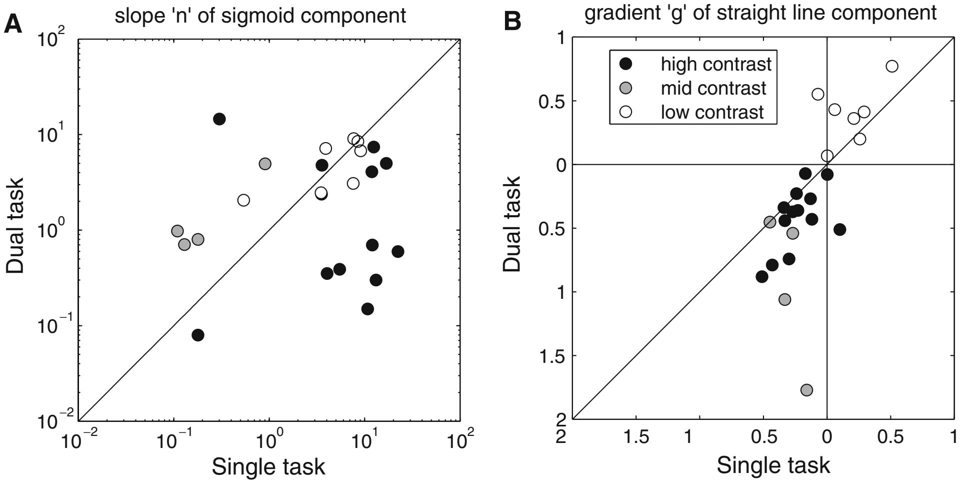

Fig. 5 Surface fitting parameters relevant for the subjects' performance as a function of attention condition (single vs. dual task). Parameter "*n*" corresponding to the slope of the sigmoid component is shown in part **a**, and parameter "*g*" corresponding to the gradient of the straight line component is shown in part **b**. Data from high contrast experiments are marked by *filled black circles*, data from the mid contrast condition are marked by a *filled gray circle* and data from low contrast experiments are marked by *open circles*. Part **a** High values correspond to reliable responses and a strongly "S shaped" functions along the target-to-reference dimension; low values correspond to less steep functions. Low values are found largely in experiments where the target-to-reference dimension was in 1 degree steps, meaning that only the steep part of the function was probed. Points below the horizontal indicate that responses were more reliable in the single task condition. Part **b** Data points above the horizontal indicate that context had an attractor effect (*low contrast target*), data points that fall below the horizontal indicate that context had a repulsive effect (*mid and high contrast target*). Attention reduced the strength of these effects irrespective of their sign. This is evident by the leftward displacement of *open circles* (*low contrast*) relative to the diagonal, i.e., larger "*g*" values in the dual task condition, and by the rightward displacement of gray and black circles relative to the diagonal, i.e., more negative "*g*" values (more repulsion) in the dual task at medium and high contrast

of the 3D surface between the single and dual task. The steepening of the sigmoid slope under the single task condition demonstrates the well known enhancement in perceptual accuracy under conditions of full attention. This effect is distinct from the attention mediated reduction of contextual influences, which also led to fewer incorrect responses in the single task in our experiment. An improvement in accuracy reduces random errors, while suppressing in contextual influences reduces the consistent bias in subjects' responses. These distinct sources of error could be separated in our experiment thanks to the two dimensions of "target-to-reference", which measured random errors, and "target-to-context bar" which measured consistent biases in response caused by contextual influence.

It might be argued that the high quality fitting which we obtained with our 3D surface model was largely due to the sigmoid component of the model, while the straight line component explained little if any of the variance in the data. This argument essentially questions the degree to which contextual modulation influenced the observer's perception. We assessed the importance of systematic contextual modulation for explaining the data by comparing the goodness of fit given by the full fitted model and a model in which the gradient of the straight line component was set to 0. Goodness of fit was assessed by normalizing the percentage variance accounted for by the number of fitting parameters (five for the full model, four for the reduced model). This measure essentially gives the percentage of variance in the data which can be accounted for by each free parameter in the model. If adding an extra parameter to the model reduces the normalized-percentage-variance-accounted-for one can infer that the new parameter contributes little explanatory power. If, however, the normalized-percentage-variance-accounted-for increases or does not change with the addition of an extra parameter, one can infer that the new parameter contributes at least as much explanatory power to the model as any of the other parameters and thus is a valuable inclusion. For the single task condition the reduced model yielded significantly better fits than the full model (median difference in normalized percentage variance accounted for $= 3.06$, 25th percentile $= 0.75$, 75th percentile, 4.3, $P < 0.001$ paired *t*-test). This indicates that in the full attention condition there was no need to include the effect of the context bars for explaining the subjects' responses. For the dual task data there was no significant difference in goodness of fit between the two models although there was a trend of better fits for the full model (median difference in normalized percentage variance accounted for was 0.83 higher for the simplified model, 25th percentile $= 3.79$ higher for the full model, 75th percentile $= 3.0$ higher for the

Table 2 Fitting parameters to quantify the influence of the context bar and the influence of attention on orientation discrimination

High contrast					Medium contrast					Low contrast				
Subject	*n*		*g*		Subject	*n*		*g*		Subject	*n*		*g*	
	Single task	Dual task	Single task	Dual task		Single task	Dual task	Single task	Dual task		Single task	Dual task	Single task	Dual task
KW	0.22	9.45	−0.43	−0.77	CP	1.24	0.15	−0.22	−0.21	MR	0.97	12.85	−0.02	0.07
WS	22.61	16.12	−0.10	−0.59	DC	0.31	3.99	−0.33	−1.04	NT	4.70	5.67	−0.09	0.57
CS	12.20	0.14	−0.12	−0.43	SJH	0.12	0.56	−0.27	−0.54	YL	9.11	7.91	0.26	0.21
DB	13.37	7.61	−0.24	−0.25	TE	0.05	1.01	−0.43	−0.46	ZI	5.65	5.59	0.22	0.36
AT	19.38	0.52	−0.22	−0.35						EA	8.26	1.31	0.31	0.34
AG	12.39	6.92	−0.32	−0.45						IS	8.42	3.42	0.06	0.33
DH	0.21	5.59	−0.34	−0.34						ER	5.48	5.15	0.54	0.78
JS	0.18	0.14	−0.30	−0.74										
NT	4.36	0.34	0.00	−0.08										
YL	12.33	6.98	−0.17	−0.07										
BP	3.00	0.01	−0.45	−0.88										
PA	5.57	0.31	−0.28	−0.37										
HS	1.71	0.03	−0.13	−0.27										
Median	5.57	0.52	−0.24	−0.37	Median	0.21	0.78	−0.30	−0.50	Median	5.65	5.59	0.22	0.34
25th	1.71	0.14	−0.32	−0.59	25th	0.10	0.45	−0.35	−0.67	25th	5.09	4.29	0.02	0.27
75th	12.39	6.98	−0.13	−0.27	75th	0.54	1.75	−0.26	−0.40	75th	8.34	6.79	0.29	0.46
SRT	$P = 0.06$		$P = 0.002$		SRT	$P = 0.63$		$P = 0.25$		SRT	$P = 0.58$		$P = 0.047$	
SRT Comp	$P = 0.06$		$P < 0.0001$											

Parameters were obtained by fitting a tilted 3D surface to the data (for details see "Results" and "Methods"). The parameter "*n*" corresponds to the slope of the surface along the target-to-reference axis and so relates to the reliability of the response. The parameter "*g*" corresponds to the gradient of the surface along the target-to-context bar axis and so relates to the effect of the context bar on the perceived target orientation. Lower rows give the median, 25th and 75th percentiles over the population. *P*-values indicate whether a significant difference for the parameter of interest occurred between single and dual task for each contrast condition separately (signed rank test SRT) and for all contrasts combined (SRT Comb.)

simplified model, $p = 0.6$, paired t-test). This indicates that the gradient parameter explained at least as much of the variance in the data as any of the other free parameters, thus accounting for the effect of the context bars was an important component of the model. These findings demonstrate that in the full attention condition the context bars had little or no influence on the observer's responses, while in the reduced attention condition they had a substantial influence.

Color counting performance

Given the difficulty of the task, subjects were generally quite good at the color counting task (25th percentile 49% correct, median 62% correct, 75th percentile 73% correct, chance performance = 25% correct). Sorting the data to only include trials where the subject counted correctly or incorrectly had no consistent effect on any of the fitting parameters. This suggests that subjects did not alternate between attending the counting task and attending the orientation task on a trial by trial basis. Errors in the counting task reflect the difficulty of the task and not an increase in the amount of attention devoted to the (secondary) orientation discrimination task.

No context bars control experiment

Two subjects participated in a control experiment in which no context bars were presented. The pattern of responses in the control experiment did not indicate any shift in the perceived orientation of the target (the respective tilt values, parameter s from the fitting, were -0.01 and -0.02). The median slope from these experiments (-0.015) was significantly different from the data in both the single task high and medium contrast experiments ($P < 0.001$, CI $= -0.32, -0.19$, two-sample t-test), but not from data in the single task of the low contrast experiments ($P = 0.052$, CI $= -0.018, 0.038$, two-sample t-test), where some subjects showed no clear effect of the context bars on the perceived target orientation. Thus, these control data demonstrate that the effects on the perceived orientation of the target observed in the previous experiments were indeed due to the presentation of the context bar and not due to some confounding variable.

Results summary

We have shown that the orientation of the context bars influenced the perceived orientation of the target. The nature of the influence was dependent on the luminance contrast of the target. At high and medium contrasts the perceived orientation difference between the target and context bar was enhanced by an average of 0.27° per degree of angular difference between target and context bars (in the single task), i.e., context bars had a repulsion effect. At low contrast the perceived orientation difference between the target and context bars was reduced by an average of 0.21° per degree of angular difference between target and context bars (in the single task), i.e., context bars had an attractor effect. The magnitude of the influence of the context bars was dependent on the orientation difference of the target from the context bars and on the allocation of voluntary attention. In the full attention condition the influence of the context bars was significantly ($P = 0.00014$, SRT, see Fig. 5) reduced by approximately 50% compared with the divided attention condition (median percentage change = 48%, 25th percentile = 28%, 75th percentile = 87%).

Discussion

This study investigated how attention and contrast influence contextual modulation of human orientation perception. The test stimulus was a dynamic series of five sequentially presented bars. We measured how the orientation of the first four "context" bars influenced the perceived orientation of the final "target" bar relative to a simultaneously presented reference. Results showed that when the target was presented at the same high contrast as the context bars, its perceived orientation was shifted away from the orientation of the context bars. This effect is similar to Westheimer's "simultaneous orientation contrast" effect (Westheimer 1990) also called the tilt illusion, or the direct tilt illusion (Wenderoth and Smith 1999). When the target was presented at a low contrast, without changing the contrast of the context bars, the effect was reversed. That is, the perceived orientation of the target was shifted towards the orientation of the context bars. Contrast-dependent switching of contextual influences has also been demonstrated by a number of physiological studies (Levitt and Lund 1997; Polat et al. 1998; Mizobe et al. 2001), but have not, to our knowledge, been reported systematically in a psychophysical setting.

We chose the spatio-temporal context in our studies, as it allowed investigating different aspects simultaneously. Firstly, the single-dual task setting allowed an investigation of the role of attention in contextual integration, under conditions where context is equivalent to noise. Secondly, the stimuli allowed to investigate the influential idea that vision is a process of Bayesian inference (Kersten et al. 1996; Kersten 1999; Young 2000 ; Guo et al. 2004, 2007). If true, the spatiotemporal context should have resulted in attractor effects at high and low contrast. We found opposite effects of spatio-temporal context at low vs. medium/high contrast, which is not in line with a simple Bayesian account of information processing. Conversely, our data can be explained by assuming differences in contrast sensitivity of overlapping facilitating and inhibiting surround areas of V1 (or higher area) neurons, whereby the inhibiting surround has lower contrast sensitivity and extends somewhat further from the receptive field centres. According to this account V1 neurons would not exploit spatio-temporal regularities in the environment for predictive coding, but for contrast dependent spatial pooling. These ideas will be explored in detail (in conjunction with electrophysiological data from V1 in awake macaque monkeys) in a forthcoming publication.

It is interesting to recall the specific stimulus conditions that trigger switching of contextual influences. Previous studies on the contrast dependence of tilt illusions demonstrate that switching does not occur for a target grating surrounded by an inducer grating (Wenderoth and Smith 1999). Kapadia et al. (2000) reported that light bars were perceived to be tilted towards the orientation of collinear flanking bars when the flankers were separated by less than 16 min of visual angle, however a repulsion of the perceived target orientation occurred for greater separations. Moreover, for intermediate separation differences (24 and 32 min) repulsion was observed for high contrast targets, while for two subjects attraction was observed for low contrast (15%) targets (keeping the flanker contrast high) closely matching our finding. These data suggest that a critical factor in the contrast dependent switching may be spatial separation of target and context bars. This is consistent with modeling (Schwabe et al. 2006) and neurophysiological studies (Polat and Norcia 1996; Polat et al. 1998; Mizobe et al. 2001; Ichida et al. 2007) which show contrast dependent switching (from response suppression to facilitation) when the context stimuli were separated from the central stimulus by several degrees.

We manipulated the allocation of voluntary attention using a single/dual task paradigm. This paradigm has been extensively used to investigate the involvement of attention in various visual processes as diverse as motion processing (Thiele et al. 2002; Thornton et al. 2002), stimulus localization (Adam et al. 2008), contrast discrimination (Huang and Dobkins 2005; Alais et al. 2006) and contextual modulation (Zenger et al. 2000). Attention is a broad term covering a wide range of cognitive processes (Knudsen 2007). Therefore it is important to define what components of attention were manipulated in the single/dual task paradigm. In our single task *spatial* attention was divided between the target and reference location. In the dual task *spatial* attention was divided between the target location, reference location and the central location, while at the same time *feature selective* attention was divided between color counting and orientation discrimination. It is worthwhile to point out that subjects were explicitly instructed to principally attend to the counting task in the dual task condition. Thus, our experiment probed the effect of high versus low levels of *spatial* attention and also the effect of *feature selective* attention. Previous results probing the effects of feature and spatial attention have often reported similar effects of these two on firing rates in macaque visual cortex (Treue and Trujillo 1999; McAdams and Maunsell 2000). Thus, while we cannot determine whether feature or spatial attention effects contributed more to our findings, it is not obvious that the two should result in different perceptual effect.

We found that the withdrawal of attention in the dual task condition enhanced the effect of the context bars on the perceived orientation of the target. This was true irrespective of whether stimulus conditions resulted in an attractor effect or whether they resulted in repulsion. Before discussing this in detail, we address the possibility that the effects were simply due to increased accuracy under conditions of full attention. We can discount this explanation for the following reason: If withdrawal of attention simply reduced accuracy, one would expect to see an increase in error rate that is unbiased, i.e., we would expect to see a more noisy distribution of choices, rather than an increase of specific errors (i.e., the biased error distribution we saw). To give a concrete example, imagine the condition where target and reference are physically identical, i.e., they have the same tilt relative to the spatiotemporal context-bar. If attention simply decreased accuracy, we would expect to see an increase in the number of erroneous reports that the target is more similar to the context-bars and the same increase in the number of reports that the target is less similar to the context-bars. This is not what we saw. We saw a strong bias towards only one of the two possible errors. This bias reflected increased attraction (i.e., increased number of reports that the target is more similar to the context-bar than the reference is to the context-bar) for low contrast stimuli, and the opposite bias of errors for the high contrast target stimuli. Thus, withdrawal of attention did not simply increase error rate, it increased reports of a specific error which reflected the sign of the influence of the spatiotemporal context (context-bars). Thus high levels of attention suppressed the effect of local context, independent of the sign of the effect. This conclusion is in line with Ito et al. finding of reduced surround facilitation under conditions of focused attention versus distributed attention (Ito et al. 1998; Ito and Gilbert 1999) and is supported by Zenger et al. finding that surround modulation (they make no claim about its nature) is weaker in a single task than a dual task condition (Zenger et al. 2000). However, our conclusion is at odds with Freeman's proposition that attention enhances contextual influences (Freeman et al. 2001, 2003). These apparently contradictory conclusions reflect differences in the experimental approach. While we specifically addressed the issue of how spatial and temporal integration is influenced by varying levels of attention directed to the target location, Freeman et al. experiments address the separate issue of whether attending to different parts of the surrounds can alter their influence on processing at the central location. The different findings are therefore not necessarily contradictory. Rather they are complementary and together show that attention alters the flow of information within the neuronal network such that task relevant information impacts on the processing at attended locations while task irrelevant information is excluded and has little impact on the processing of information at the attended location. Such flexibility could be achieved by selectively enhanced efficacy of feed-forward connections to neurons representing attended stimuli, while simultaneously suppressing lateral inputs to those neurons. The processing of attended stimuli would thus be unaffected by surrounding stimuli (suppressed lateral inputs). A recent study has demonstrated that attention to parafoveal locations changes spatial summation properties of V1 neurons in line with such a proposal (Roberts et al. 2007), and these changes could thus underlie the altered perception that we report here.

The interaction between attention and contrast has been a topic of much debate. It is well known that high levels of attention enhance performance in a number of tasks, particularly in crowded/noisy displays and when task demands are high (Lee et al. 1997; Lu and Dosher 1998; Dosher and Lu 2000; Zenger et al. 2000). This effect is also demonstrated in the current study, since the context bars induced perceptual errors and this effect was reduced in the full attention condition. Increasing the luminance contrast of a test stimulus can improve performance in a number of tasks in a manner similar to attention, suggesting that the effect of attention may be akin to increasing the "effective contrast" of a stimulus (Carrasco et al. 2004), thus supporting a "contrast gain model" of attention. The model has received significant physiological support, both from single unit recordings (McAdams and Maunsell 1999; Reynolds et al. 2000; Williford and Maunsell 2006) and fMRI studies (Carrasco 2006); (but see Williford and Maunsell (2006), Buracas and Boynton (2007)). Our data allowed us to explicitly test this proposal, because, unlike in previous studies where lowering the contrast essentially weakened but did not change the perception of the target, we demonstrate a reversal in the perception of the target between high and low contrast. Due to this dissociation, the effect of attention is distinguishable from the effect of contrast. For the low contrast experiments we demonstrated that the perceived orientation of the target was shifted towards the orientation of the context bars. This effect was reduced in the full attention condition. The attractor influence of the context bars could also be reduced by increasing the contrast of the target to an intermediate level before the repulsion effect took over. Hence when the target was presented at low contrast, the effect of attention was similar to increasing the contrast of the target. With a further increase of the target contrast, the effect of the context bar changed sign from attraction to repulsion. Under the contrast gain model of attention one would expect to find the strongest repulsion effect in the high contrast, full attention condition, as this condition should result in the highest "perceived" contrast. Contrary to this proposal we found the strongest repulsion effect in the divided attention condition. Devoting full attention to the orientation discrimination task reduced the strength of repulsion, rather than increasing it. One could argue that at high contrast attention cannot increase the perceived contrast any further due to saturation effects. However, we found strong perceptual repulsion already at a luminance contrast of 10% (medium contrast experiment). Here, attention decreased the repulsion, while it should increase the repulsion if attention was equivalent to increasing stimulus contrast. Hence, while data from the low contrast condition demonstrate how the effect of attention can appear similar to the effect of increased contrast, data from the high and medium contrast conditions clearly show that increasing the level of attention is not necessarily interchangeable with increasing the contrast of the target, in effect they had opposite effects in our study.

In the current study we have investigated how spatially and temporally separate stimuli influence the perceived orientation of a target stimulus at three levels of target contrast and high and low levels of attention. This paradigm allowed us to examine the interaction of contextual influences with stimulus contrast and attention, and the relationship between attention and contrast. We found that contrast determines the nature of contextual influences (repulsion or attraction) while the level of attention determines the strength of the influence. Thus, target contrast and attention play fundamentally different roles in the process of integrating local stimuli into global percepts. These findings have important implications for models of both attention and of contextual interactions. Our data suggest that an account of attention, whereby attention and stimulus contrast are considered to be essentially interchangeable, as in the contrast-gain model of attention, is insufficient under more complex stimulus situations.

There has been considerable recent work in modelling contextual influences. For example, Schwabe et al (2006) proposed a model describing the effects of relative contrast and spatial separation between central and flanking stimuli on V1 neuronal responses to the central stimuli. Yet more recently, Schwartz et al (2007) proposed a model describing how tilt illusions might come about through context-mediated changes in neuronal orientation tuning functions. Future models might attempt to merge descriptions of spatial and contrast dependent contextual modulation of response rates, with tuning curve-based models of contextual modulation of orientation perception. Such models could give a powerful and physiologically plausible description of the effects observed in the current study.

Acknowledgments We would like to thank P. Dayan, M.A.Gieselmann, and L.S. Delicato for valuable discussions and feedback. The work was supported by the BBSRC (BBS/B/09325), the Wellcome Trust (070380/Z/03/Z), the Royal Society, and the MRC (G78/7853).

References

Adam JJ, Davelaar EJ, van der Gouw A, Willems P (2008) Evidence for attentional processing in spatial localization. Psychol Res (in press)

Alais D, Morrone C, Burr D (2006) Separate attentional resources for vision and audition. Proc Biol Sci 273:1339–1345

Albright TD, Stoner GR (2002) Contextual influences on visual processing. Annu Rev Neurosci 25:339–379

Braun J, Julesz B (1998) Withdrawing attention at little or no cost: detection and discrimination tasks. Percept Psychophys 60:1–23

Buracas GT, Boynton GM (2007) The effect of spatial attention on contrast response functions in human visual cortex. J Neurosci 27:93–97

Carrasco M (2006) Covert attention increases contrast sensitivity: psychophysical, neurophysiological and neuroimaging studies. Prog Brain Res 154:33–70

Carrasco M, Ling S, Read S (2004) Attention alters appearance. Nat Neurosci 7:308–313

Dosher BA, Lu ZL (2000) Noise exclusion in spatial attention. Psychol Sci 11:139–146

Freeman E, Driver J, Sagi D, Zhaoping L (2003) Top-down modulation of lateral interactions in early vision: does attention affect integration of the whole or just perception of the parts? Curr Biol 13:985–989

Freeman E, Sagi D, Driver J (2001) Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. Nat Neurosci 4:1032–1036

Freeman E, Sagi D, Driver J (2004) Configuration-specific attentional modulation of flanker-target lateral interactions. Perception 33:181–194

Guo K, Nevado A, Robertson RG, Pulgarin M, Thiele A, Young MP (2004) Effects on orientation perception of manipulating the spatio-temporal prior probability of stimuli. Vision Res 44:2349–2358

Guo K, Robertson RG, Pulgarin M, Nevado A, Panzeri S, Thiele A, Young MP (2007) Spatio-temporal prediction and inference by V1 neurons. Eur J Neurosci 26:1045–1054

Huang L, Dobkins KR (2005) Attentional effects on contrast discrimination in humans: evidence for both contrast gain and response gain. Vision Res 45:1201–1212

Ichida JM, Schwabe L, Bressloff PC, Angelucci A (2007) Response facilitation from the "suppressive" receptive field surround of macaque V1 neurons. J Neurophysiol 98:2168–2181

Ito M, Gilbert CD (1999) Attention modulates contextual influences in the primary visual cortex of alert monkeys. Neuron 22:593–604

Ito M, Westheimer G, Gilbert CD (1998) Attention and perceptual learning modulate contextual influences on visual perception. Neuron 20:1191–1197

Jones HE, Wang W, Sillito AM (2002) Spatial organization and magnitude of orientation contrast interactions in primate V1. J Neurophysiol 88:2796–2808

Kapadia MK, Ito M, Gilbert CD, Westheimer G (1995) Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. Neuron 15:843–856

Kapadia MK, Westheimer G, Gilbert CD (2000) Spatial distribution of contextual interactions in primary visual cortex and in visual perception. J Neurophysiol 84:2048–2062

Kersten D (1999) High level vision as statistical inference. In: Gazzaniga MS (ed) The new cognitive neurosciences, vol 1. MIT Press, Cambridge, pp 353–364

Kersten D, Knill DC, Mamassian P, Bülthoff I (1996) Illusory motion from shadows. Nature 379:31

Knierim JJ, van Essen DC (1992) Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol 67:961–980

Knudsen EI (2007) Fundamental components of attention. Annu Rev Neurosci 30:57–78

Lee DK, Koch C, Braun J (1997) Spatial vision thresholds in the near absence of attention. Vision Res 37:2409–2418

Levitt JB, Lund JS (1997) Contrast dependence of contextual effects in primate visual cortex. Nature 387:73–76

Lu ZL, Dosher BA (1998) External noise distinguishes attention mechanisms. Vision Res 38:1183–1198

Martinez-Trujillo J, Treue S (2002) Attentional modulation strength in cortical area MT depends on stimulus contrast. Neuron 35:365–370

McAdams CJ, Maunsell JHR (1999) Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. J Neurosci 19:431–441

McAdams CJ, Maunsell JHR (2000) Attention to both space and feature modulates neuronal responses in macaque area V4. J Neurophysiol 83:1751–1755

Mizobe K, Polat U, Pettet MW, Kasamatsu T (2001) Facilitation and suppression of single striate-cell activity by spatially discrete pattern stimuli presented beyond the receptive field. Vis Neurosci 18:377–391

Nothdurft H-C (1993) The role of features in preattentive vision: Comparison of orientation, motion and color cues. Vision Res 33:1937–1958

Pelli DG, Palomares M, Majaj NJ (2004) Crowding is unlike ordinary masking: distinguishing feature integration from detection. J Vis 4:1136–1169

Polat U, Norcia AM (1996) Neurophysiological evidence for contrast dependent long-range facilitation and suppression in the human visual cortex. Vision Res 36:2099–2109

Polat U, Mizobe K, Pettet MW, Kasamatsu T, Norcia AM (1998) Collinear stimuli regulate visual responses depending on cell's contrast threshold. Nature 391:580–584

Reynolds JH, Pasternak T, Desimone R (2000) Attention increases sensitivity of V4 neurons. Neuron 26:703–714

Roberts M, Delicato LS, Herrero J, Gieselmann MA, Thiele A (2007) Attention alters spatial integration in macaque V1 in an eccentricity-dependent manner. Nat Neurosci 10:1483–1491

Schwabe L, Obermayer K, Angelucci A, Bressloff PC (2006) The role of feedback in shaping the extra-classical receptive field of cortical neurons: a recurrent network model. J Neurosci 26:9117–9129

Schwartz O, Hsu A, Dayan P (2007) Space and time in visual context. Nat Rev Neurosci 8:522–535

Thiele A (2007) Reconstructing the world: switching from segmentation to integration allows neurons in area MT to make 'sense' of the visual scene. Neuron 53:623–625

Thiele A, Rezec A, Dobkins KR (2002) Chromatic input to motion processing in the absence of attention. Vision Res 42:1395–1401

Thornton IM, Rensink RA, Shiffrar M (2002) Active versus passive processing of biological motion. Perception 31:837–853

Treue S, Trujillo JCM (1999) Feature-based attention influences motion processing gain in macaque visual cortex. Nature 399:575–579

Tzvetanov T, Womelsdorf T, Niebergall R, Treue S (2006) Feature-based attention influences contextual interactions during motion repulsion. Vision Res 46:3651–3658

Wang Q, Cavanagh P, Green M (1994) Familiarity and pop-out in visual search. Percept Psychophys 56:495–500

Wenderoth P, Johnstone S (1988) The different mechanisms of the direct and indirect tilt illusions. Vision Res 28:301–312

Wenderoth P, Smith S (1999) Neural substrates of the tilt illusion. Aust N Z J Ophthalmol 27:271–274

Westheimer G (1990) Simultaneous orientation contrast for lines in the human fovea. Vision Res 30:1913–1921

Williams AL, Singh KD, Smith AT (2003) Surround modulation measured with functional MRI in the human visual cortex. J Neurophysiol 89:525–533

Williford T, Maunsell JH (2006) Effects of spatial attention on contrast response functions in macaque area V4. J Neurophysiol 96:40–54

Young MP (2000) The architecture of visual cortex and inferential processes in vision. Spat Vis 13:137–146

Yu AJ, Dayan P (2005) Uncertainty, neuromodulation, and attention. Neuron 46:681–692

Zenger B, Braun J, Koch C (2000) Attentional effects on contrast detection in the presence of surround masks. Vision Res 40:3717–3724