Spatial attention can modulate unconscious orientation processing

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Abstract. It has recently been suggested that visual spatial attention can only affect consciously perceived events. We measured the effects of sustained spatial attention on orientation-selective adaptation to gratings, rendered invisible by prolonged interocular suppression. Spatial attention augmented the orientation-selective adaptation to invisible adaptor orientation. The effect of attention was clearest for test stimuli at peri-threshold, intermediate contrast levels, suggesting that previous negative results were due to assessing orientation discrimination at maximum contrast. On the basis of these findings we propose a constrained hypothesis for the difference between neuronal mechanisms of spatial attention in the presence versus absence of awareness.

1 Introduction

A critical question for understanding the relationship between attention and awareness is whether attentional selection can occur in the absence of awareness (Koch and Tsuchiya 2007). Specifically, does allocation of attention to an invisible event impact the neural substrates responding to that event? By 'invisible event' we refer to a visual stimulus that the observer is exposed to but (i) has no subjective impression of and (ii) performs at chance if obliged to guess about some aspect of its content, eg orientation.

A recent study (Kanai et al 2006) claimed that the effects of spatial attention are restricted to conscious events. Adaptation to an oriented grating was augmented at the attended locations only if the adaptor was clearly visible and not when the adaptor was masked by interocular suppression. This claim is at odds with reports showing that the responses of the primary visual cortex (V1) to irrelevant, invisible peripheral distractors (also masked by interocular suppression) are modulated by attentional load in a foveal task (Bahrami et al 2007). Another behavioural work (Montaser-Kouhsari and Rajimehr 2005) has also shown that spatial attention enhances orientation-specific adaptation to an adaptor rendered invisible by crowding.

It is well established that the effects of sustained spatial attention on orientation processing depend on stimulus contrast (Ling and Carrasco 2006); for example, orientation discrimination is most profoundly modulated by attention at peri-threshold contrasts but attention has little impact on orientation discrimination at supra-threshold, asymptotic contrast levels. Thus, the recent failure to find an attentional effect for invisible adaptors (Kanai et al 2006) may be due to the use of high (50%) contrast adaptor gratings that were close to the asymptotic saturation level of the contrast response function, as well as to their assessment of post-adaptation orientation discrimination with maximum contrast probes. Any subtle, contrast-dependent effects of attention may have been obliterated by employing such high-contrast stimuli (cf Blake et al 2006).

In order to address this possibility, we assessed orientation-specific adaptation to invisible adaptors, employing low-contrast adaptors that were far from the saturation

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level of the contrast response function. In addition, post-adaptation test stimuli (probes) spanning a range of contrasts were used. In order to manipulate the allocation of spatial attention, observers performed a detection task during the adaptation phase. This task required them to direct spatial attention preferentially to one hemifield, but allowed assessment of performance speed and accuracy for both attended and unattended locations. We predicted that any effects of spatial attention on adaptation to the invisible adaptor would be most likely to emerge at intermediate probe-contrast levels.

2 Methods

2.1 Participants

Five healthy volunteers (mean age 28.4 years, range 20–38 years, two females) gave written informed consent to participate in the experiment, which was approved by the local ethics committee. All participants were naive to the purpose of the experiment and had normal or corrected-to-normal vision.

2.2 Display

Viewing distance was 50 cm. Stimuli were generated with the Cogent toolbox (http://www.vislab.ucl.ac.uk/Cogent/) for Matlab (Mathworks, Inc.) and presented at 85 Hz through a CRT display (resolution, 800×600 pixels, 14 inch Sony Multiscan 110ES) for which a lookup table linearised the output luminance of the monitor. Observers viewed the display through stereoscopic mirrors. Textured black and white bars (0.5 deg width) were placed 3 deg on either side of the fixation point in order to facilitate binocular fusion (figure 1).
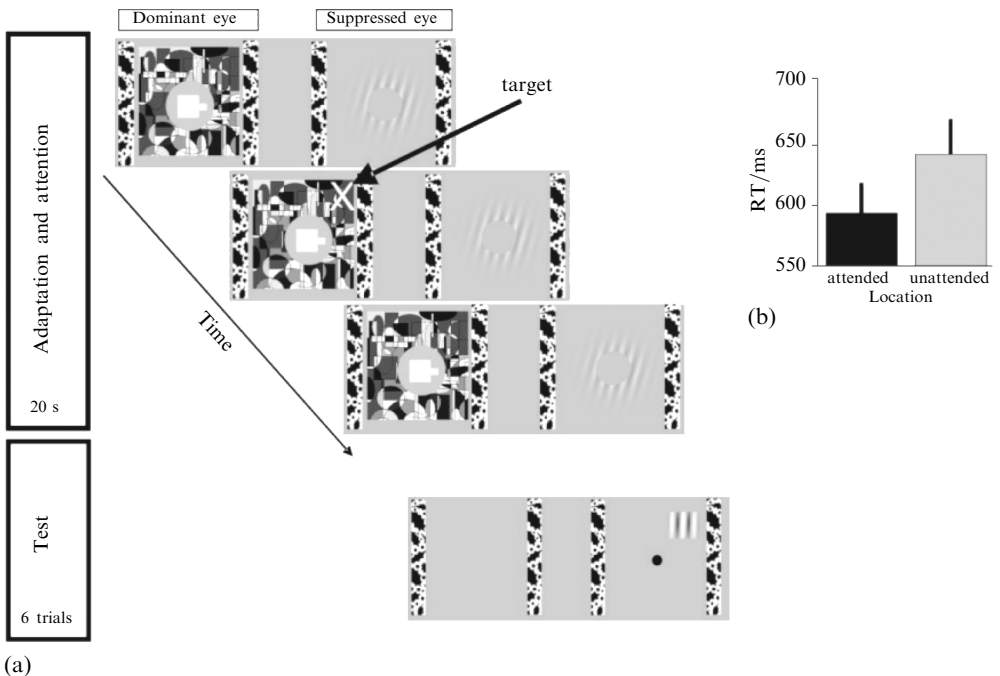
Figure 1. Experimental paradigm and attention-task results. (a) During adaptation, observers detected the occasional appearance of a white target item while maintaining fixation at a foveal white square with a small sideways protrusion indicating the side where the target was more likely to appear. The grey circle around the fixation point is added here for illustrative clarity and was not part of the stimulus array. (b) Reaction times (RTs) to targets appearing at the attended (black) and unattended (grey) locations.

2.3 Stimuli and procedure

The experimental paradigm consisted of two phases: (i) adaptation and attention (A&A) and (ii) test (figure 1a). The first phase combined a target detection task with prolonged adaptation to a grating that was suppressed from awareness. The second phase probed post-adaptation orientation discrimination over a range of contrast levels.

Each A&A period lasted 20 s. During this period, one eye was continuously exposed to an annular sinusoidal grating (0.10 contrast; 3.5 cycles deg^{-1}; inner radius: 1.1 deg; outer radius: 2.25 deg; mean luminance equal to background) that was tilted 15° either to the right (clockwise, CW) or left (counterclockwise, CCW) from vertical. The phase of the adaptor was randomised at a rate of 42.5 Hz to avoid retinal-afterimage formation. Meanwhile, the other eye was presented with arrays of randomly generated shapes of rapidly changing (~ 30 Hz) colour and form circumscribed by an outer square border (width, 5 deg). This stimulus configuration, known as continuous flash suppression (CFS), induced prolonged suppression of the adaptor grating (Fang and He 2005; Tsuchiya and Koch 2005) as verified by the control experiment detailed below.

During the A&A period, observers detected the occasional appearance of a white target item (letter 'X', width 0.7 deg; font, Arial; duration, 100 ms) in any of the four corners of the CFS stimulus. Observers reported target detection by a speeded button-press without breaking central fixation. A white square (width: 0.5 deg) with a small sideways protrusion (figure 1a) displayed at fixation indicated that the target had an 80% probability of appearing on the designated side (with an equal probability for the top and bottom locations). The informative value of this foveal cue was clearly stated for the observers. Within each adaptation period, 4 – 6 targets appeared to avoid predictability of the relative timing and total number of targets.

This detection task offers a number of advantages over previous methods. Earlier studies of attentional modulation of orientation-specific adaptation either relied on instructing the subjects to maintain spatial attention in the attended location (Kanai et al 2006; Spivey and Spirn 2000) or asked the observers to count the number of occurrences of a target in the attended location (Kanai et al 2006; Montaser-Kouhsari and Rajimehr 2005). Each of these paradigms presents a limitation.

Merely instructing the observer to attend to one side (Kanai et al 2006; Spivey and Spirn 2000) without engaging in a demanding task runs the risk that attentional resources may not be voluntarily withheld from the unattended stimulus (Lavie 1995; Lavie and Tsal 1994). According to load theory (Lavie 1995, 2005), whether or not a task-irrelevant stimulus (here, the invisible adaptor) receives attention depends on the extent to which the processing of the relevant task leaves spare capacity or exhausts full attentional capacity. If the relevant task fails to exhaust capacity (as might well be the case with voluntarily sustaining attention on one side), then excess capacity will be involuntarily allocated to the processing of irrelevant stimuli despite the instruction to ignore them.

Counting target appearances in the attended location (Kanai et al 2006; Montaser-Kouhsari and Rajimehr 2005) addresses the above issue but, importantly, does not allow for a direct comparison of performance in the attended and unattended locations as there is no assessment of performance in the unattended location. The effectiveness of the paradigm, in such a case, could only be inferred from its effectiveness at modulating the adaptation.

The task employed here overcomes both of these limitations. Attentional resources could be reliably directed to specified locations by controlling the probability of target occurrence in each location; the task was made sufficiently difficult by manipulating target number, size, and display time in a way that would produce strong effects on RT. Most importantly, since the observers responded to targets appearing in the attended as well as the unattended locations, a direct assessment of the effectiveness of the manipulation, independent of its effects on adaptation, was possible.

At the end of the A&A period the CFS and adaptor stimuli disappeared. The central fixation cross turned black, indicating the start of the test phase. In each test trial, after a variable delay of 400 to 900 ms, a tilted grating of variable contrast (tilted 2° to the left or right from vertical; contrast randomly chosen from among 6 predefined steps spanning 0.001 to 0.50; width: 0.75 deg; spatial frequency identical to the adaptor) was briefly (50 ms) displayed in one of the four corners of the stimulus array (eccentricity, 1.6°; figure 1a, test). The test probe location was randomised across trials with equal probability for all four corners. The participant's task was to decide whether the grating was tilted clockwise or counterclockwise. In the test phase, observers completed 6 test trials. Each trial began immediately after the response in the previous trial, or if no response was made, at the end of a 1500 ms response window. Observers were explicitly instructed about this restricted response window and had received prior practice (8 blocks of 32 trials) with this task with auditory feedback for mistakes before the main experiment. A blank period of 2500 ms, during which only the fixation point was displayed, followed the 6th test trial.

In order to maximise the orientation-specific adaptation to the suppressed invisible grating, we combined two features of previously demonstrated aftereffects, namely, repulsive-tilt aftereffect (TAE—Gibson and Radner 1937) and threshold-elevation aftereffect (TEAE—Blakemore and Campbell 1969; Gilinsky 1968; Regan and Beverley 1985). TAE occurs when adapting to a tilted grating makes a vertical grating appear tilted in the opposite way. TAE magnitude is maximal when the adaptor and test angles are about 10° to 15° different and with short-duration test stimuli (Wolfe 1984). TEAE is evident when adaptation to a tilted grating increases the threshold contrast for detection of test gratings of the same tilt and decreases it for the orthogonal tilt (Blakemore and Campbell 1969; Gilinsky 1968; Regan and Beverley 1985).

Previously, TAE and TEAE have been compared (Festman and Ahissar 2004) but not combined. We combined these two aftereffects by presenting the invisible adaptor gratings tilted 15° CW or CCW from vertical and measuring the contrast threshold for discrimination of a very brief (50 ms) test grating tilted 2° to the right or left from vertical. The discrimination task used here consisted of fine discriminations (of +2° or −2° tilt) around a predefined category boundary (the vertical meridian). Perceptual inference in such a case is likely to be based on sensory evidence from channels that are tuned to orientations farther away from the category boundary than the test orientation itself (Jazayeri and Movshon 2007; Regan and Beverley 1985). We therefore reasoned that an adaptor stimulus tilted 15° CW or CCW from vertical would suppress one of these maximally informative flanks for the fine-discrimination task. As a result, adaptation would tip the balance of sensory evidence derived from viewing of the test grating in favour of the opposite tilt to that of the adaptor. This would increase the likelihood of nearly vertical probes being perceived as crossing the vertical category boundary, thereby reducing the threshold for the 'different' and increasing it for the 'same' tilt conditions across 4 deg of angular distance. Moreover, the influence of channels tuned to such orientations on perceptual judgments is accentuated with increased uncertainty (eg peri-threshold contrast of the test stimulus—Jazayeri and Movshon 2007). We therefore believed that the adaptation effect would be amplified for test stimuli at contrasts near the discrimination threshold.

2.3.1 *Eye movements.* Fixation and eye blinks were monitored during orientation-discrimination trials. Horizontal eye movements were recorded with infrared light transducers in the Skalar IRIS 6500 system attached to the forehead rest (sampling rate: 1000 Hz; analog-to-digital converter card Type PCM-DAS 16d/12, Computerboards, Pittsburgh, PA) and recorded with DASYlab 5 software on a PC. Eye traces were recorded for a window of −100 to 200 ms peri-stimulus time on every trial and the equipment was recalibrated between blocks. Online monitoring and offline trial-by-trial

inspection of the data showed that participants maintained fixation on $> 93\%$ of trials. Trials in which fixation was broken (deviation $> 2°$) and those contaminated by blinks during the measurement window were removed from analysis.

2.3.2 *Quantitative analysis.* For each individual participant, we collapsed the test trials into 'same' (adaptor and test tilt) and 'different' bins. Here, 'same' and 'different' refer to whether the adaptor grating and the test stimulus were tilted in the same direction from vertical. For example, if adaptor and test were both tilted clockwise—albeit one $15°$ and the other $2°$ from vertical, respectively—then the trial would be counted as 'same'. Within each bin, we then estimated the discrimination threshold contrast (cf figures 2a and 2b for group-average graphs) by fitting the subject's performance with a psychometric function:

$$\psi(x; \alpha, \beta, \gamma, \lambda) = \gamma + (1 - \gamma - \lambda) \, F(x; \alpha, \beta),$$

where x is stimulus contrast; $\alpha, \beta, \gamma, \lambda$ are the fitted model parameters which determine the shape of the psychometric function; and F is the Weibull function:

$$F(x; \alpha, \beta) = 1 - \exp[-(x/\alpha)^{\beta}], \quad 0 \leqslant x < \infty.$$
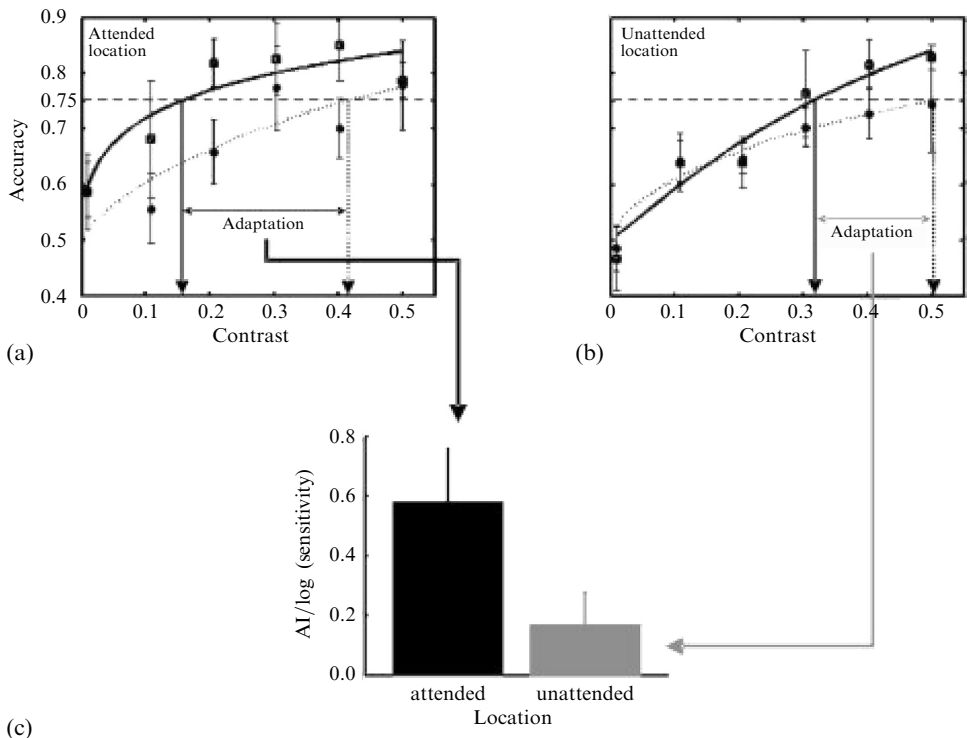
Figure 2. (a) and (b) Average orientation-discrimination accuracy as a function of contrast. Circles and dotted curves are for adaptor-test 'same'; squares and solid curves are for adaptor-test 'different'. (c) Group-average adaptation index for attended and unattended locations. All error bars stand for ± 1 SE.

We used the psignifit toolbox (http://bootstrap-software.org/psignifit/) version 2.5.6 for Matlab which implemented the maximum-likelihood method described by Wichmann and Hill (2001) for curve fitting. The contrast threshold, θ, for 75% correct orientation discrimination was estimated. An adaptation index (AI) was defined such that:

$$\text{AI} = \log(\theta_{\text{same}}) - \log(\theta_{\text{different}}).$$

As stated above, this quantitative index is a combination of TAE and contrast adaptation. In order to look at the effect of attention on adaptation at each contrast level separately, we calculated an attentional modulation index (AMI) such that:

$$\text{AMI} = (A_{\text{different}} - A_{\text{same}}) - (U_{\text{different}} - U_{\text{same}}),$$

where A and U refer to discrimination accuracy in the attended and unattended locations, respectively. This index is sensitive to interactions between attention and adaptation such that attentional modulation of adaptation would lead to a positive value of AMI whereas with an isolated main effect of either the adaptation or attention the index would not depart from zero.

2.3.3 *Control experiment.* In order to confirm the efficacy of continuous flash suppression in rendering the adaptor stimuli invisible, a control experiment followed immediately after the main experiment. The same participants viewed the same stimuli as in the adaptation phase of the main experiment and performed the attentional task. At the end of each 20 s trial, the observers were asked to make a two-alternative forced-choice (2AFC) discrimination of the orientation of the suppressed grating and to rate their confidence on a scale of 0 to 2 (0 = no awareness, 1 = doubtful; 2 = sure). Each observer completed 4 blocks of 8 trials.

3 Results

Reaction times for target detection at the attended locations during the adaptation period were significantly faster than for those appearing in the unattended location (figure 1b; $t_4 = 4.9756$; $p = 0.003$; paired t-test; see figure 3a for data for individual subjects). This confirms the effectiveness of the spatial-attention task. Hit rates were also slightly higher at the attended location (mean = 97.35%; SD = 1.72%) versus unattended location (mean = 96.49%; SD = 1.95%). Though this difference did not reach significance ($t_4 = 1.09$; $p = 0.16$; paired t-test), its direction rules out the possibility of a speed – accuracy trade-off.
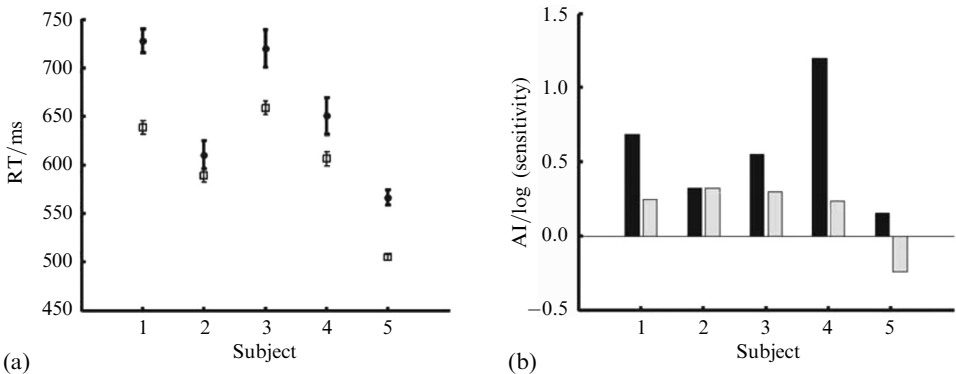

Figure 3. Data of individual observers from main experiment. (a) Reaction times to targets at the attended location were significantly faster than at the unattended location in four out of five observers ($p < 0.001$ for observers 1 and $3 - 5$; for observer 2, $p = 0.07$; independent-sample t-test, two-tailed). (b) Adaptation index (AI) was augmented in the attended locations (black bars) in the same four observers who showed a significant RT effect. All error bars stand for ± 1 SE.

Figures 2a and 2b depict the average orientation discrimination accuracy and the corresponding best fit psychometric functions for the attended and unattended locations, respectively. At the attended locations (figure 2a), the discrimination threshold for adaptor-test 'different' (solid curve and arrow) was shifted to the left compared to that of adaptor-test 'same' (dotted curve and arrow) indicating orientation-specific adaptation. At the unattended locations (figure 2b), a similar but much smaller shift was found.

We quantified this shift by an adaptation index (AI; see section 2.3.2). At the attended locations, the AI was significantly greater than zero (figure 2c; $t_4 = 3.23$; $p = 0.015$; one-sample t-test; see figure 3 for individual observers' data); in other words, the invisible adaptor induced a reliable orientation-specific adaptation. At the unattended location, the AI was not significantly greater than zero (figure 2c; $t_4 = 1.64$; $p = 0.087$; one-sample t-test). Finally, comparison of the AI in the attended versus unattended location showed that it was significantly larger at the attended location ($t_4 = 2.58$; $p = 0.03$; paired-sample t-test).

The results of a control experiment confirmed that observers were indeed unaware of the adaptor stimuli. Discrimination accuracies were consistently at chance (figure 4; $t_4 = 0.90$; $p = 0.41$; one-sample t-test comparison with the 0.50 chance level). Subjective confidence ratings did not differ significantly from zero (mean = 0.13; SD = 0.1122; $p = 0.17$; one-sample t-test comparison with zero) and did not show any correlation with discrimination accuracy (Spearman's $\rho < 0.23$; $p > 0.18$ for all participants), ruling out any residual subjective (as measured by confidence rating) or objective (as measured by 2AFC discrimination) access to the orientation of the suppressed stimulus.
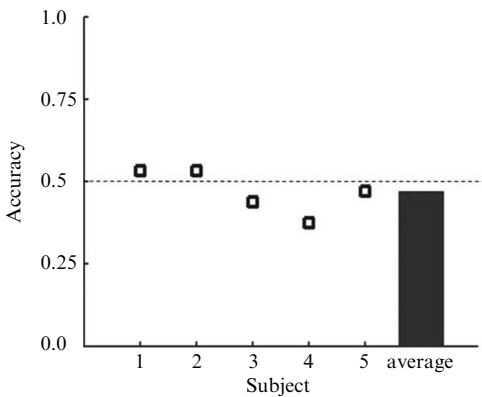
Figure 4. Discrimination performance in the control experiment. None of the five observers (individual data points) or the group average (bar) could discriminate the orientation of the invisible adaptor significantly better than chance level (dotted line).

4 Discussion

The above results demonstrate that spatial attention modulates adaptation to gratings rendered invisible by CFS; the orientation-dependent shift of the contrast-sensitivity curve for discrimination was augmented at spatial locations that were attended during adaptation. These findings are contrary to a previous report (Kanai et al 2006) but are consistent with a recent report (Bahrami et al 2007) that responses of human primary visual cortex (V1) to peripheral, invisible stimuli are modulated by the attentional requirements of a concurrent foveal task. In addition, they are in line with the finding (Montaser-Kouhsari and Rajimehr 2005) that adaptation to an illusory contour rendered invisible by crowding depends on allocation of spatial selective attention. Although the neurophysiological mechanisms responsible for the effects of crowding and CFS may differ, the allocation of attention clearly increases unconscious orientation processing, irrespective of the method that renders the oriented stimulus invisible.

The key differences between our design and that of Kanai and colleagues (2006) were that we used adaptors with 10% contrast and test stimuli with a range of peri-threshold contrast values, whereas Kanai et al (2006) used adaptors and test orientations with (supra-threshold) 50% contrast. This difference in the contrast levels used appears to have rendered our task more sensitive to reveal the effects of attention on adaptation to invisible orientation.[1]

[1] We note that we also used longer adaptation and shorter test periods: our observers adapted for 20 s and were tested with 50 ms long test probes whereas Kanai et al (2006) employed 5 s adaptation and 150 ms test times. However, it is unclear how this difference could account for the difference in the effects of attention on adaptation between the studies.

   The impact of attention on the contrast-response curve (the relationship between the stimulus contrast and the observer's response) can be characterised as either a contrast gain (figure 5a, left) or a response gain (figure 5a, right). A contrast gain enhances sensitivity, shifting the contrast-response curve horizontally, with no effect on the asymptotic response level. This effect is most prominent at intermediate contrast levels. A response gain results in elevation of the asymptotic performance, shifting the contrast sensitivity curve vertically. This effect is most prominent at maximum contrasts (see Treue 2001 for a review).
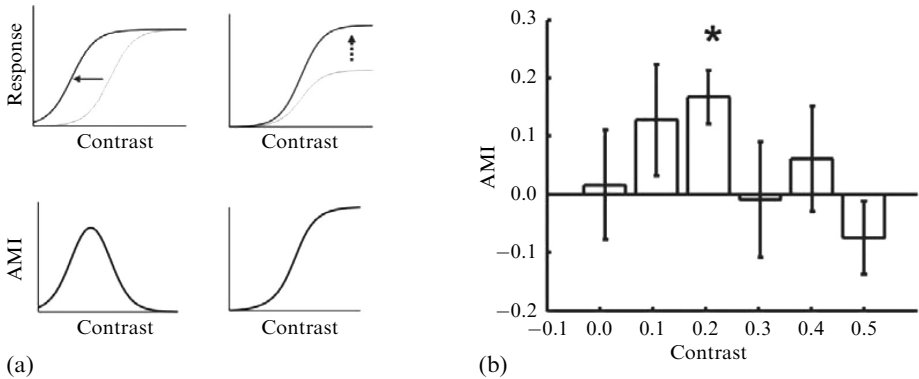
Figure 5. (a) Schematic depictions of gain mechanisms. Top: the effects of contrast (left) and response (right) gain. Solid and dotted curves refer to attended and unattended contrast-response curves, respectively. Bottom: subtraction of attended from unattended response. The effect of contrast gain is maximal at intermediate contrast levels, whereas the effect of response gain is most prominent at maximum contrast. (b) Attentional modulation index (AMI) at each level of test contrast. The augmenting effect of attention on adaptation was maximal at intermediate contrast levels (* $= p < 0.024$). This pattern is consistent with contrast gain [panel (a), bottom left]. See section 2.3.2 for the definition of AMI. All error bars stand for ± 1 SE.

   Recently, it has been suggested that in the case of orientation discrimination for visible stimuli, sustained spatial attention exerts its effect primarily by a contrast gain (Ling and Carrasco 2006). As figure 5b clearly demonstrates, the interaction between attention and adaptation (as quantified by the attentional modulation index, AMI; see section 2.3.2) was maximal at intermediate contrast levels. Importantly, this effect was much reduced at the high end of the contrast range. Thus, the effect of attention on our estimate of adaptation (figure 2c) was mainly driven by attentional modulations in an intermediate contrast range (figure 5b), in line with the suggestion that modulation of orientation processing by spatial attention is mediated by contrast gain. It is also worth noting that an advantage of using the AMI is that this index would only be positive if attention affected adaptation (in the predicted direction). Any attentional effects restricted to the test phase would not show in the AMI measure since they would affect performance irrespective of the relationship of the orientations at test and at adaptation (whether these were 'same' or 'different').

   The previous use of maximum-contrast adaptor and probes (Kanai et al 2006) may have hindered finding modulation by spatial attention driven by contrast gain. It is interesting to note that feature-based attentional modulations do produce a response gain (Treue and Martinez Trujillo 1999). Such effects are most prominent at maximum contrasts and Kanai and colleagues' (2006) method was indeed sensitive enough to reveal feature-based attentional modulation for invisible adaptors.

   A puzzling issue here is that the effect of spatial attention on adaptation to visible stimuli does not seem to rely critically on contrast gain. With the same maximum-contrast probe employed, spatial attention does modulate adaptation to visible adaptors

(Kanai et al 2006) (also see Spivey and Spirn 2000). With maximum-contrast probes, the effects of attention can only reflect a response gain. An interesting hypothesis for future research would then be that, whereas modulation by spatial attention of visible orientation processing involves a combination of contrast and response gain (Huang and Dobkins 2005; Ling and Carrasco 2006), in the absence of awareness, eg with invisible orientations, selection by spatial attention may be restricted to contrast gain.

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