Unconscious orientation processing depends on perceptual load

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The effects of perceptual load on the level of adaptation to task-irrelevant and invisible oriented gratings were examined. Participants performed a task at fixation under conditions of low (detecting color targets) or high (detecting conjunctions of color and shape) perceptual load. Simultaneously, a task-irrelevant-oriented grating was presented monocularly in a more peripheral location but was suppressed from awareness by flashing a dynamic mask stimulus at the same retinal location in the other eye. Orientation-specific adaptation to the invisible irrelevant grating was found at low perceptual load but was eliminated with high perceptual load. These results demonstrate that early unconscious processing of orientation depends on the allocation of limited attentional capacity, and conversely that the allocation of attentional capacity under low (versus high) load is insufficient to bring orientation representations to awareness.

Keywords: perceptual load, attention, orientation adaptation, unconscious processing, continuous flash suppression

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Introduction

Attention and awareness are traditionally believed to be closely linked (Driver & Vuilleumier, 2001; James, 1890; Mack & Rock, 1998; Rees & Lavie, 2001; Zeman, 2001). However, the precise nature of this link is not clear. A number of recent works have questioned this traditional view (for a review, see Koch & Tsuchiya, 2007), with some theories suggesting that attention can only be allocated to consciously accessible stimuli (Block, 1996; Lamme, 2003). However, in the Load Theory of attention (Lavie, 1995, 2005), stimulus competition for the allocation of attentional capacity occurs regardless of whether or not the observer is conscious of the stimulus representations. Load Theory asserts that the level of perceptual load

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in the processing of task-relevant stimuli determines the extent to which irrelevant stimuli are processed. Tasks involving high perceptual load that engage full attentional capacity in the processing of task-relevant stimuli leave no capacity for the processing of any task-irrelevant stimuli (conscious or unconscious alike), but in tasks of low perceptual load any spare capacity left over from relevant stimulus processing spills over to the processing of irrelevant stimuli regardless of whether or not subjects are conscious of the representations. Indeed, the level of perceptual load determines brain responses evoked by irrelevant stimuli (e.g., Rees, Frith, & Lavie, 1997; Yi, Woodman, Widders, Marois, & Chun, 2004; for a review, see Lavie, 2005) even at the earliest stages of visual processing (O'Connor, Fukui, Pinsk, & Kastner, 2002; Schwartz et al., 2005), including areas whose activity may reflect unconscious perception (Crick & Koch, 1995; Haynes & Rees, 2005). Moreover, a recent fMRI study confirmed that retinotopic activity in primary visual cortex (V1) related to the unconscious processing of invisible tool images is modulated by perceptual load (Bahrami, Lavie, & Rees, 2007).

Although these studies show that perceptual load can alter processing of irrelevant stimuli (including those that do not reach awareness) in human primary visual cortex, they neither determine whether such effects on brain activity have any consequences for behavior nor determine whether the precise nature of the neural and the mental representations is affected. Specifically, it is not clear whether unconscious representations of the basic visual feature such as orientation would depend on the level of perceptual load in a relevant task. The previous studies that investigated whether unconscious processing of orientation depends on attention have produced apparently discrepant results (Kanai, Tsuchiya, & Verstraten, 2006; Montaser-Kouhsari & Rajimehr, 2005; for a recent review, see Koch & Tsuchiya, 2007). Specifically, manipulation of spatial attention can reduce selective orientation adaptation to subjective contours rendered invisible during adaptation by crowding (Montaser-Kouhsari & Rajimehr, 2005). By contrast, Kanai et al. (2006) did not find any effect of spatial attention on selective orientation adaptation in one eye that was rendered invisible with continuous flash suppression (CFS) by bright masks in the other eye.

However, all these studies varied spatial attention by instructing the subjects to pay attention to the stimulus or away from it. Although in some cases subjects performed a task to verify that they had complied with the instruction, the extent to which successful task performance required the subjects to pay full attention to the task was not tested. A central point of Lavie's Load Theory is that merely instructing participants to pay attention to or to ignore a certain stimulus may not always guarantee that attentional resources are allocated or can be voluntarily withheld from that stimulus (Lavie, 1995; Lavie & Tsal, 1994). In Load Theory, whether or not a certain stimulus receives attention is dictated by the extent to which the task processing leaves spare capacity (in conditions of low load) or exhausts full attentional capacity (when carried under conditions of high perceptual load). If the relevant task fails to exhaust capacity, then in Lavie's account, excess capacity will be involuntarily allocated to the processing of irrelevant stimuli regardless of the instruction to ignore them.

It is therefore possible that the discrepancy in previous research is at least in part due to a difference in the level of perceptual load in the different tasks used to vary spatial attention, with tasks that may have involved lower levels of perceptual load being less effective in engaging full attention, leading to a spill-over of attention to the supposedly unattended stimulus. Specifically, the RSVP task used by Montaser-Kouhsari and Rajimehr (2005) to divert attention away from the oriented stimulus may have involved a greater level of perceptual load than the task used in the control experiments reported by Kanai et al., 2006 (see the Supplementary material) as it involved a more complex judgment (odd/even judgments for white among black digits, compared to monitoring for an "X" in Kanai et al's work). This could then explain why the spatial attention manipulation was effective in modulating unconscious orientation processing in one study but not the other.

The difference in methods used to achieve unconscious processing (crowding versus CFS) as well in the stimuli and the procedures used in these previous studies preclude, however, any direct conclusion about the role of perceptual load in their results. The purpose of the present study was therefore to determine whether unconscious processing of orientation depends on the level of load on attention in a relevant task. We manipulated perceptual load for a task presented at fixation and assessed orientation-specific adaptation to invisible, peripheral tilted gratings that were irrelevant to the task. The adapting gratings were entirely suppressed from awareness by presenting them monocularly while continuously flashing a mask stimulus in the other eye (continuous flash suppression, CFS) (Tsuchiya & Koch, 2005). On the basis of Load Theory, we predicted that increasing the attentional requirements of the foveal task will reduce adaptation to the peripheral, invisible tilted gratings.

Experiment 1

Methods

Participants

Seven healthy volunteers with normal vision (4 females, mean age: 25.4, range: 19–34) 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.

Display

Observers viewed the display through a mirror stereoscope. Textured black and white bars (0.5° width) were placed 3° on either side of the fixation point in order to facilitate binocular fusion (Figure 1a). Viewing distance was 50 cm. Stimuli were generated using the Cogent toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.) and presented at 85 Hz using a CRT display (resolution = 800 × 600, 14-in. Sony Multiscan 110ES) for which a lookup table linearized the output luminance of the monitor.

Stimuli and procedure

In each load trial, a continuous stream of 20 colored, upright, or inverted crosses each subtending 0.75° × 0.75° was displayed to one eye serially at fixation (Figures 1a and 1b). Fixation was indicated with a foveal circle 1.5° in diameter. Background was gray (mean background luminance: 65 Cd/m^2), and the crosses could appear in one of six different colors (red, green, yellow, blue, purple, and brown). Participants monitored for targets (low load: red crosses, either upright or inverted; high load: upright yellow and inverted green crosses—but not the opposite conjunctions), and there were 4–8 targets embedded in each trial sequence of 20 items. Observers were instructed to respond to targets as quickly as possible upon their appearance by a keyboard button-press. Responses were recorded as correct if they were made within 1500 ms following target onset. Each cross was presented for 250 ms followed by a 750-ms blank period. The exact same parameters were used to generate pseudorandom streams of stimuli for both high and low load trials: for each load trial, colored crosses were randomly sampled from the array of all possible cross shape and color combinations, with the constraint that two target crosses could not immediately follow one another, to avoid response-window overlap (Schwartz et al., 2005). Target items in one condition appeared as non-targets in the other condition with the same frequency. Each participant completed 4 blocks of 8 load trials for each load condition in randomized order. Task instruction was given at the beginning of each load trial by displaying either “Red Crosses” or “Upright Yellow/Inverted Green” (font: Arial; font size: 15; font color: black) to both eyes 5 degrees above the fixation point for 2000 ms. Then another sentence appeared above fixation inviting the observer to “Press any key to start.” Each load trial was then started by a button press by the observer.

During the load trial, arrays of randomly generated shapes of rapidly changing (~30 Hz) color and form circumscribed by an outer square border (width: 5°) were displayed in the periphery of the same eye that viewed the foveal stimuli (Figure 1b). Meanwhile, the other eye was continuously exposed to an annular sinusoidal grating (0.10 contrast; 3.5 cycle per degree; inner diameter: 2.2°; outer diameter: 4.5°; 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 adapter was randomized at a rate of 42.5 Hz to avoid retinal afterimage formation.

Immediately after each 20-second-long load trial (i.e., adaptation period), participants completed 6 test trials of orientation discrimination. In each trial, after a variable

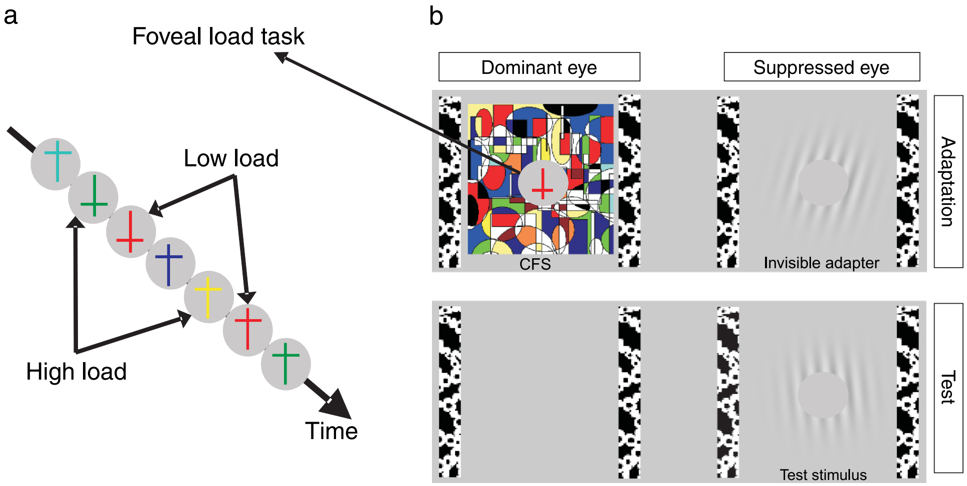

Figure 1. Stimuli and procedure. (a) Foveal load task. Exemplar sequence of foveal items indicating both high and low load targets. (b) During adaptation (top), continuous flash suppression (CFS) and the foveal task were presented to one, randomly chosen, *dominant* eye while the other, *suppressed* eye, was exposed to the adapting grating. In the test phase (bottom), test gratings were presented to the (previously) suppressed eye only. Adapting and test gratings were angled ±15° and ±2° from vertical, respectively in order to maximize adaptation strength.

delay of 400 ms to 900 ms, a tilted grating (equally likely to be 2° CW or CCW from vertical) of variable contrast (randomly chosen from among 6 predefined steps spanning 0.001 to 0.22, all other parameters identical to the adapter) was briefly (50 ms) displayed to the previously suppressed eye (Figure 1a), and the participant's task was to decide if the grating was tilted clockwise or counterclockwise. Response window was 1500 ms. If the observer did not respond within this window, next test trial automatically ensued. If they did, next test trial followed without waiting for the end of the response window. Observers were explicitly instructed about this restricted response time and had received prior practice with this task at maximum contrast (100%) and auditory feedback for mistakes before the main experiment. A blank period of 2500 ms followed after the 6th test trial in which only the fixation point was displayed. This was followed by task instruction for the next load trial.

For each individual participant, we collapsed these trials into *same* (adaptor and test tilt) and *different* bins. Here, same and different refer to the adaptor grating's tilt *relative* to that of the test stimulus. For example, if adaptor and test were both tilted clockwise—albeit one 15 and the other 2 degrees from vertical respectively—then the trial would be counted as *same*. Within each bin, we then estimated the discrimination threshold contrast (see Figures 3a and 3b) by fitting the subject's performance with a psychometric function:

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

where x is stimulus contrast; α, β, γ, and λ are the fitted model parameters which determine the shape of the psychometric function; and F is the Weibull function:

$$F(x;\alpha,\beta) = 1 - e^{\left[-(x/\alpha)^{\beta}\right]}, 0 \leq x < \infty. \tag{2}$$

We used the *psignifit* toolbox (http://bootstrap-software.org/psignifit/) version 2.5.6 for Matlab (Mathworks, Inc.), which implemented the maximum-likelihood method described by (Wichmann & Hill, 2001) for curve fitting. In this way, the contrast threshold for 81% correct orientation discrimination corresponds to the estimated α. We defined adaptation index (AI) such that

$$\mathrm{AI} = \log(\alpha_{\mathrm{same}}) - \log(\alpha_{\mathrm{different}}). \tag{3}$$

Optimization of adaptation measurement

To achieve successful suppression of the adapter gratings from awareness, it was necessary to use low contrast adapters in one eye and CFS in the other eye (thus combining flash suppression with suppression in binocular rivalry). However, the strength of orientation-specific adaptation decreases significantly with lowering visibility (e.g., suppression in binocular rivalry) and contrast of the adapters (Blake, Tadin, Sobel, Raissian, & Chong, 2006). In order to enhance the sensitivity of our method to reveal adaptation, we combined several features of orientation-specific adaptation, namely, repulsive tilt aftereffect (TAE; Gibson & Radner, 1937) and threshold elevation aftereffect (TEAE; Blakemore & Campbell, 1969; Gilinsky, 1968; Regan & Beverley, 1985), to maximize subliminal adaptation despite using low contrast, invisible adapters. After adaptation, orientation discrimination for a grating of supra-threshold contrast is maximally impaired for test angles about ~10°–15° different from the adapter; hence, after prolonged viewing of an adapter grating titled to 15° one side, a vertical test grating appears titled slightly the other way. This phenomenon is known as repulsive tilt aftereffect (Gibson & Radner, 1937) and is stronger with short-durations of test stimulus (Wolfe, 1984). 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, i.e., threshold elevation aftereffect (TEAE) (Blakemore & Campbell, 1969; Gilinsky, 1968; Regan & Beverley, 1985).

Although these characteristics of orientation specific adaptation have not been previously combined (Schwartz, Hsu, & Dayan, 2007), we anticipated that combining them would enhance the sensitivity of our measure of adaptation. We presented the invisible adapter gratings titled 15° to CW or CCW vertical for a long duration (20 second) and then measured the contrast threshold for discrimination of a briefly (50 ms) presented test gratings titled 2° to the right or left from vertical. Thus, our method targeted the angles at the peak of adaptation. In addition, we measured the effects of adaptation on fine (+2° vs. −2°) discrimination performance within the dynamic peri-threshold contrast range (i.e., [0–22%]; see Figure 1 of Regan and Beverley, 1985). As a result, we were able to counter the weakening effects (Blake et al., 2006) of continuous flash suppression and low adapter contrast.

Eye movements

Fixation and eye blinks were monitored during orientation discrimination trials. Horizontal eye movements were recorded using 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 using DASYlab 5 software on a PC. Eye traces were recorded for a −100- to 200-ms peri-stimulus time on every trial and the equipment was recalibrated between blocks. Offline analysis showed that participants maintained fixation on >95% trials. Trials in which fixation was not maintained (deviation >2 deg in the peri-stimulus time), or in which blinks occurred, were removed from analysis.

Control experiment

In order to confirm that the participants were reliably unaware of the suppressed adapting stimulus, for each participant, a control experiment followed immediately after the main experiment. Participants viewed the same stimuli as in the adaptation phase of the main experiment without performing the cross task. At the end of each 20-s trial, the observers were asked to make two-alternative forced-choice discriminations of the suppressed grating's orientation as well as 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 each.

Results

Reaction times (RTs) to targets in the foveal task were significantly slower under high compared to low load (Figure 2; $t(6) = 8.10$; $p < 0.001$; paired t-test). Error rates were slightly higher under high load condition (mean error rate = 9.15%) compared to the low load (mean error rate = 6.03%), but this difference was not significant ($t(6) = 1.654$; $p > 0.1$). The significant elevation of reaction time in the absence of any speed–accuracy trade-off confirmed the effectiveness of the load manipulation.

The orientation discrimination data from an individual observer and the group averages are depicted in Figures 3a–3d. Under low load, discrimination threshold for adaptor-test-*same* was shifted (Figure 3a, blue arrow) to the right compared to that of adaptor-test-*different* (red arrow). Under high load, a similar but much smaller shift was found for this observer (Figure 3b). Group average of orientation discrimination accuracy under low (Figure 3c) and high load (Figure 3d) showed the same pattern across the group of observers. Under low load (Figure 3c), accuracy was consistently better for adaptor-test-*different* trials (red line), and this difference was clearer at intermediate contrast levels. Under high load (Figure 3d), the separation between *same* versus *different* conditions was much smaller and less consistent.

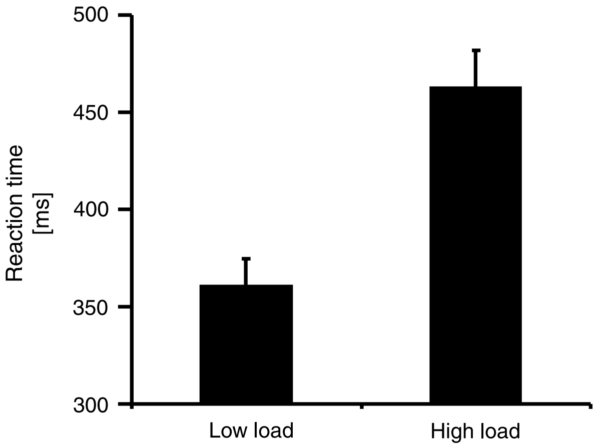

Figure 2. Reaction times in the foveal load task in Experiment 1 showed that load manipulation was effective, and detection of the high load targets was significantly slower. Error bar = 1 standard error.

To compare adaptation across load conditions quantitatively, we calculated an adaptation index (AI; see Methods section) that estimated the magnitude of the rightward shift of the contrast–response curve in the adaptor-test-*same* relative to adaptor-test-*different* condition. Under low load, AI was significantly greater than zero (Figure 3e; $t(6) = 4.41$; $p < 0.01$; one-sample t-test) indicating the elevation of contrast discrimination thresholds for test orientations of same tilt as the adaptor. Under high load, however, AI did not differ significantly from zero (Figure 3e; $t(6) = 2.04$; $p = 0.09$; one-sample t-test). Critically, a direct comparison demonstrated that AI was significantly larger under low than high perceptual load ($t(6) = 3.07$; $p = 0.02$; paired t-test).

It is worth noting here that, as depicted in Figures 3c–3d, discrimination performance at the lowest contrast levels (i.e., 1% and 5%) of the *same* condition did not depart from the expected chance level (all $p > 0.3$; one-tailed one-sample t-test comparison with 0.5) neither in low load (1% contrast: median = 0.5263; 5% contrast: median = 0.4667) nor in high load (1% contrast: median = 0.5000; 5% contrast: median = 0.5000) conditions. This is important because one might expect that at the lowest contrast levels of the *same* condition, post-adaptation bias may drive the discrimination accuracy to below chance level which, if it were true, it would have undermined the use of Weibull function for our quantitative analysis. These results therefore justified our assumptions for the curve fitting. These results are in line with the previous studies showing that orientation-specific adaptation does not induce an illusory percept of the un-adapted orientation at near zero test contrast. (see Box 3 of Clifford, 2002).

In the control experiment, discrimination accuracies were consistently at chance level (Figure 4; $t(6) = -0.281$; $p = 0.788$; one-sample t-test comparison with the 0.50 chance level). Subjective confidence ratings did not differ significantly from zero (mean ± standard error = 0.13 ± 0.074; $t(6) = 1.80$; $p = 0.122$; one-sample t-test comparison with zero) and did not show any correlation with discrimination accuracy (Spearman's $\rho < 0.2$; $p > 0.1$ for all participants), ruling out any residual subjective (as measured by confidence rating) or objective (as measured by 2-AFC discrimination) access to the orientation of the suppressed stimulus. Note that this provides a very rigorous assessment of awareness because even a momentary glimpse of the adapting stimulus during its 20-second presentation or any meaningful averaging of its orientation across display time or space (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) would have been sufficient for significant departure from chance level in the discrimination task.

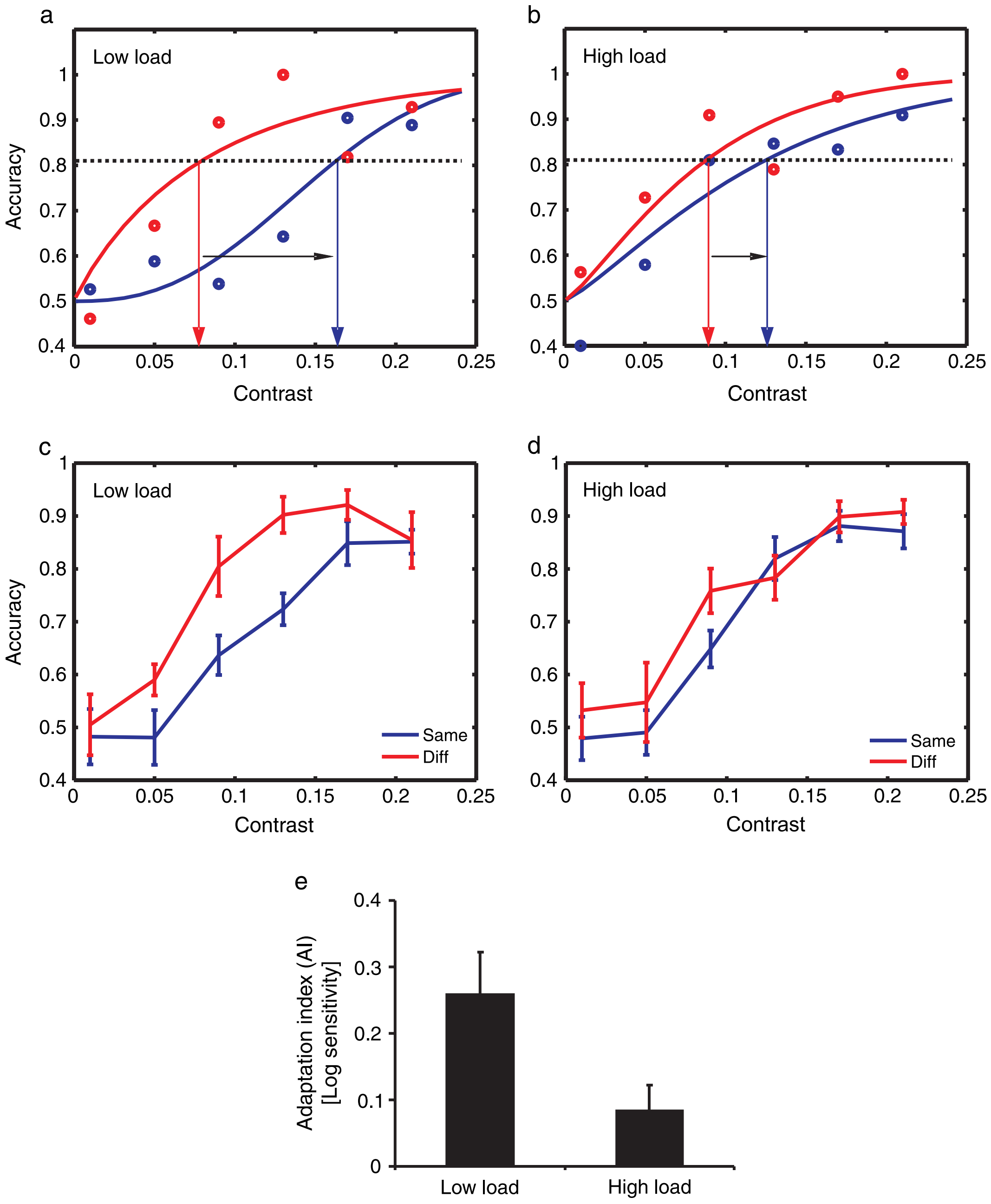

Figure 3. Experiment 1. (a, b) A representative subject's data. In each graph, abscissa and ordinate show the test grating contrast and discrimination accuracy, respectively. Red and blue curves correspond to adapter-test-*different* and adapter-test-*same,* respectively. For this participant, contrast discrimination thresholds for adaptor-test-*same* (blue arrows) are shifted to the right compared to that of adaptor-test-*different* (red arrows) under both load conditions. Importantly, the shift is larger under low load indicating stronger adaptation to invisible adapter under this condition. (c, d) Group average orientation discrimination accuracy under low (c) and high (d) load. Here too, red and blue refer to same and different adaptor-test relative tilt as in panels a and b, and the pattern of the results corroborates the same trend. (e) Group results showed that adaptation index was significantly larger under low versus high load. All error bars are 1 standard error.

Discussion

These findings confirm the prediction from Load Theory (Lavie, 1995, 2005) that increasing perceptual load at fixation would reduce the level of the adaptation for invisible peripheral gratings. However, the low load task used in Experiment 1 required color detection alone whereas the high load task concerned discrimination of conjunctions of color and shape (upward versus downward crosses; Figure 1). Thus one might question whether the effects found on orientation adaptation are due to the change in the extent to which the orientation feature was

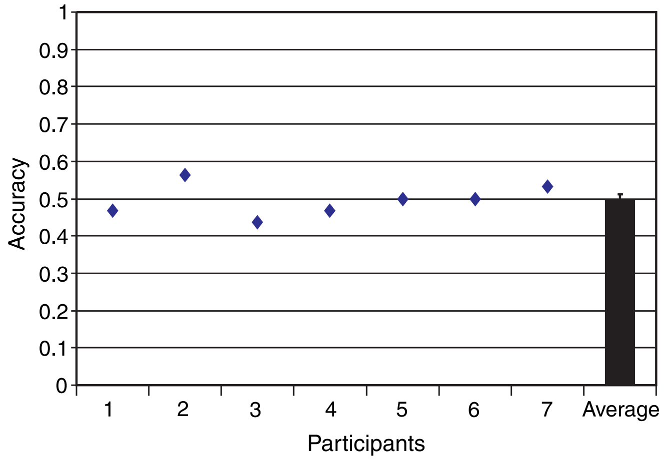

Figure 4. Control experiment confirmed the effectiveness of CFS. Accuracy was consistently at chance (0.50) in the forced-choice discrimination of suppressed stimulus orientation for all participants (diamonds) as well as the group mean (bar). Error bar = 1 standard error.

one of the attended task features (as was the case for the high load but not the low load task) rather than the level of perceptual load in the task. We note that according to feature-based attention accounts attending to a feature facilitates its processing, even in an ignored distant location (Saenz, Buracas, & Boynton, 2002, 2003) and even when it is presented under subliminal conditions (Kanai et al., 2006; Melcher, Papathomas, & Vidnyanszky, 2005). It is therefore unlikely that it is the reduced task relevance for orientation under the low load color task that led to increased orientation adaptation (compared to the high load condition).

Nevertheless, it is conceivable for example that whenever any demand on orientation processing is made at the fovea this reduces orientation processing in the periphery and hence reduces the subsequent adaptation effect.

To address this issue directly, we examined the effect of a change in the task relevance by comparing two low load tasks one involving color detection as before and one involving shape detection (e.g., upright versus inverted cross). The hypothesis that any demand on orientation processing in the fovea is sufficient to reduce orientation processing in the periphery predicts reduced adaptation in the form task compared to the color task despite both involving just low perceptual load. A feature-based attention account in which what determines whether a feature is processed (and adapted to) is its task relevance rather than the level of load in the attended task processing would predict a greater adaptation in the form task than in the color task. In contrast since both tasks involved low perceptual load, Load Theory predicts that they would both result in adaptation effects with similar magnitude irrespective of the specific feature (color or form) employed in the low load tasks.

Experiment 2

Methods

One author (DC) and five (2 female) naive but psychophysically experienced observers gave written informed consent to participate in this experiment, which was approved by the local ethics committee. None of the participants had been tested in Experiment 1. All had normal or corrected to normal vision. All procedures relating to display, stimuli, orientation discrimination task, experimental procedures, quantitative assessment, and eye movement control were identical to Experiment 1.

Foveal task

In separate consecutive sessions that consisted of 6 blocks of 8 load trials each, participants performed one of two foveal tasks. In one session, observers detected red crosses (color task). This was an exact replication of the low load condition of Experiment 1. In the other session (shape task), observers detected the occasional presence of upright crosses (of any color) among a stream of inverted colored crosses or vice versa. Target shape (upright or inverted) was randomized across blocks. All other details of the experiment were identical to Experiment 1.

Results and discussion

Exposure to the suppressed grating resulted in consistent adaptation across both shape and color tasks (Figure 5). AI was significantly larger than zero for the color ($t(5)$ =

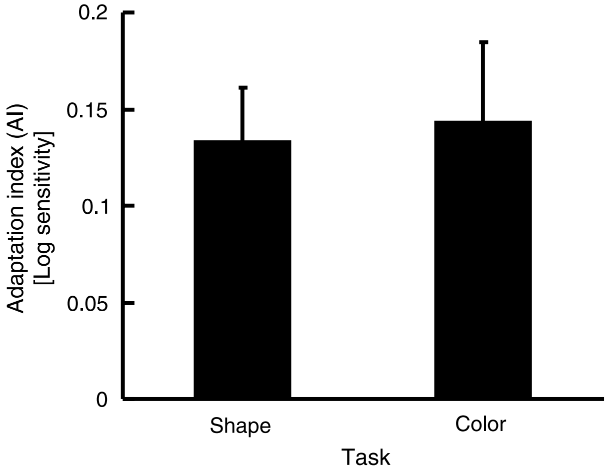

Figure 5. Experiment 2. Adaptation to the invisible distracter did not depend on the defining feature of the low load task. Group mean (n = 6) AI is plotted for shape and color task. Doing a simple shape or color task (both of which fulfilled the characteristics of low load) did not modulate the adaptation index. Error bars are 1 standard error.

3.5456; $p = 0.008$; one-sample *t*-test) as well as the shape ($t(5) = 4.9656$; $p = 0.002$; one-sample *t*-test) tasks, and there was no significant difference between the adaptation in the two tasks ($t(5) = 0.17$; $p = 0.86$; paired sample *t*-test). Compared to the low load condition in Experiment 1, the magnitude of AI was somewhat smaller in Experiment 2, but it was no less consistent judging by the inferential statistics noted above.

These results showed that when low load tasks are used, adaptation to the irrelevant suppressed grating is unaffected by the specific feature (color or form) probed by the low load tasks. Thus, we ruled out the possibility that the reduction of adaptation under high load seen in Experiment 1 was merely due to the change in the task relevance of the shape/form feature.

General discussion

The level of perceptual load in a foveal task determined the level of unconscious orientation processing. Specifically, oriented gratings presented to one eye and rendered invisible by interocular suppression produced orientation-specific adaptation, resulting in positive AI, only when the foveal task involved low perceptual load. AI was significantly reduced (indeed eliminated) when the foveal task involved high perceptual load. These results are predicted by the Load Theory. Specifically, in Load Theory stimulus competition for limited capacity resources is not restricted to conscious representations. Therefore, the consumption of most or all perceptual capacity by a foveal task with high perceptual load was expected to eliminate the unconscious processing of the peripheral orientation stimulus and thus any subsequent orientation adaptation effects. In contrast, the spill-over of spare capacity in foveal task conditions of low perceptual load was expected to result in the processing of the invisible orientation in the periphery followed thus by significant orientation–adaptation effects.

Although the predictions of Load Theory have been supported in previous research that showed the effects of perceptual load on various measures of distractor processing including brain activity (O'Connor et al., 2002; Rees et al., 1997; Schwartz et al., 2005; Yi et al., 2004), behavioral interference effects (Lavie, 2005), and measures of explicit conscious perception (Cartwright-Finch & Lavie, 2007; Lavie, 2006), these works have invariably used visible stimuli, and our present study is the first to show the behavioral effects of perceptual load on unconscious perceptual representations of invisible stimuli.

Our findings concur with our recent demonstration that unconscious retinotopic V1 activity related to the presence (vs. absence) of an invisible monocular stimulus (plus CFS in the other eye) depended on the level of perceptual load at fixation (Bahrami et al., 2007). Together the findings of both studies suggest that the level of neural activity related to unconscious orientation representations in early visual cortex, and therefore the magnitude of the aftereffect following adaptation depend on the level of perceptual load in an attended task.

However, the previous imaging data concerned the activity related to rather complex stimuli (images of tools) and therefore do not speak directly neither to the role of attention in unconscious representations of basic visual features nor to their behavioral consequences. The present study goes beyond our previous imaging findings both in providing a clear assessment of the magnitude of unconscious representations and their behavioral consequences as well as addressing the role of perceptual load in determining unconscious processing for the fundamental visual feature of orientation.

The present findings also concur with the demonstration that the magnitude of adaptation to the orientation of illusory contours rendered unresolvable by crowding (Toet & Levi, 1992; Wilkinson, Wilson, & Ellemberg, 1997) is smaller when the observers perform a demanding foveal task compared to when they pay attention to the unconscious adaptor (Montaser-Kouhsari & Rajimehr, 2005). However, it seems unlikely that their findings and those presented here share the same underlying mechanism. The suppression from consciousness due to crowding is attributed to higher level processes that pool orientation information over a larger area (Parkes et al., 2001) or alternatively to inadequate resolution of higher level, top-down mechanisms of spatial attention for individuating target items in a cluttered scene (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). CFS, however, is a form of dichoptic masking. It has been suggested (Tsuchiya, Koch, Gilroy, & Blake, 2006) that the CFS stimulus generates a rapid stream of successive transient onset and offset signals that suppress the weaker stimulus. Thus, it is conceivable that the suppressive mechanism at work in CFS may operate at a much lower level than those in crowding.

Indeed at first sight one may suggest that the contrast between the modulation of orientation adaptation by spatial attention in the Montaser-Kouhsari and Rajimehr's (2005) study and the lack of such modulation in the Kanai et al. (2006) study might be due to the use of CFS to suppress the adapting orientation in the Kanai et al. study. Our present findings, however, show that the availability of attentional resources for orientation processing determines the magnitude of adaptation even when the adapting stimulus is suppressed with the CFS masks. This suggests that previous failures to find an effect of spatial attention on orientation adaptation (Kanai et al., 2006) may reflect the use of tasks that were not sufficiently high in perceptual load. For example, this would clearly be the case when spatial attention is only varied by instruction and may also be the case for a simple letter detection task. Consistent with this proposal, we have recently found evidence (data presented at VSS 2007;

abstract: http://journalofvision.org/7/9/788/) that using a task with a high level of perceptual load but similar configuration to Kanai et al. results in significant attentional effects on adaptation to the suppressed orientations.

Conclusions

The level of perceptual load in a foveal task determined the magnitude of orientation adaptation to adapting orientation stimuli in the periphery that were suppressed with the use of CFS. The orientation adaptation index was significantly higher for low than high perceptual load. These findings generalize Load Theory to the case of unconscious processing of invisible stimuli and demonstrate that the competition of stimuli for limited capacity attentional resources is not restricted to conscious representations in contrast with the claim that attention can only act on stimuli that have already reached awareness (Block, 1996; Lamme, 2003). The results also challenge previous suggestions that attending to a stimulus (as would be the case in the conditions of low perceptual load in our study) would bring it to conscious awareness (Baars, 2005; Mandler, 2005).

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