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Attention induces conservative subjective biases in visual perception

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Although attention usually enhances perceptual sensitivity, we found that it can also lead to relatively conservative detection biases and lower visibility ratings in discrimination tasks. These results are explained by a model in which attention reduces the trial-by-trial variability of the perceptual signal, and we determined how this model led to the observed behavior. These findings may partially reflect our impression of 'seeing' the whole visual scene despite our limited processing capacity outside of the focus of attention.

There is ample evidence that endogenous spatial attention enhances perceptual processing. For example, attention increases contrast and response gains[1]. However, there is also suggestive evidence that unattended stimuli may be perceived with an inappropriately strong subjective sense of detail and vividness. For instance, in experiments of change and inattentional blindness, subjects are often surprised at how poorly they detected (changes in) unattended targets, as if they subjectively feel that they would have seen them despite the lack of attention[2]. It has also been noted that peripheral vision (which usually receives less attention than focal vision) may seem relatively detailed and vivid from a subjective point of view, despite its limited processing resolution[3] and color sensitivity[4]. One interpretation of these observations is that, in the absence of attention, we subjectively overestimate our perceptual sensitivity.

We investigated this possibility in a series of psychophysics experiments. We first examined whether attention affects detection bias (that is, one's propensity to report detection of a target). According to signal detection theory[5], perceptual sensitivity (d') is mathematically independent of subjective detection bias (or criterion, c). However, the two are often empirically related; when sensitivity is poor, subjects tend to use a conservative criterion to avoid excessive false alarms (also known as the Neyman-Pearson objective[5]). Thus, we equated d' for the detection of cued and uncued targets by using lower contrast for the cued targets (experiment 1; **Fig. 1** and **Supplementary Methods**). Equating d' allowed us to isolate the effect of attention on the criterion. By presenting a response cue after the attentional cue, we independently measured hit rates (proportion of trials in which the subject reports seeing a target when a target was presented) and false alarm rates (proportion of target responses when a nontarget was presented) for the cued and uncued stimuli (**Fig. 1**). When sensitivity was equated between the two kinds of stimuli, attentional cuing led to a more conservative detection bias (**Fig. 2a**), that is, subjects reported seeing the target less frequently in the cued locations. A series of subsequent control studies confirmed that the effects were present even under an explicit payoff structure and trial-by-trial feedback (**Supplementary Fig. 1a**,**b**), were not a result of eye movements (**Supplementary Figs. 1c**,**d** and **2**), and were largely independent of interference by the stimulus that was not probed by the response cue (**Supplementary Fig. 3**).

One could argue that the difference in physical contrast between the cued and uncued stimuli drove the effects on detection criterion. To address this concern, we conducted a second experiment in which we presented stimuli of identical contrast for the cued and uncued locations in each block, but varied the contrast value for both

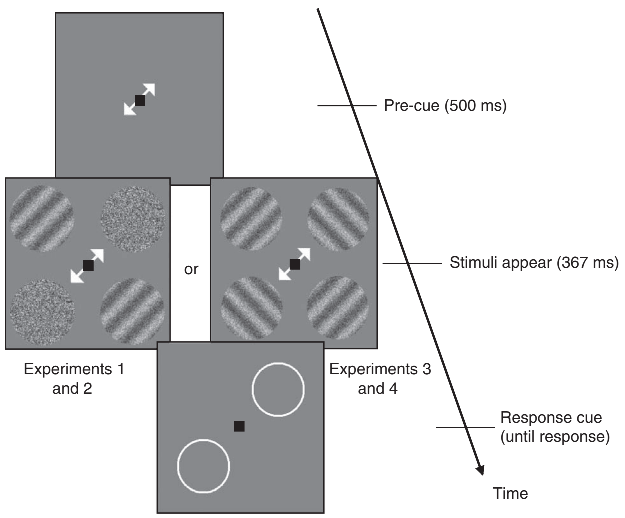

Figure 1 Task design. Each trial began with a pre-cue indicating the diagonal to which subjects should attend. After the presentation of the stimuli, a response cue indicated the diagonal for which subjects had to provide a perceptual judgment. On 70% of the trials, the response cue coincided with the pre-cue (cued trials), whereas it did not on the remaining 30% (uncued trials). This design allowed us to measure perception for both the cued and uncued locations. The stimuli were gratings of varying contrast added to noisy background. In the detection experiments (experiments 1 and 2), the gratings had random orientations. After the response cue, subjects needed to indicate whether any gratings (target) appeared in the response-cued diagonal (in the example trial above, the correct answer would be "No"). In the discrimination experiments (experiments 3 and 4), gratings tilted 45° and 135° were presented. After the response cue, subjects discriminated between the two possibilities (in the example trial above the correct answer would be "Left tilted") and rated the visibility of the grating's tilt.

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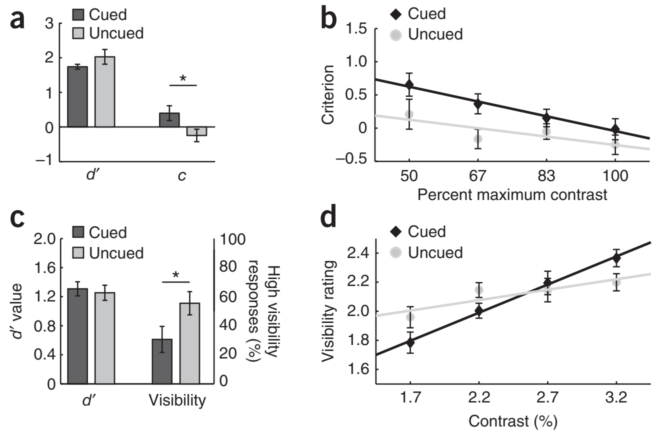

Figure 2 Results from experiments 1–4. (**a**) In experiment 1, where detection sensitivity (d') was matched ($P = 0.18$), subjects adopted a lower (more liberal) criterion for the uncued compared to the cued stimuli ($t_8 = 2.67$, $P = 0.028$). *$P < 0.05$. (**b**) In experiment 2, attention modulated the relationship between criterion and contrast, decreasing the slope of the line of best fit ($t_8 = 3.11$, $P = 0.015$). Even though contrast was matched, attention still led to a more conservative detection bias for the lowest two contrasts (both P values < 0.01), whereas there was no difference for the highest two contrasts (both P values > 0.1). Maximum contrast refers to the maximum value used for each subject (mean contrast = 2.47%, s.d. = 0.9%). (**c**) In experiment 3, in which discrimination sensitivity (d') was equated for the cued and uncued stimuli ($P = 0.27$), attention led to lower visibility ratings ($t_8 = 3.00$, $P = 0.017$). (**d**) Attention also modulated the relationship between contrast and visibility ratings, as indicated by a significantly steeper line of best fit for the cued stimuli in experiment 4 ($t_5 = 3.37$, $P = 0.02$). At the lowest two contrasts, the visibility ratings were higher for uncued stimuli ($P = 0.06$ and $P = 0.04$, respectively), whereas this relationship disappeared for the third level of contrast ($P = 0.57$) and reversed for the highest contrast ($P = 0.04$). In **d**, contrast refers to actual luminance contrast, unlike in **b**; the same levels were used for each subject. Data are means ± s.e.m.

conditions across blocks (experiment 2). In this way, we collected data at multiple sensitivity and contrast values for both the cued and uncued stimuli. We plotted the relationship between detection criterion and the physical stimulus strength (luminance contrast; **Fig. 2b**; for hit and false alarm rates plotted against stimulus contrast, see **Supplementary Fig. 4**), and found that this relationship was modulated by attentional cuing; at lower contrast levels, cuing led to a conservative detection bias. A multiple regression analysis that controlled for the effects of detection sensitivity, physical contrast and subject-specific effects confirmed that the effect of attention was to increase (that is, to make more conservative) the detection criterion ($P < 0.0001$).

These findings were explained by a signal detection theoretic model that postulates that subjects used a single unified criterion for detecting targets in both the cued and uncued locations[6] (**Supplementary Fig. 5**). The critical assumption of this model is that attention reduces the trial-by-trial variability of the internal perceptual signal. This decrease in variance enhances the signal-to-noise ratio, but also reduces the occurrence of high signal trials caused by chance fluctuations. When the same unified criterion is used for target detection in both conditions, the decreased variance for cued trials makes them less likely to cross the detection criterion, which entails fewer "yes" responses (**Supplementary Fig. 5a**,**b**). The model provides a good fit to the data from experiments 1 and 2 (**Supplementary Fig. 6a**,**b** and **Supplementary Methods**). Similar models that do not allow attention to affect the variability of the signal were unable to account for the data (**Supplementary Figs. 6** and **7**).

If attention reduces trial-to-trial variability in signal strength, one counter-intuitive implication is that uncued stimuli should also be rated as more subjectively visible in a discrimination experiment, as the criteria for high visibility rating in discrimination should behave similarly to the criterion for detection (**Supplementary Fig. 5c**,**d**). We investigated this possibility in experiment 3, in which we equated subjects' discrimination sensitivity for cued and uncued stimuli by presenting stronger contrast stimuli to the uncued location. Confirming our model's implications, we found higher visibility ratings for the uncued stimuli (**Fig. 2c**). As in experiment 1, the visibility differences in experiment 3 could be attributed to contrast differences. We then ran the discrimination task, as in experiment 2, at fixed levels of contrast (experiment 4). The relationship between visibility ratings and physical stimulus contrast was modulated by attention (**Fig. 2d**). Specifically, at low contrast levels, attention was associated with lowered visibility ratings, even when contrast was matched. Again, when the effects of the other factors, such as d' and contrast, were controlled for in a multiple regression analysis, higher attention was still associated with lower visibility ratings ($P < 0.005$). The aforementioned signal detection theoretic model again provided good fits to these results (**Supplementary Fig. 6c**,**d**). Another experiment revealed that these effects on visibility ratings generalize to a different procedure in which attention was either relatively focused or distributed across many items (**Supplementary Fig. 8**).

In summary, we found that spatial attention induces conservative biases in subjective aspects of perception, namely a conservative detection bias (lower hit and false alarm rates) and lower visibility ratings. These effects were observed when perceptual sensitivity (d') was matched or when the stimulus contrast was low. We speculate that the relatively higher hit rate and visibility rating associated with inattention may partially explain the subjective feeling of seeing objects rather vividly in the entire visual scene, even though typically little attention is paid to the periphery.

These results are explained by our signal detection theoretic model (**Supplementary Fig. 5**), which provided good fits to the data from all four experiments. One important assumption of the model is that subjects used a single unified criterion for detection of both cued and uncued targets. This assumption is supported by previous findings[7] that subjects cannot use separate criteria for distinct targets presented in the same context. This limitation in criterion setting may be a result of the limited processing resources of the prefrontal cortex, which probably contributes to criterion setting[8]. Another important idea of the model is that attention reduces the trial-by-trial variability of an internal perceptual signal, which subsequently reduces the probability with which the signal exceeds the decision criterion (a simple case of stochastic resonance[9]). Psychophysics studies have shown that attention can exclude external noise[10] as well as reduce internal noise[6]. Physiologically, attention is known to reduce the correlated noise among neuronal populations[11,12], which should have the effect of reducing the trial-by-trial variability of the averaged neuronal response of a large group of neurons. Critically, such population responses may be more important for conscious perception than single-cell spiking activity[13]. Although many single-neuron recording studies[14] and computational models (for example, ref. 15) focus on the effects of attention in boosting the perceptual signal, our findings highlight the importance of the effect of attention on reducing the variability of that signal.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS
D.R. conducted the experiments, analyzed the data and wrote the manuscript. B.M. performed the model fitting and comparison. T.G. and E.H. helped with data collection and conducted some of the control studies. F.P.d.L. conducted the eye-tracking control study. H.L. conceived the experiments, supervised the project, analyzed the data and wrote the paper.

COMPETING FINANCIAL INTERESTS
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