Report

The Scope and Limits of Top-Down Attention in Unconscious Visual Processing

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Summary

Attentional selection plays a critical role in conscious perception. When attention is diverted, even salient stimuli fail to reach visual awareness [1, 2]. Attention can be voluntarily directed to a spatial location [3–9] or a visual feature [9–14] for facilitating the processing of information relevant to current goals. In everyday situations, attention and awareness are tightly coupled. This has led some to suggest that attention and awareness might be based on a common neural foundation [15, 16], whereas others argue that they are mediated by distinct mechanisms [17–19]. A body of evidence shows that visual stimuli can be processed at multiple stages of the visual-processing streams without evoking visual awareness [20–22]. To illuminate the relationship between visual attention and conscious perception, we investigated whether top-down attention can target and modulate the neural representations of unconsciously processed visual stimuli. Our experiments show that spatial attention can target only consciously perceived stimuli, whereas feature-based attention can modulate the processing of invisible stimuli. The attentional modulation of unconscious signals implies that attention and awareness can be dissociated, challenging a simplistic view of the boundary between conscious and unconscious visual processing.

Results and Discussion

Spatial Attention Does Not Modulate TAE from Invisible Stimuli

In the first experiment, we examined whether spatial attention can target unconscious signals for invisible stimuli by using the tilt aftereffect (TAE), where prolonged viewing of an adaptation stimulus slightly tilted from the vertical causes a percept of an opposite tilt for a subsequently presented vertical stimulus [23]. A number of neurophysiological [3–5] and brain-imaging [6] studies

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have shown that spatial attention modulates cortical activity in a retinotopic fashion, even in the absence of visual stimuli [7, 8]. A case study on a blindsight patient has shown that precueing a target location in his "blind" hemifield facilitates the processing of a stimulus invisible to the patient at that location [24]. These lines of evidence suggest that spatial attention might increase the neural responses to invisible adapting stimuli and thus lead to greater TAE. Alternatively, if top-down spatial attention is limited to consciously perceived stimuli, attending to the location of an invisible stimulus should not affect adaptation at all.

The design of the experiment is illustrated in Figure 1A. We rendered adapting stimuli invisible by presenting rapidly changing Mondrian patterns presented to the other eye, a technique called *continuous flash suppression* (CFS) [25]. We manipulated spatial attention by instructing the observers to attend to one of the two spatial markers drawn on top of the Mondrian patterns (Figure 1A). The positions of the markers corresponded to the locations of the Gabor stimuli presented to the other, suppressed left eye (Figure 1A). The two adaptors had the same orientation so that the effects of feature-based attention remain constant. After adaptation of the left eye to the invisible Gabor with a tilt orientation from the vertical by 15° for 5 s, a test stimulus was presented to the eye, either at the attended or the unattended location. The observers were asked to judge whether the test Gabor stimulus with a variable orientation was tilted to the right or left. In a control experiment, we repeated the same experiment without the presentation of the Mondrian masks. In this case, both adaptors were visible to the observers. We included this control condition to confirm that the effect of spatial attention is obtained reliably with our stimulus parameters (see the Experimental Procedures in Supplemental Data available with this article online for further details).

The results (Figure 1B) show that TAE was induced by invisible adaptors (paired t test against the baseline, $T(3) = 4.73$, p < 0.05 for the attended location; $T(3) = 5.69$, p < 0.05 for the unattended location), indicating that the orientation information was processed to a certain degree for the invisible stimuli. However, the TAE magnitude was not significantly different ($T(3) = 1.45$, p = 0.24) regardless of whether the TAE was tested at the attended location (1.98° ± 0.34°; hereafter the SEM are shown to indicate interobserver variability) or at the unattended location (2.15° ± 0.29°).

On the other hand, when the adaptors were visible (Figure 1C), the TAE magnitudes were subject to attentional modulation (visible-attended, 4.71° ± 0.81°; visible-unattended, 3.86° ± 0.74°). With a two-way ANOVA, we confirmed the main effects of visibility ($F(1,3) = 22.60$, p < 0.05) and attention ($F(1,3) = 33.36$, p < 0.05) and a significant interaction ($F(1,3) = 16.99$, p < 0.05) (Figure 1D). The significant interaction between visibility and spatial attention indicates that spatial attention modulates the TAE only when the adaptors were consciously visible
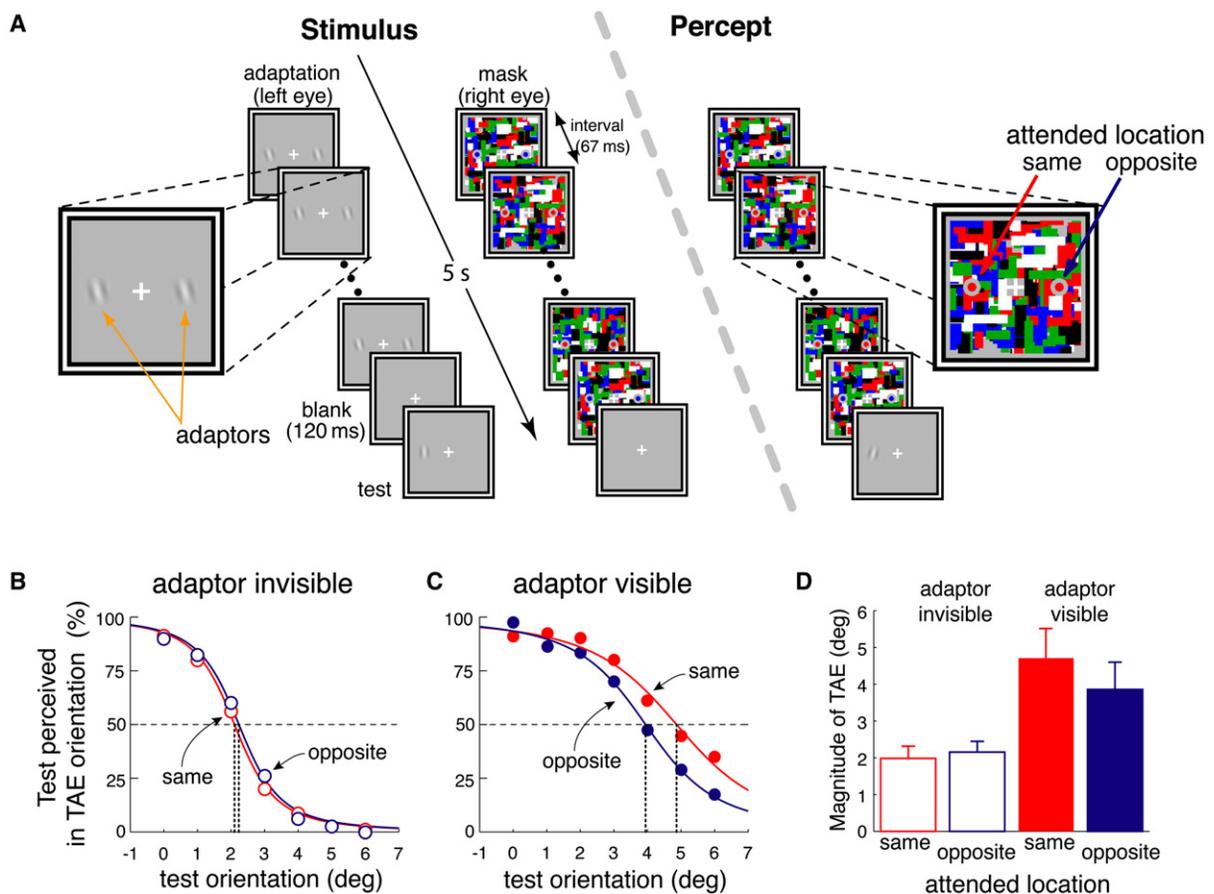
Figure 1. Stimuli and Results of the Spatial-Attention Experiment

(A) Two different sequences are dichoptically presented. On the left eye (adaptation), two oriented Gabors are presented for 5 s for inducing the TAE. These stimuli are not perceived because of the masks (Mondrian patterns) presented to the right eye. After the adaptation, a test stimulus is presented at the adapted location until a response is given.

(B) The results of the adaptor-invisible condition. The percentage of trials in which observers reported a tilt in the direction of TAE is plotted against the orientation of the test stimulus. The open red circles indicate the results of the condition in which the test was presented at the same location as the attended location, and the open blue circles indicate the condition in which the test was presented at the location opposite to the attended location.

(C) The results of the adaptor-visible condition. The solid red circles and the solid blue circles indicate the results of the attend-same and attend-opposite conditions, respectively.

(D) Summary of the results. Error bars indicate one SEM.

(visible-attended versus visible-unattended, $T(3) = 5.51$, $p < 0.05$). The attentional modulation in the visible condition ensures that the lack of attentional modulation in the invisible condition is not due to the particular parameter set used in the present experiment or to a failure of the observers to voluntarily allocate attention (more data to support this point are available in the Supplemental Data).

Feature-Based Attention Modulates TAE from Invisible Stimuli
In the second experiment, we examined whether feature-based attention can reach and modulate the TAE induced by invisible stimuli. In a previous study, it was shown that feature-based attention spreads to a brief, unattended stimulus [26], whose critical feature (i.e., motion) was presented at the subthreshold level. This suggests that feature-based attention might be able to reach processing levels where signals do not directly give rise to a conscious percept.

The design of the experiment is illustrated in Figure 2A. While adapting to an invisible adaptor presented to the left visual field of the left eye, observers continuously attended to one of the two visible targets displayed in the right visual field of the same eye (Figure 2A). One of the visible attention targets was a Gabor patch with the same tilt orientation as the adaptor, and the other target had the opposite tilt orientation. After 5 s of adaptation, a test stimulus was presented at the location of the invisible adaptor. The observers judged whether the test stimulus was tilted to the left or right. In a control experiment, we conducted the same experiment without presenting the masks and left the adapting stimuli visible to the observers (see the Experimental Procedures in the Supplemental Data for details).

The results are shown in Figure 2B. The TAE magnitude was larger ($T(3) = 6.02$, $p < 0.01$) when the attended stimulus share the same orientation as the invisible adaptor ($3.35° \pm 0.37°$) than when it had the opposite
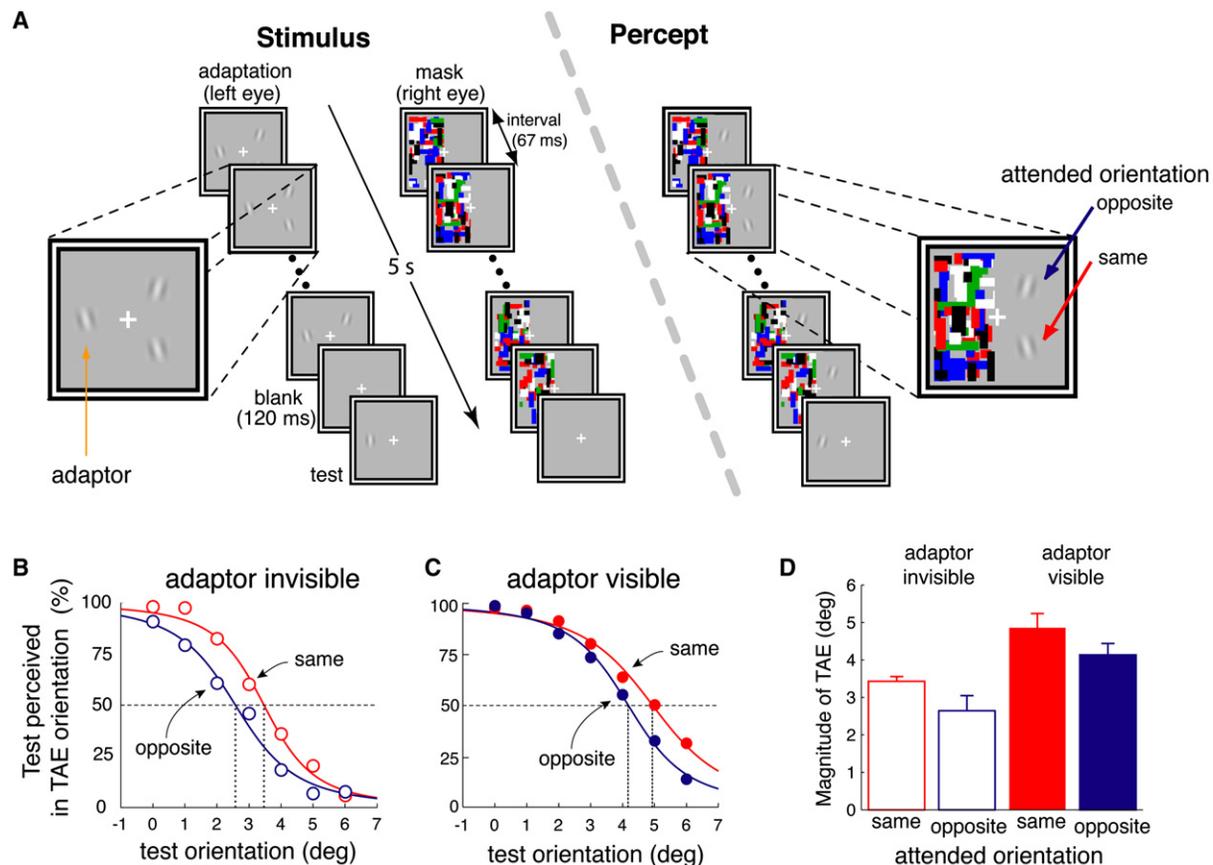
Figure 2. Stimuli and Results of the Feature-Based-Attention Experiment

(A) The adaptor was presented on the left visual field of the left eye. This was masked by the Mondrian pattern presented to the right eye. Two visible Gabors presented in the right visual field served as attention targets. One of the targets had the same tilt orientation as the adaptor (+15°), and the other had the opposite tilt orientation. A test stimulus was presented at the adapted location.

(B) The results of the adaptor-invisible condition. The percentage of trials in which observers reported a tilt in the direction of TAE is plotted against the orientation of the test stimulus. The open red circles indicate the results of the condition in which the target with the same orientation was attended, and the open blue circles indicate the condition in which the target with the opposite was attended.

(C) The results of the adaptor-visible condition. The solid red circles and the solid blue circles indicate the results of the attend-same and attend-opposite conditions, respectively.

(D) Summary of the results. Error bars indicate one SEM.

orientation ($2.54° \pm 0.08°$). As before, the invisible stimuli produced a significant TAE (attend-same, $3.35° \pm 0.09°$, paired t test against the baseline, $T(3) = 33.6$, $p < 0.01$; attend-opposite, $2.54° \pm 0.37°$, $T(3) = 6.42$, $p < 0.01$). As expected, attentional modulation was observed also in the visible condition (Figure 3C). Attending to the same-tilt target ($4.95° \pm 0.34°$) resulted in a larger TAE ($T(3) = 6.43$, $p < 0.01$) than attending to the opposite-tilt target ($4.13° \pm 0.30°$).

A two-way ANOVA revealed the main effects of visibility of the adaptor ($F(1,3) = 10.81$, $p < 0.05$) and attention ($F(1,3) = 14.51$, $p < 0.05$) but no interaction between the two factors ($F(3,3) < 1$). The main effect of visibility replicates our finding in the experiments on spatial attention; TAE is reduced when adaptors are suppressed by Mondrian patterns. The main effect of attention together with the absence of interaction confirms that the TAE magnitude both for the visible and invisible adaptors can be modulated depending on the orientation of the distant attended target. This suggests that feature-based attention has the ability to reach and modulate unconscious signals arising from invisible adapting stimuli.

The individual data for the spatial attention experiment and the feature-based attention are summarized in Figure 3. Although there is an interobserver variability in TAE magnitudes, the pattern of attentional modulation was consistent for all observers. This consistency corroborates our conclusions.

Our present study demonstrates that top-down feature-based attention but not spatial attention can modulate the TAE magnitudes to unconsciously processed visual stimuli. Previous neurophysiological and brain-imaging studies showed that spatial attention enhances the neural activity at the attended location even in the absence of physical stimuli [7, 8]. Moreover, one previous study found that attending to a spatial location invisible to a blindsight patient facilitated reaction times to the target presented at that location [24]. Despite this, we found no evidence of attentional modulation by top-down spatial selection.

According to population coding models of orientation perception, the TAE is thought to arise from an imbalance in population activity caused by selective adaptation of neurons responsive for that particular orientation
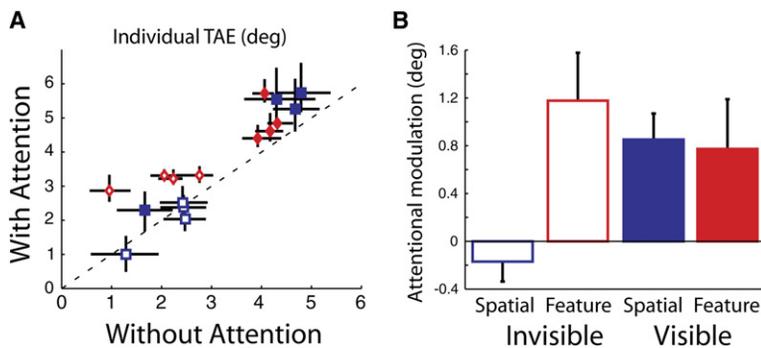
Figure 3. Comparison between Spatial Attention and Feature-Based Attention

(A) Summary of individual data. Open symbols indicate the conditions where adaptors were invisible. Blue squares denote the data points from the spatial attention experiment, and red diamonds denote the data points from the feature-based attention experiment. Data points above the diagonal line drawn along the identity indicate attentional modulation. Error bars indicate 95% confidence intervals calculated by a bootstrap method.
(B) The mean of attentional modulation (TAE magnitude for attended condition subtracted by TAE magnitude for unattended condition) across observers is summarized per condition. Error bars indicate one SEM.

[27–29]. In this sense, it is possible that spatial attention produces a generic enhancement of the entire neural population but has no influences on the TAE magnitude. Spatial attention might increase the total activity level at the attended location, but the nonselective attentional effects on the whole population do not result in a modulation of TAE magnitudes. This idea may reconcile the generic influence of spatial attention and the lack of attentional modulation for the TAE from invisible stimuli. It should be noted that our control experiment (Figures 1D) as well as a past study [30] have shown that spatial attention as such has the ability to modulate the TAE when the adaptors are visible and feature-based attention is constant. This indicates that when adaptors are visible, spatial attention as such must have orientation-selective effects, but the orientation specificity appears to be lost for invisible adaptors. It remains to be seen whether the absence of effects of spatial attention to invisible stimuli is limited to the case of TAE or generalized to other types of adaptation effects.

In contrast to spatial attention, feature-based attention did modulate adaptation to invisible stimuli and offered empirical evidence that top-down attention can be dissociated from awareness [17–19]. Other studies have found that attention can affect priming from invisible stimuli [31, 32]. These lines of evidence for the dissociation between awareness and attention implies a potential confound for neurophysiological studies searching for the neural correlates of visual awareness. Some studies use attentional modulation of neuronal activity as a marker of facilitated visual processing leading to a conscious percept (e.g., [9]). Others look for neuronal correlates of perceptual changes in effects such as binocular rivalry [33–37]. However, attentional modulation of unconscious sensory signals implies that neural activities exhibiting a percept-dependent modulation may not necessarily be directly linked with visual awareness. Instead, they could reflect the effects of attention on unconscious signals via attended or consciously perceived stimuli. As has been emphasized in recent fMRI studies [38], the dissociation of attentional effects from awareness will become essential when one tries to determine the neural activity associated with conscious percept [19].

Finally, the present study supports the notion that spatial attention and feature-based attention are based on distinct neural mechanisms [39, 40]. Electrophysiological studies have shown that the effects of spatial attention are delayed and lag behind the initial transient responses to a stimulus onset [40–42], whereas feature-based attention has both an early and continuing effect and modulates even the initial transient responses [40]. Interestingly, several lines of evidence suggest that the initial feedforward sweep elicited by a stimulus onset does not give rise to visual awareness, whereas later responses do correlate with the conscious percept [43]. Our findings and these physiological results offer interesting parallels regarding feature-based attention and early unconscious processing versus spatial attention and late conscious processing.

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