Adaptation and exogenous attention interact in the early visual cortex: A TMS study

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Summary [250/250 words]

Our capacity to process information is constrained by the limited energy available to the brain and the high energy cost of cortical computation [1]. To help manage limited resources and optimize our sensitivity to visual information, adaptation diminishes sensitivity for repetitive stimuli, whereas attention enhances the representation of relevant information [2]. Transcranial magnetic stimulation (TMS) to early visual cortex (V1/V2) eliminates the response-gain effect of exogenous (involuntary) attention on contrast sensitivity: the benefit at the attended location and the cost at the unattended location [3]. Here we investigate whether adaptation modulates the exogenous attentional effect on perception under TMS to V1/V2. Observers performed an orientation discrimination task while attending to one of two stimuli, with or without adaptation. Following a valid, neutral or invalid attentional cue, two cortically-magnified Gabor patches were presented in the stimulated region (matching each observer's phosphene location) and its contralateral symmetric region. A response cue indicated the patch whose orientation observers had to discriminate. The response cue either matched—target stimulated—or did not match—distractor stimulated—the stimulated side. Without adaptation, the exogenous attention response-gain effect emerged in the distractor-stimulated condition–increased contrast sensitivity at the attended location and decreased at the unattended location–but these effects were eliminated in the target-stimulated condition, consistent with our previous findings. Critically, after adaptation, response gain of exogenous attention was observed in both distractor-stimulated and target-stimulated conditions. These results reveal that (1) adaptation and attention interact in the early visual cortex, (2) adaptation shields exogenous attention from TMS effects.

Keywords: adaptation, contrast sensitivity, exogenous attention, phosphene mapping, psychophysics, transcranial magnetic stimulation (TMS), visual cortex

Results [2485/2,500]

We cannot process all the information available in the environment at once, given the limited metabolic resources in the brain and the high energy cost of cortical computation. To maximize perceptual performance, energy must be allocated according to task demands. Both visual adaptation and attention help manage the limited energy, optimizing visual processing and sensitivity [1,4]. These two mechanisms work in opposite directions: On the one hand, adaptation reduces the visual system's response to repetitive stimuli while enhancing sensitivity to non-adapted stimulus features [5], allowing the visual system to continuously adjust to redundancies in the environment. For example, prolonged viewing of a stimulus recenters contrast sensitivity away from the adaptor [2,5-8]. Adaptation reduces sensitivity via contrast gain: the contrast response function (CRF) shifts rightward, increasing contrast thresholds, and observers require higher contrast level to reach the same performance than before adaptation (**Figure 1A**; [2,9-12]. On the other hand, covert spatial attention–the selective processing of information at a specific peripheral location without concurrently moving our eyes–enhances contrast sensitivity [3,4,13-19]. Because orientation discriminability is contingent upon contrast sensitivity, we discriminate stimulus orientation better when attention is allocated to its location than elsewhere [2-4,13,14,20-27]. In short, visual adaptation suppresses the processing of a visual stimulus whereas attention enhances its processing [2].

There are two types of covert spatial attention: Endogenous attention is voluntary, conceptually-driven (top-down), and sustained, whereas exogenous attention is involuntary, stimulus-driven (bottom-up), and transient [4,28,29]. Visual information processing is enhanced at the attended location and impaired at the unattended location, because of a "push-pull" mechanism [3,24,30,31]. Exogenous attention primarily alters the CRF via response gain: an increase in the upper asymptote at the attended location and a decrease at the unattended location (**Figure 1B**; [3,4,13,19]). When jointly manipulated, adaptation and attention affect contrast sensitivity: while adaptation decreases contrast sensitivity via contrast gain, exogenous attention still alters sensitivity via response gain [2] (**Figure 1C**).

Transcranial magnetic stimulation (TMS) induces a magnetic field that alters the local electric field in the brain [32-37]. Effects of TMS on perceptual and cognitive performance are state-dependent [3,11,14,38-44]: when the initial state of the neuronal population is active, TMS suppresses activity, but when the initial state is suppressed, TMS disinhibits the neuronal population in motion perception [40,44], adaptation [11,39], covert attention [3,14] and presaccadic attention [43] studies [38,41,42].

We know that TMS on early visual cortex (V1/V2) extinguishes the benefit and cost exerted by exogenous attention on contrast sensitivity [3] (**Figure 1D**). In that study, observers were instructed to perform an orientation discrimination task and two TMS pulses were applied to the occipital pole while two stimuli were simultaneously presented. A response cue indicated the patch whose orientation observers had to discriminate. The response cue either matched—target stimulated—or did not match—distractor stimulated—the stimulated side. When the distractor side was stimulated, exogenous attention yielded the typical effect via response gain: benefit and cost in performance in the valid and invalid cue conditions, respectively (**Figure 1D**, solid lines). This finding is consistent with the effect of exogenous attention without TMS [13,19]. But when the target side was stimulated, the response gain was eliminated; all three conditions had similar performance (**Figure 1D**, dashed lines). This study provides supporting evidence for the state-dependent effect of TMS: suppressing activity at the attended location and disinhibiting suppressed activity at the unattended location.

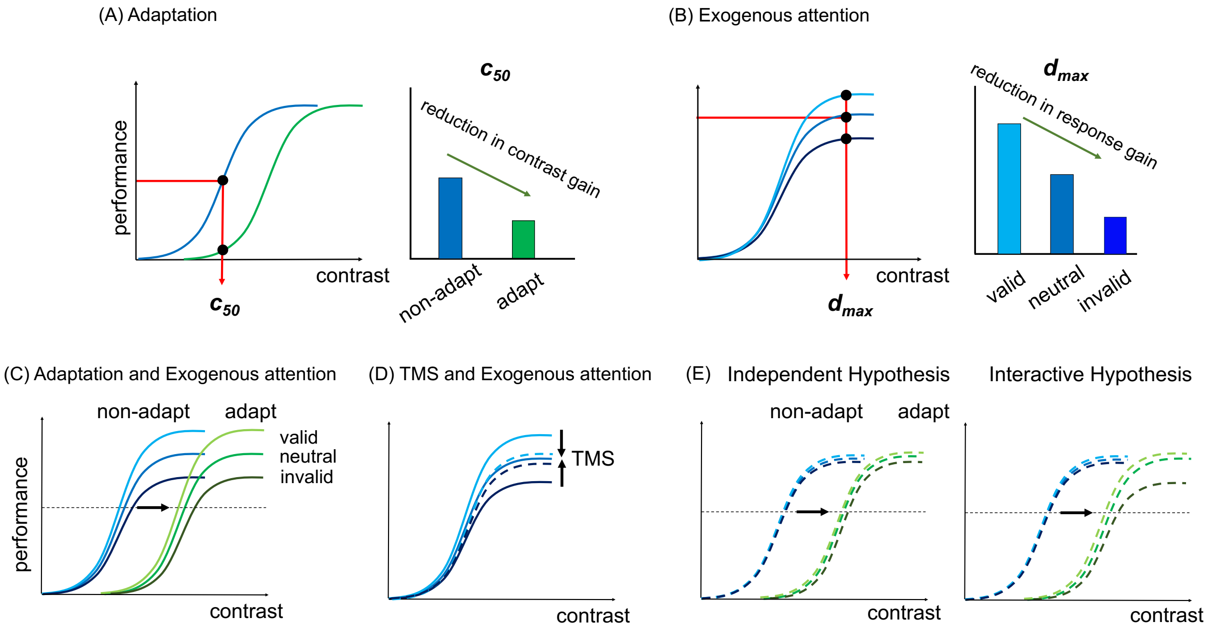

Figure 1. Effects of adaptation and attention effects on contrast sensitivity. (**A**) Adaptation reduces contrast gain: The c_{50} (semi-saturation point) is higher in the adapted than non-adapted condition [2,9-11]. (**B**) Exogenous attention modulates performance via response gain: performance at d' max (asymptote) is highest in the valid, followed by neutral and invalid trials [2-4,13,19]. (**C**) Exogenous attention restores contrast sensitivity via response gain even if adaptation depresses overall contrast sensitivity via contrast gain [2]. (**D**) TMS to the target will disrupt the response gain brought by exogenous attention [3]. (**E**) Hypotheses: If the effects of adaptation and attention are independent in the early visual cortex, we should observe that the attentional effect is still eliminated by TMS after adaptation (left panel). Otherwise, the attentional effect will still emerge under the influence of TMS after adaptation (right panel).

Both adaptation [11,39,45] and exogenous attention [3] alter activity in early visual cortex. Here, we investigated whether adaptation and attention are independent or interactive by examining if TMS eliminates exogenous attentional effects after adaptation. Were these independent processes, adaptation would not modulate the effect of TMS on exogenous attention–TMS would still extinguish attentional benefits and costs (**Figure 1E**, left panel). Were these interactive processes, adaptation would modulate the effect of TMS on exogenous attention (**Figure 1E**, right panel).

We titrated the tilt angle needed to achieve 75% correct discrimination performance and derive the semi-saturation point (c_{50}; **Figure 1A**) of the CRF for each individual. The asymptote level was set at 80% contrast for all observers (d_{max}; **Figure 1B**; see **Methods**). Ten observers discriminated whether a stimulus was tilted counterclockwise or clockwise off vertical at c_{50} or d_{max} contrasts. We tested observers' performance at these two contrasts across attention, adaptation, and TMS conditions to infer contrast gain and response gain mechanisms.

The adaptation and non-adaptation sessions were administered on different days. In the adaptation sessions, observers experienced flickering Gabors (100% contrast) followed by an attentional cue and the stimuli. In the non-adaptation sessions, the procedure was the same but without the flickering Gabors (**Figure 2A**). Observers received two TMS pulses separated by 50 ms during target presentation (**Figure 2B)**. We presented the two stimuli in the TMS stimulated region and its symmetric location in the other hemifield; the stimulus was presented for each observer according to their phosphene location (**Figure 2C**). In half of the trials, the response cue instructed observers to report the orientation of the stimulus at the stimulated region (contralateral to TMS; target-stimulated), and in the other half, the symmetric region (ipsilateral; distractor-stimulated). In each case, the test was either preceded by a valid, invalid or neutral cue, with equal probability (**Figure 2A**; see **Methods**).

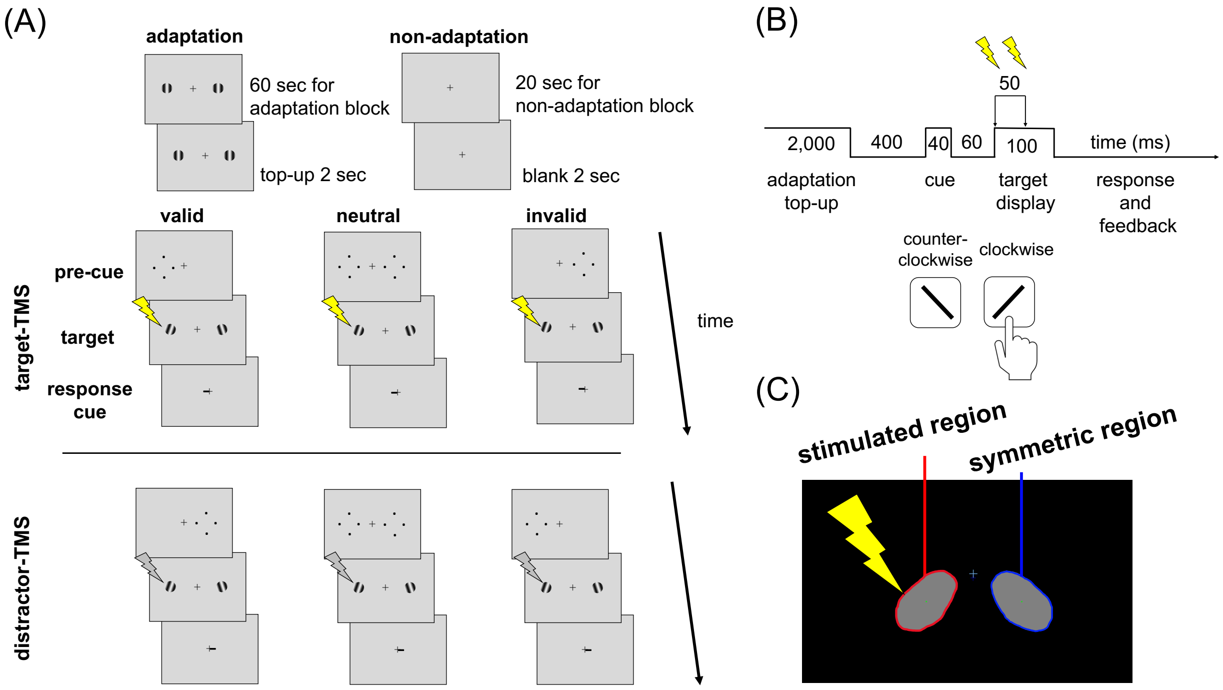

Figure 2. The Psychophysics-TMS task. (**A**) The experimental design: Observers performed the adaptation or non-adaptation blocks in different experimental sessions. In the valid trial, the peripheral cue matched the location of the response cue. In the invalid trial, the peripheral cue mis-matched the location of the response cue. In the neutral trial, the peripheral cues were shown on both sides. In the target-TMS condition (middle panel), the response cue indicated the target in the stimulated region. In the distractor-TMS condition (bottom panel), the response cue indicated the target in the non-stimulated region (and the distractor was stimulated). (**B**) Trial timeline. Two TMS pulses were given during target presentation (separated by 50 ms). (**C**) Phosphene mapping: observers were stimulated near the occipital pole before they started the psychophysics-TMS task. They were instructed to draw the perceived phosphene outline using the cursor. This phosphene mapping procedure was repeated at the beginning of every session.

The adaptation effect

To examine adaptation's effect on contrast sensitivity, we first assessed performance in the distractor-stimulated, neutral condition (**Figure S1)** –in which we neither expected an effect of TMS nor attention. A 2 (adaptation, non-adaptation) X 2 (c_{50}, d_{max}) within-subject analysis of variance (ANOVA) revealed higher performance (*d')* in the d_{max} than c_{50} conditions ($F(1,9)= 55.66$, $p<.001$) and an interaction ($F(1,9)=10.68$, $p=.01$): Performance was lower in adaptation than non-adaptation at c_{50} contrast, *d'* ($t(9)=2.98$, $p=.016$), and only marginally so at the d_{max} contrast ($t(9)=-1.9$, $p=.091$). This finding is consistent with adaptation depressing contrast sensitivity primarily via contrast gain [2,9-11].

To explore the effects of attention under different adaptation conditions, we conducted a 4-way within-subject ANOVA on attention (valid, neutral, invalid), adaptation (adapt, non-adapt), TMS (distractor-, target-stimulated), and contrast (c_{50}, d_{max}). There was no 4-way interaction [$F(2,18)=0.13$, $p=.88$], but there were 3-way interactions among attention, adaptation, and TMS [$F(2,18)=7.03$, $p=.005$] and attention, adaptation and contrast [$F(2,18)=3.82$, $p=.041$]. There were main effects of attention [$F(2,18)=6.18$, $p=.009$], adaptation [$F(1,9)=22.89$, $p<.001$] and contrast [$F(1,9)=113.4$, $p<.001$]. To interpret these 3-way interactions, we assessed the attention effect under TMS for c_{50} and d_{max} without and with adaptation.

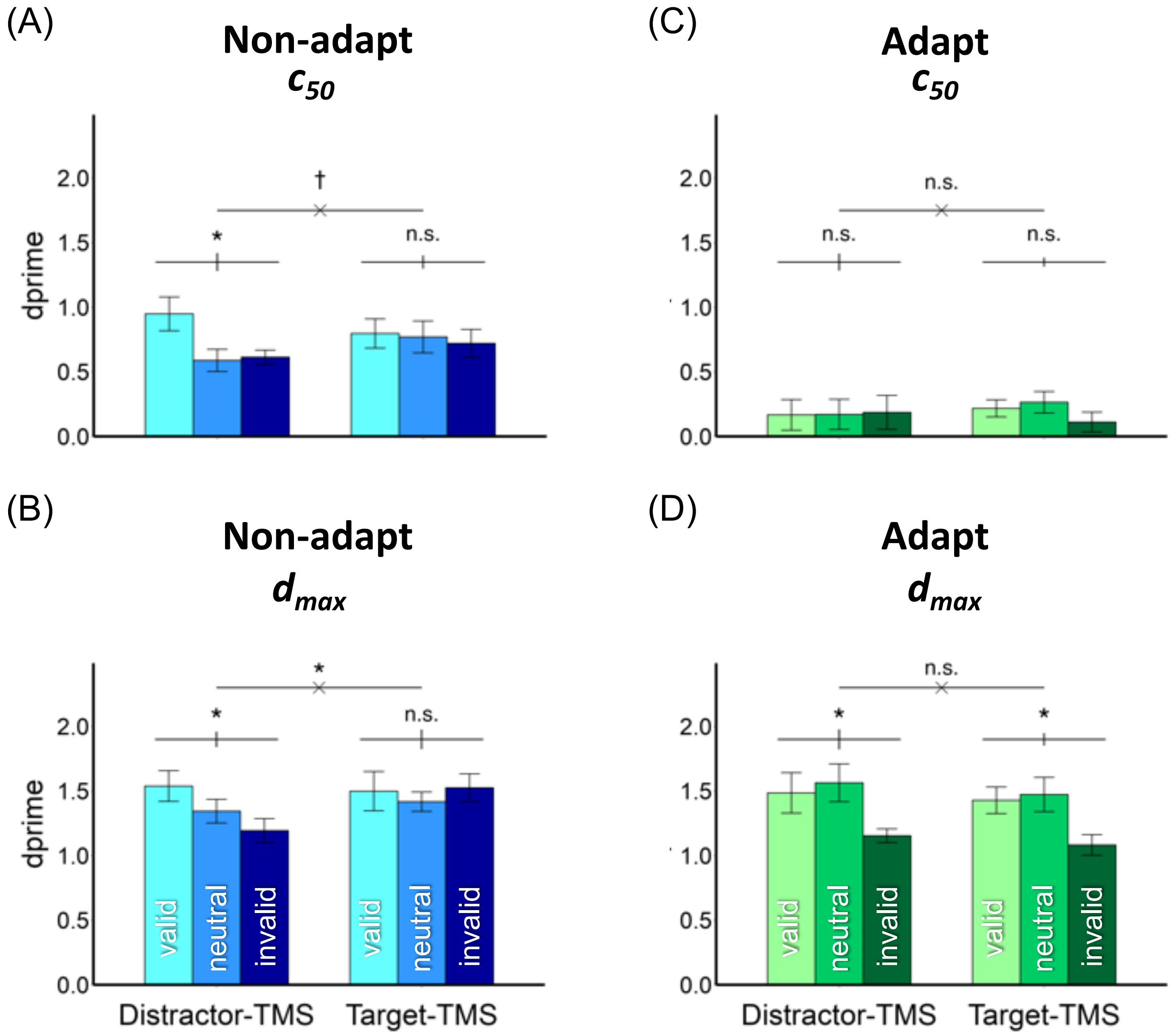

Figure 3. Performance as indexed by *d'* in the (A) non-adapt c_{50} condition, (B) non-adapt d_{max} condition, (C) adapt c_{50} condition, (D) adapt d_{max} condition. The error bars within the bar plots depict ±1 SEM (Cousineau corrected) of the condition. The error bars above the bar plots indicate ±1 SEM of the difference between the valid and invalid conditions. * $p < .05$, † $p < .1$, n.s. $p > .1$.

The attentional effect under TMS without adaptation

We examined the attentional effect without adaptation using within-subjects ANOVAs on attention (valid, neutral, invalid) and TMS (distractor-TMS, target-TMS). For c_{50} (**Figure 3A**), there was no main effect of TMS [$F(1,9)<1$], but there were a marginal main effect of attention [$F(2,18)= 2.89$, $p=.082$] and of its interaction with TMS [$F(2,18)=2.72$, $p=.093$]: the attentional effect was only observed in the distractor-stimulated (valid–invalid: $t(9)=2.42$, $p=.038$) but not the target-stimulated condition (valid–invalid: $t(9)=0.75$, $p=.47$).

For d_{max} (**Figure 3B**), there were no main effects of attention [$F(2,18)=1.24$, $p=.314$] or TMS [$F(1,9)<1$], but they interacted [$F(2,18)=4.82$, $p=.021$] because the attentional effect was observed in the distracter-stimulated condition (valid–invalid: $t(9)=2.91$, $p=.017$) but not the target-stimulated condition (valid - invalid: $t(9)=-0.17$, $p=.866$). The finding that TMS eliminated the exogenous attentional effect is consistent with Fernández and Carrasco [3].

The attentional effect under TMS with adaptation

For c_{50} (**Figure 3C**), there were neither main effects nor an interaction (all $F<1$). For d_{max} (**Figure 3D**), a main effect of attention was observed ($F(2,18)=8.03$, $p=.003$), but no effect of TMS or its interaction with attention (both $F<1$). This result indicates that after adaptation, TMS did not influence the effect of exogenous attention on contrast sensitivity.

To quantify the overall attentional effects, we calculated the difference in the valid *d'* and invalid *d'* values by conducting a 4-way ANOVA for attention (valid, invalid), contrast (c_{50}, d_{max}), adaptation (adapt, non-adapt), and TMS (target-, distractor-stimulated) conditions (**Figure 4**). There was a 3-way interaction among adaptation, attention and TMS [$F(1,9)=13.32$, $p=.005$] and a marginal interaction among adaptation, attention and contrast [$F(1,9)=3.79$, $p=.083$].

A 3-way ANOVA on adaptation, attention, and TMS condition revealed a 3-way interaction on c_{50}, [$F(1,9)=5.1$, $p=.05$] and a marginal 3-way interaction on d_{max} [$F(1,9)=3.8$, $p=.083$]. These results suggest that adaptation modulated the effect of TMS on exogenous attention.

Figure 4 shows the comparison between the attentional effect with (y-axis) and without adaptation (x-axis). In the distractor-stimulated condition, for c_{50} (**Figure 4A**), a 2-way ANOVA on adaptation and attention revealed a marginal interaction [$F(1,9)=4.2$, $p=.071$] due to an effect of attention for the non-adapted [$F(1,9)=5.88$, $p=.038$] but not for the adapted [$F(1,9)<1$] conditions. For d_{max} **(Figure 4B**), there were neither main effects nor interactions (*ps*>.1). The individual data points in the scatterplot are along the diagonal.

In the target-stimulated condition, for c_{50} (**Figure 4C**), the 2-way ANOVA revealed a main effect of adaptation [$F(1,9)=57.89$, $p<.001$], but neither a main effect of attention nor an interaction (*ps* >.1). For d_{max} (**Figure 4D**), the 2-way ANOVA revealed a marginal interaction [$F(1,9)=4.83$, $p =.056$]. Post-hoc analysis of the interaction showed that there was an attentional effect in the adapted condition [$F(1,9)=13.24$, $p=.005$] but not in the non-adapted condition [$F(1,9)<1$]. Note that in the scatterplot, most points lie in the upper left diagonal. The scatterplot here provides supporting evidence across observers that after adaptation, TMS did not eliminate the effect of attention on performance.

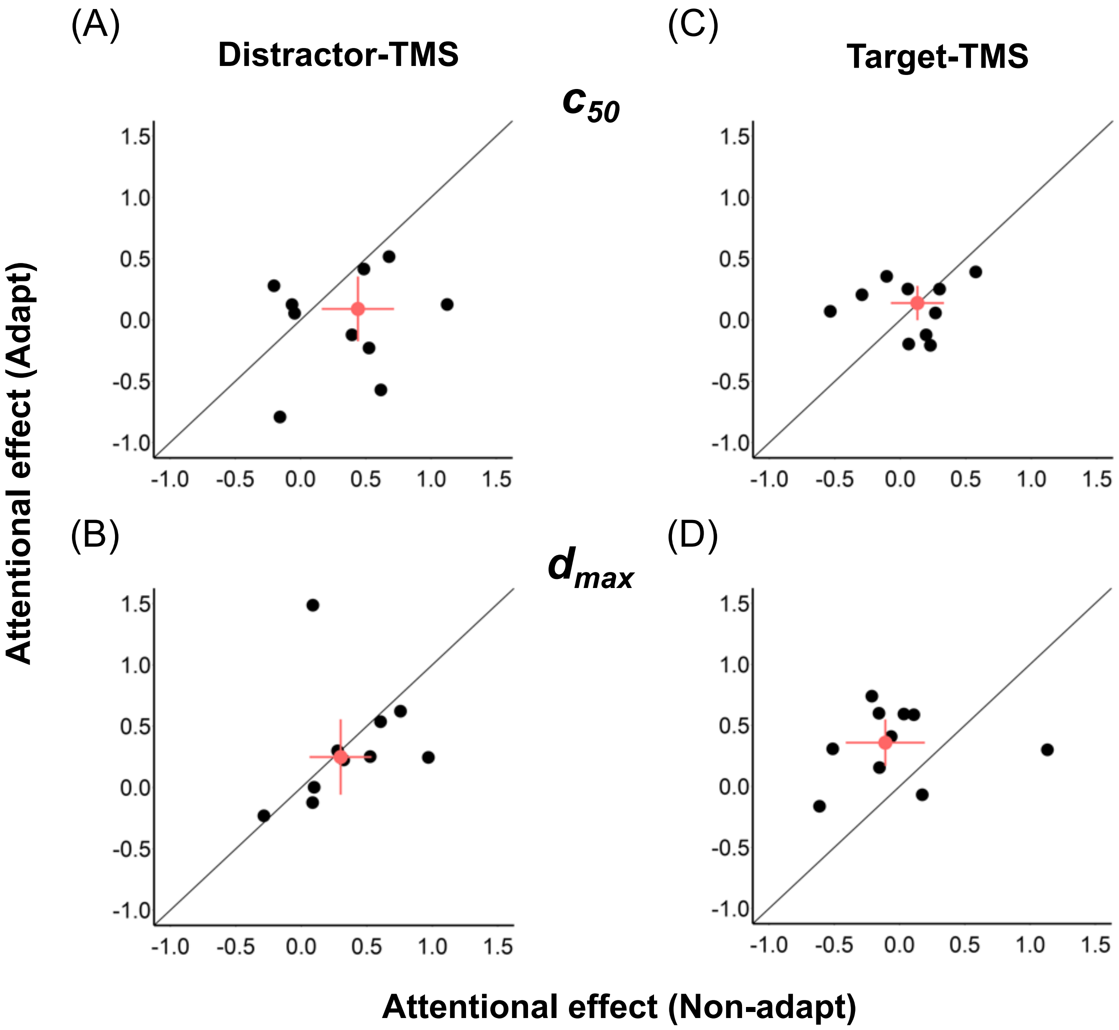

Figure 4. The attentional effect in the adapted (y-axis) and the non-adapted (x-axis) conditions for each observer in (A) distractor-TMS) c_{50}, (B) distractor-TMS d_{max}, (C) target-TMS c_{50}, (D) target-TMS d_{max}. The red circle indicates the average across observers and the error bars indicate ±1 SEM of the attentional effect.

Discussion

We manipulated brain state through visual adaptation and attention in a psychophysical experiment while applying non-invasive brain stimulation, TMS, to investigate the relation between adaptation and attention in the early visual cortex. In the distractor-stimulated condition, in which no effect of TMS is expected, we demonstrated (1) a contrast gain effect of adaptation (**Figure S1**), and (2) a response gain effect of exogenous attention (**Figure 3B**). These findings are consistent with an adaptation and attention study without neurostimulation [2]. The phosphene mapping procedure we adopted was similar to previous studies [3,14,43,46-50]. TMS-induced phosphenes are confined to the contralateral visual hemifield. Thus, the distractor-stimulated condition was an ideal control condition (see Methods) and the target-stimulated condition was the only one in which TMS disrupted target processing.

In the target-stimulated condition, (1) TMS to early visual cortex eliminated the exogenous attentional effect on contrast sensitivity (**Figure 3B**), replicating Fernández and Carrasco [3]; and

(2) adaptation eliminated the effect of TMS on attention (**Figure 3D**). These findings reveal that adaptation and attention interacted in the early visual cortex: by altering the brain state, adaptation enabled exogenous attention to exert its effects on performance and prevented it from being eliminated by TMS.

In the distractor-stimulated conditions, we observed typical adaptation and attentional effects, further indicating that it served as an ideal control condition. Specifically, adaptation shifted the CRF toward the 100%-contrast adaptor via contrast gain (**Figure 1A**) [2,9-12,51]. Additionally, exogenous attention multiplicatively enhanced the firing rate of a neuron as a function of contrast via response gain (**Figure 1B**) [31]. We also observed a contrast gain of exogenous attention in the non-adapted condition, consistent with previous studies not using TMS [2,31]. Specifically, in the distractor-stimulated condition, higher d_{max} was observed in the valid than invalid trials in both adapted and non-adapted conditions [2-4,13,19].

TMS effects on human cortex are state-dependent [3,11,14,38-44]: TMS suppresses the excitatory activity, leading to a performance decrement, and the inhibitory activity (i.e., disinhibition), leading to a performance enhancement [3,11]. In our case, when attention was deployed to the target location, neural processing was enhanced at that location and depressed elsewhere. Thus, TMS eliminated the benefits in the valid condition while restoring the cost in the invalid condition, consistent with the state-dependent effect of TMS. In the target-stimulated condition without adaptation, we replicated the extinction of exogenous attention's effects on performance, consistent with [3]. These results confirm that the early visual cortex plays a causal role in the effect of exogenous attention on contrast sensitivity.

In the target-stimulated condition after adaptation, however, the effect of exogenous attention was not eliminated by TMS. TMS decreased the performance in the valid trials but did not improve performance in the invalid trials. In the invalid adapted state at d_{max}, performance was suppressed by both adaptation and the invalid cue, thus, the brain state may have been too suppressed for TMS to enable reactivation. These results suggest that the state-dependency effect of TMS has its limits: when brain activity is suppressed to a floor level, TMS could not reactivate it. Adaptation reduced contrast gain (i.e., the performance at c_{50}; **Figure S1**), as in previous studies [2,9-12]; however, adaptation can also suppress neural activity [52,53] and behavior [54] at higher contrasts [53]. By using adaptation, attention and TMS to alter the brain state simultaneously, we provide evidence of the interaction between adaptation and attention in the early visual cortex.

It has been reported that TMS impairs performance without adaptation, but restores performance after adaptation [11]. We did not observe these effects. The following non-mutually exclusive factors may underlie this discrepancy: First, performance after adaptation at the c_{50} contrast was low. We titrated performance at ~75% accuracy for c_{50} in the non-adapted, neutral condition and tested it in the adapted condition, where the accuracy for neutral trials was 51% in distractor-stimulated and 56% in target-stimulated condition, in line with 53% accuracy for the same condition in Perini et al. [11]. Again, neural activity may have reached a floor level and could not be reactivated. Second, the protocols differed: We stimulated one of the hemispheres during the task with two pulses and the intensity ranged from 58% to 65%. Perini et al. [11] gave a single pulse at the center of the occipital pole with an intensity around 70%-80%. Third, instead of the no-TMS condition, we used a distractor-stimulated condition. Future studies can systematically examine how the protocol may influence the effects of TMS on cortical excitability and adaptation's perceptual consequences.

By altering neural activity in V1/V2 with TMS, we reveal that the effect of exogenous attention, otherwise eliminated by TMS, was preserved by adaptation. This interaction between adaptation and exogenous attention provides a possible neural correlate for the psychophysical interaction of the effect reported in texture segmentation [55], where adaptation to high spatial frequencies eliminated the effect of exogenous attention at central locations, as this task is also supported by the early visual cortex [56-60]. But adaptation and attention do not always interact at the behavioral level; they have independent effects on contrast sensitivity [2] and perceived speed [61].

We used a psychophysics-TMS protocol to investigate how adaptation modulates the effect of exogenous attention in the early visual cortex. We replicated the typical contrast gain of adaptation and response gain of exogenous attention. Importantly, the extinction of exogenous attention effects on contrast perception occurred when the target was disrupted by the TMS in the non-adaptation condition but not in the adaptation condition. We propose that the state-dependent effect of TMS has its limits, especially when the brain state may have reached a floor level. Thus, adaptation shielded the attentional effect from disruption by TMS.

METHODS DETAILS

Observers

Ten observers participated in 4 experimental sessions, which is similar to the observer number in previous TMS studies [3,39,40,43,47,48,50] All observers were naïve to the purpose of the experiment and provided informed consent before participating in the experiment. All observers were free from neurological disorders and had normal or corrected-to-normal vision. This study followed the protocol of the safety guidelines for TMS research and was approved by the University Committee on Activities Involving Human Subjects at New York University.

Apparatus

The stimuli were presented on a gamma calibrated ViewPixx LCD monitor with 120 Hz refresh rate and 1920 × 1080 resolution. EyeLink 1000 (Eyelink SR) was used to monitor observers' gaze (right eye) to make sure that observers were fixating at the fixation cross throughout the task and ensure that we were measuring a covert attentional effect. If observers moved their eyes (deviation $>$ 1 dva) or blinked during the trial, the trial would stop and be repeated at the end of the block.

Stimuli

The stimuli were generated using MATLAB (MathWorks, Natick, MA) and the Psychophysics toolbox [62,63]. The fixation cross consisted of two perpendicular lines (length=0.25 degree; width=0.06 degree) at the center of the screen. The Gabor patches (2 cpd) were presented on the left and right visual field, and the position was matched to the center of the reported phosphene by each observer [range: 4.24 – 13.77 dva away from the center]. The size of the Gabors were adjusted according to the cortical magnification factor [64] : $M = M_0(1+0.42E+0.000055E^3)^{-1}$. The attentional cues consisted of four solid black dots (0.1 dva wide), which surround the two Gabors (1 dva from the Gabor's edge, 2 above/below, 2 left/right).

Transcranial magnetic stimulation and phosphene mapping

The TMS pulses were given by a 70 mm figure-of-eight coil positioned at the occipital cortex with a Magstim Rapid Plus stimulator (3.5T) and triggered with MATLAB Arduino board.

Stimulation intensity was the same throughout the experimental sessions for each observer and determined by the individual's phosphene threshold (58%–65% of maximum stimulator output, mean = 61.3%, SD = 2.36%).

The phosphene mapping procedure was as the one used in previous studies [3,14,43,46-50]. Observers were seated 57 cm from the monitor in a dark room and were instructed to fixate at a dark-blue fixation at the center of a black background. A train of seven TMS pulses at 30 Hz and 65% intensity of the maximum output was applied on the occipital area of the scalp. Observers were instructed to draw the outline of the perceived phosphene on the screen using the mouse and the coil location was recorded accordingly. The center of the phosphene drawing was used as the coordinates of the Gabor's location in the psychophysics task, where one Gabor was presented in the phosphene region (i.e., the stimulated region), and the other was presented in the symmetric region in the other hemifield (**Figure 2C**). The phosphene threshold was determined by two pulses spaced 50 ms apart at the same coil location. The intensity of the TMS pulse was adjusted accordingly until observers reported seeing phosphenes 50% of the time. The same phosphene mapping procedure was administered at the beginning of each session. The observer's head was calibrated to match Brainsight software's 3D head template, which ensured that the stimulation was given to the same location with the millimeter level of precision.

We used a lower intensity for the psychophysics-TMS task to ensure that no phosphenes were perceived during the main experimental task (conducted on mid-gray background). During the psychophysics-TMS task, if the stimulated region matched the response-cued region, it was a target-stimulated condition; otherwise, it was a distractor-stimulated condition (**Figure 2A**).

TMS over occipital cortex affects the contralateral hemifield [3]. Thus, the distractor-stimulated condition can be considered as a control condition (similar to a no-TMS condition), and the target-stimulated condition was the one in which TMS should disrupt target processing. Importantly, in our experimental design, observers could not know whether they were experiencing a valid or invalid cue trial and whether they were in a target-stimulated or distractor-stimulated trial until the response cue appeared. Thus, the current experimental design eliminated the need for a sham condition (see [65]).

Psychophysics-TMS task

After the phosphene mapping and before performing the psychophysics-TMS task in each session, we assessed the semi-saturation point and the asymptote of the CRF (i.e., the c_{50} and d_{max}) by titrating the tilt angle and the contrast level for each observer. They participated in thresholding tasks without adaptation and attention manipulation. We first conducted an adaptive staircase procedure to determine the tilt level (0.5° to 6° relative to vertical) that corresponds to approximately 75% orientation discrimination accuracy when the Gabor patches were presented with 80% contrast using the Palamedes toolbox [66]. Then, using the tilt level obtained from this tilt staircase task, we conducted a contrast staircase and varied the contrast of the Gabor from 5% to 30% to again achieved approximately 75% accuracy using the same toolbox. The d_{max} contrast was fixed at 80% based on pilot data and previous studies [13,25]. The orientations of the left and right Gabors were independent of each other.

For the psychophysics-TMS task, **Figure 2A** shows the experimental procedure. The adaptation and non-adaptation sessions were administered on different days to ensure that the adaptation effect did not carry-over to other conditions. The order of the adaptation and non-adaptation sessions was counterbalanced between observers.

In the adaptation blocks, observers were adapted to two cortically-magnified 100%-contrast Gabor patches (2cpd) on a mid-gray background flickering for 60 seconds in a counter phase manner at 10 Hz at the beginning of each block, followed by 2 seconds of top-up before each trial started. This top-up was applied to ensure that the adaptation continued throughout the block. In the non-adaptation blocks, a mid-gray screen was presented for 20 seconds followed by 2 seconds of blank at the beginning of each trial. Observers were instructed to fixate at the center and pay attention to the flickering Gabors during the adaptation phase.

After 400 ms of inter-stimulus interval (ISI), a valid, neutral, or invalid peripheral cue (40 ms) presented around a Gabor (1 dva away from the Gabor edge), followed by a 60 ms ISI, then two Gabor patches presenting at the center of placeholders (i.e., the center of the phosphene outline) on the left and right visual fields for 100 ms. Observers' task was a two-alternative forced-choice orientation discrimination task (either counterclockwise or clockwise relative to the vertical) of the Gabor patch being indicated by the response cue, via button press. During the target presentation, observers received two single pulses (separated by 50 ms) of TMS with the power at the sub-threshold level (**Figure 2B**). A feedback tone (400 Hz, 150 ms) was given after an incorrect response.

The whole experiment consisted of 4 sessions, and each session contained 10 blocks of 48 trials. Each observer completed 1920 trials in total, which included of 80 trials per condition (two different levels of contrast: c_{50} and d_{max}; three attentional conditions: valid, neutral, and invalid; two adaptation conditions: adaptation and non-adaptation; two stimulated conditions: target-stimulated and distractor-stimulated (**Figure 2A**).

Quantification and statistical analysis

Task performance indexed by *d'* [z(hit rate) – z(false alarm rate)] across conditions. The correct discrimination of clockwise trials were considered as hits and incorrect discrimination of counter-clockwise trials were considered as false alarms [3,14,25,31].

Repeated-measures ANOVAs were administered to assess the statistical significance. ANOVAs were computed in R [67].

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