Cue-induced temporal attention affects contrast response function by response gain

Chengxu Jing
Sichuan University of Science and Engineering
Yongjie Zeng
Sichuan University of Science and Engineering
Wenxia Li
Sichuan University of Science and Engineering
Yao Chen
Shanghai Jiao Tong University
Dan Huang (danhuang81@suse.edu.cn)
Sichuan University of Science and Engineering

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Abstract

Orienting attention to a specific point in time has been shown to improve the contrast sensitivity at the attended time point and impair it earlier or later. This phenomenon could be explained by temporal attention increasing the effective contrast of target presented at the attended time point which leads to changes in contrast psychometric function by contrast gain. Another explanation is that temporal attention proportionally amplifies the amplitude of (behavioral or neural) response to contrast, resulting in alterations in contrast psychometric function by response gain. To explore the underlying mechanism, we adopted a temporal cueing orientation discrimination task using audio pre-cues composed of different frequency components to induce different attentional bias in time domain and targets of various contrast intensities to measure contrast psychometric functions. Obtained psychometric functions for contrast sensitivity were fitted for different conditions with discrepant attention states in time. We found that temporal attention manipulated by cue affected contrast psychometric function by response gain, indicating that multiplying contrast response of visual target occurring at the selected point in time by a fixed factor is a crucial way for temporal attention to modulate perceptual processing.

Introduction

There is a confliction between the numerous visual information flooding our eyes every moment and the limited resources in our brain that can be used to process them. To solve this incompatibility, a crucial procedure named selective attention is employed to select important visual information and then process it with priority while the rest is ignored. The selection by attention can be based on space to focus on the locations that most likely contain targets, on feature such as color or direction to concentrate on the traits that the targets are likely to have, or on time to attend to the moments that the targets have a high chance of occurring, termed spatial attention, featural attention, temporal attention (or temporal expectation) respectively. Because of the importance of attention in visual information processing, perception and behavior, its mechanisms have been intensively explored with psychophysical, neuroimaging and neurophysiological methods (Maunsell and Treue, 2006;Carrasco, 2011;Nobre and van Ede, 2018).

Contrast is a fundamental character of visual stimulus. How attention affects contrast sensitivity is one of the key questions in research on attention. With the increase of the contrast of a visual stimulus, the (behavioral or neural) response to the stimulus initially becomes larger and reaches a plateau after the contrast goes beyond a certain level, forming an s-shape contrast response function (CRF). In theory, when the stimulus is selected by attention, corresponding contrast response function could be modulated by attention with different patterns (Sclar et al., 1989). CRF could be shifted leftwards by attention with obvious alteration in the response to the visual stimulus with intermediate contrast and not others (contrast gain, Fig. 1B), indicating that attention acts by increasing the effective contrast of the stimulus, as if the stimulus is of higher contrast when it is attended. Attention could also drive CRF upwards with an enhancement of the response to the stimulus with a fixed scale regardless of the contrast of the stimulus (response gain, Fig. 1A), reflecting a multiplicative increase in the amplitude (not the contrast) of the attended visual signal. Moreover, attention could mediate CRF in a way just like a mixture of response and contrast gains (Fig. 1C). Empirically, different modulation patterns including response gain (Morrone et al., 2002;Ling and Carrasco, 2006;Pestilli et al., 2007), contrast gain (Reynolds et al., 2000;Martinez-Trujillo and Treue, 2002;Ling and Carrasco, 2006;Li et al., 2008) and mixture gain (Huang and Dobkins, 2005;Williford and Maunsell, 2006;Buracas and Boynton, 2007) have been found in experiments investigating spatial attention and its effects on CRF. A normalized model in which the size of attention field plays a key role has been proposed to explain the various modulation patterns revealed in distinct experiments (Reynolds and Heeger, 2009). According to this model, changing the size of attention field can lead to discrepant effects of spatial attention on CRF: when the scope of spatial attention is large and the stimulus is relatively small, spatial attention modulates the contrast psychometric function by contrast gain, while attention modulation leads to change in CRF by response gain when attention field is small combined with a comparatively large stimulus. Hence previous reported different influences of spatial attention on CRF could be due to the uncontrolled size of attention field in these studies. The predictions of the normalized model on how the size of attention field affects the pattern of the mediation of spatial attention on CRF have been verified by consequent psychophysical (Herrmann et al., 2010a) and electrophysiological studies (Itthipuripat et al., 2014). Besides spatial attention, the normalized model has also predicted that featural attention can only lead to changes in response gain regardless of the size of the featural extent of the attention field which has been also confirmed by a following empirical study (Herrmann et al., 2012). These abundant researches demonstrate the importance of exploring the effects of attention on CRF and set good examples to illustrate how this type of study can greatly deepen our understandings of the underlying mechanisms of attention in general and the distinctions among subtypes of attention.

In contrast to the plentiful studies concerning the influence of spatial and featural attention on CRF, there are few investigations about the effects of temporal attention on CRF. It is widely accepted that temporal attention can modulate visual perception. Previous studies have demonstrated that targets appearing at moments predicted by the rhythmic structure gain perceptual benefits compared with those embedded in arrhythmic structure (Mathewson et al., 2010;Cravo et al., 2013;de Graaf et al., 2013). A perceptual tradeoff has also been revealed for voluntary temporal attention, with the evidence that when attention was directed to a cued point in time, there were perceptual improvements at the anticipated time and also impairments earlier and later (Denison et al., 2017). These reported effects of temporal attention on perception only indicate that just like spatial and featural attention, temporal attention has the ability to lead to changes in CRF, but give no clue to the detailed pattern by which temporal attention alters CRF. A psychophysical study (Rohenkohl et al., 2012a) asked subjects to discriminate the orientations of targets with various contrasts that were embedded in a stream of noise patches separated by a fixed (regular condition) or jittered (irregular condition) intervals and fitted the collected behavior data with psychometric functions for contrast sensitivity for each condition. They found that temporal expectation modulated contrast psychometric function by contrast gain. Temporal attention generated in different temporal structures are functionally and neurally distinct (Coull et al., 2000;Correa and Nobre, 2008;Rohenkohl et al., 2011;Trivino et al., 2011;Breska and Deouell, 2014;Correa et al., 2014;Breska and Ivry, 2018;Amit et al., 2019). But only temporal attention generated by rhythms has been explored in this research, meaning that how temporal expectation induced in other settings (especially in cueing tasks that recruit informative cues to manipulate attention and are commonly used in researches on spatial and featural attention) influences CRF still remains unclear. Additionally, the task in their study was not rendered difficult enough such that observers' performance asymptotes were at nearly 100% accuracy (ceiling), thus leaving insufficient room for response gain (if any) to manifest itself when the targets were embedded in the rhythmic structure (see their Fig. 2a). There are limitations in previous research on temporal attention and the effect of temporal expectation on the CRF is still unknown. Answering this question is beneficial for our understanding of temporal attention and helps to form a comprehensive picture about the underlying mechanisms of attention and whether these mechanisms parallel those found in spatial and featural attention.

In the aim of investigating how cue-induced temporal expectation affects CRF, we adopted a temporal-cueing paradigm with audio cues composed of different frequency components to direct attention to distinct points in time, combined with the variations in the stimulus contrast to gain psychophysical functions under different attentional states. Computational modeling and fitting were conducted to determine how CRFs were altered by temporal expectation.

Methods

Observers. Seven subjects (age 20–23 years, 5 males, 2 female) participated in the experiments. All subjects were naïve to the purpose of the experiments. They had normal or corrected-to-normal vision and provided informed consent. All experimental procedures were conformed to the ethical standards of the Ethical Committee of Sichuan University of Science & Engineering and the guidelines of the Declaration of Helsinki. The number of subjects in the present study was comparable to those listed in previous studies investigating effects of attention on CRF (Ling and Carrasco, 2006;Herrmann et al., 2010a). According to a research on psychophysical statistics (Anderson and Vingrys, 2001), the significant effect revealed with this sample size exists in the majority of the average population.

Apparatus. A gamma-corrected 23.8-inch liquid crystal display (LCD) monitor (TITAN ARMY, T24FG, Shenzhen, China, 1920 × 1080 pixels, 100 Hz refresh rate) was used to display the visual stimuli with a mean luminance of 15.5 cd/m^2. The subject was seated 57 cm in front of the screen with his/her head stabilized by a chin rest. The eye movements were monitored by an infrared imaging-based eye tracker (Tobii X60; Tobii Technology AB, Stockholm, Sweden). Stimulus presentation and data collection were achieved using MATLAB (MathWorks) with Psychtoolbox extension (Brainard, 1997;Pelli, 1997). Audios were presented via the computer speakers. Data analyses were conducted with the Statistical Package for Social Sciences (SPSS, Inc.) and OriginPro software (OriginLab Corporation).

Stimuli and Procedure. Stimulus placeholders being presented throughout all trials and experimental sessions were used to eliminate spatial uncertainty and assist fixation which were corners of a 2º×2º grey square outline centered on the center of the screen with a width of 0.08º(Fig. 2A). Subjects were instructed to fixate within the square enclosed by the placeholders while performing the task. An audio pre-cue was played for 200 ms to signify the start of a trial. The pre-cue could be high-frequency (4800 Hz) or low-frequency (600 Hz) pure tone, or their combination. 1000 ms after the pre-cue, a target (T1, a Gabor patch, 3º×3º,σ = 0.4°, 4 cycles/deg) was presented for 30 ms which was located within the placeholders and at the center of the screen. The Gabor was tilted slightly away from either horizontal or vertical (randomized on each trial). 250 ms after the disappearance of T1, another target (T2) appeared on the screen with all settings same as the preceding one. Tilts and axes were independent for T1 and T2. An audio response cue (pure tone of high-frequency with 4800 Hz or low-frequency with 600 Hz) with 200 ms duration was played 500 ms after the vanishing of T2. Observers were instructed to discriminate the orientation of the target indicted by the response cue (report T1 for high-frequency response cue, report T2 for low-frequency response cue) and press key '6' if this target was tilted clockwise (CW) from its closest cardinal axis (i.e. horizontal or vertical), or press key '4' if the tilt was counter-clockwise (CCW) (Fig. 2B). A visual feedback was sent at the center of the screen (correct: a green cross; incorrect: a red line) after the key response. The next trial began after a random intertrial interval (ITI) between 1000 to 1500 ms. Those trials that had reaction times (time interval between the response cue and the response onset, RT) shorter than 150 ms were considered as incorrect to prevent guessing. Trials with fixation breaks (the fixation went outside a 2° window) were stopped immediately without being counted and repeated at the end of the run. Accuracy was emphasized for performing the task. The purpose of adopting two options (vertical and horizontal) for main axes of Gabor patches was twofold: firstly, decreasing the number of trials in which T1 and T2 were same; secondly, preventing observers from implementing a tactic of judging whether the two consecutive Gabor stimuli were identical or different and using this information to benefit orientation discrimination.

The audio pre-cue was adopted to introduce a temporal attentional bias to T1 or T2 or none of them when the subject was performing orientation discrimination task. Depended on the relationship between the pre-cue and the response cue, the pre-cue was valid if the two were matched and was invalid if the two were not of the same type. The pre-cue which was a mixture of the high-frequency and low-frequency tones was neutral and provided no useful information on which of the upcoming targets should be paid attention to. The pre-cues were valid/neutral/invalid in 60%/20%/20% of the total trials. Before experiments got started, subjects were explicitly told that the pre-cues were informative regarding the targets whose orientation would be discriminated and reported at the end of each trial and that there was a benefit in using the pre-cues to perform the task.

The contrasts of T1 and T2 within a trial were the same but varied from trial to trial. To obtain a complete contrast response function, in each trial the contrast for the two targets was randomly chosen from a set of contrasts ranging from 6 to 67% in 7 log increments.

In a pretest, each observer's orientation discrimination threshold for the tilt of Gabor patch from its main axis was measured with a three-down one-up staircase procedure to find out the 79%-correct points for the discrimination. The threshold value of each subject were used as the tilted angles of Gabor to its main axis in the following formal experiments. 2800 ~ 3920 trials were collected per subject.

Data Analysis and Statistics. For each subject, perceptual sensitivity values (d') and reaction times were assessed for each pre-cueing condition (valid, invalid and neutral) and for each contrast level. Sensitivity was calculated according to the formula:

$$d' = z[hitrate] - z[falsealarmrate]$$

where z corresponds to the inverse normal (z score). A correct response to the tilt of the stimulus relative to its closest cardinal axis was regarded as a hit (for example key press “6” to a clockwise tilt to the main axis) while a wrong reply (such as key press “4” to a clockwise tilt) was considered as a false alarm.

For each pre-cueing condition and for each contrast level, the mean sensitivity value across subjects was calculated. The averaged d' values were fitted (via nonlinear least-squares) to the Naka–Rushton contrast response model (Albrecht and Hamilton, 1982;Sclar et al., 1990) :

$$d'(\mathrm{c}) = \frac{d_{max} * c^n}{c^n + c_{50}^n} + M$$

where $d'(\mathrm{c})$ represents sensitivity d' as a function of contrast c, c_{50} is the contrast corresponding to half the saturating response (threshold), n is the exponent which determines the slope of the function, d_{max} controls the asymptote performance at high contrasts, and M represents the response at the lowest contrast level which is 0 for d'. c_{50} and d_{max} are free parameters varied for different pre-cueing conditions (valid, invalid and neutral), while the exponent n was treated as one free parameter, constrained to have the same value across conditions.

The confidence intervals of the fitted d_{max} and contrast c_{50} was determined by a bootstrap procedure (Fig. 3A). In detail, a resampled dataset was generated by randomly resampling with replacement of individual psychophysical trials, which was refitted subsequently. We repeated this procedure involving resampling and refitting 1000 times to generate bootstrap distributions of the fitted parameters from which the confidence intervals for each parameter were extracted. Another bootstrap procedure (Yuval-Greenberg et al., 2014;Grubb et al., 2015) was used to determine whether there were significant changes in two key parameters (d_{max}, c_{50}) between two discrepant pre-cueing conditions (such as trials with valid versus invalid pre-cues). Specifically, we randomly shuffled the labels of these two conditions to be explored, separately for each contrast level, and separately for each subject. Based on the new labels, the shuffled data was refitted to yield new parameter estimates for d_{max} and c_{50} for each pre-cueing condition respectively, followed by the calculation of the difference in d_{max} and c_{50} between these two conditions. After 1000 times repetition of this procedure, a null distribution for the difference of d_{max} between trials with valid and invalid pre-cues was generated. The difference in d_{max} observed in our actual experiment was then compared with the null distribution. The P-value reported is the proportion of null distribution values greater than or equal to the actual change in d_{max} to reflect the probability of response gain change. P-value for the difference in c_{50} was computed in a same manner except that the

P-value reported is the proportion of null distribution values less than or equal to the actual change in c_{50} to illustrate the likelihood of contrast gain change.

Results

Based on assessment, best-fitting value for the exponent of the psychometric functions was 1.55 for our data (**Supplementary Fig. 1**). We also used the reported exponent values in previous researches measuring contrast-response functions psychophysically and electro physiologically (Sclar et al., 1990;Herrmann et al., 2010a) and got the same results (data not shown).

Cue-induced Temporal Attention Modulates Contrast Perception By Response Gain

Considering the main purpose of assessing the modulation of temporal attention induced by the pre-cue, data were collapsed across the reported targets. The mean contrast response functions under discrepant pre-cueing conditions (valid, invalid, neutral) were shown in Fig. 3A. It could be seen that no matter what the pre-cue was, d' increased with the increase of target contrast and saturated at high contrast, forming a typical s-shape curve. Importantly, the two psychometric functions representing perceptual sensitivity under valid and invalid pre-cueing conditions were not overlapped with each other but had an order with the one obtained in trials with valid pre-cues being always above the line indicating invalid pre-cueing condition. The curve depicting the neutral condition constantly laid between the other two psychometric functions. The clear separation of these three functions demonstrates the influence of temporal attention on the perception of contrast.

A decrease in threshold c_{50} with no change in asymptote d_{max} induced by attention is typical in contrast gain model while response gain model is characterized by an attentional boost in asymptote d_{max} in concomitant with no alternation in c_{50}. The parameters of the fitted psychometric functions representing trials with discrepant (valid/neutral/invalid) pre-cues were compared to determine how cue-induced temporal attention affects perceptual sensitivity. c_{50} values for valid, neutral and invalid pre-cues were 0.111 (90% confidence interval = [0.101, 0.124]), 0.118 (90% confidence interval = [0.094, 0.151]), 0.119 (90% confidence interval = [0.085, 0.163]) respectively (Fig. 3A, left column) and were not significant different from each other (valid vs. neutral, $p = 0.627$; valid vs. invalid, $p = 0.578$; neutral vs. invalid, $p = 0.961$). The scenario was different for d_{max} (Fig. 3A, left column). The d_{max} value of CRF representing valid pre-cue was 2.55 (90% confidence interval = [2.45, 2.64]), which was not only significantly larger ($p < 0.001$) than its counterpart (1.26, 90% confidence interval = [1.10, 1.42]) obtained under invalid pre-cueing condition but also differed significantly ($p < 0.001$) from the d_{max} value of the CRF under neutral pre-cueing condition (1.79, 90% confidence interval = [1.64, 1.94]). Additionally, there was significant difference ($p < 0.001$) between the d_{max} values of the two CRFs under neutral and invalid pre-cueing conditions. For the psychometric functions from individual observers, a one-way ANOVA for repeated measures was used to analyze the influence of temporal attention induced by cue by including pre-cue type as the factor (valid, invalid, neutral). Pre-cue type did not show significant influence on c_{50} values ($F(1,6) = 0.420$, $p = 0.541$; Fig. 3A middle column) while d_{max} values were affected significantly by pre-cue type ($F(1,6) = 12.059$, $p = 0.013$; Fig. 3A right column). These observed effects of attention modulation on d_{max} in combination with the fact that no influence of attention was found on c_{50} from both the averaged and the individual data indicate that temporal attention induced by cue modulates perceptual sensitivity d' via response gain. Furthermore, the revealed differences in perceptual sensitivities between the valid and neutral pre-cueing conditions illustrate the enhancement of temporal attention on the perception of the attended target (attentional benefit) while the discovered decrease in perceptual sensitivity when the temporal cue was invalid compared with the neutral pre-cueing condition demonstrates the impairment of temporal attention on the perception of ignored distractors (attentional cost).

Previous study using similar paradigm to investigate the effect of temporal attention on sensitivity has demonstrated that sensitivity d' was comparable for T1 and T2 (Denison et al., 2017). We also divided our data based on whether the reported target was T1 or T2 and analyzed the CRFs of the two subgroups for each pre-cueing condition to assess whether temporal attention modulated the perception of T1 and T2 with the same pattern. Regardless of the reported target, the CRF denoting perceptual sensitivity under valid pre-cueing condition was always at the top, with the psychometric function representing neutral pre-cueing condition in the middle and the curve describing invalid pre-cueing condition at the bottom of the three (Fig. 3B left column, Fig. 3C left column). When the reported target was T1, the c_{50} values for different pre-cueing conditions were quite similar (valid: 0.111, 90% confidence interval = [0.095, 0.129]; neutral: 0.114, 90% confidence interval = [0.079, 0.164]); invalid: 0.097, 90% confidence interval = [0.057, 0.151]) (Fig. 3B, left column) and did not differ significantly from each other (valid vs. neutral, $p = 0.897$; valid vs. invalid, $p = 0.466$; neutral vs. invalid, $p = 0.667$). However, CRFs representing discrepant pre-cueing conditions had significantly different d_{max} values (valid vs. neutral, $p < 0.001$; valid vs. invalid, $p < 0.001$; neutral vs. invalid, $p < 0.001$) with the largest d_{max} value under the valid pre-cueing condition (2.50, 90% confidence interval = [2.35, 2.67]), the smallest d_{max} value under invalid pre-cueing condition (1.09, 90% confidence interval = [0.93, 1.30]) and the medium d_{max} value when the pre-cue was neutral (1.68, 90% confidence interval = [1.47, 1.98]). The analyze of one-way ANOVA for repeated measures showed that pre-cue type did not significantly impact c_{50} value ($F(1,6) = 0.03$, $p = 0.868$; Fig. 3B middle column) but had significant influence on d_{max} value ($F(1,6) = 23.40$, $p = 0.003$; Fig. 3B right column). Same pattern was found when T2 was the reported target. There were no significant differences (valid vs. neutral, $p = 0.509$; valid vs. invalid, $p = 0.075$; neutral vs. invalid, $p = 0.435$) among the similar c_{50} values of different pre-cueing conditions (valid: 0.112, 90% confidence interval = [0.096, 0.126]; neutral: 0.122, 90% confidence interval = [0.091, 0.167]); invalid: 0.147, 90% confidence interval = [0.094, 0.228]) (Fig. 3C, left column) but the d_{max} values for discrepant pre-cueing conditions (valid: 2.59, 90% confidence interval = [2.45, 2.74]; neutral: 1.90, 90% confidence interval = [1.69, 2.20]); invalid: 1.46, 90% confidence interval = [1.21, 1.79]) differed significant from each other (valid vs. neutral, $p < 0.001$; valid vs. invalid, $p < 0.001$; neutral vs. invalid, $p = 0.014$). Meanwhile, the significant impact of pre-cue type on d_{max} was observed with one-way ANOVA for repeated measures ($F(1,6) = 4.14$, $p = 0.043$; Fig. 3C right column) but pre-cueing method was not a significant influential factor for c_{50} ($F(1,6) = 1.13$, $p = 0.330$; Fig. 3C middle column). Based on these results, it could be concluded that temporal attention induced by cue modulated psychometric function by response gain no matter the reported target was T1 or T2, indicating the independence of the modulation pattern on the order of the reported target.

Together, these results illustrate that in our experiment perceptual sensitivity for contrast was modulated by temporal expectation which was manipulated by cue. Additionally, our data was fitted by response gain model but not contrast gain model or the mixture model. Meanwhile, our data also showed perceptual tradeoffs due to temporal attention, illustrated by the enhanced perceptual sensitivity for the target occurring at the attended time point and the worsened perception for the distractor happening at the unattended time point.

Impacts Of Cue-induced Temporal Attention On Reaction Time

The effects of cue-induced temporal attention on RT were also observed with a similar pattern as for perceptual sensitivity d'(Fig. 4), illustrated by fastest RTs on trials with valid pre-cues (Mean ± SEM: 0.511 ± 0.015 s), slowest RTs on trials that were invalid pre-cued (0.645 ± 0.019 s), and intermediate RTs on neutral trials (0.538 ± 0.008 s). The mean RTs of different conditions were submitted to a three-way analysis of variance (ANOVA) for repeated measures with pre-cue type (valid, invalid, neutral), target contrast (seven levels) and reported target (T1, T2) as three factors. It was not surprising that significant main effect of pre-cue type was observed ($F(2,12) = 55.440$; $p < 0.001$). There was also a significant main effect of reported target ($F(1,6) = 7.967$; $p = 0.028$), reflecting a faster discrimination for tilt of T2 than T1(Fig. 4B, C), which might be due to subject being more prepared for orientation discrimination at the appearance of late T2 than early T1. No significant main effect of target contrast was found ($F(6,30) = 3.290$; $p = 0.399$), indicating that in our experiment RT was not influenced by the contrast of target, and other factors that could lead to changes in RT such as motor preparation (Correa, 2012) or criterion changes (Carrasco & McElree,2001) played more influential roles on RT. The two-way interaction effects of the three pairs were not significant (Pre-cue type × Target contrast: $F(12,72) = 1.301$, $p = 0.303$; Pre-cue type × Reported target: $F(2,12) = 3.973$, $p = 0.064$; Target contrast × Reported target: $F(6,36) = 2.554$, $p = 0.093$). The three-way interaction effect of all three factors was also not significant ($F(12,72) = 1.297$; $p = 0.307$).

The results on RT demonstrate that the observed changes in contrast sensitivity induced by temporal attention could not be attributed to speed-accuracy tradeoff.

Discussion

In the present study, we demonstrate that directing attention to a pre-cued time point affects the perception of relevant events with enhanced contrast sensitivity for the target occurring at the attended time (attentional benefit) and deteriorated contrast sensitivity for the distractor happening at the unattended time (attentional cost). Importantly, we compare the psychometric functions for contrast sensitivity when attention was directed to different time points by temporal cue, and find that this cue-induced temporal attention results in an upward shift in the psychometric function, a typical characteristic of response gain model of attention, indicating that temporal attention can modulate visual perception by proportional scaling of the response to contrast.

According to distinct criterions, temporal attention can be further divided into different subclasses. There are four types of well-known temporal structures that temporal expectation can be generated from: 1) associations, characterized by predictive temporal relations between successive stimuli (Griffin et al., 2002;Jaramillo and Zador, 2011;Denison et al., 2017); 2) hazard rates, meaning that the probability of the occurrence of an event varies over time in a predictive manner (Ghose and Maunsell, 2002;Cravo et al., 2011); 3) rhythms, with repeated temporal structure composed of simple events(Jones, 1976;Rohenkohl et al., 2012b); 4) sequences, with complex recurring temporal structures (Nobre and van Ede, 2018). In the present study, an audio pre-cue was used to indicate the time of the appearance of the target to be reported. Clearly, there was a strong temporal association between the pre-cue and the behavioral-relevant target in our temporal cueing experiment, with no existence of repetitive temporal structure in a trial and the likelihood of target occurrence did not change over time. A distinction between endogenous (also referred to goal directed, controlled or top-down) and exogenous attention (also named as stimulus driven, automatic, bottom-up) in the temporal domain has also been suggested and empirically investigated (Coull and Nobre, 2008;Rohenkohl et al., 2011) with the former being generated spontaneously by exposure to stimuli with rhythmic or predictable temporal structure and the later directing attention to specific time by informative cue. Obviously, the cue-induced temporal expectation in our study was driven by goal and should be categorized as endogenous attention. This elucidation of the type of temporal attention explored in our study is especially important when comparing our study with other researches.

Regardless whether it is driven by goal or external stimulus and no matter what temporal structure it is generated from, the ability of temporal expectation to affect visual perception is well recognized. A typical illustration is the widely observed high and low perceptual sensitivities for the events occurring at the anticipated and the unexpected time respectively ascribed to the modulation of temporal attention (Correa et al., 2005;Rohenkohl et al., 2014;Denison et al., 2017). Our study adds new empirical evidence for the power of temporal attention to modulate perception which includes the boost for the attended target and the suppression for the disregarded distractor. In addition, our work goes further than previous researches and extends to a follow-up question: how does temporal attention exert its effect on visual perception? Our results show that temporal attention induced by cue affects contrast psychometric function by response gain, indicating that temporal attention proportionally amplifies the responses to stimuli as a function of contrast intensity which consequently leads to changes in perceptual processing for visual stimuli. However, Rohenkohl and colleagues have observed the typical phenomenon of contrast gain in their behavioral study on temporal attention-a leftward shift of the contrast psychometric function induced by temporal attention, illustrating that temporal expectation enhances the effective contrast of attended target to modulate perception (Rohenkohl et al., 2012a). This discrepancy could be due to distinct ways of manipulating temporal attention in these two studies. In our study, an audio pre-cue was used to direct attention to the first or second visual stimulus of the incoming short sequence of two visual targets with predictable timing. In the work of Rohenkohl, temporal expectation was manipulated by rhythmic stimulation, with the targets being embedded in a stream of rhythmic (with fixed interstimulus interval) or arrhythmic (with variable interstimulus interval) noise patches. The time of the occurrences of targets could be anticipated when the stream of stimuli was periodic but could not be expected for the stream without rhythm. Previous works have provided evidence supporting that temporal expectations generated by cues and rhythmic stimuli emerge from different mechanisms (Rohenkohl et al., 2011;Trivino et al., 2011;Breska and Deouell, 2014), which can lead to the discrepant modulation patterns of temporal attention observed in our study and the work of Rohenkohl and coworkers. Moreover, in the work of Rohenkohl, the performance accuracies of subjects almost reached ceiling level (100%) when the target had high contrast intensity, leaving no space for response gain to present itself. This possible ceiling effect makes their observed contrast gain change in contrast response function by temporal attention debatable. Given all these probable explanations, further investigation is needed to determine the actual source for the difference between the results of our study and theirs.

The effect of modulation of temporal attention on contrast psychometric function could be impacted by many factors. Figuring out these influential factors is another related and important question. The size of the temporal extent of the attention field is one factor that need to be paid attention to. Studies on spatial attention have demonstrated that the stimulus size and the relative size of the spatial scope of attention can determine whether spatial attention modulates CRF by contrast or response gain. A research on featural attention has found that unlike spatial attention, featural attention leads to changes in response gain regardless of the size of the featural extent of the attention field. In light of these previous studies, it is natural to ask whether changing the size of the temporal extent of the attention field can lead to changes in the pattern of gain effects in psychometric functions. The present study does not provide direct answer to this question, even though in our experiment, subjects needed to attend to both of the two stimuli (T1 and T2) occurring at different times when the pre-cue was neutral but only focused on one event (T1 or T2) in trials with invalid or valid pre-cues, meaning that the temporal extent of the attention field under neutral condition was broader than under other conditions. It is promising for future study to systemically vary the size of the temporal extent of the attention field and explore the changes in the attention gain effects in psychometric functions. Besides the size of temporal extent of the attention field, the type of temporal structure is another possible influential factor worthy of further investigation. As above-mentioned, temporal attention generated by different temporal structures originate from distinct underlying mechanisms. Rigorous experiments are needed to examine whether these subtypes of temporal attention affect psychometric functions with the same pattern.

Other studies have investigated the modulation patterns of cue-induced spatial (Herrmann et al., 2010b) and feature attention (Herrmann et al., 2012) on CRFs and find that these types of attention can alter the contrast psychometric function by response gain. Combined our study with these previous works, it can be seen that enhancing the contrast response of stimulus proportionally is a general mechanism for cue-induced attention to modulate contrast perception. Moreover, the amplitude of the modulation of temporal attention on contrast sensitivity observed in our study is comparable to the strength of the effect of spatial attention on CRF revealed in the research of Herrmann and coworkers (Herrmann et al., 2012), which demonstrates that attention that is non spatial can modulate perception with the same power as the spatial attention.

In conclusion, our results provide empirical evidence that temporal attention manipulated by cue affects contrast psychometric function by response gain, indicating that temporal attention can multiplicatively boost the contrast response of stimuli appearing at the attended time to shape visual perception.

Declarations

Ethics approval and consent to participate:

All participants provided informed consent. All experimental procedures were conformed to the ethical standards of the Ethical Committee of Sichuan University of Science & Engineering (Approval number: 20210758) and the guidelines of the Declaration of Helsinki.

Consent for publication:

All authors gave final approval for publication.

Competing interests:

The authors declare no competing financial interests.

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Data availability statement

All data, or code generated or used during the study are available from the corresponding author upon reasonable request.

Authors’ contributions

D.H. devised the project, and drafted the manuscript; C. J. and Y. Z. collected the data, carried out the data analyses; W. L. and Y. C. participated in the design of the study and helped write the paper.

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Figures

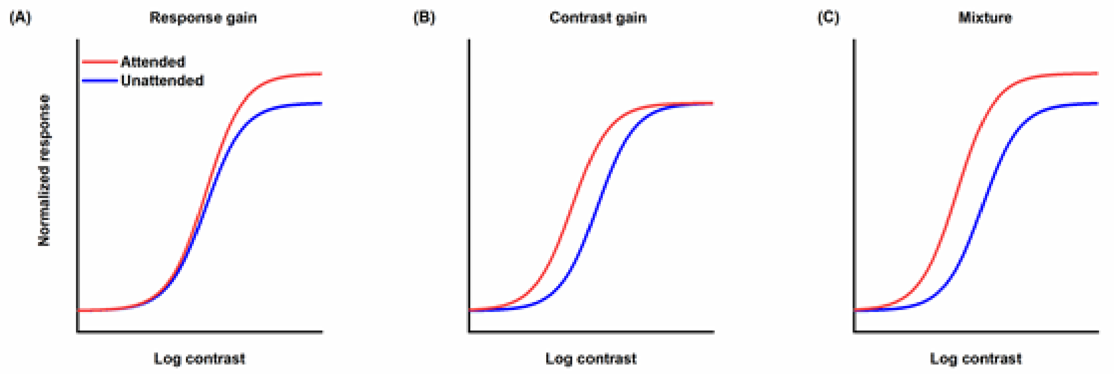

Figure 1

Different forms of the effects of attention modulation on contrast response function. **(A)** Response gain. **(B)** Contrast gain. **(C)** A mixture of response and contrast gains. Red lines represent responses as a function of contrast when stimuli are attended. Blue lines denote responses to unattended stimuli.

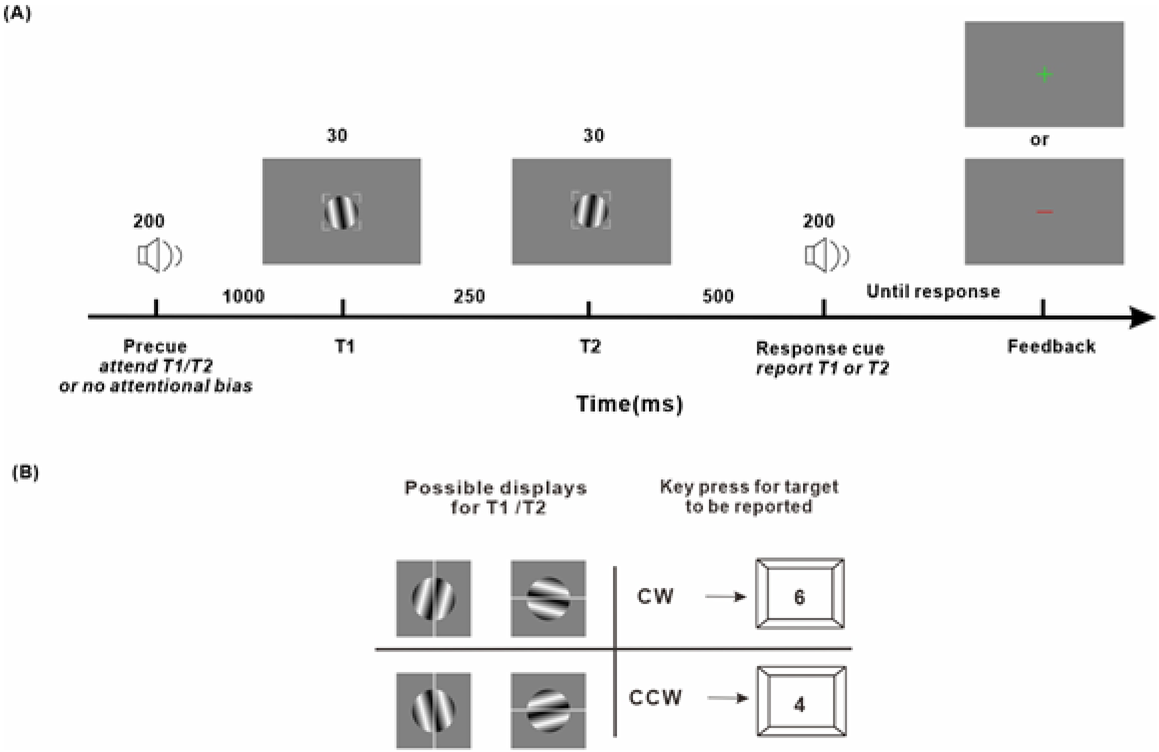

Figure 2

Experiment protocol and response strategy. **(A)** Trial sequence. Observers were asked to judge the tilt (clockwise or counter-clockwise) of a sinusoidal grating patch (T1 or T2, indicated by the response cue) with respect to its main axis. **(B)** Stimulus display and response scheme. Observers discriminated clockwise versus counter-clockwise tilts relative to either the vertical or horizontal axis depending on which was the closest cardinal axis of the target to be reported (indicated by gray line for demonstration purpose and not shown during the experiment). Press key “4” if the tilt was CCW while press key “6” if the tilt was CW. All stimuli, pre-cues and response cues were presented in randomly interleaved trials. Tilt magnitudes were determined for each observer using a staircase procedure.

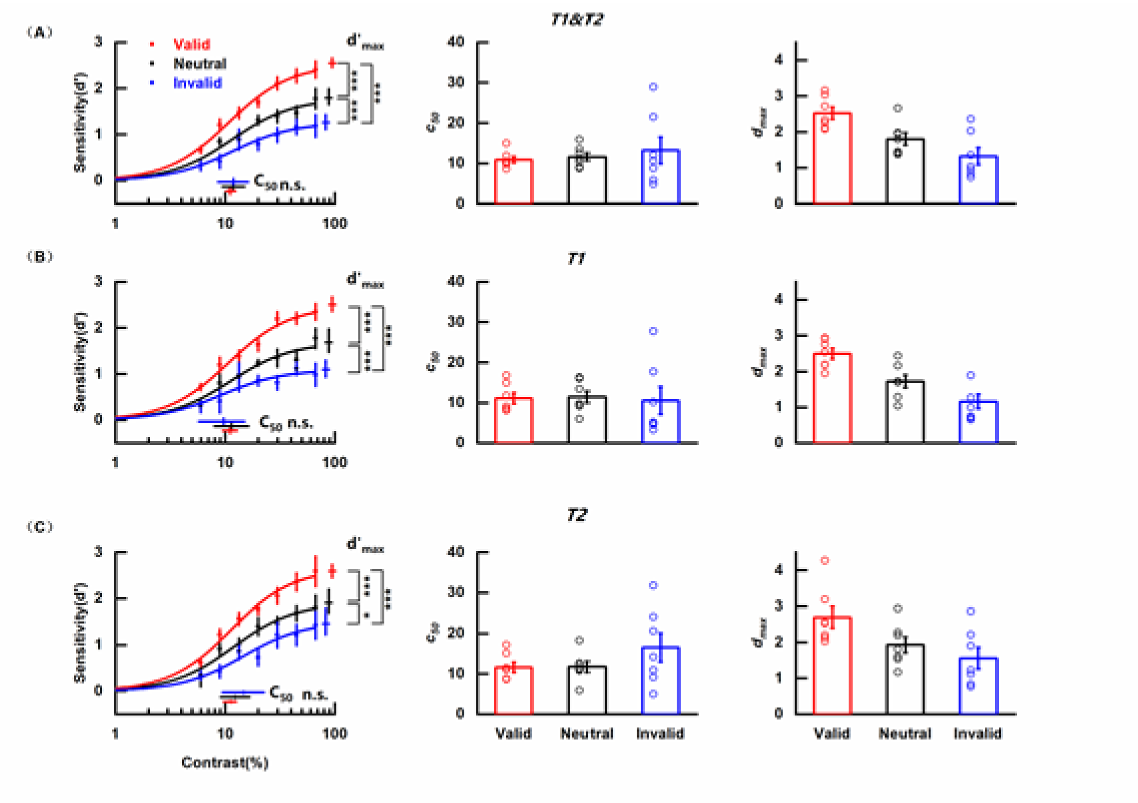

Figure 3

Effects of cue-induced temporal attention on contrast sensitivity **(A)** Left column: contrast response functions for different pre-cueing conditions. Data were collapsed across the reported targets. Each data point denotes the mean across observers under corresponding pre-cueing condition. Red, blue and black symbols and lines indicate valid, invalid and neutral pre-cues respectively. Error bars on data points represent standard errors of the mean which have been adjusted to remove between-subject variability (Cousineau, 2005;Morey, 2008;Franz and Loftus, 2012;Baguley, 2013). Error bars on parameter estimates are 90% confidence intervals, obtained by bootstrapping. Middle column: parameter estimates of threshold c_{50} for trials with different pre-cues for each participant. Open symbols denote data of individual subjects. The bars indicate the means of the parameter estimates across the subjects under corresponding conditions. Error bars represent standard errors of the mean. Right column: same as the middle column but for parameter estimates of asymptote performance d_{max}. * $p < 0.05$, *** $p < 0.001$. **(B)** Same as **(A)**, but only including the trials in which the reported target was T1. **(C)** Same as **(A)**, but only including the trials in which the reported target was T2.

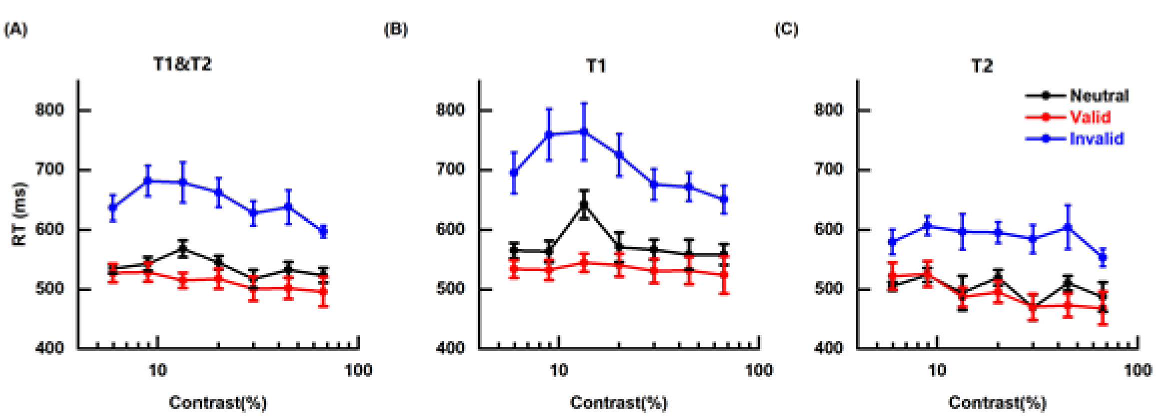

Figure 4

Effects of cue-induced temporal attention on reaction time **(A)** mean reaction times (RTs) across targets, plotted for different pre-cues as a function of contrast intensity. Error bars on data points denote adjusted standard errors of mean (Cousineau, 2005;Morey, 2008;Franz and Loftus, 2012;Baguley, 2013). **(B)** same as **(A)** but only for trials in which the reported target was T1. **(C)** same as **(A)** but only for trials in which T2 was the reported target.

Supplementary Files

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