

Temporal attention improves perception similarly at foveal and parafoveal locations

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Temporal attention, the prioritization of information at a specific point in time, improves visual performance, but it is unknown whether it does so to the same extent across the visual field. This knowledge is necessary to establish whether temporal attention compensates for heterogeneities in discriminability and speed of processing across the visual field. Discriminability and rate of information accrual depend on eccentricity as well as on polar angle, a characteristic known as performance fields. Spatial attention improves speed of processing more at locations at which discriminability is lower and information accrual is slower, but it improves discriminability to the same extent across isoeccentric locations. Here we asked whether temporal attention benefits discriminability in a similar or differential way across the visual field. Observers were asked to report the orientation of one of two targets presented at different points in time at the same spatial location (fovea, right horizontal meridian, or upper vertical meridian, blocked). Temporal attention improved discriminability and shortened reaction times at the foveal and each parafoveal location similarly. These results provide evidence that temporal attention is similarly effective at multiple locations in the visual field. Consequently, at the tested locations, performance fields are preserved with temporal orienting of attention.

Introduction

Attention selects relevant information in both space and time (Coull & Nobre, 1998; Kingstone, 1992). Both kinds of selection are important for understanding sensory and cognitive processing, yet much less is known about the temporal than spatial aspects

of vision and attention. In natural vision, we often have predictions about when relevant events will occur, which can be used to direct temporal attention (review by Nobre & van Ede, 2018). Temporal attention is the prioritization of information at specific points in time (Nobre, Correa, & Coull, 2007; Nobre & Rohenkohl, 2014; Nobre & van Ede, 2018). Voluntary temporal cueing studies have found both speed and accuracy benefits for attended compared to unattended time points (accuracy: Correa, Lupiáñez, & Tudela, 2005; Davranche, Nazarian, Vidal, & Coull, 2011; Denison, Heeger, & Carrasco, 2017a; Rohenkohl, Gould, Pessoa, & Nobre, 2014; Samaha, Bauer, Cimaroli, & Postle, 2015; reaction time: Coull & Nobre, 1998; Miniussi, Wilding, Coull, & Nobre, 1999; for a review, see Nobre & Rohenkohl, 2014). By studying the effects of temporal attention on perception, we can better understand the dynamics of visual perception.

To understand these dynamics, a critical distinction must be made between temporal attention—prioritization of task-relevant time points—and temporal expectation—prediction of stimulus timing regardless of task relevance. By precueing observers to one of two fixed time points, here we manipulate temporal attention while maintaining expectation constant (Denison et al., 2017a; Denison, Yuval-Greenberg, & Carrasco, 2018). Thus, this task requires precise cognitive control to attend to the precued time point from trial to trial.

Recently, we have used this task to demonstrate the benefits and costs of temporal cueing on task performance. Directing voluntary attention to a point in time leads to better discriminability at that time and worse discriminability at earlier and later times (Denison et al., 2017a). It is unknown whether and

Citation: Fernández, A., Denison, R. N., & Carrasco, M. (2019). Temporal attention improves perception similarly at foveal and parafoveal locations. *Journal of Vision*, 19(1):12, 1–10, <https://doi.org/10.1167/19.1.12>.

<https://doi.org/10.1167/19.1.12>

Received June 28, 2018; published January 16, 2019

ISSN 1534-7362 Copyright 2019 The Authors



how temporal attention affects different visual field locations. This knowledge is necessary to establish whether temporal attention compensates for heterogeneities in discriminability and speed of processing across the visual field.

Discrimination across the visual field is heterogeneous. Acuity is highest at the fovea and diminishes pronouncedly in the periphery (e.g., Carrasco, Williams, & Yeshurun, 2002; Chen, 2008; Strasburger, Rentschler, & Jüttner, 2011; Staugaard, Petersen, & Vangkilde, 2016). Greater eccentricity is also associated with poorer contrast sensitivity (e.g., Regan & Beverley, 1983; Virsu & Rovamo, 1979), spatial resolution (e.g., Carrasco & Frieder, 1997; review by Carrasco & Barbot, 2015), texture segmentation (e.g., Gurnsey, Pearson, & Day, 1996; Yeshurun & Carrasco, 1998), and visual search (e.g., Carrasco, Evert, Chang, & Katz, 1995; Carrasco & Frieder, 1997; Carrasco, McLean, Katz, & Frieder, 1998; Madison, Lleras, & Buetti, 2018). Crowding (e.g., Pelli, Palomares, & Majaj, 2004; Toet & Levi, 1992) and positional uncertainty (e.g., Michel & Geisler, 2011) also increase with eccentricity.

Discrimination is also heterogeneous at isoecentric locations with different polar angles. This phenomenon is called “performance fields” (Altpeter, Mackeben, & Trauzettel-Klosinski, 2000; Carrasco, Talgar, & Cameron, 2001; Mackeben, 1999) and includes two visual field asymmetries. First, discriminability is better along the horizontal than the vertical meridian. This horizontal–vertical anisotropy (HVA) has been reported in a variety of visual tasks (e.g., Abrams, Nizam, & Carrasco, 2012; Carrasco et al., 2001; Greenwood, Szinte, Sayim, & Cavanagh, 2017; Mackeben, 1999; Rijdsdijk, Kroon, & van der Wildt, 1980; Rovamo & Virsu, 1979). Second, discriminability is greater (e.g., Abrams et al., 2012; Carrasco et al., 2001; Talgar & Carrasco, 2002) and apparent contrast is higher (Fuller, Rodriguez, & Carrasco, 2008) at the lower vertical meridian than the upper vertical meridian (UVM), a pattern known as the vertical meridian asymmetry (VMA). Both the HVA and the VMA become more pronounced with increasing eccentricity and spatial frequency (Cameron, Tai, & Carrasco, 2002; Carrasco et al., 2001; Fuller et al., 2008).

The rate of information accrual as measured using the speed–accuracy trade-off procedure (Reed, 1973) also differs depending on eccentricity. The speed–accuracy trade-off procedure provides conjoint measures of discriminability and rate of information accrual. Accrual is faster at perifoveal (9°) than parafoveal (4°) locations (Carrasco, McElree, Denison, & Giordano, 2003). Likewise, reaction times are slower at foveal than parafoveal locations (Poletti, Rucci, & Carrasco, 2017). Furthermore, rate of

information accrual also differs across isoecentric visual field locations: It is faster along the horizontal than vertical meridian and slowest at the UVM, a heterogeneity known as temporal performance fields (Carrasco, Giordano, & McElree, 2004).

Much research has investigated whether and how covert spatial attention interacts with eccentricity and polar angle. Allocating spatial attention covertly (without moving the eyes) in an involuntary manner (exogenous spatial attention) enhances discriminability at the attended location, and this effect increases with eccentricity (e.g., Carrasco et al., 2002; Carrasco & Yeshurun, 1998). However, at the same eccentricity, exogenous spatial attention enhances discriminability across all polar angles by a similar degree (Cameron et al., 2002; Carrasco et al., 2001; Carrasco et al., 2002; Roberts, Ashinoff, Castellanos, & Carrasco, 2017; Roberts, Cymerman, Smith, Kiorpes, & Carrasco, 2016) so that the shape of the performance field remains. In contrast, exogenous spatial attention speeds information accrual (Carrasco & McElree, 2001) similarly across eccentricity (Carrasco, Giordano, & McElree, 2006) but differentially for isoecentric locations (Carrasco et al., 2004), speeding up processing more at slower than at faster locations; that is, it compensates for differences in processing speed, effectively eliminating heterogeneities in temporal performance fields.

Both spatial and temporal performance fields have diverse perceptual consequences. For instance, illusory contours (Rubin, Nakayama, & Shapley, 1996) and crowding (Greenwood et al., 2017) vary across isoecentric locations in accord with spatial performance fields. Similarly, the magnitude of the line-motion illusion varies across isoecentric locations (Fuller & Carrasco, 2009) in accord with temporal performance fields.

Given that the magnitude of the effect of spatial attention on visual performance varies across some but not all locations, it is important to know whether temporal attention varies with visual field location or, conversely, whether it affects discriminability similarly at multiple locations in the visual field. In the present study, we investigated whether the effects of temporal attention on discriminability vary with spatial location. We assessed the effect of voluntary temporal attention on discriminability at the fovea and two isoecentric, parafoveal (4°) locations. We tested the two isoecentric parafoveal locations associated with the highest and lowest performance levels (right horizontal meridian [RHM] and UVM, respectively). We considered two hypotheses: (a) Equal benefit hypothesis: If temporal attention operates uniformly at different locations in the visual field (similar to the effect of spatial attention on discriminability), then we should expect attentional

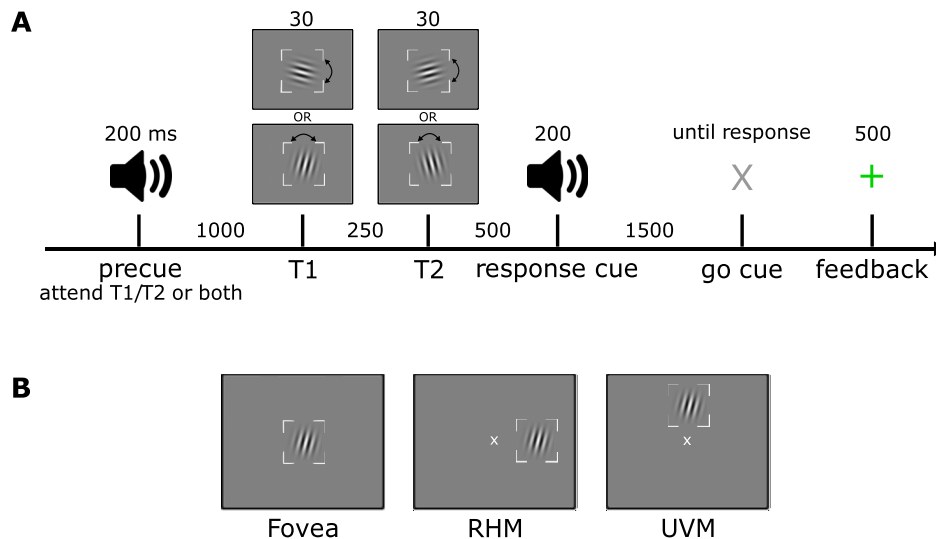


Figure 1. (A) Schematic depiction of a trial sequence at the fovea. Each target could be tilted clockwise or counterclockwise about either the vertical or horizontal axis. (B) All tested locations (blocked by session).

effects with equal benefits at all tested locations. (b) Compensation hypothesis: If temporal attention compensates for visual field heterogeneities (similar to the effect of spatial attention on speed of processing), we should expect the greatest attentional effect at the UVM, at which both discrimination and speed of processing are worst.

100 Hz refresh rate). An Apple iMac computer was used to control stimulus presentation and collect responses. Stimuli were generated using MATLAB (MathWorks, Natick, MA) and the Psychophysics toolbox (Brainard, 1997; Pelli, 1997).

Stimuli

The task and stimuli were very similar to our recent study (Denison et al., 2017a), but the stimulus locations differed (Figure 1). Central fixation was a white letter “X” subtending 0.5° of visual angle. The stimuli were 4 cycles/ $^\circ$ sinusoidal gratings with a Gaussian spatial envelope (standard deviation of 0.7°). Depending on the session, stimuli were presented at fixation or at a parafoveal location, either the UVM or RHM, at 4° eccentricity (Figure 1B). Stimulus contrast was 100% so that the targets would be highly visible. Two targets (T1 and T2) were presented on each trial. Each target was tilted clockwise or counterclockwise about the vertical or horizontal axis, and each target’s tilt was independently determined. Stimulus placeholders were corners of a $4.25^\circ \times 4.25^\circ$ white square outline with a width of 0.08° centered on the target location. These placeholders were present throughout all trials and experimental sessions to eliminate spatial uncertainty. Stimuli were presented on a midgray background (57 cd/m^2). Auditory cues consisted of pure sine wave tones presented through the computer’s speakers. There were three possible auditory cues: high (1,300 Hz) indicating to attend to T1, low (250 Hz)

Methods

Participants

Eleven observers (six male, aged 21–33), including authors A.F. and R.N.D., participated. One observer’s data was removed because discriminability was at ceiling for vertical orientations and below chance for horizontal orientations, leaving 10 observers. The number of observers needed was determined by a power analysis of the data we reported in experiment 1 of Denison et al. (2017a). All observers provided written informed consent and had normal or corrected-to-normal vision. All experimental procedures were in agreement with the Helsinki declaration and approved by the university committee on activities involving human subjects at New York University.

Apparatus

Observers sat in a dark room 57 cm away from a color-calibrated CRT monitor ($1,280 \times 960$ resolution;

indicating to attend to T2, or both tones together, indicating to attend to both targets (neutral trial).

Procedure

Observers were asked to discriminate the orientation of one of two grating patches. During each experimental session and on each trial, two targets (T1 and T2) were presented serially at the same spatial location separated by a stimulus onset asynchrony of 250 ms. Placement of the stimuli varied depending on the session. Each observer was tested twice at the three spatial locations (fovea, RHM, UVM) for a total of six sessions per observer. Location order was randomized for each observer.

Each session consisted of five 64-trial blocks for a total of 320 trials. Trial order was counterbalanced to maintain an equal number of trials for each precue, target, and orientation combination on a block-by-block basis. At the beginning of each trial, a precue tone was presented 1,000 ms before the first target and instructed observers to attend to one (with 100% validity) or both targets (neutral). Target presentation lasted 30 ms. A response cue 500 ms after stimulus presentation indicated which target's orientation to report. On valid trials, the response cue matched the precue; on neutral trials, the response cue was equally likely to indicate T1 or T2. For a trial timeline, see Figure 1A. Observers reported the tilt of the probed target by pressing a key (1 = counterclockwise, 2 = clockwise) on a keyboard. A “go” cue, the fixation cross turning gray 1,500 ms after the response cue, indicated the start of the response period. This response delay was included to emphasize accuracy and reduce speed–accuracy trade-offs. Response time was unlimited, and reaction times were calculated from the start of the response period. After each response, observers received visual feedback in the form of a green “+” or red “–” presented at fixation for 500 ms. In addition, percentage correct was also presented at the end of each block.

To accurately compare attentional effects among visual field locations, we ensured that neutral discriminability was matched across all tested locations within each observer. Before each experimental session, a staircase procedure was used to titrate discrimination accuracy to 75% on neutral trials, independently for each target (T1 and T2) and location (fovea, RHM, UVM)—in total, six thresholds. Observers started each session with their tilt thresholds, and thresholds were adjusted on a block-by-block basis to maintain accuracy for neutral trials at 75%. To acquaint observers with the task and reduce uncertainty about the target timing, each observer trained for two 1-hr sessions at a nonexper-

imental location (lower right quadrant) on neutral trials only before running their first experimental session.

Eye tracking

To ensure that observers were centrally fixating, online eye tracking was used. Eye position was recorded using an Eyelink 1000 eye tracker (SR Research) with a sampling rate of 1,000 Hz. Each trial began once the observer fixated on the central cross. Trials in which observers broke fixation (blinked or deviated their eye position more than 1.5° from the center of the screen) between the precue and the response cue were stopped and repeated at the end of the experimental block. Observers were allowed to move their eyes and blink during the response period and between trials.

Results

For each target and cueing condition, sensitivity (d') was calculated at each location. Correct discrimination of clockwise orientations was arbitrarily chosen as hits. False alarms were trials in which observers incorrectly discriminated counterclockwise orientations (e.g., Dugué, Roberts, & Carrasco, 2016; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010).

Performance on neutral trials

We first examined performance on neutral trials (Figure 2A). Our titration procedure was successful: Discriminability was equivalent across the tested locations. Next, tilt thresholds were assessed at each visual field location (Figure 2B) to confirm that our observers had typical performance fields; greater tilt thresholds indicate worse discriminability, and lower thresholds indicate better discriminability. The HVA predicts higher thresholds for the UVM than the RHM. A two-way, within-subjects ANOVA (location: fovea, RHM, UVM; target: T1, T2) revealed a main effect of location, $F(2, 18) = 16.51, p = 0.0001, \eta_G^2 = 0.25$, but no main effect of target or significant interaction between location and target. Peripheral thresholds were significantly higher than foveal thresholds: fovea versus RHM, $t(39) = 3.39, p = 0.01, d = 0.08$; fovea versus UVM, $t(39) = 4.95, p < 0.00001, d = 0.12$, and UVM thresholds were higher than RHM thresholds, $t(39) = 2.63, p = 0.01, d = 0.06$. Observers, therefore, had normal performance fields for discriminability.

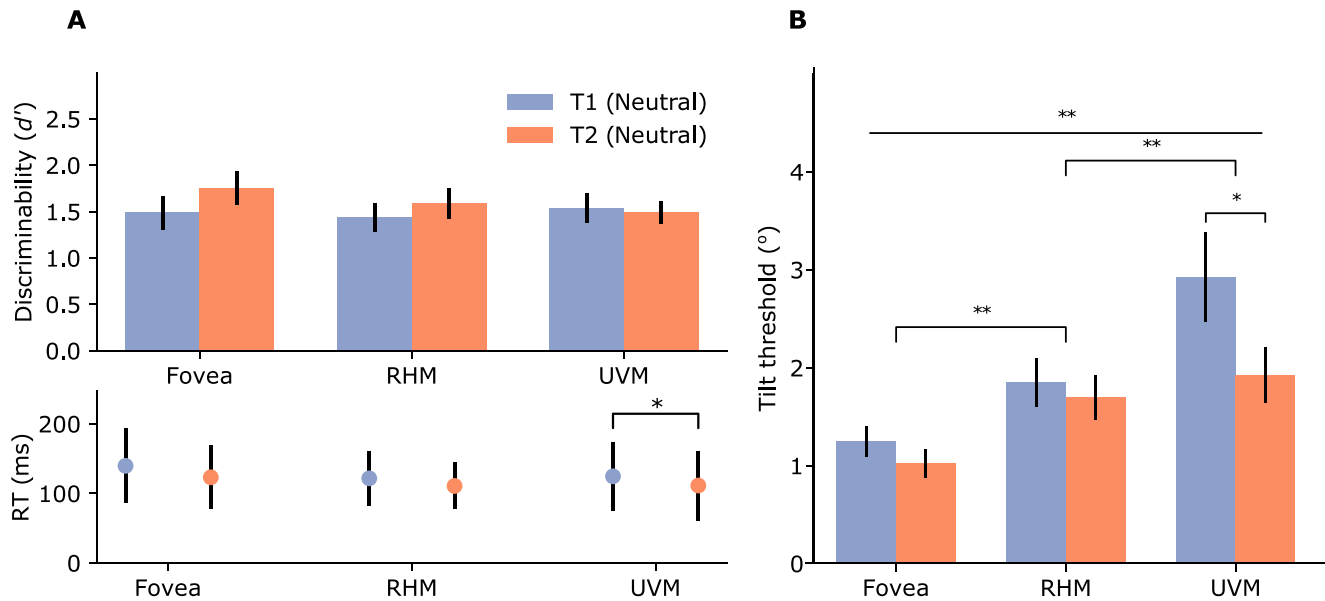


Figure 2. (A) Mean discriminability and reaction time for each target and location, neutral trials only. (B) Mean orientation threshold for each target and location, neutral trials only. Error bars represent the *SEM*. $n = 10$. Significance line with no end ticks represents a main effect of location; those with end ticks represent pairwise comparisons between locations or between targets for a single location. * $p < 0.05$; ** $p < 0.01$.

Effects of temporal attention

To determine whether temporal attention varied with visual field location, we performed a three-way, within-subjects ANOVA (precue: valid, neutral; location: fovea, RHM, UVM; target: T1, T2).

The main effect of target was not significant, $F(1, 9) < 1$. The other two main effects were significant: (a) location, $F(2, 18) = 4.549$, $p = 0.0252$, $\eta_G^2 = 0.06$, with higher discriminability at the fovea than at the two parafoveal locations: fovea versus RHM, $t(39) = 2.87$, $p = 0.006$, $d = 0.07$; fovea versus UVM, $t(39) = 2.51$, $p = 0.01$, $d = 0.06$, and (b) precue, $F(1, 9) = 13.967$, $p = 0.0046$, $\eta_G^2 = 0.14$, with higher discriminability for the valid than the neutral cue (Figure 3A). The only significant interaction, precue \times target, $F(1, 9) = 10.075$, $p = 0.0113$, $\eta_G^2 = 0.04$, revealed that the benefit of the valid precue was greater for T1 than T2. The interaction of target \times location was not significant, $F(2, 18) = 1.961$, $p = 0.170$. Importantly, attention affected all locations to a similar degree (Figure 3B and C) as indicated by its nonsignificant interaction with the other factors: precue \times location, $F(2, 18) = 1.395$, $p = 0.273$; precue \times target \times location, $F(2, 18) = 0.159$, $p = 0.854$. In line with these results, we found a significant correlation between the benefits at the two parafoveal locations: $r = 0.44$, $p = 0.05$ across observers.

These results were confirmed by a Bayesian model selection approach (Masson, 2011). We transformed

the sum of squared errors obtained from our ANOVAs to arrive at an estimated Bayes factor as well as Bayesian information criterion probabilities ($pBIC$) for the null (H_0) and alternative (H_1) hypotheses given data set D. For the interaction of precue and location, the Bayes factor favored the null hypothesis with odds 4.74 to 1: $pBIC(H_1|D) = 0.175$ and $pBIC(H_0|D) = 0.825$. For the three-way interaction of precue, target, and location, the Bayes factor produced odds of 16.72 to 1: $pBIC(H_1|D) = 0.06$ and $pBIC(H_0|D) = 0.94$. A Bayes factor greater than three and a $pBIC(H_0|D)$ value between 0.75 and 0.95 are considered “positive” evidence for the null hypothesis (Masson, 2011; Raftery, 1995). These analyses therefore provide positive evidence in favor of attention affecting all locations in a similar fashion.

To ensure we could rule out speed–accuracy trade-offs, we assessed reaction time. A three-way, within-subject ANOVA on reaction time revealed a main effect of precue, $F(1, 9) = 8.2$, $p = 0.018$, $\eta_G^2 = 0.0036$. Observers responded faster on valid than on neutral trials (Figure 3A), ruling out speed–accuracy trade-offs. No differences were found across the tested locations, $F(2, 18) < 1$, or targets, $F(1, 9) = 2.89$, $p = 0.12$, and none of the interactions were significant (all $ps > 0.1$). The observed fast reactions times were due to the temporal predictability of both the response and go cue. Responses were prepared at the response cue and rapidly dispatched at the go cue.

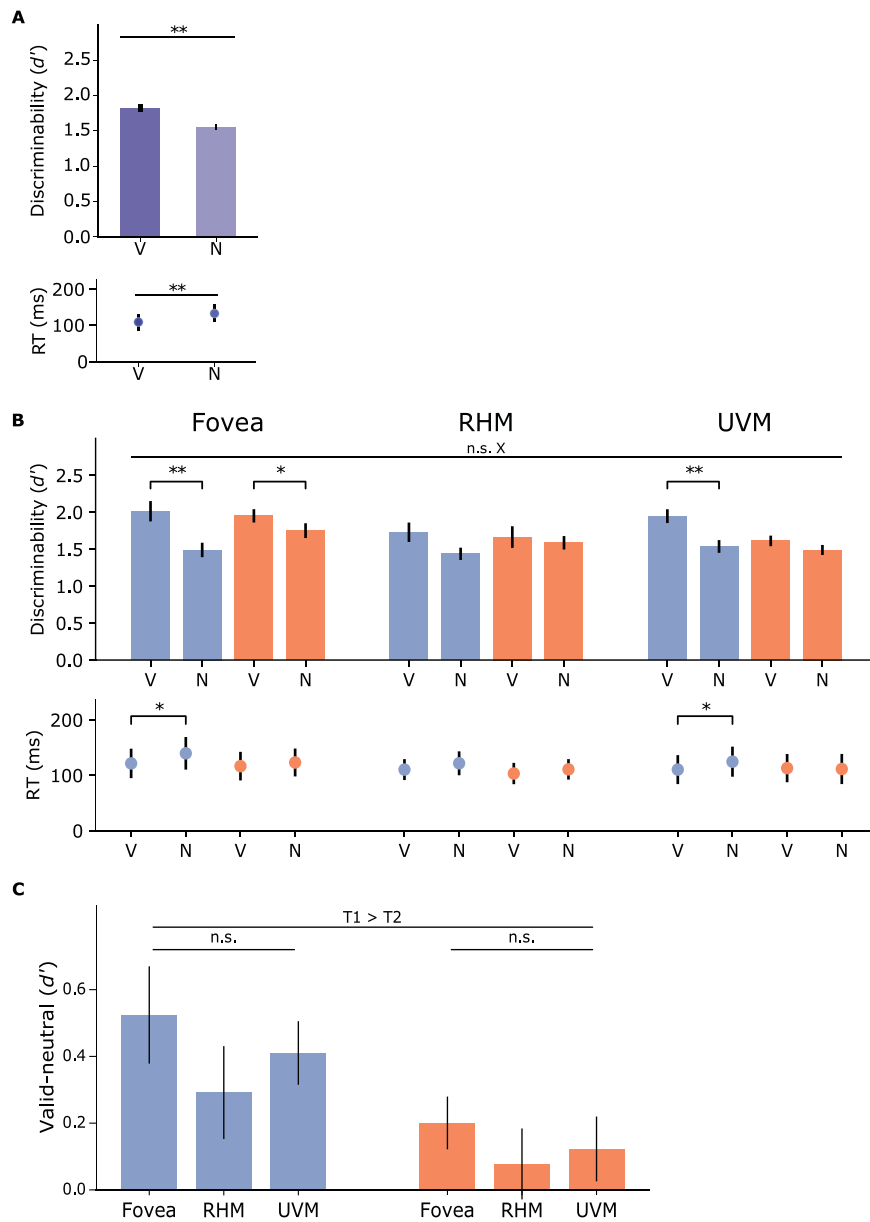


Figure 3. (A) Mean discriminability and response times across locations and targets. V = valid, N = neutral. (B) Mean discriminability and response times for each location, target, and precue combination. “ns X” represents no significant precue \times target \times location interaction. (C) Attentional benefits (valid – neutral). Error bars represent the SEM. $n = 10$. “T1 > T2” represents significant precue \times target interaction. $*p < 0.05$; $**p < 0.01$.

Discussion

Does temporal attention vary with visual field location? We found that it does not. Overall performance was better for valid than for neutral precues, but these attention-related improvements were similar at all tested locations. Previous studies have reported that voluntary temporal attention improves performance both in the fovea (Correa et al., 2005; Davranche et al., 2011; Miniussi, Rao, & Nobre, 2002; Samaha et al., 2015) and at peripheral locations (Coull & Nobre, 1998; Denison et al., 2017a; Griffin, Miniussi, & Nobre, 2002). Here we directly compared the effect of temporal attention at foveal and parafoveal spatial locations. Our findings support the equal benefit hypothesis: Temporal attention improved discriminability similarly at all tested spatial locations.

Indeed, we found no indication of a compensatory effect of attention, i.e., more impact of temporal attention at locations where discriminability is worse and information accrual slower. When examining thresholds (neutral performance, without attention), we found significant differences across all locations with best discriminability at the fovea, then the RHM and worst discriminability at the UVM, consistent with the literature on eccentricity effects (e.g., Carrasco & Frieder, 1997; Virsu & Rovamo, 1979) and performance fields (e.g., Abrams et al., 2012; Carrasco et al., 2001). Therefore, although observers had normal performance fields, temporal attention did not compensate for the inhomogeneities across the visual field. This is similar to the effect of exogenous spatial attention on discriminability (e.g., Cameron et al., 2002; Carrasco et al., 2001).

Attention benefitted T1 more than T2. One may wonder whether this is because the task was more difficult for T1 than for T2. This explanation is unlikely because both difficulty as measured by d' in the neutral condition was matched for the two targets and difficulty as measured by tilt threshold in the neutral condition was not significantly different between the two targets. Further, a difficulty account would predict the greatest attentional effect at the UVM, at which the task is most difficult, followed by the RHM and then fovea. However, this was not the case; if anything, attention improved discriminability more consistently at the fovea (Figure 3B).

In contrast to the increasing benefit of spatial attention with eccentricity, our results show that temporal attention benefits discriminability to a similar degree at the tested foveal and parafoveal locations. When stimuli are presented parafoveally, observers may have deployed their covert spatial attention to the target location because stimuli appeared at a constant location throughout an experimental block. Any effect of spatial attention would have been constant across the two intervals in a trial and across trials. When stimuli are presented foveally, the effect can be attributed solely to

temporal attention. Although selective covert spatial attention can be allocated within the foveola when stimuli are very small (Poletti et al., 2017), the stimuli in the current study covered the entirety of the fovea, so selective spatial attention is not expected to play a role in performance. The finding that the magnitude of the effect of temporal attention is similar at the fovea and parafovea then rules out a possible contribution of covert spatial attention at the parafoveal locations.

Temporal attention benefited both peripheral locations in a similar fashion. Temporal attention, like exogenous spatial attention, therefore, does not change the shape of the performance fields for discriminability. This is in line with the idea that performance fields are determined by visual rather than attentional constraints (Cameron et al., 2002; Carrasco et al., 2001). Both photoreceptor and retinal ganglion cell densities vary across retinal locations and limit spatial resolution (Curcio & Allen, 1990; Curcio, Sloan, Kalina, & Hendrickson, 1990; Watson, 2014). It is unclear how much these initial sampling factors contribute to the characteristic shape of performance fields. Recently, it has been established that preneural factors, such as optics (simulated as typical human wave front and defocus) and cone density, contribute only a small amount to performance fields (Kupers, Carrasco, & Winawer, 2018). Substantial additional asymmetries must arise in retinal ganglion cell or cortical processing.

The current study adds to the growing body of evidence that voluntary temporal attention improves not only reaction times, but also perceptual judgments (Correa et al., 2005; Davranche et al., 2011; Denison et al., 2017a; Rohenkohl et al., 2014; Samaha et al., 2015). Although temporal attention has been discussed in a variety of contexts (Dux & Marois, 2009; Martens & Wyble, 2010), it has often not been directly manipulated. Temporal precues provide a straightforward way to manipulate temporal attention (Nobre & Rohenkohl, 2014), allowing any perceptual effects of the precues to be unambiguously attributed to voluntary temporal attention. Although most previous studies using precues have presented only one target per trial, the use of two targets per trial has clear advantages. In one-target tasks, if a target does not appear at the first time point, the observer can reorient attention to the second time point, knowing that the target is sure to appear then. Therefore, attention and expectation are not dissociated (whenever a target at the second time point is highly relevant, it is also fully predictable). In a two-target task, on the other hand, the trial sequence is the same on every trial, so attention and expectation are dissociated for both time points. The two-target task has revealed not only perceptual benefits at the attended time points, but also perceptual costs at unattended time points, demonstrating the selectivity of temporal attention (Denison et al., 2017a). It has also been used to dissociate the effects of attention and

expectation on microsaccades, revealing that the stability of fixation increases not only at expected times (Amit, Abeles, Carrasco, & Yuval-Greenberg, 2019; Dankner, Shalev, Carrasco, & Yuval-Greenberg, 2017), but also around attended time points (Denison et al., 2018). A possible complication in two-target tasks is that the precue gives temporal information pertaining to both an absolute time (e.g., 1,000 ms after the precue) and serial order (e.g., the first target in the sequence). Varying the temporal interval between the two targets has shown that the degree to which a temporal precue affects perceptual sensitivity depends on the precise interval and, therefore, is not merely determined by serial order (Denison, Carrasco, & Heeger, 2017b). The continued use and development of behavioral protocols that manipulate temporal attention while controlling for other factors will advance the expanding effort to understand how we attend dynamically across time.

Future studies concerned with the interaction of temporal attention with performance fields could test more spatial locations to characterize the performance fields more extensively. For instance, it may be informative to test additional isoeccentric locations, as discriminability differences are more pronounced at the meridians and decrease as locations get closer to intercardinal locations (Abrams et al., 2012), and to place stimuli at farther eccentricities, because information accrual is faster at perifoveal than at parafoveal locations (Carrasco et al., 2003).

In conclusion, temporal attention appears to operate similarly at different visual field locations, despite pronounced low-level differences in visual processing. Spatial performance fields for discriminability remain intact during both spatial and temporal orienting of attention at locations at which visual field inhomogeneities are pronounced. Thus, in natural vision, we can voluntarily direct temporal attention similarly across locations at different eccentricities and polar angles for which discriminability and speed of information accrual differ.

Keywords: temporal attention, spatial vision, performance fields

Acknowledgments

We acknowledge the contribution of Carrasco Lab members. This research was supported by NIH National Eye Institute R01 EY019693 and R01 EY016200 to MC, F32 EY025533 to RND, and T32 EY007136 to New York University.

Commercial relationships: none.
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