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BRIEF REPORT

Adaptive visual selection in feature space

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Abstract
Visual perception relies on efficient selection of task-relevant information for prioritized processing. A prevalent mode of selection is feature-based selection, and a key question in the literature is the shape of the selection profile—that is, when a feature is selected, what is the landscape of priority for all features in that dimension? Past studies have reported conflicting findings with both monotonic and nonmonotonic profiles. We hypothesized that feature selection can be adaptively adjusted based on stimulus factors (feature competition) and task demands (selection precision). In three experiments, we manipulated these contextual factors in a central task while measuring selection profile in a peripheral task. We found a nonmonotonic, surround suppression, profile when feature competition and selection precision was high, but observed a monotonic profile when these factors were low. Furthermore, manipulation of selection precision alone can shape selection profile independent of feature competition. These findings reconcile previous conflicting results and importantly, demonstrate that feature selection is highly adaptive, allowing flexible allocation of processing resources to ensure efficient extraction of visual information.

Keywords Vision · Attention · Feature · Control

Introduction

Visual attention is responsible for selecting task-relevant information for prioritized processing from the myriad of input that arrives at our eyes. Effective selection of both spatial and nonspatial information, such as features and objects, is critical for accurate perception and adaptive behavior (Carrasco, 2011; Liu, 2019; Yantis, 2000). A key question for understanding the mechanisms of attention is the way attentional resources are distributed. Here, we define this distribution as the *selection profile*—that is, when attention selects one location or feature, what is the landscape of priority for other locations or features?

While the current study will focus on feature-based attention, it is useful to briefly consider the selection profile of spatial attention. One of the earliest model of spatial attention is the "attentional spotlight," where attention selects an oval-shaped region and everything outside this region is ignored (Posner et al., 1980). Subsequent work refined this model by showing that the selected region can vary in size and have a smooth boundary (Eriksen & James, 1986; LaBerge et al., 1997). These models assume that the strength of spatial attention declines monotonically as a function of the distance away from the attended location. More recent work, however, has shown that the spatial selection profile can assume a nonmonotonic, "Mexican-hat" shape, such that it decreases from the attended location but recovers for further locations (Bahcall & Kowler, 1999; Cutzu & Tsotsos, 2003; Mounts 2000). This profile is termed "surround suppression," as it resembles the center-surround antagonistic receptive field of early visual neurons. Consistent with these behavioral results, subsequent physiological studies reported neural signals exhibiting a Mexican-hat shaped activity profile (reviewed in Hopf et al., 2010).

In this study, we focus on the analogous question in feature-based attention (i.e., the selection profile in the feature space). In a series of seminal neurophysiological experiments (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999), it was found that attending to a motion direction modulated neuronal activity in area MT monotonically as a function of the difference between the attended direction and the neuron's preferred direction. This finding led to the formulation of the feature-similarity

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gain model, which was further supported by a number of human psychophysical studies that showed monotonic attentional modulation in behavioral performance (Ho et al., 2012; Paltoglou & Neri, 2012; Wang et al., 2015). However, other studies have reported evidence for a non-monotonic selection profile in the feature space that resembles a Mexican-hat shape in behavioral performance (Fang et al., 2019; Fang & Liu, 2019; Störmer & Alvarez, 2014; Tombu & Tsotsos, 2008) and neural response (Bartsch et al., 2017; Störmer & Alvarez, 2014).

It is not clear what factors contribute to the expression of different selection profiles and, in particular, what conditions promote surround suppression. On the one hand, given its resemblance to the center-surround antagonistic receptive field structure of early visual neurons (e.g., retinal ganglion cells), surround suppression might be universal and perhaps even immutable (Treue, 2014). On the other hand, the selection profile may adapt to stimulus and task contexts, given that attentional control can be considered part of the highly flexible cognitive control system (Chun et al., 2011; Courtney, 2004). In the current study, we tested the overall hypothesis that feature-based selection is adaptive to contextual factors to efficiently extract task-relevant information.

First, consider the stimulus context. From a functional point of view, the Mexican-hat profile is useful in reducing interference from distracters similar to the target but would be less useful when distracters are distinct from the target. Thus, an adaptive feature-based selection should not exhibit surround suppression in the latter situation. Second, consider the task context. We reasoned that if surround suppression helps isolate the target feature among distracters, the precision level of target selection could impact the selection profile. A surround suppression mechanism should be more useful when the target is defined by a precise feature than when it is only coarsely defined.

We developed a novel dual-task paradigm to investigate how these contextual factors modulate the selection profile for visual features. We presented a central target among a stream of masks along with two peripheral grating stimuli (Fig. 1). Participants attended to a cued orientation in the center stream while monitoring for a contrast change in the peripheral gratings. Contextual factors were manipulated in the central task, while the peripheral task was used to measure the selection profile. In this paradigm, spatial attention is held constant throughout the experiment, but the similarity between the cued orientation and the grating orientation is systematically manipulated. Thus, performance modulation on the peripheral grating can be attributed to attending to different features in the center (i.e., a global modulation of feature-based attention). Many previous studies have demonstrated that feature-based attention indeed exerts a global effect (e.g., Liu & Hou, 2011; Sàenz et al., 2003; White & Carrasco, 2011)—a property exploited by our design to isolate feature-based attention from spatial attention.

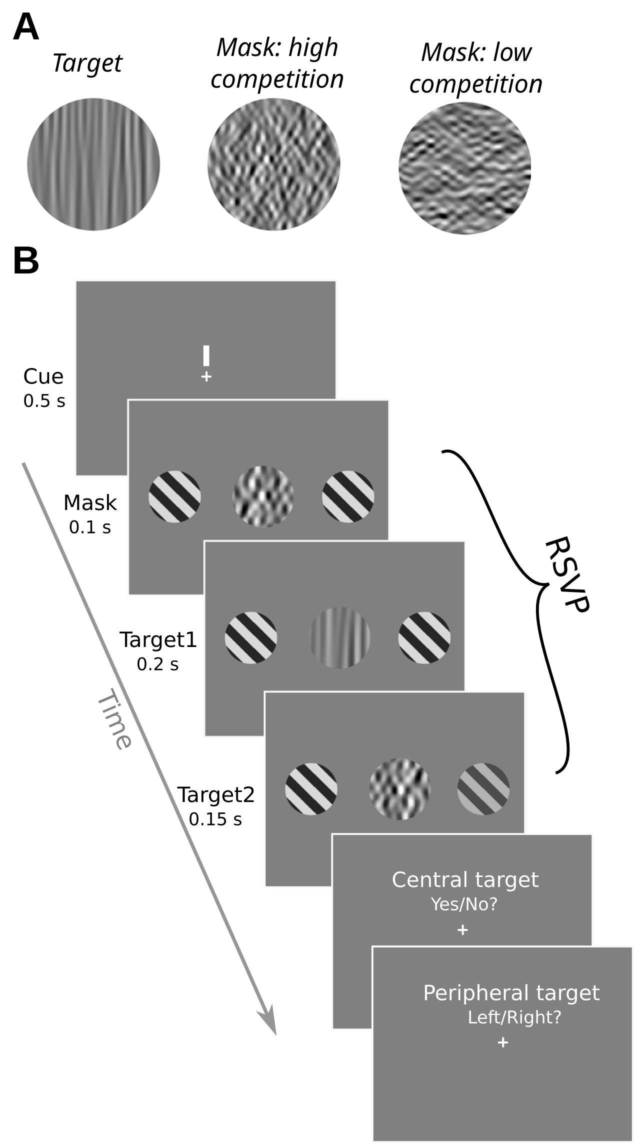

Fig. 1 Stimuli and task of Experiment 1. **A** Example images for the orientation signal and two types of masks. **B** Trial schematic with timing information. *Note*. The stimuli were not drawn to scale for illustration purposes

Experiment 1

In Experiment 1, we manipulated the target-mask similarity in the central task, which we refer here as *feature competition*, and examined its effect on the selection profile measured by the peripheral task. If attentional modulation is sensitive to stimulus context, we should observe a surround suppression profile when feature competition is high, and a reduction (or absence) of such effects when feature competition is low.

Methods

Preregistration

The study design, hypotheses, analysis plan, and sampling plan were preregistered online (https://osf.io/r9cqu).

Participants and sample size

Ten students from Michigan State University participated in this experiment. All had normal or corrected-to-normal visual acuity. Participants gave informed consent and were compensated at the rate of $10 an hour. The experimental protocol was approved by the Institutional Review Board at Michigan State University.

The sample size was determined based on the effect size estimated from our previous study using a similar design (Experiment 1 in Fang & Liu, 2019), in which we observed an effect size of 0.88 for a surround suppression at an intermediate cue–target offset via a *t* test. Using G*Power (Faul et al., 2007), we estimated that 10 participants would allow us to detect this effect with 80% power ($\alpha = 0.05$).

Visual stimulus and apparatus

There are three types of stimulus: signal, mask, and peripheral grating (Fig. 1A). Both the signal (i.e., orientation target) and mask were generated by filtering Gaussian noise in the spatial frequency and orientation domain with specific filters, as described below. We first filtered Gaussian noise images with a spatial frequency bandpass filter (0.16 to 5.09 cycles per degree). To generate the signals, these images were further filtered with an orientation filter in a narrow band (±5°) around a specific orientation, which could be one of eight fixed values from 10° to 167.5° with a step size of 22.5° to avoid cardinal orientations. The masks were generated similarly, except the orientation filters covered a wider range. For the high-competition condition, the masks were filtered in a range close to the signal orientation (±5° to ±45°), whereas for the low-competition condition, the masks were filtered in a range dissimilar to the signal orientation (±50° to ±90°). A randomly generated initial Gaussian noise was used for each stimulus instance, thus producing unique textures for each individual image of the signal and mask. The orientation signal and masks thus contained similar spatial frequency content, but with different levels of similarity in the orientation content. The peripheral stimulus consisted of square wave gratings (0.9 cycles per degree) in one of the eight fixed orientations as the signal. All three types of stimulus were enclosed in a circular aperture with the same size (5.4°).

Stimuli were generated using MGL (Gardner et al., 2018), a set of custom extensions implemented in MATLAB (The MathWorks, Natick, MA), and were presented on a 21-in. CRT monitor (1,024 × 768 pixels, 100-Hz refresh rate) at a viewing distance of 90 cm. The monitor was gamma corrected to achieve a linear luminance output, and the background was set at the mid-gray level of the monitor (57 cd/m^2). A chin rest was not used due to COVID concerns, and we instructed participants to remain still to maintain the viewing distance throughout the experiment. Participants also wore face masks during the experiment.

Task and procedure: Orientation cueing (main task)

We used a dual task (central-peripheral) paradigm to manipulate and measure feature-based attention (Fig. 1B). At the onset of each trial, a fixation dot (white, 0.3°) and an orientation precue (white line, length: 0.4°, thickness: 0.05°) appeared for 500 ms. After a 200 ms interstimulus interval, the visual stimuli were shown for a total duration of 800 ms. The central location contained a rapid serial visual presentation (RSVP) of the masks and a potential signal, which was updated at 10 Hz (100 ms per image). In half of the trials, an orientation signal was presented for 200 ms with a random delay between 50 ms and 500 ms after stimulus onset. The contrast of the orientation signal was determined in a threshold pretest (see below). In the other half of the trials, the mask underwent a contrast change for 200 ms with the same temporal parameter and contrast as the signal. By equating the contrast of the signal and mask, the target in the central task can only be identified by its orientation feature, but not by the abrupt change in contrast. The orientation of the cue and signal was always identical and was randomly drawn from one of the eight possible orientations on each trial (from 10° to 167.5° with a step size of 22.5°). Participants were instructed to attend the cued orientation and report the presence or absence of the signal.

Two peripheral gratings appeared simultaneously with the central RSVP at an eccentricity of 8.0°. The gratings had a fixed contrast (0.4) and remained static throughout the trial, with one of them briefly reducing its contrast for 150 ms (dimming). The timing of the dimming event was randomly selected with the constraint that it always occurred at least 140 ms after the offset of the central target, when it was present, and with the same timing on target-absent trials (assuming a target would have occurred). The two gratings were always in the same orientation, which was randomly selected from the set of eight fixed orientations, independently from the randomly selected orientation of the central signal. The location of the dimming event (left or right) was randomly chosen on each trial, and participants were instructed to report the location of the dimming event (left or right). The asynchrony between the target events in the central and peripheral tasks was to reduce response interference (Pashler, 1994). Participants were instructed to maintain central fixation throughout the trial. We did not monitor eye position with an eye tracker. However, given the demanding central task, the bilateral presentation of the peripheral gratings, and the brevity of the target events, eye movements toward the peripheral gratings would be counterproductive for task performance. Thus, we believe our participants mostly likely maintained central fixation, which is also our own anecdotal experience with the task.

After the stimulus presentation, two displays were shown that prompted participants to respond to the central task first, followed by the peripheral task. They used their index and middle fingers of the right hand to respond to the central task ("present" vs. "absent) and those fingers on the left hand to respond to the peripheral task ("left" vs. "right") by pressing one of two buttons under each hand. Participants had unlimited time to respond to each prompt. They were informed that the precue was always valid (when the orientation signal was present) and that they should pay particular attention to the cued orientation to detect the central target, as well as maintain high accuracy on the peripheral task. A tone was played after each incorrect response.

There were two within-subject factors in the experiment: feature competition and cue-grating offset. Feature competition was manipulated by presenting masks in the central RSVP of either similar (high competition) or dissimilar (low competition) orientation content to the precued orientation. To encourage the adaptation of a stable selection profile, the high- and low-competition conditions were conducted in two separate sessions on different days, with the order counterbalanced across participants. On each trial, the orientations of the cue and peripheral grating were independently sampled from one of eight fixed values (see above), thus yielding eight possible cue-grating offsets: 0°, ±22.5°, ±45°, ±67.5°, and 90°. Each participant completed six blocks of 80 trials in each competition condition (480 trials per condition, 960 trials total). The only exception was one participant who completed five blocks of trials in the high-competition condition due to logistical issues (400 trials).

Task and procedure: Contrast threshold pretest

Our primary goal was to obtain an accuracy-based measure of the selection profile using the peripheral task. We also needed the central task to be sufficiently challenging to encourage participants to attend to the cued orientation. To achieve these goals, we first calibrated task difficulty for each participant in a threshold procedure before they performed the main task in each session. The threshold task was identical to the main task described above, with two exceptions. First, the orientation of the peripheral gratings was set to be the same as the signal. Second, the RMS contrast of the signal, as well as the magnitude of the peripheral dimming, were controlled by separate QUEST staircases (Watson & Pelli, 1983) targeting an intermediate level of performance (~75%). Two independent staircases per task were randomly interleaved in two blocks of 60 trials each (four staircases in total). The average of the threshold values from the two staircases for each task was used in the main task (signal contrast and dimming magnitude) in the same session, which lasted 1–1.5 hr. Participants were encouraged to take breaks between blocks.

Results and discussion

Given the circular and symmetric nature of the orientation space, we collapsed the clockwise or counterclockwise offset and calculated task performance as a function of the absolute orientation offset (five levels: 0°, 22.5°, 45°, 67.5°, and 90°). This also increased the number of trials per offset, yielding more stable measures of performance.

Accuracy in the central task was at an intermediate level (M = 77.5%) and only exhibited minor variations among competition and offset conditions (Fig. 2A). A two-way repeated-measures analysis of variance (ANOVA) did not reveal any significant main effect or interaction (all ps > 0.4). This outcome was expected, given that we calibrated task performance in each competition condition with the threshold procedure.[1]

For the peripheral task, performance exhibited a different pattern for the high- and low-competition conditions. For the high-competition condition, we observed a nonmonotonic profile such that the lowest performance occurred at 45° offset, exhibiting a surround suppression effect and replicating previous findings (Fang & Liu, 2019; Tombu & Tsotsos, 2008). However, in the low-competition condition, a monotonic profile emerged without any hint of surround suppression. This difference in selection profiles was confirmed by a two-way repeated-measures ANOVA, which revealed a significant main effect of offset, $F(4, 9) = 6.56$, MSE = 0.001, $p < .001$, $\eta_p^2 = 0.42$, and importantly, a significant interaction between offset and competition, $F(4, 9) = 6.17$, $MSE = 0.02$, $p < .001$, $\eta_p^2 = 0.41$. We further examined the surround suppression effect in the high-competition condition by comparing performance at 45° against 0° and 90° offsets via planned t tests. Both tests revealed significant differences, 45° vs. 0°: $t(9) = 2.27$, $p < .05$; 45° vs. 90°: $t(9) = 3.21$, $p < .05$, indicating that performance at 45° offset was reliably lower than the cued orientation (0°) and the

[1] We also analyzed the central task data using the signal-detection measures. The sensitivity measure (d') gave essentially the same results as proportion correct. This was also true for Experiment 2. However, because Experiment 3 used a discrimination task and could not be subject to a signal-detection analysis, we report proportion correct for all experiments to be consistent throughout the paper.

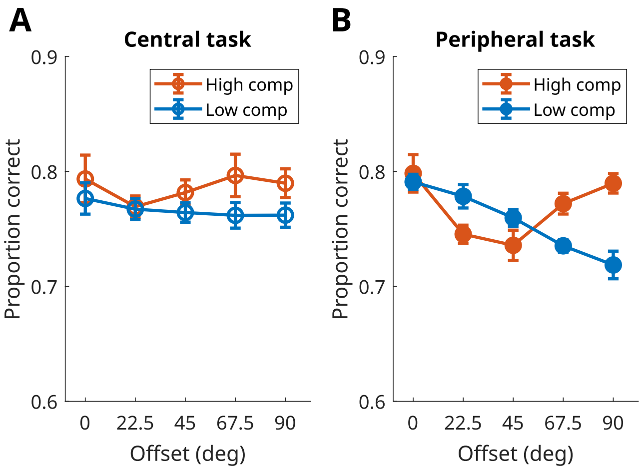

Fig. 2 Data for Experiment 1. **A** Accuracy for the central task. **B** Accuracy for the peripheral task. Error bars are estimated within-subject standard errors (Cousineau, 2005)

orthogonal orientation (90°), a hallmark of the nonmonotonic surround suppression effect.

Recall that the central target, a low-contrast orientation signal, was presented on half of the trials. Thus, we further examined whether the selection profiles measured in the peripheral task depended on the presence of the central target. This analysis revealed reliable effects for offset and target presence, but no interaction between these factors for either competition condition (Fig. S1 in Supplemental Materials). Thus, the peripheral task was more difficult when the central target was present, but the shape of the selection profiles remained similar regardless of its presence.

Overall, these results support our hypothesis that feature competition can modulate the selection profile of feature-based attention. When the masks had similar orientation content as the cued orientation (high competition), a surround suppression profile was observed. When the masks contained very different content to the cued orientation (low competition), a monotonic profile was observed. This pattern makes adaptive sense. Because surround suppression reduces interference from similar distracters, it would be more useful when stimulus competition is high, but less so when stimulus competition is low. Thus, feature selection is adaptive and sensitive to stimulus context.

Experiment 2

Experiment 1 showed that selection profile can be flexibly adjusted to stimulus factor. Here, we examined whether it can be modulated by top-down task demand. We reasoned that surround suppression would be most useful if the task requires the selection of a precise feature value. In this case, suppression of nearby distracters, if present, would benefit task performance. However, if the target itself is broadly defined, then it would be less useful to engage surround suppression as the "nearby distracters" are not well defined in the first place. Indeed, a surround suppression mechanism could potentially suppress a target feature, making it less advantageous. Thus, we tested the scenario where attention is deployed to a broad range of features. The experiment was similar to the high-competition condition of Experiment 1, except that the orientation signal in the central task could occur over a broad range. We hypothesized that surround suppression would be weaker, or even abolished, with this manipulation.

Methods

Preregistration

The study design, hypotheses, analysis plan, and sampling plan were preregistered online (https://osf.io/qajmz).

Participants and sample size

A new group of 10 students from Michigan State University participated in this experiment. All had normal or corrected-to-normal visual acuity. Consent, compensation, and sample size considerations were the same as in Experiment 1.

Visual stimulus and apparatus

Stimulus and apparatus were identical to those of Experiment 1, except that only the high-competition masks were used in this experiment. In addition, the precue was a double fan-shaped object spanning 40° (white, diameter: 0.4°), which we refer to as "range cue" in the following (see Fig. 3A inset for an illustration).

Task and procedure

The task and procedure were nearly identical to the high-competition condition of Experiment 1, so only a brief description is provided here, with the emphasis on the differences between experiments. Trial structure and timing were identical to Experiment 1. As in Experiment 1, participants detected the presence of an orientation signal in the central RSVP stream. However, the key difference was that the precue was the range cue spanning 40°, which indicated that the signal could be any orientation in the cued range. On each trial, the center of the range cue was randomly selected from one of the eight fixed orientations as in Experiment 1. The signal was present on half of the trials, and if present, its orientation was randomly selected from the 40° range cued on that trial. The peripheral stimuli and task remained

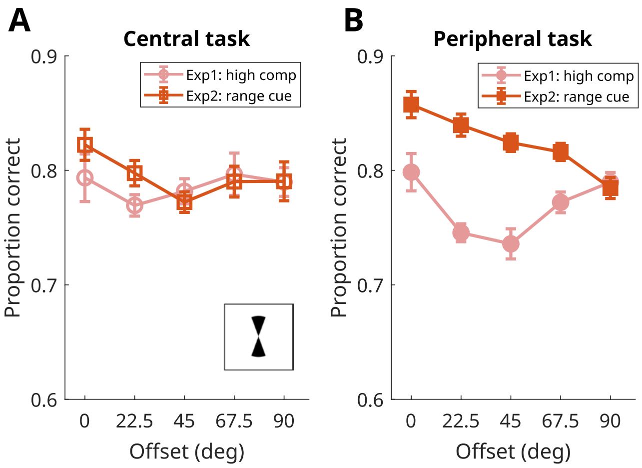

Fig. 3 Data for Experiment 2. **A** Accuracy for the central task. Inset shows an illustration of the range cue in the vertical orientation. **B** Accuracy for the peripheral task. Error bars are estimated within-subject standard errors (Cousineau, 2005). Data from the high-competition condition of Experiment 1 are replotted here in a lighter color for comparison purposes

identical to those of Experiment 1. Similar to Experiment 1, participants reported the presence/absence of the central orientation signal and the location (left/right) of the dimming event on the peripheral gratings. Participants were instructed to attend to all the orientations indicated by the range cue.

Similar to Experiment 1, the RMS contrast of the central orientation signal, as well as the magnitude of peripheral dimming, were determined in a threshold task using QUEST. During the threshold task, the orientation of the peripheral gratings was always aligned with the center of the range cue. Each participant completed two blocks (60 trials per block) of the threshold task at the beginning of the session. After that, they completed six blocks (80 trials per block) of the main task in the same session. Due to logistic issues, one participant completed four blocks of the main task. All participants completed all trials in a single session, which lasted 1–1.5 hrs.

Results and discussion

Given that the only difference between this experiment and the high-competition condition in Experiment 1 was the use of the range cue, we can compare the data across the two experiments to examine the effect of attending to a range of orientations. Accuracy data from Experiment 2 are shown in Fig. 3, and, in addition, we replotted data from the high-competition condition in Experiment 1. We then used two-way mixed-factor ANOVAs with experiment (1 vs. 2) as the between-subject factor and offset (0°, 22.5°, 45°, 67.5°, and 90°) as the within-subject factor to assess the impact of cue precision on the selection profile.

For the central task, performance was at the intermediate level ($M = 79.2\%$). There was a slight trend of decreasing accuracy with larger offsets (Fig. 3A). However, this effect was not reliable (no significant main effect nor interaction from ANOVA, all $ps > .35$). For the peripheral task, accuracy exhibited a monotonic decline as a function of offset (Fig. 3B). The ANOVA revealed a significant main effect of offset, $F(4, 72) = 5.08$, $MSE = 0.001$, $p < .01$, $\eta_p^2 = 0.22$, and importantly, a significant interaction between offset and experiment, $F(4, 72) = 5.93$, $MSE = 0.001$, $p < .001$, $\eta_p^2 = 0.25$. The analysis thus indicated that cue precision had a differential effect on the selection profile across experiments. Similar to Experiment 1, we also examined whether the presence of the central target had an impact on the selection profile and found that overall performance on the peripheral task was lower when the central target was present, but the shape of the selection profiles was similar regardless of its presence (Fig. S2 in Supplementary Materials).

These results showed that a low precision cue abolished the suppressive surround in the feature space, consistent with our prediction. It is noteworthy that we used high-competition masks in this experiment. Thus, task demands appear to be able to override stimulus factors in shaping attentional selection. Overall these results suggest that the selection profile of feature-based attention can be flexibly tuned to top-down task demands.

Experiment 3

In Experiment 3, we further probed the malleability of the selection profile. We reasoned that if attending to a range of orientations abolished surround suppression, then attending to a precise orientation might restore it, even in the low-competition condition. Therefore, our starting point is the low-competition condition in Experiment 1. Recall that the cue did indicate the precise signal orientation in that condition. However, because participants only needed to detect the signal among masks with very different orientation content, they did not have to focus their attention exclusively on the cued orientation. Thus, in this experiment, we induced highly focused attention to the cued orientation in the central task. If feature-based attention is flexibly tuned to task demands, we should observe a surround suppression profile, even in the presence of low-competition masks.

Methods

Preregistration

This study was not preregistered, but the study plan closely followed the first two experiments.

Participants and sample size

A new group of 10 students from Michigan State University participated in this experiment. All had normal or corrected-to-normal visual acuity. Consent, compensation, and sample-size considerations were the same as in Experiment 1.

Visual stimulus and apparatus

Stimulus and apparatus were identical to those of Experiment 1, except that only the low-competition masks were used in this experiment.

Task and procedure

The task and procedure were nearly identical to the low-competition condition of Experiment 1, so only a brief description is provided here, with the emphasis on the differences between experiments. Trial structure and timing were identical to Experiment 1. The key difference from Experiment 1 is that the central task was a fine orientation discrimination, instead of detection, to induce a more focused state of attention. The same line cue was presented at the beginning of each trial. However, an orientation signal was presented on every trial, rotated by 7.5° either in the clockwise or counterclockwise direction from the cued orientation. Participants were instructed to attend precisely to the cued orientation and report the relative rotation direction of the central target from the cue (clockwise or counterclockwise), using their right index and middle fingers. The peripheral stimuli and task remained identical to those of Experiment 1.

Similar to Experiment 1, the RMS contrast of the central target, as well as the magnitude of peripheral dimming, were determined in a threshold task using QUEST. During the threshold task, the peripheral gratings were always in the same orientation as the precue. Each participant completed two blocks (60 trials per block) of the threshold task at the beginning of a session. After that, they completed six blocks (80 trials per block) of the main task in the same session. All participants completed all trials in a single session, which lasted 1–1.5 hrs.

Results and discussion

We compared Experiment 3 and the low-competition condition of Experiment 1 to examine the effect of highly focused attention on the selection profile (Fig. 4). For statistical inference, we again used two-way mixed-factor ANOVAs as in the previous experiment. For the central task, performance was similar across offsets and was at an intermediate level ($M = 65.2\%$), which was lower than the low-competition condition of Experiment 1 (Fig. 4A). The ANOVA

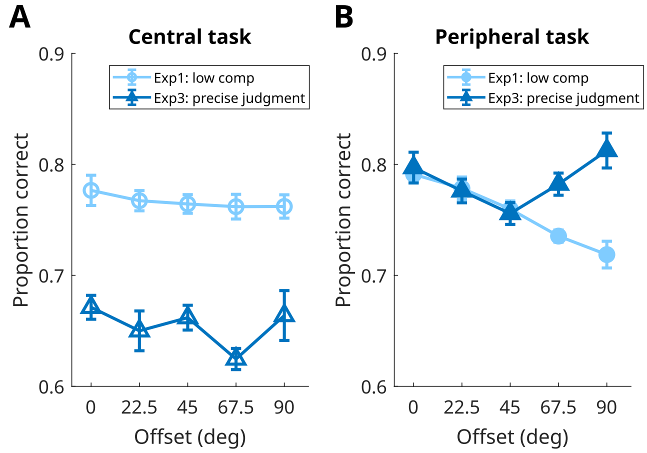

Fig. 4 Data for Experiment 3. **A** Accuracy for the central task. **B** Accuracy for the peripheral task. Error bars are estimated within-subject standard errors (Cousineau, 2005). Data from the low-competition condition of Experiment 1 are replotted here in a lighter color for comparison purposes

revealed a significant main effect of experiment, $F(1, 18) = 13.72$, $MSE = 0.023$, $p < .01$, $\eta_p^2 = 0.43$, without any other significant effects (all *ps* > 0.3). Thus, the central task here was more difficult than was that in Experiment 1, likely due to the need to discriminate the small orientation difference between the cue and central target.

For the peripheral task, we observed a nonmonotonic pattern such that accuracy was lowest at the 45° offset, consistent with a surround suppression profile. The ANOVA revealed a significant main effect of offset, $F(4, 72) = 3.29$, $MSE = 0.001$, $p < .05$, $\eta_p^2 = 0.16$, and a significant interaction between offset and experiment, $F(4, 72) = 6.32$, $MSE = 0.001$, $p < .001$, $\eta_p^2 = 0.26$. These results showed that highly focused attention had a differential effect on the selection profile. We further conducted planned *t* tests comparing performance at 45° against 0° and 90° offsets in Experiment 3, with both tests returning significant differences, 45° vs. 0°: $t(9) = 2.62$, $p < .05$; 45° vs. 90°: $t(9) = 2.70$, $p < .05$, thus confirming a surround suppression pattern.

These results demonstrate that when participants narrowly focused their attention on a specific orientation, a surround suppression effect emerged. Remarkably, such an effect was observed with low-competition masks where there was no interference from nearby distracters. This finding suggests that deploying attention in a highly focused state can proactively suppress representations of nearby features, even when such features are not present.

We note that, unlike the previous two experiments, where the difficulty of the central task was equated, here, the central task was more difficult than the low-competition condition in Experiment 1. This can be attributed to the small orientation offset between the cue and central target (7.5°). We used a small offset intentionally in order to induce a highly focused state of attention. In doing so, the task might have approached the hard limit in orientation discrimination and our thresholding procedure was unable to perfectly titrate the performance level. However, we do not think the lower performance in the central task complicates our interpretation of the peripheral task as the purpose of the central task was simply to induce a focused state of feature attention while the peripheral task was held constant across experiments. Furthermore, overall performance in the peripheral task was still equated between experiments (Fig. 4B).

General discussion

We examined the flexibility of feature-based attention in shaping the selection profile. We found that when there was strong feature competition, or a demand for high selection precision, a nonmonotonic, surround suppression profile was observed. However, when feature competition was low or selection was coarse, a monotonic profile was observed. These results thus support our hypotheses that feature-based attention is deployed adaptively to efficiently select task relevant information.

The feature-similarity gain model was informed by the monotonic attentional modulation of neuronal responses (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999) and was further supported by human psychophysical studies that found monotonic performance modulation (Ho et al., 2012; Paltoglou & Neri, 2012; Wang et al., 2015). However, other studies have reported the nonmonotonic surround suppression profile (Fang et al., 2019; Fang & Liu, 2019; Störmer & Alvarez, 2014; Tombu & Tsotsos, 2008). An outstanding question is what can account for discrepancies across these studies? In our previous work, we have pointed out that a relatively dense sampling of a feature space is necessary to detect a surround suppression effect, and a coarse sampling would likely only detect a feature-similarity gain profile (Fang et al., 2019; Fang & Liu, 2019). Some of the previous studies used relatively sparse sampling (e.g., Liu et al., 2007; Sàenz et al., 2003; Wang et al., 2015), and hence could have missed the suppressive surround.

However, this explanation is unlikely to account for other studies in the literature which have sampled the feature space relatively densely (e.g., Ho et al., 2012; Paltoglou & Neri, 2012), including the original study in monkey MT (Martinez-Trujillo & Treue, 2004). The current results shed light on factors that promote the expression of surround suppression—feature competition and selection precision—and help explain the absence of surround suppression in earlier studies. Indeed, both factors appear to be low in these studies: subjects tended to detect/locate a target feature that was quite distinct from distracter features, with the latter often in different locations from the target. We recognize that this literature is quite heterogenous with a variety of dependent measures and feature dimensions, and further research is necessary to examine the generalizability of our account. However, our results revealed a systematic modulation of the selection profile and suggest that feature competition and selection precision are two important factors in shaping the selection profile.

Our finding on the effect of stimulus context is reminiscent of previous work showing the “off-channel gain” effect, which occurs when searching for a target that is very similar to distracters (e.g., Navalpakkam & Itti, 2007; Scolari & Serences, 2009; Yu & Geng, 2019). In this case, it appears that participants would attend to a feature that is shifted away from both the target and distracter, which, according to computational analysis, is more optimal than attending to the target feature, as it can enhance target-distracter distinctiveness. The current study differs from these previous studies in some key aspects. Aside from the methodological differences (e.g., the use or probe trials to measure attentional template in visual search vs. dual-task procedure to measure selection profile), perhaps the most important difference is that previous studies presented distracters on one side of the target in the feature space to elicit the repulsion effect, whereas, in our study, the distracter features in the masks were always on both sides of the target, which is not expected to lead to any shift (and none observed). Thus, these effects (shifting template vs. surround suppression) might reflect different mechanisms of adaptive attentional control. More work is necessary to compare and relate these phenomena in the future.

Regardless of the underlying causes of template shift and surround suppression, they are both manifestations of attentional control tuned to stimulus context. This raises the question of whether these effects are obligatory responses to stimulus context, or they can also be modulated by top-down task goals. Utilizing our dual-task paradigm, we further probed the impact of task demands on the selection profile and found that a pure top-down manipulation of selection precision modulated the surround suppression effect. Indeed, Experiments 2 and 3 pitched feature competition against selection precision, and the latter was able to override the former in modulating the selection profile. Specifically, we observed a nonmonotonic, surround suppression profile when selection was precise, and a monotonic, feature-similarity gain profile when selection was coarse, regardless of the level of feature competition between the target and masks. These results demonstrate that attention-induced surround suppression is subject to pure top-down regulation and hence is likely of different origins than the prevalent center-surround antagonism in early vision, which is largely based on fixed, feedforward connections. Our results thus suggest that top-down modulations alone are sufficiently flexible to adjust the selection profile independent of stimulus factors.

An important future question concerns the neural mechanisms through which top-down signals modulate the selection profile. Although the exact neural mechanism of attention-induced surround suppression is unknown, computational modeling work has suggested candidate mechanisms that could guide the interpretation of the current findings. An influential computational model of top-down attention is the selective tuning model (Tsotsos et al., 1995), a multilayer neural network model in which higher-level units send feedback signals to lower-level units in a propagating, winner-take-all process. Such a process prunes lower units that do not represent the target yet are connected to the higher units and thus creates a surrounding area around the target with attenuated activity. This model naturally explains the spatial surround suppression effect induced by spatial attention (Hopf et al., 2010). With appropriate connectivity patterns among feature-tuning units, this model can also exhibit surround suppression in the feature space (Tsotsos, 2011). Given the top-down nature of the feedback signal in this model, it is conceivable that such feedback can be flexibly adjusted based on task demands, a possibility supported by our results. Future work at the neural circuit level is needed to test the details of such models.

Regardless of the exact neural mechanisms of attention-induced surround suppression, our results show that this effect is not hardwired nor obligatory but is under adaptive control with a high degree of flexibility tuned to stimulus contexts and task demands. Such flexibility provides an adaptive and efficient mechanism to extract task-relevant features from the rich visual environment.

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Data and code availability All data and code are openly available at https://osf.io/pk5cq/.

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Author contributions T.L. and M.F. conceptualized and designed the experiment. M.F. and T.L. implemented the task and analyzed the data. M.F. and S.S. collected data. M.F. and T.L. analyzed data. T.L. wrote the original draft manuscript. T.L., M.F., S.S. reviewed and edited the manuscript.

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