



Limited featured-based attention to multiple features

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ARTICLE INFO

Article history:

Received 4 April 2012

Received in revised form 22 August 2012

Available online 13 September 2012

Keywords:

Attention

Feature

Capacity

Motion

Coherence

ABSTRACT

Attending to a feature (e.g., color or motion direction) can enhance the early visual processing of that feature. However, it is not known whether one can simultaneously enhance multiple features. We examined people's ability to attend to multiple features in a feature cueing paradigm. Each trial contained two intervals consisting of a random dot motion stimulus. One interval (noise) had 0% coherence (no net motion), while the other interval (signal) moved in a particular direction with varying levels of coherence. Participants reported which interval contained the signal in one of three cueing conditions. In the one-cue condition, a line segment preceded the stimuli indicating the direction of the signal with 100% validity. In the two-cue condition, two lines preceded the stimuli, indicating the signal would move in one of the two cued directions. In the no-cue condition, no line segment appeared before the dot stimuli. In several experiments, we consistently observed a lower detection threshold in the one-cue condition than the no-cue condition, showing that participants can enhance processing of a single feature. However, detection threshold was consistently higher for the two-cue than one-cue condition, indicating that participants could not simultaneously enhance two motion directions as effectively as one direction. This finding revealed a severe capacity limit in our ability to enhance early visual processing for multiple features.

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1. Introduction

Attention is thought to be an adaptive mechanism that has evolved to cope with a capacity limit in information processing (Anderson, van Essen, & Olshausen, 2005; Carrasco, 2011). It allows us to selectively process a small set of information from the vast amount of sensory input. Importantly, attention can be allocated voluntarily according to goal-relevant features, as in the example of searching for a particular colored fruit in the jungle. This type of attention is commonly referred to as feature-based attention.

A basic finding in the literature is that feature-based attention can modulate early sensory representations (Maunsell & Treue, 2006). For instance, a single-unit recording study has demonstrated direction-specific attentional modulation of neuronal activity in monkey middle temporal (MT) area during a motion perception task (Treue & Martinez-Trujillo, 1999). Psychophysical tasks in humans further support these findings. For example, attending to a direction in a compound motion stimulus modulates motion aftereffects (Lankheet & Verstraten, 1995), suggesting that attention can bias activity in low-level direction-selective mechanisms. These early observations were further corroborated by later

studies utilizing psychophysical (Arman, Ciaramitaro, & Boynton, 2006; Liu & Hou, 2011; Liu & Mance, 2011; Saenz, Buracas, & Boynton, 2003; White & Carrasco, 2011), brain imaging (Liu, Larsson, & Carrasco, 2007; Saenz, Buracas, & Boynton, 2002; Serences & Boynton, 2007), and neurophysiological (Cohen & Maunsell, 2011; Martinez-Trujillo & Treue, 2004) measures. Furthermore, these attention-modulated sensory responses could be the mechanism underlying target selection during visual search. Indeed, such a conjecture is supported by the finding of enhanced neuronal response in V4 during visual search when the stimulus within a neuron's receptive field matched the target feature (Bichot, Rossi, & Desimone, 2005).

Although these studies of feature-based attention have shown that participants can selectively modulate representations of a single feature, it is not known how many features one can simultaneously modulate. This question pertains to the capacity limit of attentional modulation, and its answer will provide useful constraints on models of attention. In the domain of spatial attention, similar questions have been investigated by systematically varying the size of attended region and demonstrating a decrease in processing power and resolution with larger attended areas—a phenomenon likened to a “zoom lens” (Castiello & Umiltà, 1990; Eriksen & St James, 1986). However, analogous questions for visual features have not been addressed. In the current study, we investigated how efficiently one can attend to multiple features.

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A related question has been addressed in a number of recent studies using visual search. In those studies, it was found that participants can use two different features to guide search (Adamo et al., 2008; Beck, Hollingworth, & Luck, 2012; Irons, Folk, & Remington, 2012; Moore & Weissman, 2010). In some cases, participants were just as efficient in constraining search based on one vs. two features (Beck, Hollingworth, & Luck, 2012; Becker, Alzhabi, & Jelinek, 2011; Moore & Weissman, 2010). To the extent that visual search involves the enhancement of feature-specific sensory responses (Bichot, Rossi, & Desimone, 2005), these studies could imply that early sensory responses can be modulated for two features efficiently. However, this is not a foregone conclusion, as attentional selection might also be implemented by later, post-perceptual processes such as selective pooling of information in a post-perceptual decisional stage (Eckstein, 2011). In addition, visual search is a complex task that involves both spatial and feature selection and the typical performance measure of reaction time is difficult to relate to the state of early sensory representations. These considerations prompted us to use a threshold psychophysical task to examine how well attention can simultaneously modulate early sensory representations for multiple features.

We chose to test direction of motion as it offers a continuous scale for ease of manipulating feature similarity, and it is also the most widely used in studies of feature-based attentional modulation of early sensory responses. We tested participants' ability to detect global motion signals using the classic random dot motion stimulus (Newsome & Pare, 1988). Performance on this task has been shown to be causally linked to MT neuronal activity (Parker & Newsome, 1998), thus offering a proxy for testing attentional effects on neural activity in early visual processing.

2. Experiment 1a: cueing one or two directions with fixed directions

In this experiment, we compared whether participants can attend to two directions as well as to one direction. Importantly, we tested participants' ability to attend to two *distinct* directions, as when two directions are very similar, they become essentially one direction (De Bruyn & Orban, 1988). For this purpose, we tested two maximally dissimilar configurations: orthogonal directions and opposite directions. We used a cueing paradigm to manipulate feature-based attention to motion.

To quantify performance, we measured coherence threshold to detect a weak motion signal in a two interval forced choice (2-IFC) procedure. Two random dot moving patterns were shown on each trial, one in each interval. One pattern moved in one of four possible directions at varying level of coherence (*signal*), whereas the other pattern had zero coherence (no net motion). Participants reported the interval that contained the motion signal. For the baseline condition, no prior information about the signal direction was provided; for the one-cue condition, a single cue informed participants about the signal direction; for the two-cue condition, two cues (either orthogonal or opposite) indicated the possible directions of the signal (Fig. 1). Cues were always valid, thus prompting participants to attend to the cued direction(s).

2.1. Methods

2.1.1. Participants

A total of eleven observers participated in this experiment. Two participants were authors (T.L. and M.J.), while the remaining nine participants were graduate and undergraduate students at Michigan State University and were naïve as to the purpose of the experiment. All participants had normal or corrected-to-normal vision. Participants gave informed consent and all (except the authors)

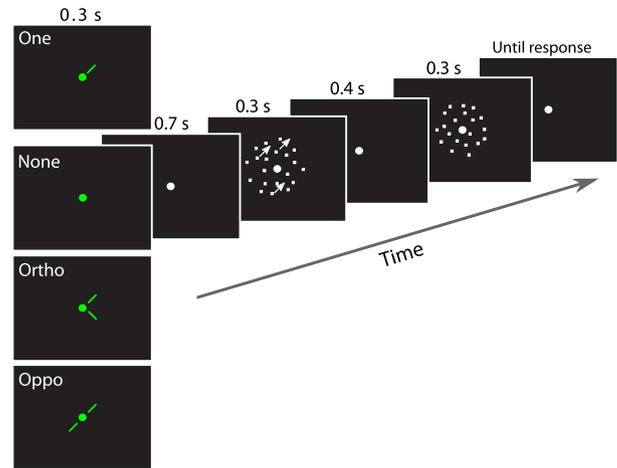


Fig. 1. Schematic of a trial in Experiment 1a. At the beginning of the trial, one of the four possible cue types was presented.

were compensated at the rate of \$10/h. All experimental protocols were approved by the Institutional Review Board at Michigan State University.

2.1.2. Visual stimuli

Visual stimuli were generated using MGL (<http://gru.brain.riken.jp/doku.php?id=mgl:overview>), a set of OpenGL libraries running in Matlab (Mathworks, Natick, MA). The random dot motion stimulus was based on classic studies in neurophysiology (Newsome & Pare, 1988). The motion stimulus consisted of white moving dots (size: 0.05°) in a circular aperture (6°), presented on a dark background. The circular aperture was centered on the fixation point (white, size: 0.3°), which was surrounded by a small occluding region (0.7°) of the background luminance such that no dots would appear too close to the fixation point. The dots were plotted in three interleaved sets of equal number, with an effective density of $16.8 \text{ dots/deg}^2/\text{s}$ and a speed of 4 deg/s . Each single dot was presented on the screen for one video frame (16.7 ms). Importantly, only a portion of dots moved in a particular direction between frames, while the rest of the dots were re-drawn in random locations. The proportion of coherently moving dots (motion coherence) is the key stimulus parameter that we manipulated to measure performance. The stimuli were presented on a 19" CRT monitor refreshed at 60 Hz and set at a resolution of 1024×768 . Observers were stabilized with a chinrest and viewed the display from a distance of 114 cm in a dark room.

2.1.3. Task and procedure

Observers detected the presence of coherent motion in a 2-IFC task. Each trial started with a cue display for 0.3 s, followed by a 0.7 s fixation interval, after which two intervals of random dot motion stimuli were shown, each for 0.3 s, and separated by 0.4 s (Fig. 1). One interval always contained 0% coherent motion (noise) while the other interval contained a motion stimulus at one of six coherence levels: 2%, 4%, 8, 16%, 28%, and 49% (signal). The presentation order of the signal and noise intervals was randomized. Observers were instructed to report which interval contained the coherent motion signal by pressing the "1" or "2" key on the numeric keypad of a standard computer keyboard. Observers were instructed to respond as accurately as possible. A sound was played as feedback on incorrect trials. An inter-trial interval of 1.2 s followed their key press response.

The motion signal moved in one of four directions on any given trial: 45° , 135° , 225° , and 315° (i.e., the four inter-cardinal directions). To manipulate feature-based attention, we presented one

of four types of cue displays at the beginning of a trial. In the baseline (no-cue) condition, the fixation dot turned green to indicate the impending motion stimulus; in the one-cue condition, an additional green line segment (length: 0.3° , center 0.65° to the fixation) was shown to indicate the direction of the motion signal; in the orthogonal cue condition, two green line segments were shown in one of four possible pairings of orthogonal directions (i.e., 45° – 135° , 135° – 225° , 225° – 315° , 315° – 45°); in the opposite cue direction, two green line segments were shown in one of two possible pairings of opposite directions (i.e., 45° – 225° , 135° – 315°). The direction cues were always valid: in the one-cue condition, the motion signal always moved in the cued direction; in the two-cue conditions, the motion signal moved in one of the two cued directions. Observers were instructed to use the cue information and attend to the cued direction(s), as it would help them to detect the signal. Note the 1 s cue-to-stimulus interval was much longer than that for typical cueing studies, and should be sufficient for participants to use direction cues, according to previous studies that had measured the time course of their effect (Ball & Sekuler, 1981; Liu, Stevens, & Carrasco, 2007).

Observers performed the task in blocks of 48 trials, within which the type of cue (no-cue, one-cue, orthogonal cues, opposite cues) was held constant. Cue type was indicated by a prompt at the beginning of each block. Within a block, the direction, the coherence level of the motion signal, and the cue pairings in the two-cue conditions were all randomized. Sixteen blocks of trials were run, with four blocks for each cue type. The order of blocks was pseudo-randomized such that for every four blocks, each of the four cue types occurred once in a random order. This ensured there were no consistent order effects among the cueing conditions. The experiment took approximately 1 h to complete.

The majority of our observers (except the authors) were not familiar with the random dot motion task. In our experience using this task, there is a considerable perceptual learning effect for observers who have never seen this type of stimulus. Thus, in addition to the main experiment, we also ran a practice session for these observers, using exactly the same procedure as the no-cue condition described above. Observers performed the motion detection task in 48-trial blocks until their coherence threshold did not show a sizeable drop in consecutive 3-block units. On average, the practice session was 10 blocks long (i.e., 480 trials), with a range of 6–15 blocks across observers. The practice session always took place before the main experiment on a different day.

2.1.4. Data analysis

Proportion correct data were fitted with a three-parameter Weibull function:

$$p = 0.5 + (0.5 - \lambda) \left\{ 1 - \exp \left[- \left(\frac{x}{\alpha} \right)^\beta \right] \right\}$$

where p is the proportion correct, x is the coherence, α is the location parameter, β is the slope, and λ represents deviation from 1 at the upper asymptote (e.g., due to pressing the wrong buttons). Fits were performed using maximum-likelihood estimation, as implemented in *psignifit* (Wichmann & Hill, 2001). Threshold was defined as the coherence level corresponding to $p = 0.75$ (75% correct).

2.2. Results and discussion

Overall performance on the task showed a monotonic increase as a function of the motion coherence of the signal, which was well fit by a sigmoid function such as Weibull (Fig. 2A). Compared to the baseline condition (no cue), a single cue shifted the psychometric function to the left, indicating that a weaker motion signal was

needed to detect the motion signal at the same criterion performance. Both the orthogonal and opposite two-cue conditions also shifted the psychometric function to the left, but to a smaller extent than the one-cue condition, indicating a smaller cueing benefit. To quantify the cueing effect, we fitted individual participant data with Weibull functions and obtained thresholds, defined as the coherence of the motion signal that produced 75% correct performance. Fig. 2B shows the group-averaged thresholds for the four cueing conditions, which were significantly different from each other as assessed with a one-way repeated measures ANOVA ($F(3,30) = 6.93$, $p < 0.005$). Post-hoc paired comparisons showed that the three cueing conditions all had lower threshold than the baseline no-cue condition, and that the one-cue condition had a lower threshold than the orthogonal cue condition (paired t -test, all $p < 0.05$). No other comparisons reached significance. We also examined the slope parameter of the psychometric function, which did not differ among conditions (ANOVA, $F(3,30) = 2.16$, $p > 0.1$).

These results show that knowing the direction of an upcoming motion target facilitates its detection. This finding is also consistent with an earlier study that found increased sensitivity for detection of a low-contrast motion stimulus when its direction was known vs. unknown (Ball & Sekuler, 1981). The coherence measures we used have been shown to be closely related to direction-selective neural responses in early visual areas, particularly MT (Britten et al., 1992; Newsome & Pare, 1988), hence we believe that the coherence threshold is a better measure of the modulation of direction-selective mechanisms in early visual processing than the contrast threshold indexed by the task in Ball and Sekuler (1981).

Our results also showed intermediate coherence thresholds for the two-cue conditions, suggesting that although participants can attend to two directions to some extent, they cannot attend as efficiently as attending to one direction. This result revealed a capacity limitation in simultaneously attending to multiple directions. Although the orthogonal and opposite cues produced overall similar thresholds, the latter is numerically lower, making it statistically indistinguishable from the one-cue condition. We suspect this could be due to alternative strategies used for opposite cued trials—although we instructed participants to attend to two directions, they might have attended to a single axis of motion on these trials. This axis strategy essentially translates direction discrimination to orientation discrimination. Indeed, a number of participants spontaneously reported to have used such a strategy during debriefing. Additionally, there is evidence of mutual inhibition between opposite direction-selective mechanisms in early visual processing (Heeger et al., 1999; Qian & Andersen, 1994), which could aid the detection of weak signals. For example, if the observer registered a suppressed activity in a particular channel (e.g., upward), it could signal the stimulus moving in the opposite direction (e.g., downward). Thus both strategic and architectural factors might aid participants to attend to opposite directions. These factors could make it difficult to interpret results on opposite-cued trials, which will not be considered further in this report.

Our main finding in this experiment was that performance on the orthogonal cue condition was impaired relative to the one-cue condition, suggesting that feature-based selection has a limited capacity. In the next experiment, we sought to replicate this finding when the motion signal could move in more possible directions. But before that, we performed a control experiment to test the role of uncertainty reduction during our experiment.

3. Experiment 1b: pre-cue vs. post-cue

Under certain circumstances, performance improvement in spatial cueing paradigms can be explained by more efficient pooling of

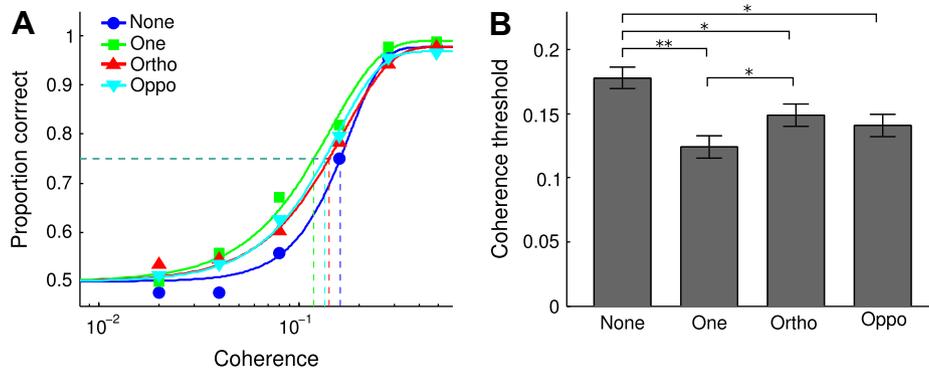


Fig. 2. Data for Experiment 1a. (A) Group average accuracy and fitted psychometric functions for each cueing condition (None: no cue, One: one cue, Ortho: two orthogonal cues, Oppo: two opposite cues). (B) Average threshold for each of the cueing conditions. Error bars are the estimated within-subject standard error from the ANOVA following the method of Loftus and Masson (1994). Asterisks indicate the significance level in paired *t*-tests (* $p < 0.05$, ** $p < 0.01$).

sensory information in the decision stage (Eckstein, Shimozaki, & Abbey, 2002; Shiu & Pashler, 1994). Although the attentional effects we observed in Experiment 1a are consistent with the notion that feature-based attention modulates early sensory responses, a post-perceptual decisional explanation might also account for our result. For example, consider a trial in the one-cue condition, where the first interval contained a weak signal moving in the upward-left direction and the second interval contained noise. On occasion, the participant might fail to perceive the actual motion signal in the first interval and erroneously perceived motion in the downward-left direction in the second interval. But because the cue pointed to the upward-left direction, the participant could guess (correctly) that the signal was actually in the first interval. Thus, knowing the target direction could improve one's guessing strategy.

To evaluate this post-perceptual account of the cueing effect, one can use post-cues to eliminate decisional noise/uncertainty (e.g., Luck et al., 1994; Yeshurun, Montagna, & Carrasco, 2008). If the direction cue facilitated a post-perceptual decisional strategy in Experiment 1a, it should exert a similar effect when the same cue was presented after the stimulus (e.g., knowing the direction of the target can still facilitate guessing in the above scenario). On the other hand, if the direction cue enhanced sensory processing of the motion stimulus, it should only affect performance when presented before the stimulus. In this experiment, we tested these two alternatives by comparing the effect of a pre-cue vs. a post-cue regarding the direction of the motion signal.

3.1. Methods

3.1.1. Participants

Six observers participated in this experiment (including the three authors). All observers had normal or corrected-to-normal vision and were compensated at \$10/h (except the authors). Four of the observers also participated in Experiment 1a.

3.1.2. Stimuli, task, and procedure

The experiment was identical to Experiment 1a with the following exceptions. There were three conditions: baseline (no-cue), pre-cue, and post-cue. The first two conditions were identical to the no-cue and one-cue condition of Experiment 1a. The post-cue trials were identical to the pre-cue trials, except that the cue (green line segment) was presented 0.2 s after the second random dot motion stimulus disappeared (duration: 0.3 s), rather than at the beginning of the trial. Observers were instructed that the cues were always valid and they should use them to detect the coherent motion signal. There were four 48-trial blocks for each cueing condition (12 blocks total), pseudo-randomized such that every three

blocks contained a random permutation of the three cue types. All observers in this experiment were familiar with the random dot motion stimulus and thus were not trained in a practice session.

3.2. Results and discussion

Compared to the baseline (no-cue) condition, the pre-cue shifted psychometric function to the left, but the post-cue did not produce a noticeable shift of the psychometric function (Fig. 3A). Group averaged coherence thresholds (Fig. 3B) were significantly different from each other (ANOVA, $F(2,10) = 7.55$, $p < 0.05$). Post-hoc comparisons showed that the threshold was significantly lower for the pre-cue condition than the no-cue and post-cue conditions (paired *t*-test, all $p < 0.01$), but did not differ between the no-cue and post-cue conditions (paired *t*-test, $p > 0.8$). The slope of the psychometric function also did not differ among conditions (ANOVA, $F(2,10) < 1$).

Again, we observed a reliable cueing effect comparing the pre-cue and no-cue condition, replicating Experiment 1a. Critically, the post-cue did not produce any observable benefits, suggesting that reducing noise/uncertainty in the decisional stage cannot account for the cueing benefits associated with the pre-cue. We believe the more plausible explanation of the cueing effect is an improved sensory representation of the motion signal due to feature-based attention. Such a conclusion is consistent with many other studies using direction cues to manipulate attention to motion stimuli. In particular, an attention-induced motion aftereffect provides strong evidence that direction-selective mechanisms in early visual processes can be modulated by attention (Arman, Ciaramitaro, & Boynton, 2006; Lankheet & Verstraten, 1995; Liu & Mance, 2011).

4. Experiment 2: cueing one or two directions with varying directions

In Experiment 1a, we found only a limited performance improvement due to two cues. A potential explanation for such a limited cueing effect was that the cues were not very informative. Recall that there were four fixed target directions throughout the experiment. Although this fact was not explicitly mentioned to participants, it was likely that participants realized this constraint during the experiment. Thus, compared to this (essentially four-cue) baseline, the modest increase in information (from four possibilities to two possibilities) might not sufficiently motivate participants to use the cues. To test the role of cue informativeness and to further replicate our finding, we allowed the target to move in many more directions in this experiment. Furthermore, due to

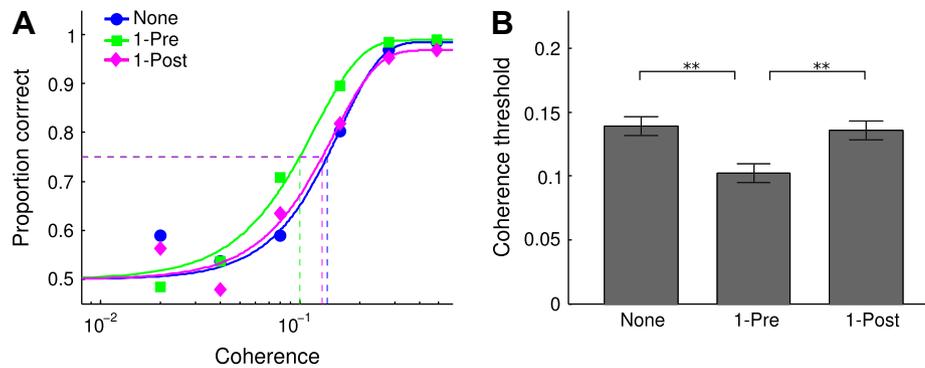


Fig. 3. Data for Experiment 1b. (A) Group average accuracy and fitted psychometric functions for each cueing condition (None: no cue, 1-Pre: one pre-cue, 1-Post: one post-cue). (B) Average threshold for each of the cueing conditions. Error bars are the estimated within-subject standard error (Loftus & Masson, 1994). Asterisks indicate the significance level in paired *t*-tests (* $p < 0.05$, ** $p < 0.01$).

the potential difficulty in interpreting results of opposite cues (see Section 2.2), we only tested orthogonal cues in the two-cue condition.

4.1. Methods

4.1.1. Participants

Eleven observers participated in this experiment (including the three authors). All observers had normal or corrected-to-normal vision and were compensated at \$10/h (except the authors). Four of the observers had participated in Experiment 1a and four of the observers had participated in Experiment 1b (three observers participated in both Experiments 1a and 1b, two of whom were authors).

4.1.2. Stimuli, task, and procedure

The experiment was identical to Experiment 1a with two exceptions. First, we dropped the opposite cue condition, for the reasons discussed above, such that three cueing conditions remained: baseline (no-cue), one-cue, and orthogonal cue. Second, instead of four fixed directions, the motion signal moved in any one of 72 possible directions, ranging from 0° to 355° in 5° intervals. The cue always pointed to the signal direction in the one-cue condition, whereas in the orthogonal cue condition, one cue pointed to the signal direction and the other cue pointed to a direction $\pm 90^\circ$ away (the sign randomly determined on each trial). There were twelve 48-trial blocks, with four blocks per cueing condition. Block order was pseudo-randomized as in Experiment 1b. In this experiment, there were six naïve observers who underwent a separate practice session as in Experiment 1a. The average length of the practice session was 10.5 blocks (504 trials, range: 6–12 blocks).

4.2. Results and discussion

Cueing one direction shifted the average psychometric function to the left relative to the baseline (no-cue) condition. Cueing two orthogonal directions also shifted the psychometric function to the left, but to a smaller degree (Fig. 4A). A one-way ANOVA revealed a significant effect of condition on coherence threshold ($F(2,20) = 16.7$, $p < 0.001$, Fig. 4B). Post-hoc comparisons showed a significant difference in all pair-wise comparisons (all $t(10) > 2.27$, all $p < 0.05$), i.e., threshold for the one-cue condition was lower than the two-cue condition, which was lower than the no-cue condition. The slope of the psychometric function did not differ among the conditions (ANOVA, $F(2,20) = 2.41$, $p > 0.1$).

Coherence threshold in the baseline (no-cue) condition was higher in this experiment compared to Experiment 1a, indicating

an overall harder task when the target could move in many more possible directions. However, the pattern of the results remained essentially the same as in Experiment 1a: cueing one direction lowered threshold while cueing two orthogonal directions also lowered threshold, but to a smaller degree. Thus, increasing the cue informativeness did not overcome the drop in performance in the two-cue condition relative to the one-cue condition. These results thus replicated Experiment 1a and provided evidence for a severe capacity limit in terms of how many features can be simultaneously attended.

5. Experiment 3: validity effects with cueing one or two directions

In this experiment, we consider several possible mechanisms for the observed limit in attending to two directions. One possibility is that participants can attend to both directions during each trial, but with a lower efficacy. We refer to this scenario as “both”. It could result from rapidly switching between the two cued directions within a trial or sharing limited attentional resources across both cued directions in parallel. In neural terms, this could translate to smaller modulation magnitude or less precise (wider spread) modulation along the feature dimension, or a combination of both.

Alternatively, the observed limit in attending to two directions might result because participants were only able to use one directional cue during a trial. There are multiple possible mechanisms that could operate under this scenario. First, it is possible that participants realized that it was difficult to simultaneously attend to both cued directions and therefore they voluntarily picked one of the cued directions to attend to on a particular trial. This would be an explicit strategy. A second alternative is that participants had a strategy to attend to both directions but limits in the attentional system allowed only one direction to be effectively attended on each trial. These two alternatives would produce the same performance outcome and thus we will refer to them as “one-at-a-time” scenarios. However, the two “one-at-a-time” scenarios differ in terms of the participants’ strategies. Thus, we can differentiate between these two possibilities by inquiring about participants’ explicit strategy (so far we have not queried their strategies). Finally, it is possible that participants utilized both cues, but doing so resulted in participants attending to the mean direction indicated by the two cues (vector average). We refer to this scenario as “middle”, which is a reasonable heuristic given the mean direction is relatively close (45° away) to both of the cued directions. Indeed, a previous study found evidence for such a strategy in a somewhat similar task (Ball & Sekuler, 1980).

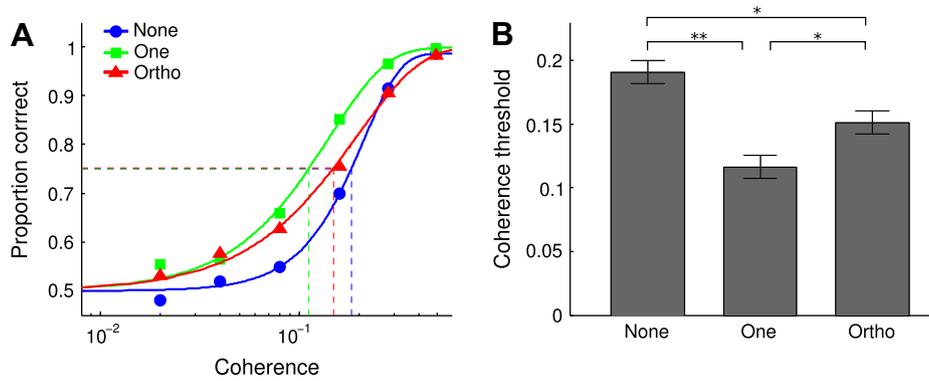


Fig. 4. Data for Experiment 2. (A) Group average accuracy and fitted psychometric functions for each cueing condition (None: no cue, One: one cue, Ortho: two orthogonal cues). (B) Average threshold for each of the cueing conditions. Error bar is the estimated within-subject standard error (Loftus & Masson, 1994). Asterisks indicate the significance level in paired *t*-tests (**p* < 0.05, ***p* < 0.01).

In Experiment 3, we introduced a cue validity manipulation and a post-experiment query about observers’ strategy. Doing so should allow us to differentiate between the alternative scenarios outlined above. Like previous experiments, the task in Experiment 3 was a 2-IFC of the interval that the contained coherent motion. On the majority of the trials, the motion signal moved in a cued direction (valid cue), whereas it moved with a 45° offset to the cued direction on a minority of the trials (invalid cue). The introduction of this validity manipulation produces precise predications about performance under the “one-at-a-time” and “middle” scenarios that should allow us to reject these scenarios if they are incorrect. The set of specific predications are presented in Fig. 5 and the logic supporting these predications is outlined below.

If participants attended to the mean direction (the “middle” scenario), then in two-cue trials they should attend to the direction 45° from each cue, which was the direction of motion presented during the invalid trials. Thus two-cue invalid trials should perform like valid trials in the one-cue condition. In addition, the direction of the signal on valid two-cue trials should be 45° from the actual attended mean direction and thus should behave like invalid trials in the one-cue condition (first row of predications, Fig. 5). By contrast, if participants attended to one of the cued directions in the two-cue condition (the “one-at-a-time” scenario), then the invalid trials should yield the same performance in one-cue and two-cue conditions (second row of predications, Fig. 5). These three equalities are exact predications and are mutually exclusive.

There were many other possible comparisons not listed in Fig. 5; however, none of them provide a diagnostic test between these alternative models because one can derive different predications under each model by varying how much weaker (amplitude) and less precise (tuning width) attentional modulation is in the two-cue than the one-cue condition. For example, all models can predict a higher performance for the two-cue invalid than two-cue valid trials, given suitable parameters of attentional tuning. Similarly, the “both” model turns out to be a more difficult model to reject as it does not produce any equality predications. Simple simulations showed that it can exhibit a variety of behavior depending on assumptions of tuning parameters. However, our hope is that the results can provide some insights regarding the plausibility of the other models.

5.1. Methods

5.1.1. Participants

Twelve observers participated in this experiment (none of the authors participated). All observers had normal or corrected-to-

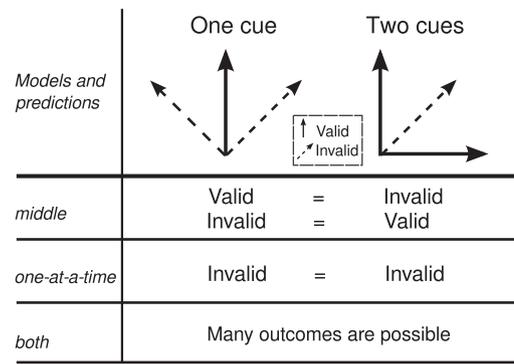


Fig. 5. Stimulus schematic and predications tested in Experiment 3. The solid arrows indicate the cued directions and the dashed arrows indicate the uncued directions in which the signal moved on invalid trials. Note the actual directions can vary greatly from 0° to 360° but the relative spacing of directions remain the same. The lower half of the figure shows the predications by three models considered (for details see text).

normal vision and were compensated at \$10/h. Two of the observers also participated in Experiment 2, and one observer participated in all previous experiments.

5.1.2. Stimuli, task, and procedure

The experiment was very similar to Experiment 2 with two main exceptions.

First, we measured percent correct performance at a fixed level of motion coherence. Coherence was first determined for each participant in a threshold procedure, which was identical to the no-cue condition in Experiment 2. Briefly, two random dot motion stimuli were presented and observers made 2-IFC judgment reporting the interval that contained coherent motion, with the coherence levels varying across trials (method of constant stimuli). Each participant performed the threshold task until suitable psychometric functions were obtained (average: 252 trials, range: 144–432 trials). We fitted each participant’s psychometric function with a Weibull (see Section 2.1.4) and used the 75% correct threshold as the coherence level for the cueing experiment (see below).

Second, we manipulated cue validity in this experiment. There were again three cue types: no-cue, one-cue, two-cue (orthogonal), which were run in blocks of either 30 trials (no-cue) or 60 trials (one-cue and two-cue). We collected fewer trials for the no-cue condition as it did not directly bear on the predications of different models (see Fig. 5), the main objective in this experiment. The timing of events within a trial was identical to previous experiments

(see Fig. 1), and the signal coherence was fixed at individually determined level obtained via the thresholding procedure (see above). In the one-cue blocks, the signal moved in the cued direction on 80% of the trials (valid cue), and moved in $\pm 45^\circ$ from the cued direction (equally frequent clockwise and counterclockwise) on 20% of the trials (invalid cue). In the two-cue blocks, the signal moved in one of the cued directions on 80% of the trials (valid cue), and moved in the mean direction (45° away from both cued directions) on 20% of the trials (invalid cue). Valid and invalid trials were randomly interleaved within a block. There were nine blocks in total, with three blocks for each cue type and the block order randomized as in Experiment 1b. As before, participants were instructed to report the interval that contained the coherent motion signal. They were told that on the majority of cued trials, the signal would move in the cued direction(s), but on a minority of trials, it would move in some other direction. They were instructed to attend to the cued directions to maximize their performance, but were not told the exact directions of the signal on invalid trials.

After the completion of the experiment, participants were queried if they used any strategy in performing the task. In particular, they were asked whether they picked only one direction to attend on the two-cue trials.

5.2. Results and discussion

Average signal coherence as determined by the thresholding procedure was 0.18 (s.d. = 0.03) in this experiment. As expected, given the coherence was thresholded at 75% correct, mean proportion correct in the no-cue condition was 0.76 (s.d. = 0.05). Because the model predictions concern only the one-cue and two-cue conditions (Fig. 5), the no-cue condition will not be considered further. We conducted planned comparisons using paired *t*-tests to evaluate these predictions (Fig. 6). We first note a robust validity effect in the one-cue condition: valid cues yielded significantly better performance than invalid cues ($t(11) = 4.00$, $p < 0.005$). We next evaluated the three equality predictions listed in Fig. 5. We found significantly higher performance for the valid one-cue compared to the invalid two-cue trials ($t(11) = 2.47$, $p < 0.05$), as well as for the invalid one-cue than the valid two-cue trials ($t(11) = 3.42$, $p < 0.01$). Furthermore, performance on the invalid one-cue trials was not different from that on the invalid two-cue trials ($t(11) = 0.84$, $p > 0.4$). Lastly, all but one participant reported to have attended to two directions in the two-cue condition during post-experiment query. The one participant reported to have attended to the middle direction, but his/her data essentially mirrored the pattern of the group data: both one-cue conditions were higher than two-cue conditions (e.g., one-cue valid: 0.91 vs. two-cue invalid: 0.75).

These results allow us to rule out two alternatives discussed above. First, the “middle” model, where participants attended to the mean direction on two-cue trials, can be rejected, with both of its predictions contradicted by the data. Second, participants did not voluntarily pick one direction to attend on two-cue trials, as shown by the post-experiment query. Thus we can eliminate the strategic version of the “one-at-a-time” model. However, the critical prediction of the “one-at-a-time” model, that the invalid trials should be equivalent in one-cue and two-cue conditions, cannot be rejected. This leaves the “one-at-a-time” model in which the limit is imposed by the attentional system a viable model. Given its flexibility, the “both” model can also accommodate the present data under certain assumptions about the change in modulation magnitude and precision, and thus it also remains a viable model.

Interestingly, our results stand in contrast to a previous study that found evidence for the “middle” model (Ball & Sekuler, 1980). Although that study was couched in terms of stimulus uncertainty, the effects investigated can be construed as

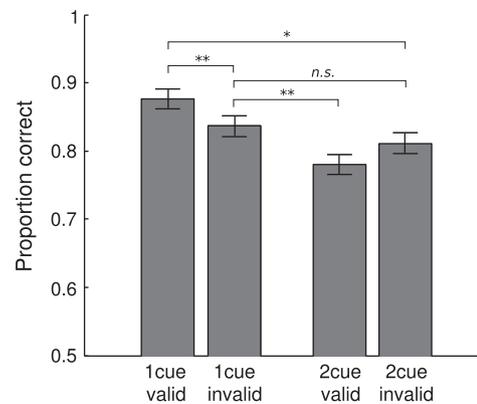


Fig. 6. Proportion correct data in Experiment 3. Error bar is the estimated within-subject standard error (Loftus & Masson, 1994). Asterisks indicate the significance level in paired *t*-tests (* $p < 0.05$, ** $p < 0.01$).

feature-based attention. In that study, researchers presented static dots which started to move and measured participant’s reaction time to detect the motion onset. In different blocks, the dots either moved in one of fixed directions (60° , 90° , 120° , the certain condition), or two possible directions (60° and 120° , the uncertain condition), which was analogous to our one-cue and two-cue conditions. In the uncertain condition, dots would move in the mean direction (90°) on a small portion of the trials. They found reaction time to the 90° probe to be equivalent to the certain directions, supporting the notion that participants attended to the mean direction. Our comparison of valid one-cue vs. invalid two-cue was analogous to their comparison, but we found worse performance in the latter condition. Although these results seemingly contradict each other, there are many procedural differences between these experiments that make it difficult to directly compare the results. The stimulus, task, and dependent measure were all different. Also, the two directions were 60° apart in their experiment, whereas they were 90° apart in our experiment. Thus the mean direction was further away from the cued directions in our experiment (45°) than in theirs (30°). Furthermore, directions were fixed throughout their entire experiment, whereas directions were much more variable and cued on a trial-by-trial basis in our experiment. Lastly, their data were collected on two highly experienced psychophysical observers, whereas we tested twelve naïve observers. All these factors might contribute to the differences in results. However, our results clearly showed that participants did not adopt the “attend to the middle” strategy, either explicitly or implicitly, in our experimental setup.

6. General discussion

We used the classic random dot motion stimulus to measure coherence thresholds for detecting weak motion signals while manipulating feature-based attention to directions. Our results showed a consistent pattern: attending to one direction improved detection performance, while attending to two directions simultaneously led to a smaller improvement. These results demonstrate a capacity limit of feature-based attention in that multiple direction cues cannot be used to increase motion sensitivity as effectively as a single direction cue.

6.1. A limit in feature-similarity gain

Three aspects of our experimental design allowed us to examine how feature-based attention affects early visual processing. First, it is worth noting that our results cannot be explained by a degraded working memory representation in the two-cue condition. This is

because two items (two cues) are well below the capacity limit of working memory, which has a capacity of 3–4 items, by most measures (Cowan, 2001; Luck & Vogel, 1997). In other words, participants should know which two directions were cued on each trial (our own observations support this conjecture) and hence there was no failure in memory. Second, we used the random dot motion task which is generally believed to depend on direction-selective mechanisms in early visual areas (Britten et al., 1992; Newsome & Pare, 1988). Third, our stimuli were presented in a single location (the center of display), eliminating potential contributions from spatial attention. Thus we believe that our cue manipulation indexes the limit by which attention can affect the early sensory mechanisms. The predominant framework in understanding how feature-based attention influences early visual processing is the feature-similarity gain model (Treue & Martinez-Trujillo, 1999). According to this model, attending to a feature enhances activity in units tuned to that feature and suppresses activity in units tuned to faraway features. The strongest evidence for this model comes from single-unit recording studies that measured MT neurons' direction tuning curves under attentional manipulation (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999), as well as modeling results from human psychophysical and fMRI experiments (Ling, Liu, & Carrasco, 2009; Liu, Larsson, & Carrasco, 2007). In the context of this framework, our current results suggest that the feature-similarity gain mechanism cannot effectively modulate two distinct neuronal populations.

A recent study manipulated the reliability/uncertainty of an orientation cue in an orientation discrimination task (Herrmann, Heeger, & Carrasco, *in press*). Participants were cued to attend to either a single orientation or a range of orientations (60° wide). These authors found a better discrimination performance in the former than the latter case. A similar finding was also reported by Ball and Sekuler (1981) for direction cues that varied in the degree of uncertainty. Our results are consistent with the general conclusion of these studies that attentional modulation is less effective with multiple cues than a single cue. Notably, in the studies that manipulated cue uncertainty (Ball & Sekuler, 1981; Herrmann, Heeger, & Carrasco, *in press*), participants had to attend to a range of features, whereas in our study participants only needed to attend to two distinct directions. Even so, we found a lower performance level in the two-cue than one-cue condition, thus providing strong evidence for a severe capacity limit in feature-specific attentional modulation.

6.2. Implications for visual search studies

It is interesting to consider our results in light of recent findings that showed participants could maintain attentional control setting (ACS) for multiple features during visual search. For example, Beck, Hollingworth, and Luck (2012) asked participants to search for a colored Landolt-C target in a multi-element array that required gaze shifts (overt attention). When participants were cued to search for the target first among items of one color and then among items of another color, there was a switch cost when participants switched between ACSs such that the fixation duration just prior to fixating an item of a new color was longer than typical. But when participants were cued to search for the target among items of both colors, there was no switch cost, indicating that participants maintained two search templates simultaneously (see also Becker, Alzhabi, and Jelinek (2011) for a similar finding). These results, along with other results using the contingent attentional capture paradigm (Adamo et al., 2008; Irons, Folk, & Remington, 2012; Moore & Weissman, 2010), suggest that participants can set their attention for more than one feature.

Our finding of worse performance in the two-cue than one-cue condition implies that multiple ACSs probably operate at later

stages of processing during visual search. That is, they do not operate by simultaneously modulating early feature-selective mechanisms for multiple target features. These later stages presumably consisted of read-out and monitoring of sensory input, prioritization of competing input, and planning of responses. However, one caveat is that the visual search studies cited above all used color as the guiding feature, whereas the majority of feature-based attention studies, including the current study, use directions of motion. It is possible that attentional capacity differs for motion and color. Further research using both search and non-search paradigms and a variety of feature dimensions is needed to map out the landscape of capacity limit across tasks and feature dimensions.

6.3. Potential mechanisms for attentional limit

What are possible mechanisms that underlie the smaller cueing effects in two-cue vs. one-cue condition? In Experiment 3, we considered several alternatives and were able to exclude two of them. Namely, observers did not voluntarily pick one of the cued directions to attend, nor did they attend to the mean direction of the two cued directions. This left us with two viable models: the “one-at-a-time” model, where feature-based attend can only modulate one direction of motion (even though observers tried to attend to both), and the “both” model, where feature-based attention can modulate two directions, but with a reduced efficacy for each direction (e.g., a smaller gain and/or wider tuning width). These two models essentially encapsulate the distinction between a serial process and a limited-capacity parallel process. It is well known that distinguishing between these two processes is extremely difficult due to model mimicry (for a review, see Townsend & Wenger, 2004). Similarly, our data do not provide unequivocal evidence favoring either model.

A parallel can be drawn to these functional/behavioral considerations in terms of plausible neural mechanisms. For example, if attentional control areas (e.g., the dorsal frontoparietal cortex) can only send one top-down signal to modulate visual cortex, it would be consistent with the “one-at-a-time” (serial) model. However, if two top-down signals can be issued to the visual cortex, but the simultaneous modulations partially cancel out each other due to certain intrinsic circuit constraints such as normalization (Carandini & Heeger, 2012; Heeger, 1992), it would be consistent with the “both” model.

Future work using more sophisticated behavioral measures (e.g., the tuning profile of attending to one vs. two directions), as well as physiological measures in both the attentional control areas and visual cortex, will likely shed light on the mechanism responsible for the impaired performance when attending to multiple features. For now, we conclude that although feature-based attention can modulate early sensory responses, it is also subject to a strong capacity limit in how many features can be simultaneously attended.

Acknowledgment

This work was supported in part by a grant from the National Institutes of Health (R01EY022727) to T.L.

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