Attention to multiple locations is limited by spatial working memory capacity

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What limits the ability to attend several locations simultaneously? There are two possibilities: Either attention cannot be divided without incurring a cost, or spatial memory is limited and observers forget which locations to monitor. We compared motion discrimination when attention was directed to one or multiple locations by briefly presented central cues. The cues were matched for the amount of spatial information they provided. Several random dot kinematograms (RDKs) followed the spatial cues; one of them contained task-relevant, coherent motion. When four RDKs were presented, discrimination accuracy was identical when one and two locations were indicated by equally informative cues. However, when six RDKs were presented, discrimination accuracy was higher following one rather than multiple location cues. We examined whether memory of the cued locations was diminished under these conditions. Recall of the cued locations was tested when participants attended the cued locations and when they did not attend the cued locations. Recall was inaccurate only when the cued locations were attended. Finally, visually marking the cued locations, following one and multiple location cues, equalized discrimination performance, suggesting that participants could attend multiple locations when they did not have to remember which ones to attend. We conclude that endogenously dividing attention between multiple locations is limited by inaccurate recall of the attended locations and that attention poses separate demands on the same central processes used to remember spatial information, even when the locations attended and those held in memory are the same.

Introduction

One way attention can improve perceptual processing is by prioritizing the analysis of task-relevant over task-irrelevant sensory inputs (Broadbent, 1958). Accordingly, when more than one location or object is task relevant, attention may need to be divided to allow selection of noncontiguous stimuli. Several studies have examined whether observers can select sensory information independently from separate locations. Some suggested that attending multiple locations requires selection of one contiguous area of the visual field, encompassing all task-relevant stimuli (C. Eriksen & St. James, 1986; C. Eriksen & Yeh, 1985; W. Eriksen & Hoffman, 1973; Posner, Snyder, & Davidson, 1980), thus negating the possibility that spatial attention may be truly divided. Others concluded instead that dividing attention among noncontiguous locations is possible (Bichot, Cave, & Pashler, 1999; Castiello & Umiltà, 1992; Gobell, Tseng, & Sperling, 2004). This is particularly true when the display does not contain novel onset distractor stimuli, which automatically capture attention (Hahn & Kramer, 1998). Awh and Pashler (2000) extended the generality of this result by demonstrating that observers can also suppress processing of novel onset distractors, at least partially, even when they occur between attended locations. Both neurophysiological and imaging studies, which indicated that neural activity and hemodynamic responses evoked by targets at separate locations can be simultaneously modulated by attention, even when

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signals evoked by distractors at intervening locations are not (McMains & Somers, 2004; Muller, Malinowski, Gruber, & Hillyard, 2003), have provided evidence consistent with the idea that attention can be split. Evidence from attentional tracking experiments, designed to examine the effects of target selection by minimizing those of processes, which may follow selection, such as target identification and memory (e.g., Duncan & Humphreys, 1989; Palmer, 1990), suggested initially that multiple targets can be selected in parallel (Pylyshyn & Storm, 1988). However, the generality of this conclusion was challenged by a number of observations. Attentional tracking can be improved by presenting targets in opposite visual hemifields, suggesting that tracking multiple objects in the same visual hemifield is not done in parallel (Alvarez & Cavanagh, 2005). Others found that when targets and distractors are closely spaced and moving unpredictably, increasing the number of targets from one to two leads to decrements in tracking performance. To account for these effects, it was suggested that attentional tracking is limited by how frequently samples of the targets' location can be obtained by the observers and since the overall sampling rate cannot be increased indefinitely, whenever the number of targets is increased, the sampling rate for each target must be diminished (d'Avossa, Shulman, Snyder, & Corbetta, 2006). A radical view has been put forth suggesting that perceptual processes have access to sensory information only through temporally discrete (VanRullen & Koch, 2003; VanRullen, Reddy, & Koch, 2005) and spatially limited "snapshots" (Dubois, Hamker, & VanRullen, 2009), so that in general two or more locations cannot be simultaneously attended. Accordingly, the ability to analyze simultaneous targets is limited by how rapidly attention can be moved among locations (Hogendoorn, Carlson, VanRullen, & Verstraten, 2010). Others have suggested that the ability to spatially divide attention is limited, but can be achieved by trading off the number of attended locations against the spatial resolution of the selection signal (Franconeri, Jonathan, & Scimeca, 2010).

A different account of the limitations inherent to attending multiple locations may be drawn from work on spatial working memory by Bays and Husain (2008). Having observed that the precision in recalling the positions of visual targets decreases with the number of targets, the authors inferred that the resolution of spatial recall is limited by a finite resource that is shared between memorized locations. The obvious inference from this model of spatial working memory is that precise selection of information from a visual display may be limited by the resolution of a top down signal, which is diminished when multiple locations are held in working memory. Accordingly, the ability to attend multiple locations may be limited by the accuracy of the spatial information held in working memory rather than attentional processes per se.

In the present study, we explore whether attending multiple locations places any limitation on performance and if it does, whether the limitation reflects attentional or working memory factors. To address this issue, we tested performance in a demanding motion-direction discrimination task. We manipulated the number of attended locations by cueing, prior to the onset of the motion stimulus, one or multiple locations likely to contain the one RDK moving coherently. Since the observers' spatial uncertainty will affect discrimination performance (e.g., Pelli, 1985), we were careful to match the amount of information one and multiple location cues provided about the target location. According to Bayesian models of attention, which provide a theoretically principled account of the effects of spatial cues on perceptual decisions and treat cues as spatial priors, cueing effects are entirely attributable to changes in the observer's spatial uncertainty (Eckstein, Drescher, & Shimozaki, 2006; Eckstein, Shimozaki, & Abbey, 2002; Shimozaki, Eckstein, & Abbey, 2003). Therefore, only the amount of spatial information provided by a cue should determine the size of attentional effects, the quality of sensory data at attended and unattended locations being unaffected by attention (Eckstein, 2011). We reasoned that if human observers use all the information provided by the cues and approximate the performance of a Bayesian ideal observer, then their accuracy should be the same following one and multiple location cues, as long as the cues are matched for the amount of information provided. However, under some conditions we found that discrimination accuracy was less after multiple rather than one-location cues. Moreover, diminished discrimination accuracy was associated with inaccurate recall of the cued locations, suggesting that limitations in dividing attention are a result of working memory limited capacity, rather than an inability to divide attention spatially.

Experiment 1

Experiment 1 was designed to measure the effect of attending one and two locations on motion discrimination performance. One-location and two-location cues were used to direct attention to the likely location of coherent motion. The cues were matched for the amount of information they provided about the target location, to ensure that the observers' spatial uncertainty was matched.

Methods

Participants

Three of the authors and three naive participants (five males) completed three sessions of 600 trials each, on three consecutive days. Each session lasted approximately 45 min.

Naive participants gave written informed consent. All the study protocols were approved by the Bangor University School of Psychology Ethics Committee.

Stimuli and apparatus

Stimuli were generated on an Apple Mac Pro 1.1 (Apple, Inc., Cupertino, CA), using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) for MATLAB© (Mathworks, 2008a, Natick, MA). Stimuli were presented on the screen of a LaCie Electron 22blue CRT monitor (Lacie, Paris, France) with a refresh rate of 60 Hz, placed 70 cm from the participant. The participants' head position was restrained by a chinrest. The target display contained four RDKs, one in each corner of the screen, lasting 400 ms. Each RDK contained 100 dots in positive contrast. Each dot diameter was 0.15°. The dots' speed was 6.17°/s, with a lifetime of three frames. Each RDK covered a circular aperture of 7.26° in diameter, centered at an eccentricity of 10.9° along the main diagonals. Dots' luminance was 62.4 cd/m^2 while the background's luminance was 0.1 cd/m^2. The target RDK consisted of a 200-ms period of coherent motion in one of four directions (left, right, up, or down). Coherent motion was preceded and followed by 100-ms periods of incoherent motion.

Procedure

The percentage of coherently moving dots, namely the stimulus coherence, was determined in a preliminary session. In this session, four RDKs were presented following a temporal cue, consisting of a color change at the point of fixation lasting 1.0 s. The participants had to report the direction of motion of the coherently moving RDK, either left, right, up, or down, by pressing the corresponding arrow key on a keyboard. Threshold motion coherence was determined using a two to one staircase procedure with a 2% coherence step. The level of coherence resulting in an accuracy of 70% was estimated by data interpolation and used during the main experimental sessions. During this training presession, participants were given visual feedback about their discrimination accuracy on each trial.

In the main experimental sessions, the following cues were used: (a) a probabilistic, one-location cue, which indicated correctly on 81% of the trials the location where the target RDK would appear; (b) two-location cue, which consisted of two oblique colored lines abutting the fixation point. One of the two cued locations always contained the coherent motion; (c) two-location anticue, which highlighted two locations where the target motion would never appear; (d) a neutral cue, consisting of four oblique lines pointing to all RDK locations. The different cue types and trial structure are shown in Figure 1.

Information theoretic measures of spatial uncertainty

To provide an objective measure of the observers' spatial uncertainty and the value of the different cues in reducing the uncertainty regarding the target location, we used information theory (Shannon, 1948). The entropy, or initial uncertainty, $H(L)$, is the log-likelihood of coherent motion appearing at the *i-th* location, l_i, averaged over all locations.

$$H(L) = -\sum_{i=1}^{4} p(l_i) \cdot \log_2 p(l_i) \quad (1)$$

When four RDKs are presented, the initial spatial uncertainty is 2.0 bits, since the observer knows that each of the four RDKs is equally likely to contain coherent motion. Following the cue, the observer's spatial uncertainty is reduced by an amount equal to the information transmitted (IT) by the cue, assuming that the observer can make full use of the cue. For partially valid, one-location cues, the IT is a function of the cue reliability r, namely the probability that the coherent motion appears at the cued location. The IT is given by the following expression:

$$\mathrm{IT}(r) = H(L) + \left[r \cdot \log_2 r + (1-r) \cdot \log_2\left(\frac{1-r}{3}\right)\right] \quad (2)$$

For example, a probabilistic, one-location cue will transmits 1.0 bits of information at a reliability of $r = 0.81$.

For multiple locations cues indicating which subset of the RDKs will contain the coherent motion, the IT varies with the number of locations cued, c.

$$\mathrm{IT}(c) = H(L) + \log_2\left(\frac{1}{c}\right)$$

For example, a cue indicating two of the four locations transmits 1.0 bits of information. Therefore, probabilistic and multiple location cues can be matched in terms of spatial information they provide, even though they instruct different spatial distributions of the expected target location. Table 1 summarizes the initial uncertainty, IT, and residual spatial uncertainty for each cue type in both Experiments 1 and 2.

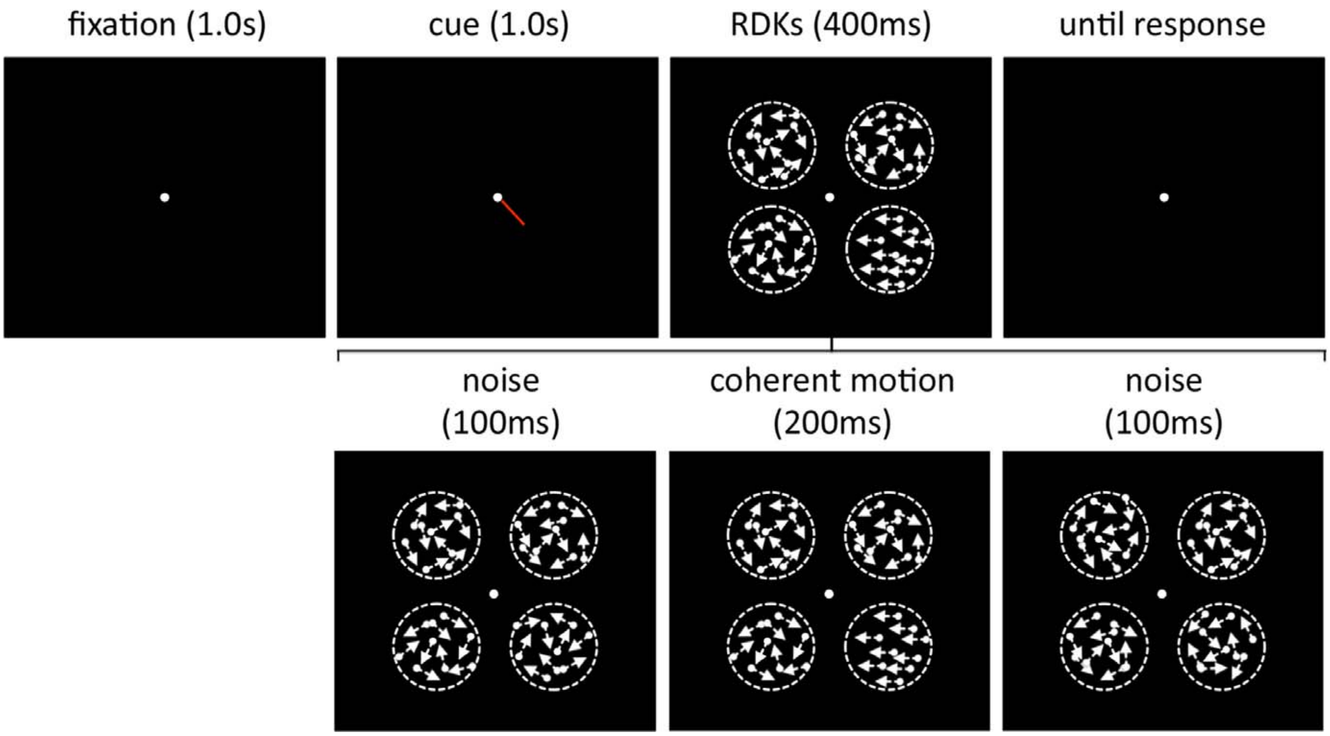

Figure 1. Trial event structure in Experiment 1. Participants maintained fixation for 1.0 s, followed by a central cue. This was either a partially valid single-location cue, shown in the figure, a two-location cue, a two-location anticue, or a neutral cue. One second after cue onset, four RDKs appeared for 400 ms. One of the RDKs contained a 200-ms long interval of coherent motion in one of the four cardinal directions. A fixation marker remained visible until the motion direction was reported by a key press.

Results and discussion

The aim of the analysis was to establish: (a) whether the cue was utilized; (b) whether one- and two-location cues were as effective in directing attention and improving discrimination accuracy; and (c) whether the distance between cued locations, following two-location cues, affected discrimination performance.

One- versus two-location cues

We compared discrimination accuracies when neutral, one-, or two-location cues preceded the target display. Figure 2A shows individual participants' accuracies and Figure 2B the group averaged accuracies according to the cue type. Overall, the data indicate that participants used both one- and two-location cues

Cue type	Cued target probability	RDKs	Initial uncertainty (bits)	Information transmitted (bits)	Uncertainty postcue (bits)
Experiment 1					
One location	0.81	4	2.0	1.0	1.0
Two location	0.5	4	2.0	1.0	1.0
Experiment 2					
One location	0.84	6	2.5850	1.5850	1.0
Two location	0.5	6	2.5850	1.5850	1.0
One location	0.7	6	2.5850	1.0	1.5850
Three location	0.33	6	2.5850	1.0	1.5850
One location	1.0	6	2.5850	2.5850	0.0

Table 1. Spatial uncertainty associated with each cueing condition in Experiments 1 and 2. *Notes*: One-, two-, and three-location cues were used. The probability that the target would appear at a cued location varied between 0.33 and 1.0. Initial spatial uncertainty increased with the number of RDKs. The IT by the one-location, 81%-reliable cue and two-location cue was matched, equalizing the spatial uncertainty following one- and two-location cues in Experiment 1. In Experiment 2, the IT by the one-location, 84%-reliable cue and the two-location cue was matched and so the IT by one-location, 70%-reliable cue and the three-location cue, thus equalizing the spatial uncertainty following one- and two-, as well as one- and three-location cues.

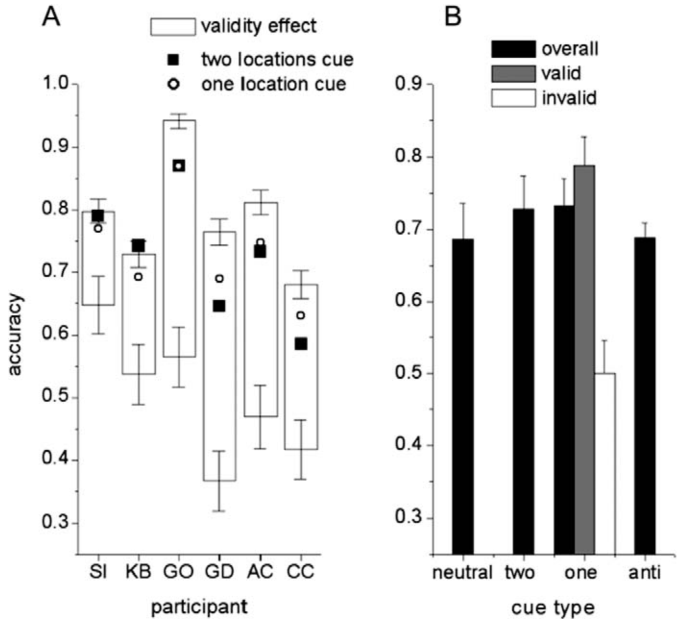

Figure 2. (A) Motion discrimination accuracy by participants. Bars indicate the size of the validity effect. The upper and lower edges are the accuracies on valid and invalid trials respectively for the 0.81-reliable cue, the circles are the overall accuracies in the single cue condition, whereas black squares are the accuracies when the two-location cue was used. Error bars represent bootstrapped estimates of standard error. (B) Motion discrimination accuracy by cue type. Gray bars indicate overall accuracies, the empty bar represents accuracy on valid trials, and the filled bar on invalid trials in the single cue condition.

effectively in reducing their uncertainty about the upcoming target location. Motion discrimination accuracy was significantly greater when cueing one or two locations than on neutrally cued trials, $t(5) = 3.50$, $p < 0.05$ and $t(5) = 2.61$, $p < 0.05$, respectively. Moreover, following the one-location cue, participants were more accurate on valid than invalid trials, $t(5) = 2.73$, $p < 0.05$, suggesting that they used the spatial information provided by the cue. The one- and two-location cues, which provided the same amount of spatial information, were associated with virtually identical average accuracies, $t(5) = -0.28$, $p = 0.79$, suggesting that the single cue and the two-location cues were as effective in reducing the observers' spatial uncertainty.

The two-location anticue was not as effective as the two-location cue in improving accuracy, $t(5) = 2.81$, $p < 0.05$, and not significantly different from a neutral cue, $t(5) = 0.28$, $p = 0.79$. This result suggests that cue utilization may also be affected by factors other than the spatial information provided by the cue.

Cue configuration

In order to test further the effect of dividing attention, we measured accuracy as a function of cue configuration in trials where the target was preceded by the two-location cue. Cues were grouped according to the distance between cued locations, which varied over two levels: The cued locations occupied either contiguous quadrants or quadrants located across the fixation point. There was no significant difference between accuracies when cued locations were in contiguous or opposite quadrants, $F(1, 5) = 0.02$, $p = 0.88$.

In summary, one- and two-locations cues that provided the same amount of information were as effective in improving motion discrimination accuracy. Secondly, two-location cues were as effective when the cued RDKs occupied adjacent or opposite visual quadrants. These findings suggest observers can attend two locations as effectively as one, whether the locations are in adjacent or opposite visual quadrants. Finally, the anticue was not effective in improving discrimination accuracy as the remaining cues, even though it provided the same amount of information. This result is in contrast with a previous report showing that equally informative, 100% valid and 100% invalid cues are as effective at driving attention (Eckstein, Pham, & Shimozaki, 2004). However, others found that endogenously evoked shifts of attention can follow noninformative cues (e.g., Tipples, 2002). Similarly, task-irrelevant social cues can evoke shifts of attention (Driver et al., 1999), suggesting that shifts of attention not always reflect the information content of the cue. Consistent with this idea and most relevant to our result is the finding that cues can paradoxically direct attention to the expected location of distractors (Lahav & Tsal, 2013; Tsal & Makovski, 2006). While these findings are problematic for the idea that attentional effects mainly reflect changes in uncertainty, they are not particularly relevant to the issue addressed in the remainder of this paper, which examines a different set of limitations in the deployment of spatial attention.

Experiment 2: Cueing effects when spatial uncertainty is increased

In the previous experiment, we observed similar performance following one- and two-location cues. The generality of this result may be limited by the modest demands placed on divided attention by the simplicity of the cueing and stimulus conditions used. Therefore, we augmented the demands on spatial attention by increasing the number of RDKs to six and the number of cued locations to three. For one location, either partially or fully valid, multiple location and neutral cues were used. Partially valid, one-location cues and multiple location cues were matched for the amount of

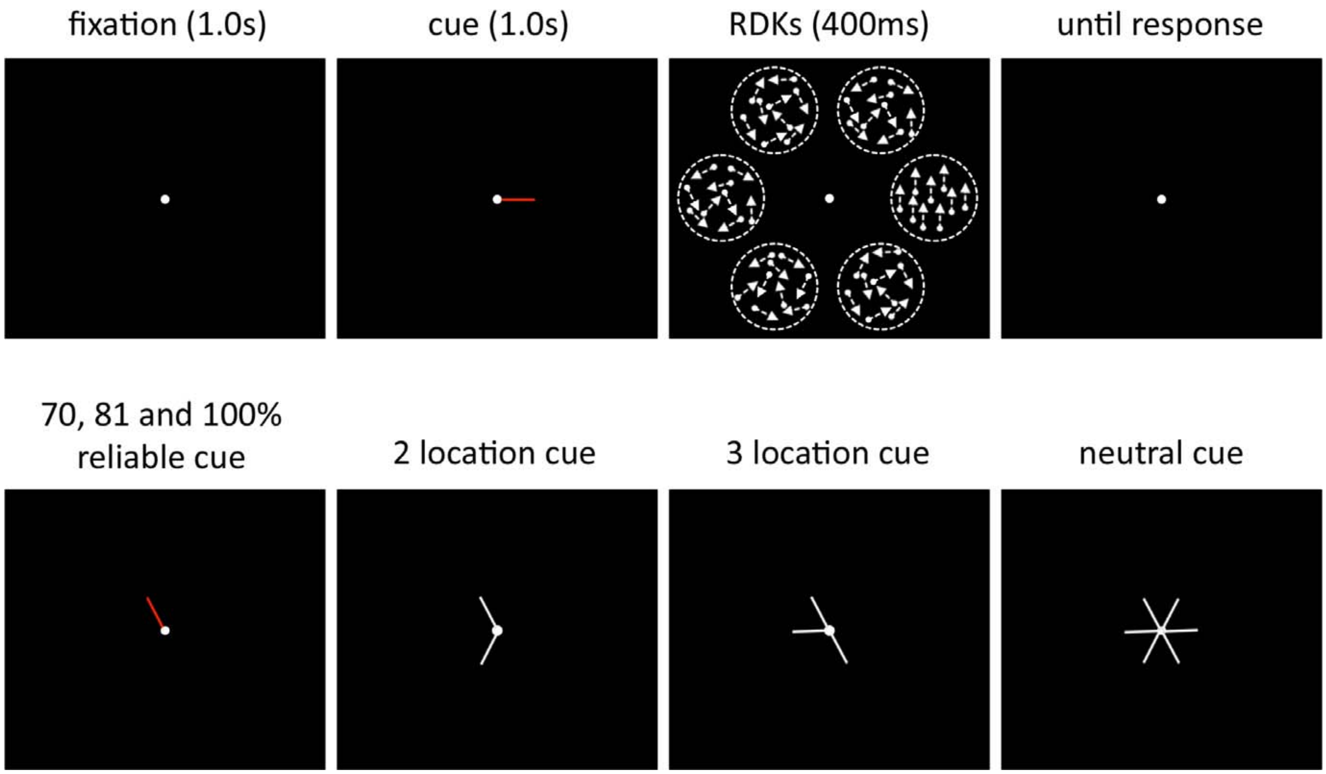

Figure 3. Trial event structure in Experiment 2. Six cue types were used. These included 0.7-, 0.84-, or 1.0-reliable, one-location cues, a two-location cue, a three-location cue, and a neutral cue. The target displays always contained six RDKs.

information they provided. Table 1 provides a summary list of the various cueing conditions.

Methods

Participants

Nine naive participants underwent six sessions of 600 trials each on consecutive days.

The stimuli consisted of six RDKs presented at an eccentricity of 15.9° from the center of the screen, spaced at 60° intervals in the radial direction. One-, two-, and three-location cues preceded displays containing six RDKs. One of the RDKs contained coherently moving dots. The reliability of the one-location cues varied over three levels: 0.70, 0.84 and 1.0. Both the 0.84-reliable cue and the two-location cue transmitted approximately 1.59 bits of spatial information, while the 0.70-reliable cue and the three-location cue transmitted 1.0 bits of spatial information. Table 1 summarizes the spatial uncertainty values associated with each of the cueing conditions and how the initial uncertainty is reduced by the information provided by the various cue types.

The cue color indicated the reliability of one-location cues. Participants learned the relation between cue color and cue reliability during a training presession. Data from the presession were not included in the final analysis. A neutral cue, which provided no spatial information, was also used, and consisted of six oriented lines abutting the central fixation point. Figure 3 shows the trial event structure and the cue types used in Experiment 2.

Procedure

The order of trials containing the various cue types was randomized within blocks. Six of the participants completed three additional testing sessions, which contained trials with stimuli preceded by two- or three-location cues only. These data were used exclusively to examine the effect of cue configuration. Each of the 30 combinations of one target and two cued locations, and 60 combinations of one target and three cued locations were presented an equal number of times, for a total of 900 trials for the two-location cue and 1,800 trials for the three-location cue. The analysis of the effects of cue configuration was carried out by dividing the trials according to the distance between the cued locations. For both two- and three-location cues, the distance between cued locations varied over three levels. Following two-location cues, the cued locations could be either adjacent, separated by one or two intervening RDKs. Following three-location cues, the cued locations could all be adjacent or two of the them could have been separated by an intervening RDK, or each

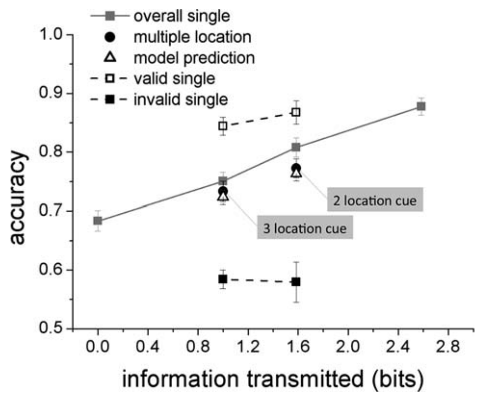

Figure 4. Motion discrimination accuracy as a function of IT. Filled gray squares are overall, group-averaged accuracies following one-location and neutral cues. The accuracy on neutrally cued trials (IT = 0.0 bits) was smaller than the accuracy following one-location, 0.70-reliable cues (IT = 1.0 bits), 0.84-reliable cues (IT = 1.58 bits), and fully valid cues (IT = 2.58 bits). Empty and filled black squares are accuracies on valid and invalid trials, respectively. Filled circles are accuracies following three and two-location cues, which are individually labeled in the Figure. Triangles represent performance predicted to follow one-location probabilistic cues providing the same IT as multiple-location cues after adjusting for the effects of memory inaccuracies. These latter estimates were only obtained from those participants who had also completed the recall experiment (the difference between group average accuracies for all nine participants and those for participants who completed the recall experiment being less than 1.0% in all cueing conditions). Error bars represent standard error of the mean (*SEM*).

cued location was separated from the others by one intervening RDK.

Results and discussion

The aim of the analysis was to establish whether (a) cue utilization varies with the reliability of the cue; (b) whether one and multiple location are equally effective in directing attention; and (c) whether the spatial configuration of multiple location cues affects their effectiveness in directing attention.

Figure 4 shows the group averaged overall accuracy for probabilistic cues and multiple location cues as a function of the cue IT. Discrimination accuracies on valid and invalid trials following one-location, partially valid cues, are also shown separately.

Cue reliability

First, we examined in trials where the stimulus was preceded by a partially valid cue, the effects of cue validity (valid, invalid) and cue reliability (0.70, 0.84) using a two-way, repeated measures ANOVA. There was a significant main effect of cue validity, $F(1, 8) = 110.13$, $p < 0.001$; however, neither the effect of cue reliability, $F(1, 8) = 0.71$, $p = 0.42$, was significant, nor the interaction of cue reliability by cue validity, $F(1, 8) = 1.18$, $p = 0.31$, suggesting that changes in cue reliability between 0.7 and 0.84 had minor effects, if any, on cue utilization. However, a one-way repeated measures ANOVA, which only included valid trials preceded by one-location cues (reliability: 0.70, 0.84, and 1.00) revealed a significant effect of cue reliability, $F(2, 16) = 12.43$, $p < 0.001$, suggesting that over a broader range, cue reliability did affect cue utilization, the average accuracy difference on valid trial following 100% and 70% reliable cues being 3.3%.

One versus multiple location cues

The conclusion that participants were able to use the information provided by the cues was further buttressed by the finding that overall discrimination accuracies on trials preceded by the 0.7-reliable cue and the three-locations cues were both significantly greater than accuracies on neutrally cued trials, $t(8) = -5.65$, $p < 0.001$ and $t(8) = -6.19$, $p < 0.001$. However, overall accuracies were on average 1.7% lower when three locations were cued than when a 0.70 reliable cue was used, $t(8) = -2.50$, $p < 0.05$, despite the fact that both cue types carried the same amount of spatial information. Similarly, overall accuracy was 3.6% lower following two-location than 0.84-reliable cues, $t(8) = -2.70$, $p < 0.05$. These data suggest that accuracy is lower when attending multiple locations than when attending one location, at least when displays contained six RDKs.

Cue configuration

Finally, we examined the effects of multiple location cues spatial configuration. No significant effect of cue configuration was found when cueing two, $F(2, 8) = 0.17$, $p = 0.85$, or three locations, $F(2, 10) = 0.75$, $p = 0.49$, suggesting that dividing attention did not appreciably modulate the effectiveness of multiple location cues.

There are two possible explanations for the performance decrements observed when cueing two or three locations compared to one. The first is that distributing attention over multiple locations carries a cost over maintaining an undivided attentional focus. However, this account is difficult to reconcile with the finding that there was no difference in performance when one- or two-location cues were used and the target display contained only four RDKs, or the finding that the configuration of multiple location cues did not modulate their effectiveness. An alter-

Cue type	IT (bits)	Memory load (bits)
One location, 0.70-reliable	1.0	2.5850
One location, 0.84-reliable	1.5850	2.5850
One location, 1.0-reliable	2.5850	2.5850
Two location	1.5850	3.9069
Three location	1.0	4.3219

Table 2. The IT and memory load associated with each cue type. *Notes*: As the number of cued locations increased, so did the memory load; however, the IT decreased. Moreover, the reliability of one-location cues affected the IT, but did not affect the memory load.

native explanation to the accuracy decrement found when dividing attention between multiple locations is that it reflects increased memory demands when attending two or three locations compared to one location. That is, cueing multiple locations may have breached the capacity to recall the locations cued, leading participants to either confound cued with uncued locations or ignore the cues. It is important to note that the demands associated with storing the identity of the cued locations in memory do not only depend on the number of locations cued, but also on the number of RDKs. An objective measure of the memory load, M, associated with each cueing condition can be easily computed using information theory to demonstrate this very fact. The memory load, in bits, is the number of binary values required to uniquely specify the cued location(s). This value can be computed as follows:

$$M(c) = \log_2 \frac{n!}{(n-c)!c!} \quad (3)$$

where n is the number of RDKs and c is the number of cued locations. For example, when the number of RDKs is four, there are six possible two-location cues and the memory load associated with remembering one of these combinations will be 2.59 bits. However, when the number of RDKs is six, there are 15 possible two-location cues and the memory load associated with remembering one of these combinations will therefore be 3.91 bits. The implication of the fact that memory load increases with both the number of cued locations and the number of RDKS for a limited capacity process like spatial working memory is obvious. When the number of cued locations is two and the number of RDKs is four, the capacity limits of visual working memory may not have been breached by the memory load associated with remembering which two locations were cued. However, when the number of RDKs is six, the memory load associated with remembering the two locations cued may have breached working memory capacity, leading to inaccurate recall of the locations cued. Table 2 lists the IT and memory load, in bits, for each cue type to demonstrate that they are largely independent.

Experiment 3: Attention interferes with recall of multiple location cues

To test the hypothesis that inaccurate recall of cued locations may limit the attentional benefits of multiple location cues, we asked participants to recall the cued locations in two conditions. In the first, participants reported the cued locations and the target motion direction in separate blocks. In the second, participants were required to report either the cued locations or the target motion direction in the same block. The comparison of recall performance when participants only recalled the cued locations in blocked trials or also had to attend the cued locations in order to prepare to discriminate motion in mixed trials was used to examine whether attending the cued locations places additional demands on memory.

Methods

Naive participants were tested in two separate experiments; one where three locations were cued and one were two locations were cued. One participant did not complete the experiment with two-locations cues. Therefore, the results include data from seven participants with three-locations cues, and six participants with two-locations cues. All the participants had taken part in the previous experiment.

Two trial types were used: participants either recalled the cued locations or reported the motion direction. In recall trials, a spatial cue lasting 1.0 s was presented initially. Immediately after the cue offset, six circular placeholders appeared, which outlined the boundaries of the RDKs. However, no RDKs were shown. The participants placed the cursor by moving the hand-held mouse over the apertures corresponding to the recalled cued locations. The event structure of motion discrimination trials was identical to the one used in Experiment 2. Participants performed the two tasks either in pure or mixed blocks. In the mixed blocks, participants were not aware of the trial type until either the motion or recall display appeared. It should be emphasized that in all conditions, participants never reported both the locations cued and the direction of motion in the same trial. Trials containing two- and three-location cues were run in separate sessions. Recall with one-location cues was not tested since preliminary testing in three of the participants showed performance to be

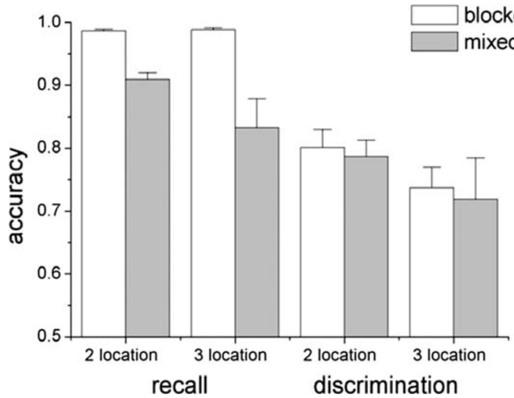

Figure 5. Recall and motion discrimination accuracies following two- and three-location cues. The empty bars are the group-averaged, recall and discrimination accuracies in blocked trials. Gray bars are the accuracies when discrimination and recall trials were interleaved in random order. Error bars represent *SEM* across participants.

at ceiling both in the pure (100% accuracy) and mixed blocks (>99% accuracy).

Results and discussion

Recall and discrimination accuracies are shown in Figure 5. In pure blocks in which participants only recalled the cued locations, recall performance was at ceiling, the group average accuracies being 98.7% when recalling two and 98.8% when recalling three cued locations. However, in mixed blocks, recall was poorer, the accuracies being 90.9% when recalling two and 83.2% when recalling three locations. The effects of block type, pure versus mixed, was significant, $t(5) = 45.50$, $p < 0.001$ and $t(6) = 23.56$, $p < 0.001$, for recalling two and three locations respectively. In contrast, motion discrimination accuracy was not significantly different between pure blocks and mixed blocks whether two, $t(5) = -0.33$, $p = 0.75$, or three locations were cued, $t(6) = 0.23$, $p = 0.83$.

A question of interest is whether inaccurate recall of the cued locations could account for the discrimination accuracy decrements observed when two or three locations were cued. To get some insight into the issue, recall accuracies in mixed block trials were used to calculate an adjusted measure of the IT by the cues, which accounted for the information loss due to inaccuracies in spatial recall.

We compute the information about target location provided by two- (IT2) and three-location cues (IT3), adjusted for inaccuracies in memory recall, as the difference in spatial uncertainty before and after the cue appears. The uncertainty following multiple location cues is the expected value of the negative logarithm of the probability of two events: (a) the target appears at one of the recalled cued locations or (b) the target appears at one of the locations not recalled. For example, if the observer recalls correctly both locations cued in 60% of the trials, but recalls one cued location correctly and the other incorrectly in 40% of the trials, the probability that the target will appear at one of the recalled locations is 40%, the probability that it will appear at one of the locations not recalled is 5%, the probability that the target will appear at either one of the locations recalled is 80%, and the probability that it will appear at any of the four locations not recalled is 20%. The formulas to compute the IT by inaccurately recalled cues is then the following:

$$IT2 = \log_2(6) - \left[-\left(p_2 + \frac{p_1}{2}\right)\log_2\left(\frac{2p_2 + p_1}{4}\right) - \left(p_0 + \frac{p_1}{2}\right)\log_2\left(\frac{2p_0 + p_1}{8}\right) \right]$$

$$IT3 = \log_2(6) - \left[-\left(\frac{3p_3 + 2p_2 + p_1}{3}\right) \times \log_2\left(\frac{3p_3 + 2p_2 + p_1}{9}\right) - \left(\frac{3p_0 + 2p_1 + p_2}{3}\right) \times \log_2\left(\frac{3p_0 + 2p_1 + p_2}{9}\right) \right] \quad (4)$$

where p_0, p_1, p_2, and p_3 are respectively the probability that none, one, two, or three of the cued locations are recalled correctly. The recall adjusted IT was estimated for each participant. The reliability of a one-location probabilistic cue transmitting the same amount of information was then computed. Finally, the discrimination accuracy associated with a cue whose reliability level matched the recall adjusted IT was estimated by linear interpolation. The group-averaged estimates are shown in Figure 4. The recall-adjusted discrimination accuracies were not different from those observed in Experiment 2 when two, $t(5) = -0.78$, $p = 0.47$, or three, $t(6) = 1.91$, $p = 0.10$, location cues were used. We conclude that imprecise recall of the cued locations can account for differences in discrimination accuracy when cueing one and multiple locations.

Experiment 4: Marking the cued locations improves accuracy following two-location cues

If attending multiple locations is limited by inaccurate recall of the cued locations, then visually marking the cued locations throughout the trial should improve discrimination accuracy, because the markings would act as vicarious memory.

Cue type	Marked cue locations	Unmarked cue locations
Neutral	0.69 ± 0.02	0.70 ± 0.02
One location ($r = 0.84$)	0.85 ± 0.02	0.87 ± 0.01
Two location	0.87 ± 0.02	0.83 ± 0.02

Table 3. Group averaged accuracies for each cue type are reported separately for blocks where the cued locations were marked and unmarked.

Methods

Participants

Seven naive participants completed two sessions each. In the initial session the observers familiarized themselves with the task. In the second session, after their coherence threshold was measured, they completed 780 trials in the main task.

Stimuli and procedure

The stimuli and trial structure were the same as those used in Experiment 2, except for the following differences. Only three cue types were used including: (a) a neutral cue; (b) one-location, 84%-reliable cue; and (c) a two-location cue. Six white annular placeholders centered on each of the RDKs locations were constantly visible. The inner diameter of the placeholders was 7.3° and the outer diameter 7.5°. In half of the blocks the placeholders did not change color and therefore did not provide any information about the locations cued. In the other half of the blocks, when the central cue appeared, the placeholders at the cued locations turned red. After 1.0 s the central cues were removed, but the placeholders at the cued locations remained red until the participants' response. Participants completed two blocks of each condition in alternating order. The initial block type was counterbalanced between participants.

Results and discussion

Table 3 lists the group average discrimination accuracies for each cue type when the cued locations were visually marked and when they were not. Discrimination accuracy following two-location cues was higher when the cued locations were marked than when they were not, while the overall accuracy following the one-location cue showed the opposite pattern. The interaction of number of cued locations (one vs. two) and visual marking (present vs. absent) was significant, $F(1, 6) = 8.057$, $p = 0.03$, suggesting that visually marking the cued locations did improve accuracy following two-location cues, but not one-location cues. Moreover, neither on valid trials (data not shown), following the one-location cue, nor on neutrally cued trials was the accuracy greater on marked than unmarked blocks, suggesting that the effects of visually marking the cued location on discrimination accuracy are unlikely to reflect low-level sensory interactions between the placeholders and the coherent motion. These result are consistent instead with the prediction of the recall-based hypothesis, namely that discrimination decrements following multiple location cues reflect inaccurate recall, since providing a vicarious memory by marking the cued locations improved discrimination accuracy following multiple, but not one-location cues.

Discussion

There is currently disagreement whether attention can (Awh & Pashler, 2000; Bichot, Cave, & Pashler, 1999; Gobell et al., 2004; Kramer & Hahn, 1995) or cannot be divided among noncontiguous locations (e.g., Dubois et al., 2009; C. Eriksen & St. James, 1986; C. Eriksen & Yeh, 1985; Jonides, 1983; McMains & Somers, 2004; Muller et al., 2003; Posner et al., 1980; Pylyshyn & Storm, 1988) without incurring a cost.

To understand where limitations arise when attention needs to be divided spatially, we examined performance in a motion discrimination task in which the target display was preceded by cues for either one or multiple locations. Our goal was to determine whether the number of locations cued affected the effectiveness of cueing once the amount of spatial information provided by different cues was properly accounted for. In general, we found that cueing the location of the coherently moving RDK improved discrimination accuracy. Moreover, when the display contained four RDKs, accuracy was identical when targets were preceded by one- and two-location cues. However, when the visual stimulus contained six RDKs, cues indicating two and three locations did not improve discrimination accuracy as much as a one-location cue. Since multiple and one-location cues were matched for the amount of spatial information provided, the difference could not be attributed to factors intrinsic to the cue.

If the finding that cueing one or two locations was equally effective when four RDKs were used suggests that attention can be distributed according to the spatial demands of the task, then how could one account for the finding that multiple cues were less effective than single cues when six RDKs were displayed? One possibility is that the costs of dividing attention become apparent only when greater demands on attentional resolution are placed either by more tightly spaced stimuli (Cavanagh, Hunt, Afraz, &

Rolfs, 2010; Franconeri et al., 2010; He, Cavanagh, & Intriligator, 1996), or when attentional resolution is traded off against the number of attended locations (Alvarez & Franconeri, 2007; Franconeri, Alvarez, & Enns, 2007). The other possibility is that memory demands are increased when displays contained six compared to four RDKs, leading participants to either forget the cued locations or confuse cued and uncued locations. This latter hypothesis is not, prima facie, in keeping with estimates of visual working memory capacity reported in previous studies. These have indicated that humans can recall accurately visual details of three or four objects (e.g., Luck & Vogel, 1997; Zhang & Luck, 2008) and that the amount of spatial information available in working memory to guide a two-dimensional reaching movement exceeds 4.5 bits (Georgopoulos & Massey, 1988), suggesting that recalling two or three locations should be well within working memory's capacity limits.

However, we reasoned that using cues for directing attention may require more than just remembering the cued locations. For example, it has been argued that cueing engages processes that shift attention to the cued location and keep it there (Posner et al., 1980; Posner & Petersen, 1990), operations that, at least on logical grounds, are not required when simply remembering spatial data. We examined the possibility that attending the cued locations may interfere with their representation in working memory, by asking participants to recall the cued locations, under two different conditions. In the blocked condition, participants had to perform the recall task on each trial. In the mixed condition instead, recall and motion-discrimination trials were randomly interleaved. Recall accuracy was at ceiling in the blocked trials, but it dropped significantly in mixed trials when participants could not anticipate whether they would have to recall the cued location or perform the discrimination task, and thus had to shift attention on every trial. Moreover, motion-discrimination accuracy was not different between blocks in which participants only discriminated motion direction and blocks in which recall and discrimination trials were mixed, suggesting that the demands placed on attention by the memory of the cued locations were no different in blocked and mixed trials. Since in recall trials the motion display did not appear and therefore no motion discrimination was required, the recall decrements observed in mixed blocks are unlikely to depend on increased demands posed by performing a dual task. Rather, the difference should be accounted for in terms of the preparatory processes associated with shifts of attention, which were engaged in mixed blocks, but not in recall-only blocks.

To provide evidence for the hypothesis that working memory demands may limit the distribution of attention, we calculated the amount of spatial information lost because of memory inaccuracies to predict the discrimination accuracy that should have been observed following one-location cues, matched for the amount of spatial uncertainty. Once the effect of recall imprecision was taken into account, motion-discrimination accuracy when cueing multiple locations was no worse than that predicted if an equally informative, one-location cue had been used. This result shows that recall inaccuracies could account for the accuracy differences observed when cueing one versus multiple locations. Finally, in Experiment 4 we tested directly the hypothesis that inaccurate recall of the cued locations accounts for the discrimination decrements observed following multiple location cues. We compared discrimination accuracy when transient central cues and stable visually markings where used to indicate the likely target locations. Discrimination accuracies following two-location, but not one-location, cues, were improved by visually marking the cued locations, indicating that minimizing the memory demands of multiple location cues improves discrimination accuracy.

Our findings are consistent with the widely held belief that visual working memory and attention are intimately related processes (Chun, Golomb, & Turk-Browne 2011; Downing, 2000; Theeuwes, Kramer, & Irwin, 2011). Some have suggested that rehearsal of visual information in working memory relies on attentional mechanisms, since when attention is allocated to locations other than those simultaneously held in working memory, recall is impaired (Awh & Jonides, 2001; Awh, Jonides, & Reuter-Lorenz, 1998; Lawrence, Myerson, & Abrams, 2004; Smyth & Pelky, 1992, Smyth & Scholey, 1994). Crucially, when no spatial shift of attention is required, perceptually demanding tasks do not interfere with spatial memory (Awh et al., 1998), implying that interference between attention and working memory arises when they operate on a shared spatial representation. However, neither the view that attention is required to keep spatial information in memory, nor the opposite view that capacity limits for attention and working memory are largely independent (Fougnie & Marois, 2006; Zhang, Xuan, Fu, & Pylyshyn, 2010), can account for the finding that the recall of cued locations was worse when participants also had to attend those locations. Our findings indicate instead that following endogenous, central cues processes holding the cued locations in working memory and processes shifting attention to those locations compete for the same limited capacity resources. The suggestion that attention may not be an essential component for rehearsal of spatial information in working memory (Belopolsky & Theeuwes, 2009) is in keeping with our conclusion.

Keywords: spatial attention, spatial uncertainty, memory load, motion discrimination, information theory

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