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Visual Search for Motion–Form Conjunctions: Selective Attention to Movement Direction

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ABSTRACT. In 2 experiments requiring visual search for conjunctions of motion and form, the authors reinvestigated whether motion-based filtering (e.g., P. McLeod, J. Driver, Z. Dienes, & J. Crisp, 1991) is direction selective and whether cuing of the target direction promotes efficient search performance. In both experiments, the authors varied the number of movement directions in the display and the predictability of the target direction. Search was less efficient when items moved in multiple (2, 3, and 4) directions as compared with just 1 direction. Furthermore, precuing of the target direction facilitated the search, even with "wrap-around" displays, relatively more when items moved in multiple directions. The authors proposed 2 principles to explain that pattern of effects: (a) interference on direction computation between items moving in different directions (e.g., N. Qian & R. A. Andersen, 1994) and (b) selective direction tuning of motion detectors involving a receptive-field contraction (cf. J. Moran & R. Desimone, 1985; S. Treue & J. H. R. Maunsell, 1996).

IN THE PRESENT STUDY, we were concerned with the mechanisms underlying a particular type of easy conjunction search, namely, search for targets defined by a conjunction of motion and form. McLeod and his colleagues (McLeod, Driver, & Crisp, 1988; McLeod, Driver, Dienes, & Crisp, 1991) proposed a two-stage account of motion–form conjunction search, with a *motion filter* that segregates the moving from the stationary items operating at the first stage, followed by parallel search of the moving items at the second stage. Although the idea of motion-based filtering is not controversial, precisely how the filtering works is not well understood (e.g., Müller & von Mühlenen, in press; von Mühlenen & Müller, in press). Two open issues of importance in this context concern whether motion-based filtering is direction selective and whether cuing of the target direction promotes efficient search performance. Before developing this issue and describing how we addressed it in the present experiments (see ensuing section, "Is motion-based filtering direction-selective?"), we reviewed the evidence and theoretical accounts for efficient search for motion–form conjunctions.

Efficient Search for Motion–Form Conjunctions

One of the most influential accounts of visual attention and selection has been provided by Treisman's feature integration theory (FIT; Treisman & Gelade, 1980; Treisman & Sato, 1990). As its major tool, FIT has used the analysis of search reaction times (RTs) as a function of the number of items in the display (the display size). Two different patterns of RT–display size functions are typically observed. Which pattern is found depends on the nature of the target and nontarget objects. When the search involves a target that differs from the nontargets in a single salient feature (e.g., a vertical line among horizontal lines), the search RT functions are essentially flat, supporting the notion that targets are detected by a spatially parallel process. In contrast, when the target is defined by a conjunction of features, each of which is separately present among the nontarget items (e.g., a red X among red Os and green Xs), the search RT functions are linearly increasing, and the slope ratios between negative (target-absent) and positive (target-present) responses are approximately 2:1. This pattern has been taken as indicative of a spatially serial, item-by-item search process, where search is exhaustive on negative trials and self-terminates upon detecting a target on positive trials. According to FIT, serial search is required to conjoin the separable features present at a location involving focal attention.

However, McLeod and his colleagues have shown that not all conjunction searches require serial scanning of display items, posing a problem to classical FIT (Treisman & Gelade, 1980). In particular, McLeod et al. (1988) reported that targets defined by a conjunction of movement and form can be detected in parallel. In the task used by McLeod et al. (1988), participants had to search for a moving X among moving Os and stationary Xs. To account for the flat search RT functions, the researchers proposed a two-stage process. At the first stage, a movement filter, which operates in parallel, segregates the display into two sets, moving and stationary items. The filter represents only the moving items. At the second stage, the moving items are searched. Because there is only one moving X among the moving Os represented by the filter, the task is effectively reduced

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to the detection of a single-featural form difference between the target and nontargets, permitting the search to operate in parallel.

Treisman and Sato (1990) proposed an augmented version of FIT to accommodate that exception. Treisman's original theory suggested that features (e.g., form, color, movement) are represented in separate feature maps. If the task requires a conjunction of two or more features, focal attention must be serially allocated to locations specified in a master map. The main modification in the revised theory is that if a feature distinction is particularly salient, detector units in nontarget feature maps can inhibit nontarget locations on the master map, so that they can be excluded from serial search. In other words, in search for conjunctions of motion and form, scanning would effectively be restricted to the moving stimuli, and parallel search would result. A very similar proposal is made in guided search (GS; Cave & Wolfe, 1990; Wolfe, 1994), except that potential target locations on the master map receive excitation from target-compatible feature maps (rather than the nontarget locations receiving inhibition from target-incompatible feature maps).

The existence of motion-based filtering thus is not controversial and can be accommodated by most general theories of visual search. However, precisely how motion-based filtering works is not well understood. One as yet unresolved issue concerns whether motion-based filtering is inherently direction selective, operating only on items moving in a particular direction at a time, or whether it can operate on all moving items simultaneously, irrespective of their movement direction(s).

Is Motion-Based Filtering Direction-Selective?

McLeod et al. (1991) examined the direction selectivity of motion-based filtering. In their first experiment, they used displays of items that moved in four orthogonal directions (rather than just one direction as in previous work; McLeod et al., 1988). Their participants could search for a motion–form conjunction target in parallel (positive search rate of 5 ms/item), even though there were multiple movement directions and the direction in which the target moved was not known in advance. In another experiment, McLeod et al. (1991) further observed that search of items moving in two opposite directions was efficient whether or not the movement direction of the target was predictable (Experiment 2b). In other words, search was parallel regardless of whether the target had to be searched within one, two, or four movement direction sets. In contrast, parallel search failed when the target—unpredictably on a trial—could be a member of either the moving or the stationary set of items (Experiment 2a). The researchers took this pattern of results to indicate that efficient search for motion–form conjunction targets (a) does not require the tuning of the motion filter to a particular movement direction but (b) does require that participants be able to consistently set themselves for a moving target.

Although the search rate effects reported by McLeod and his colleagues were clear, a full consideration of their data, including the base times (the y-intercepts of the search RT functions), does leave the possibility that direction tuning plays an important role in motion-based filtering. McLeod and his colleagues found little difference in positive search rates when there was only one movement direction (3 ms/item; McLeod et al., 1988, Experiment 1) as compared with four movement directions (5 ms/item; McLeod et al., 1991, Experiment 1). However, there was a marked difference in base times, which were around 500 ms with one movement direction and 650 ms with four movement directions. This base-time effect, taken together with the absence of a search-rate effect, is consistent with the alternative account that search is parallel *within* movement directions (i.e., involves movement direction-based filtering), but serial *across* directions.

In the present experiments, we examined the alternative account, which is similar to Pashler's (1987) clumping model, by systematically varying the number of directions in which the moving items moved and the predictability of the target movement direction. The results were at variance with an account of parallel search within movement directions and serial search across directions. However, there were effects of number of movement directions and advance knowledge of target direction (including an interaction), inconsistent with the findings of McLeod et al. (1991). On the basis of a GS framework (e.g., Wolfe 1994), we proposed an alternative account to the original motion-filter model, which can accommodate these effects by incorporating principles derived from recent neurophysiological work on color-based attention (Moran & Desimone, 1985; Treue & Maunsell, 1996) and transparent-motion perception (e.g., Qian & Andersen, 1994; Snowden, Treue, Erickson, & Andersen, 1991).

EXPERIMENT 1

We designed Experiment 1 to test whether motion–form conjunction search operates in parallel within movement directions but serially across directions. If there are multiple directions, participants might tune into one direction at random and search all items moving in that direction in parallel. If the direction set contains a target, it might "pop out," and a positive response could be given. If not, the direction set might be rejected, another set selected to tune into, and so forth, until either a target is detected or all directions are eliminated from the search. In the latter case, a negative response could be given. According to this alternative to the account put forward by McLeod et al. (1991), the number of movement directions should have little effect on the search rates, but it should have an effect on the base time, which should increase linearly with the number of movement directions. Such base-time effects are to be expected when the movement direction of the target is unknown. In contrast, when the target direction is known, participants should be able to directly tune into that direction. This alternative account cannot be properly assessed on the basis of the available experiments

(McLeod et al., 1988, Experiment 1; McLeod et al., 1991, Experiment 1). Although the two experiments compared were methodologically similar, the participants were different; in the 1988 experiment, the target direction was always known in advance, whereas in the 1991 experiment, it was not.

In Experiment 1, we systematically examined the effect of the number of movement directions on both the search rates and the base times when the target direction was either unknown or known to the participant. All moving items were Os (with one possible target X) that could move in one, two, three, or four orthogonal directions (up, down, left, right). In Experiment 1a, the target direction was unknown. We expected that if search can operate in parallel across only one movement direction set, the base times, but not the search rate, should increase with the number of movement directions. In Experiment 1b, the target direction was known in advance. No effect of the number of movement directions on the base times was expected in this condition, because participants should be able to directly tune into the target direction.

Method

Participants

The same 4 participants took part in Experiment 1a and Experiment 1b. They were all men; aged between 21 and 42 years; 2 had normal vision, and 2 corrected-to-normal vision. They were paid for their participation. All participants received thorough practice on the task in one or more preexperimental sessions (of 768 trials).

Apparatus

The stimuli were presented on a Tektronix 608 X-Y monitor (CRT) with a fast-decay P15 phosphor. The CRT was driven by a LSI 11/23 computer through a CED 502 interface (with D-to-A converters). Refreshing of the display and sampling of digital inputs were controlled by Shepherd's (1984) EMDISP software system. The laboratory was dimly illuminated to eliminate reflections on the CRT. Participants responded by pressing designated keys (initiate block of trials, respond target present/absent) on a hand-sized keypad in front of them, which was sampled by the laboratory interface. Participants viewed the CRT from a distance of 33 cm, with the viewing distance maintained through the use of a chin rest.

Stimuli

The total screen area subtended approximately 22° × 16° of visual angle. Displays consisted of 5, 10, 20, or 30 items, including the target on positive trials. As a rule, one fifth of all items were stationary and four fifths were moving at a constant speed of 2.2° per s. The position of each moving item was increased every 20 ms by 0.044°, which produced the impression of a smooth, continuous motion. Displays were shown for a maximum time of 2440 ms, during which the moving items could cover a distance of 5.4°. Otherwise, displays were terminated by the participant's response.

The stimuli were crosses rotated by 45° (Xs) and circles (Os), both 0.36° in height and width.[1] For each display, the starting position and movement direction of each item were determined individually by dividing the display into an invisible square matrix with cells of size 1.35° × 1.35°. The size of the matrix decreased with decreasing display size, so that the relative density of the display items would be reasonably constant across the different display sizes. With 30-item displays, the display area was divided into 12 × 12 cells; with 20-item displays, into 10 × 10 cells; with 10-item displays, into 8 × 8 cells; and with 5-item displays into 6 × 6 cells. The display area increased with the number of items from 8.1° × 8.1°, to 10.8° × 10.8°, to 13.5° × 13.5°, and to 16.2° × 16.2° for 5-, 10-, 20-, and 30-item displays, respectively.[2] We controlled for item eccentricity with respect to the display center by presenting displays containing less than the maximum number of items at random positions within the maximum display area (this is a two-dimensional variant of the procedure used by McLeod et al., 1988, for the horizontal-display dimension). Moving items moved on horizontal and vertical tracks (left, right, up, down). We varied the number of movement directions. There were one, two, three, or four movement directions, with each direction and combination of directions being presented equally often. Moving items traversed in 2440 ms a maximum of four cells.

Forty-eight displays (item arrangements) were generated for each of the 16 combinations between display size (5, 10, 20, or 30 items) and number of movement directions (one, two, three, or four directions) by using the following procedure. The (starting) coordinates of each display item on the matrix were determined randomly except for the following constraints: Only one item was permitted to occupy a cell; and moving items were not permitted (a) to leave the matrix during the (maximum) course of the movement, (b) to collide with a sta-

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[1] A pilot experiment presenting stationary items only was carried out to ascertain that the form discrimination required in the subsequent experiments could be performed in parallel. The task required detection of a stationary X among stationary Os in displays containing 9, 17, or 25 items. The search rates of 6 participants averaged 2.3 ms/item on positive trials and 4.3 ms/item on negative trials, indicating that the form discrimination was indeed easy.

[2] The increase in display area with increasing item number is in contrast to the work of McLeod et al. (1991, Experiment 1), whose display area was constant at 11° × 8°. One potential problem with their procedure is that the item density varied as a function of the display size. There is an unavoidable trade off between item density and the size of the display area. Which display parameter is more important to control for in motion–form conjunction search is debatable (Berger & McLeod, 1996; Müller & Found, 1996).

tionary item or other moving items, or (c) to move in tandem with another item on the same track in the same direction without being separated by at least one cell. If one of these criteria was violated, new coordinates were randomly chosen until all criteria were met. Stationary items were placed first, and moving items, second. For the latter, the direction of movement was changed after each valid placement of an item. All item coordinates were generated in advance (i.e., they were the same for all participants). The target was a moving X. The nontargets were stationary Xs and moving Os. See Figure 1 for example displays with 20 items and 1 – 4 movement directions.

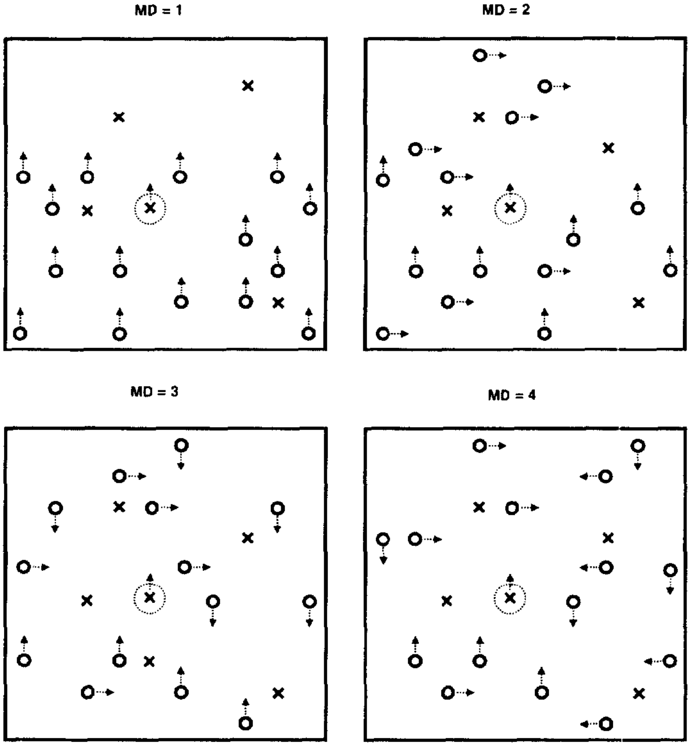

FIGURE 1. Four examples of displays used in Experiment 1. The displays contain 20 items moving in one (MD = 1), two (MD = 2), three (MD = 3), or four (MD = 4) orthogonal directions (movement direction indicated by dotted arrows). The target is a moving X among stationary Xs and moving Os. The movement direction of the target is either not specified (Experiment 1a) or specified in advance of a trial (Experiment 1b).

A trial started with the presentation, for 500 ms, of either a fixation cross (Experiment 1a, target direction unknown) or an arrow pointing up, down, left, or right (Experiment 1b, target direction known) in the center of the display (line size: 1°). There was then a 500-ms blank interval, followed by the display of stationary and moving items. The display stayed on until either the participant responded or the maximum display duration of 2,440 ms was reached. Responses were timed from the onset of the display. The intertrial interval was 1500 ms.

Design and Procedure

Both experimental conditions (a and b) comprised the following three variables: movement (one, two, three, or four directions), target (absent or present), and display size (5, 10, 20, or 30 items). There were 48 trials for each factorial combination between these variables, giving a total of 1,536 (32 × 48) experimental trials for Experiment 1a and for Experiment 1b. The experiment was subdivided into four sessions of 768 trials each, two sessions per day. The order of experimental conditions (1a and 1b) was counterbalanced across participants and days. The various combinations of movement, target, and display size were presented in random order within a session. At the beginning of each session, participants were given 96 (unrecorded) practice trials. Each session was subdivided into blocks of 48 trials, with short breaks between blocks. Each block started with 5 unrecorded warming-up trials. Whenever possible, we conducted experimental sessions on consecutive days.

Instruction

Participants initiated a block by pressing one of two designated keys on the response keypad. To each display (trial), participants had to make the appropriate response on the keypad according to whether the target was absent or present. Participants were instructed to respond as quickly and accurately as possible. If participants made an error, they were alerted to this event by a computer-generated "bleep."

Results

The overall mean RTs for the correct positive and negative trials are shown in Figures 2a and 2b for Experiments 1a and 1b, respectively. The corresponding mean base RTs and mean search rates are listed in Table 1, along with mean R^2 values and associated standard deviations as measures of the amount of variance explained by the individual linear regressions to indicate their goodness of fit.

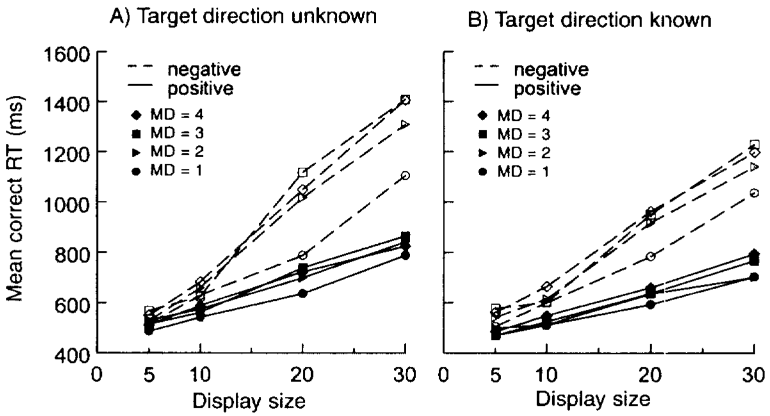

FIGURE 2. Mean correct positive and negative reaction times (RTs) as a function of the display size for each number of movement directions (MD) condition, separately for Experiment 1a (A. Target direction unknown) and Experiment 1b (B. Target direction known).

TABLE 1
Mean Base Times (ms), Search Rates (ms/Item), and Linearity for the Individual Search Reaction Time Functions (Mean R^2 and *SD*) in Experiment 1

	Trial							
	Positive				Negative			
Target direction	Base	Rate	R^2	*SD*	Base	Rate	R^2	*SD*
Unknown (Experiment 1a)								
MD = 1	421	11.8	.98	.011	389	22.8	.96	.047
MD = 2	457	12.6	.98	.018	361	31.8	.99	.012
MD = 3	433	14.6	.99	.007	345	36.0	.97	.009
MD = 4	459	12.5	.99	.011	358	34.7	.99	.003
Known (Experiment 1b)								
MD = 1	418	9.3	.97	.023	390	21.0	.98	.034
MD = 2	445	8.7	.96	.023	399	24.9	.98	.017
MD = 3	408	11.8	.99	.007	390	27.7	.97	.011
MD = 4	424	12.2	.98	.018	423	26.1	.98	.016

Note. MD = number of movement directions.

Experiment 1a (Target Direction Unknown)

RT analysis. We analyzed the RT data by a three-way repeated-measures analysis of variance (ANOVA) with main terms for target (present or absent), display size (5, 10, 20, or 30 items), and movement (1, 2, 3, or 4 directions). All three main effects were significant: target, $F(1, 3) = 28.35$, $p < .05$; display size, $F(3, 9) = 43.75$, $p < .01$; and movement, $F(3, 9) = 14.42$, $p < .05$. Positive RTs were faster than negative RTs; RTs increased with display size and varied with number of movement directions. Furthermore, all two-way interactions were significant: Target × Display Size, $F(3, 9) = 42.16$, $p < .01$; Target × Movement, $F(3, 9) = 13.33$, $p < .01$; and Display Size × Movement, $F(9, 27) = 11.07$, $p < .01$. Negative RTs were more affected than positive RTs by display size, with search rates of 31.3 and 12.9 ms/item, respectively. Number of movement directions also had a greater effect on negative RTs than on positive RTs and caused a change in search rates. The three-way interaction was significant, $F(9, 27) = 10.22$, $p < .01$, indicating that the changes in search rate attributable to the varying number of movement directions were greater on negative than on positive trials.

Base time and search rate analysis. We examined the individual base RT estimates by separate one-way ANOVAs for positive and negative trials with the main term for movement. There were no significant movement effects, either for positive trials, $F(3, 9) = 2.73$, *ns*, or for negative trials, $F(3, 9) = 2.64$, *ns*. The positive-trial base RTs averaged 443 ms, and the negative-trial base RTs, 363 ms. A priori tests of contrasts revealed no evidence to support the hypothesis that base RTs increase linearly with number of movement directions: positive trials, $F(1, 3) = 2.74$, *ns*; negative trials, $F(1, 3) = 1.82$, *ns*.

We also examined the individual search rate estimates by two one-way ANOVAs for positive and negative trials with the main term for movement. The movement effect was significant for negative trials, $F(3, 9) = 19.49$, $p < .05$, but not for positive trials, $F(3, 9) = 1.81$, *ns*. A post hoc Tukey test (HSD = 5.91 ms/item, $\alpha = .05$) revealed the negative-trial search rates to be significantly faster when items moved in only one direction (movement = 22.8 ms/item) than when they moved in multiple directions (movement = 31.8 ms/item, 36.0 ms/item, and 34.7 ms/item for two, three, and four directions, respectively). However, the differences between two, three and four movement directions were not significant (average search rate for movement > 1 = 34.2 ms/item). The positive trials showed a very similar pattern of movement effects; however, search-rate differences were too small to reach significance (although there was a marked difference between movement = 1 and movement > 1 in terms of overall RTs, 51 ms, compared with a 150-ms difference for negative RTs). The positive-trial search rates were significantly greater than zero, $F(1, 3) = 33.07$, $p < .01$, averaging 12.9 ms/item. Such search rates may be described as approaching "quite efficient search" (Wolfe, 1998, p. 21; defined by search rates between 5 and 10 ms/item).

In summary, there was no systematic linear effect of number of movement directions on the base RTs. However, there was a significant slowing in negative search rates between one and multiple movement directions.

Error analysis. The overall error rates were 5.0% misses (in positive trials) and 1.0% false alarms (in negative trials). Misses and false-alarm rates were arcsine transformed and analyzed separately by two-way ANOVAs with main terms for movement and display size (target effects were not of interest in this context). For misses, only the display size main term reached significance, $F(3, 9) = 6.41$, $p < .05$; misses increased from 2.0% with 5-item displays to 9.9% with 30-item displays. The false alarm rates showed no significant variation.

Experiment 1b (Target Direction Known)

RT analysis. A three-way ANOVA (Target × Display Size × Movement) of the RT data revealed essentially the same pattern of effects as in Experiment 1a (see Figure 2b). All main effects and two-way interactions were significant: target, $F(3, 9) = 16.80$, $p < .01$; Target × Display Size, $F(3, 9) = 31.85$, $p < .01$; Target × Movement, $F(3, 9) = 6.35$, $p < .05$; Display Size × Movement, $F(9, 27) = 8.81$, $p < .01$. The three-way interaction was only marginally significant: Target × Display Size × Movement, $F(9, 27) = 2.36$, $p < .10$.

Base time and search rate analysis. Again, we examined the base RT estimates by separate one-way ANOVAs for positive and negative trials with the main term for movement. There was no significant movement effect for positive trials, $F(3, 9) = 1.81$, *ns*, and for negative trials the effect only approached significance, $F(3, 9) = 4.69$, $p < .10$. A post hoc Tukey test (HSD = 32.26 ms, $\alpha = .05$) for the negative trials showed the base RT to be significantly slower with four movement directions (423 ms) than with one or three movement directions (390 ms and 390 ms, respectively). No other comparisons were significant. A priori tests of contrasts revealed no significant linear increase in base RTs with number of movement directions, either for positive trials, $F(1, 3) = 0.28$, *ns*, or for negative trials, $F(1, 3) = 4.89$, *ns*. Overall, the average base RTs were 424 for positive and 401 ms for negative trials.

We examined the search-rate estimates for positive and negative trials by one-way ANOVAs with the main term for movement. They revealed a significant movement effect for negative trials, $F(3, 9) = 12.35$, $p < .05$, but not for positive trials, $F(3, 9) = 2.85$, *ns*. The movement effect on the negative search rate showed the same pattern as in Experiment 1a (Tukey test, HSD = 3.56 ms/item, $\alpha = .05$). Search rates were significantly faster when items moved in only one direction (21.0 ms/item) than when items moved in multiple directions (24.9 ms/item, 27.7 ms/item, and 26.1 ms/item for two, three, and four directions, respectively), with no significant differences between two, three, and four directions (average search rate for multiple directions = 26.2 ms/item). The positive-trial search rates showed a very similar, but nonsignificant, pattern of movement effects (averaged across display size, positive RTs were 42 ms faster with movement in a single direction than with movement in multiple directions, which compares with 98 ms for negative RTs). The mean positive search rate was 10.5 ms/item and significantly greater than zero, $F(1, 3) = 92.11$, $p < .01$.

In summary, the RT results were consistent with those of Experiment 1a: There was no systematic linear effect of number of movement directions on the base RTs, but there was a significant slowing in negative search rates between one and multiple moving directions.

Error analysis. The overall error rates were 3.9% misses and 0.8% false alarms. Misses and false-alarm rates were arcsine transformed and analyzed separately by two-way ANOVAs with main terms for movement and display size. For misses, only the display size main term reached significance, $F(3, 9) = 48.36$, $p < .01$. Misses increased from 2.5% with 5-item displays to 6.8% with 30-item displays. The false-alarm rates showed no significant variation.

Comparison Between Experiments 1a and 1b

RT analysis. To further explore the effects of knowing in advance the movement direction of the target, we compared the RT data of Experiments 1a and 1b by a four-way ANOVA with an additional main term for target direction (unknown or known), which revealed, among other effects, the four-way interaction to be significant, $F(9, 27) = 3.28$, $p < .05$. This interaction was further examined by two Target Direction × Display Size × Movement ANOVAs performed separately for positive and negative trials. See Table 2 for a listing of the effects involving target direction.

On average, positive RTs were 57 ms faster, and negative RTs were 67 ms faster when the target direction was known in advance than when it was unknown. The advantage of knowing the target direction was somewhat smaller when items moved in one direction rather than in multiple directions (positive trials: 44 vs. 61 ms, respectively; negative trials: 28 vs. 80 ms, respectively). The same pattern of effects was also evident in the negative-trial search rates: They were significantly faster when the target direction was known than when it was unknown (24.9 vs. 33.1 ms/item, respectively), and this difference was smaller with one movement direction (21.0 vs. 22.8 ms/item, respectively) than with multiple directions (26.2 vs. 34.2 ms/item, respectively).

Error analysis. Analogous Target Direction × Movement × Display Size ANOVAs of the miss and false-alarm rate data revealed no effects involving target direction. Therefore, the RT differences between Experiments 1a and 1b were not confounded by differential speed–accuracy trade offs.

TABLE 2
Results of Target Direction × Display Size × Movement ANOVAs, Performed Separately for the Positive and Negative Trials of Experiment 1

	Trial					
	Positive			Negative		
Variable	*df*	*F*	*p*	*df*	*F*	*p*
TD	1, 3	8.30	< .07	1, 3	9.49	< .06
TD × MD	3, 9	5.05	< .05	3, 9	4.91	< .05
TD × DS	3, 9	2.59	.18	3, 9	23.10	< .01
TD × MD × DS	9, 27	8.88	.23	9, 27	4.26	< .01

Note. Only effects involving target direction are listed. TD = target direction (unknown or known). MD = number of movement directions (one, two, three, or four). DS = display size (5, 10, 20, or 30 items). ANOVA = analysis of variance.

Discussion

In summary, in neither subexperiment (1a, 1b) were there any systematic linear effects of the number of movement directions. However, both experiments showed significant differences in negative-trial search rates between one movement direction and multiple movement directions. Thus, qualitatively, the results were similar regardless of whether the target direction was known in advance (Experiment 1b) or unknown (Experiment 1a). However, uncertainty as to the target direction tended to slow RTs. Furthermore, while directional uncertainty had little effect on the positive-trial search rates (11.7 ms/item on average, suggesting quite efficient search),[3] the negative-trial search rates were slowed when there were multiple movement directions.

This pattern of effects is inconsistent with an account that assumes parallel search within movement directions but serial search across directions. Although the positive-trial search rates approached the criterion for parallel search, there was no linear increase in base RTs with the number of movement directions. However, the results are also inconsistent with accounts that assume that number

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[3] The positive search rates reported by McLeod et al. (1991) tended to be somewhat faster (clearly below 10 ms/item) than those in the present experiments. This difference may be attributable to the ratio between stationary and moving items, which was 1:1 in the experiments of McLeod et al. but 1:4 in the present experiment (i.e., the present displays contained a greater number of moving items for a given display size). If this ratio is important, it would point toward some form of parallel-continuous processing of all types of items—stationary and moving—in the display, with moving items influencing search efficiency more than stationary items. This was confirmed by von Mühlenen and Müller (in press).

of directions and advance knowledge of the target direction have no effect on search performance (McLeod et al., 1991). The pattern of results that requires explanation is (a) why advance knowledge (cuing) of target direction expedited search (even with only one movement direction), (b) why multiple movement directions impaired search performance (even when the target direction was known), and (c) why the advantage conferred by direction cuing was larger when items moved in multiple directions. This pattern of results suggests that motion–form conjunction search may involve some form of direction tuning of the motion system, which is more complex than the parallel–serial account considered at first. However, before attempting to develop such an account, we had to rule out a trivial explanation for the advantage of knowing the target direction in advance. This was the purpose of Experiment 2.

EXPERIMENT 2

In Experiment 1, there was a RT advantage when the target direction was known (marginally significant main effect of target direction), especially with multiple movement directions (significant Target Direction × Movement interaction). This advantage may simply stem from the direction cue's providing information about the likely display region in which the target is to be found. For example, when the target was an upward moving item, its initial position could not be in the upper part of the display. Thus, to optimize their search, participants may simply have made an eye movement toward the more likely display region, facilitating target detection in the direction-known condition relative to the direction-unknown condition. In other words, performance may not have been based on direction tuning of the motion system, but rather on maximizing information intake from the selected parts of the display.

We designed Experiment 2 to distinguish between those opposing accounts by using wrap-around displays in which moving items could disappear at one end of the display area and reappear at the other end. Thus, the position of the target at the start of a trial could be anywhere in the display, not just in the region opposite to its movement direction. If the advantage for the direction-known condition were replicated, this would rule out an account of selective information intake from particular display regions.

Method

Participants

Six new participants, 2 women and 4 men, took part in Experiment 2. Their ages ranged between 17 and 31 years. They all had normal or corrected-to-normal vision. They were paid £4.00 per hour. All participants received thorough practice on the task in one or more pre-experimental sessions.

Apparatus

The CRT was driven by an Interactive Electronics Systems point plotter (Finley, 1985), controlled by a Dell 433/M PC. Participants' responses (target present or target absent) were recorded by use of the right and left buttons of a serial Microsoft mouse, with the track ball removed to improve timing accuracy (Segalowitz & Graves, 1990). The same apparatus was used in the following experiments.

Stimuli

The stimuli in Experiment 2 were the same as in Experiment 1: Participants searched for a moving X among stationary Xs and moving Os. There were up to four movement directions, and the target direction was either unknown or known in advance. The following changes were made in comparison with Experiment 1:

1. The items moving in a particular direction were wrapped around—that is, they were continuously, point-by-point, disappearing at the display boundary in movement direction (e.g., upper boundary) and reappearing at the opposite boundary (e.g., lower boundary). This continuous wrap-around of items occurred in all directions in which items moved on a given trial (e.g., when there were four movement directions, out-and-in moving occurred across all boundaries). Apart from out-and-in moving being allowed in Experiment 2, all other constraints on the initial positions of the display items were the same as in Experiment 1. Importantly, this meant that the target could always be in any part of the display, regardless of its movement direction. As a result, all regions in the display were possible target positions, throughout the duration of a trial.
2. In the direction-known condition, the (cued) target direction was blocked rather than randomized across trials as in Experiment 1b. This was done to facilitate the participants' making use of the direction cue.
3. On half of all trials, items moved in only one movement direction (movement = 1); in the other half they moved in two, three, or four movement directions (movement > 1). This was done to reduce the number of trials and seemed permissible on the basis of the data of Experiment 1, which had shown little difference in performance between displays with more than one movement direction.
4. The display size was either 10, 20, or 30 items.

Design and Procedure

Forty-eight trials were generated for each combination of display size (10, 20, or 30 items), movement (one direction or multiple directions), target (present or absent), and target direction (unknown or known)—a total of 1,152 trials, which were presented to the participants in two sessions. Each session consisted of 12 blocks of 48 trials each. Target direction was randomized across trials within a block in the direction-unknown condition but constant throughout a block in the direction-known condition. On each trial, participants were provided with a noninformative direction cue (a cross) in the direction-unknown condition or an informative cue (an arrow) in the direction-known condition.

Results

The mean correct RTs are shown in Figures 3a and 3b for Experiments 2a and 2b, respectively. Mean base RTs and mean search rates are listed in Table 3, along with mean R^2 values and associated standard deviations.

RT Analysis

The RT data showed a pattern similar to those in Experiment 1. We analyzed RTs by a four-way repeated-measures ANOVA with main terms for target direction (unknown or known), target (present or absent), display size (10, 20, or 30 items), and movement (single or multiple directions). The analysis revealed the target effect, $F(1, 5) = 310.18, p < .01$, the display size effect, $F(2, 10) = 452.89, p < .01$, and the Display Size × Target interaction, $F(2, 10) = 378.25, p < .01$, to be significant. RTs were faster on positive than on negative trials, and they increased with display size, especially for negative trials.

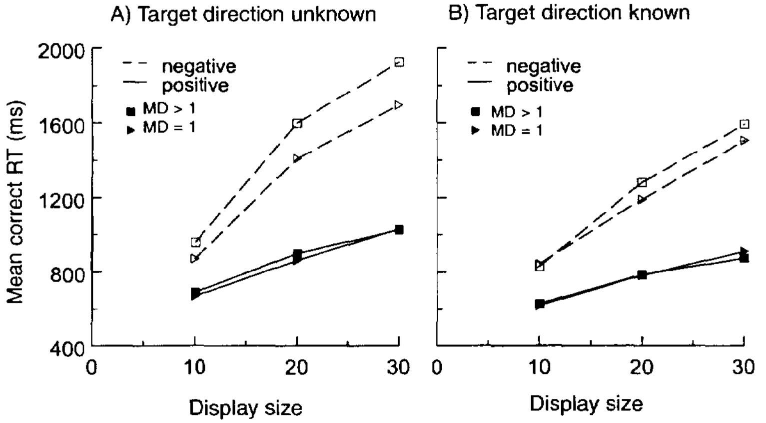

FIGURE 3. Mean correct positive and negative reaction times (RTs) as a function of the display size for each number of movement directions (MD), separately for Experiment 2a (A. Target direction unknown) and Experiment 2b (B. Target direction known).

TABLE 3
Mean Base Times (ms), Search Rates (ms/Item), and Linearity for the Individual Search Reaction Time Functions (Mean R^2 and *SD*) in Experiment 2

	Trial							
	Positive				Negative			
Target direction	Base	Rate	R^2	*SD*	Base	Rate	R^2	*SD*
Unknown								
MD = 1	494	18.0	.96	.044	502	41.2	.96	.053
MD > 1	536	16.8	.90	.152	527	48.3	.95	.065
Known								
MD = 1	479	14.5	.98	.013	518	33.1	.97	.021
MD > 1	517	12.3	.87	.132	473	38.1	.96	.043

Note. MD = number of movement directions.

Several effects involving movement were significant. RTs were, on average, 59 ms faster with one movement direction than with multiple directions: movement, $F(1, 5) = 33.57$, $p < .01$. However, this advantage was more marked for negative (112 ms) than for positive (6 ms) trials, Movement × Target, $F(1, 5) = 51.25$, $p < .01$. The same pattern held for the search rates, which were somewhat faster overall with one direction (26.8 ms/item) than with multiple directions (28.9 ms/item), Movement × Display Size, $F(2, 10) = 4.62$, $p < .05$. However, this search rate advantage was entirely attributable to negative trials (6.1 ms/item advantage) rather than to positive trials (−1.7 ms/item disadvantage), Movement × Target × Display Size, $F(2, 10) = 6.34$, $p < .05$.

Furthermore, several effects involving target direction were significant. RTs were overall 150 ms faster when the target direction was known than when it was unknown, target direction, $F(1, 5) = 42.79$, $p < .01$. This advantage was larger for negative (202 ms) than for positive (97 ms) trials, Target Direction × Target, $F(1, 5) = 10.10$, $p < .05$, and larger when items moved in multiple movement directions (184 ms) compared with one direction (115 ms), Movement × Target Direction, $F(1, 5) = 7.27$, $p < .05$. Similarly, search rates were overall faster when the target direction was known (24.5 ms/item) than when it was unknown (31.1 ms/item), Target Direction × Display Size, $F(2, 10) = 12.55$, $p < .01$, and this advantage was significantly larger for negative trials (9.2 ms/item) than for positive trials (4.0 ms/item), Target Direction × Target × Display Size, $F(2, 10) = 6.86$, $p < .05$.

Error Analysis

The overall error rates were 7.5% misses and 1.5% false alarms. Miss and false-alarm rates were arcsine transformed and analyzed separately by three-way

ANOVAs with main terms for target direction, movement, and display size. For misses, only the display size main term was significant, $F(2, 10) = 12.88, p < .01$. Misses increased from 3.6% with 10-item displays to 11.2% with 30-item displays. For false alarms, the Target Direction × Display Size interaction reached significance, $F(2, 10) = 7.76, p < .05$. False alarms, although rare overall, showed a somewhat different pattern of decrease across display size when the target direction was known (2.6%, 1.2%, and 1.3% for 10, 20, and 30 items, respectively) from when it was unknown (1.5%, 1.9%, and 0.4% for 10, 20, and 30 items, respectively). Taken together, the error data (misses varying only with display size and low percentages of false alarms) provide no evidence to suggest that the RT differences obtained between combinations of target direction and movement conditions (see preceding RT data) were confounded by differential speed–accuracy tradeoffs.

Comparison With Experiment 1

RT analysis. We compared the RT data of Experiments 1 and 2 by an ANOVA with the variables experiment, target direction, target, movement, and display size. (To permit comparison, we combined the data of Experiment 1 across the two-, three-, and four-movement conditions and excluded the 5-item display-size condition.) There was a significant experiment main effect, $F(1, 8) = 25.25$, $p < .01$. Furthermore, the Experiment × Display Size interaction, $F(2, 16) = 13.13$, $p < .01$, the Experiment × Target interaction, $F(1, 8) = 23.92$, $p < .01$, and the Experiment × Display Size × Target interaction, $F(2, 16) = 18.58$, $p < .01$, were significant. Not surprisingly, in Experiment 2, RTs were, on average, 285 ms slower and search rates 8.2 ms/item slower than in Experiment 1; these differences were more marked on negative trials (409 ms, 12.7 ms/item) than on positive trials (161 ms, 3.7 ms/item). Of the theoretically more interesting interactions involving experiment, target direction, and movement, only the Experiment × Target Direction interaction was significant, $F(1, 8) = 6.27$, $p < .05$: The advantage of knowing the target direction was larger in Experiment 2 than in Experiment 1 (150 vs. 67 ms, respectively). The fact that all other interactions were nonsignificant means that Experiments 1 and 2 showed very similar patterns of movement and target direction effects. These effects are summarized in Table 4, which contains the average RTs, base rates, and search rates as functions of movement, target direction, and target, averaged across Experiments 1 and 2.

Error analysis. The error percentages were somewhat lower in Experiment 1 than in Experiment 2 (misses: 4.5% vs. 7.5%, respectively; false alarms: 0.8% vs. 1.5%, respectively). However, differential speed–accuracy tradeoffs are unlikely to account for the RT differences between the two experiments.

TABLE 4
Reaction Times (ms), Base Times (ms), and Search Rates (ms/Item), Averaged Across Experiments 1 and 2

	Trial					
	Positive			Negative		
Target direction	Mean	Base	Rate	Mean	Base	Rate
Unknown						
MD = 1	734	458	14.9	1,043	446	32.0
MD > 1	768	489	15.0	1,202	441	41.3
Known						
MD = 1	670	449	11.9	956	454	27.1
MD > 1	683	472	11.6	1,033	439	32.2

Note. MD = number of movement directions.

Discussion

In general, Experiment 2 confirmed the findings of Experiment 1. The most important finding was that the advantage of knowing the target direction in advance was also manifest with wrap-around displays. In fact, the advantage was nearly twice as large as in Experiment 1, in terms of both overall RT (136 ms vs. 62 ms; witness the significant Experiment × Target Direction interaction) and search rate (6.6 vs. 3.7 ms/item). One potential problem with the direction cue in Experiment 1 was that it may have provided information about the likely display region in which the target was to be found at the start of a trial. Experiment 2 clearly argued against this as a confounding variable, because, with the wrap-around displays used, the target direction cue provided *no* information about likely target locations. This leaves the alternative account that advance knowledge of target direction improves search efficiency by permitting the motion system to be tuned to that direction.

The larger advantage of knowing the target direction in Experiment 2 relative to Experiment 1 may be attributable, at least in part, to the target direction's being blocked in the target-direction-known condition of Experiment 2 (i.e., the target always moved in the same direction within a block of trials), whereas target direction was variable across trials in Experiment 1. Direction tuning of the motion system may be more efficient when the target direction is kept constant across trials. Some evidence in support of this possibility was provided by a post hoc analysis of the positive RTs under target-direction-unknown conditions for intertrial dependencies, according to whether the target direction on a given trial was the same as or different from the direction on the preceding trial (unfortunately, only the raw data of Experiment 2 could be examined in this fashion; the data of Experiment 1 could not, as the LSI 11/23 system was no longer functioning). There was a small, but reliable, RT advantage when the directions of consecutive targets were the same rather than different (923 vs. 936 ms), without a difference between opposite and orthogonal (i.e., different) direction trials.[4]

Another noteworthy finding was the increased search rates in Experiment 2 relative to Experiment 1. On average, the wrap-around displays slowed the positive search rates by 4.1 ms/item and the negative search rates by 14.1 ms/item. One reason for this might be that the continual disappearance and reappearance of the moving items were diverting attention to the edges of the display, at the expense of more central items. Another possibility is that wrap-around displays violate a normal assumption underlying guided-search behavior: If a display region can be eliminated from the search as not containing a target, it does not need to be reinspected at a later time. To some extent, this assumption is violated by all moving displays, especially those with several directions of movement. However, wrap-around displays violate this assumption most consistently because the target can be in any part of the display at any time during a trial. This heightened uncertainty would increase the need for rechecking, resulting in steeper search rates. (However, see Horowitz & Wolfe, 1998, who argued that such uncertainty should have no influence on the search rates.)

In addition to replicating the advantage of knowing the target direction in advance, Experiment 2 also replicated the interaction of this effect with number of movement directions: The cuing advantage, in terms of overall RT, was larger with multiple movement directions (especially for negative trials). Combined across Experiments 1 and 2, the cuing advantages were 71 vs. 93 ms (movement = 1 vs. movement > 1) for positive trials and 101 vs. 200 ms (movement = 1 vs. movement > 1) for negative trials. It was not immediately apparent whether the overall search RT advantage conferred by advance knowledge of target direction and by items moving in one direction only was attributable to improved search rate rather than to base RT parameters of the search RT functions. However, a closer analysis of the data (see Table 4) suggests that the primary effect was on the search rates, rather than on the base RT. However, because the Target Direction × Movement × Display Size interaction was not significant (which may not be surprising, given the relatively fast search rates), we considered only overall RT effects in the General Discussion.

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[4] The advantage for same-direction trials would appear to be inconsistent with the findings of Raymond, O'Donnell, and Tipper (1998), who reported degraded motion-direction sensitivity when the attended direction in a transparent "prime" display with two orthogonal directions matched the direction in a second, unidirectional "probe" display. However, a direct comparison between the two sets of data is difficult because of the different paradigms used (visual search efficiency vs. sensitivity to motion direction of dot patterns).

GENERAL DISCUSSION

Summary of Results

The main results of the present experiments can be summarized as follows:

1. The base RTs did not increase with the number of movement directions in the display, and the positive-trial search rates approached quite efficient search.
2. Search was less efficient when items moved in multiple directions compared with just one direction, especially on negative trials (positive trials exhibited a reliable difference only in terms of overall RT; negative trials showed a difference in terms of both overall RT and search rate). Search efficiency differed little between conditions in which items moved in two, three, or four directions.
3. Advance knowledge (cuing) of the target direction facilitated the search. Direction cuing produced faster search rates (and overall RTs) on positive and negative trials. The cuing benefits cannot be attributed to better predictability of the display region in which the target is to be found at the start of a trial, because benefits were also manifest with wrap-around displays in which the target location was completely unpredictable.
4. The benefit of knowing the target direction was overall larger with multiple movement directions than with one movement direction, especially on negative trials.

We first considered the implications of our results for the original motion-filter account of McLeod and his colleagues (McLeod et al., 1988, 1991). Next, we developed an alternative conceptual framework to provide something like a *representations and algorithms* level account (Marr, 1982) of the data. Finally, several suggestions are advanced of how this account could be neuronally implemented in the brain (*hardware implementation* level account; Marr).

Implications for the Motion-Filter Account

Overall, the aforementioned results are consistent with the existence of some kind of motion filter. According to the account proposed by McLeod and his colleagues (McLeod et al., 1988, 1991), the motion filter segregates the moving from the stationary items, with only the moving items represented in the filter. Search across the reduced set of moving items can then proceed very efficiently, as it requires detection only of a single form-different item represented in the filter (McLeod et al., 1988). If the form discrimination required is easy (e.g., X versus O), the target may be discerned directly within the filter, permitting highly efficient search, whether the moving items move in only one direction or in multiple directions (McLeod et al., 1991).

The present findings do not fundamentally challenge those of McLeod et al. (1991): Search can indeed operate *relatively* efficiently over the whole set of moving items, irrespective of the number of movement directions and the predictability of the target direction. There was no support for an alternative interpretation of the data of McLeod et al. (1988, 1991), according to which search operates in parallel within movement directions but serially across directions (when the target direction is unknown). However, the present experiments did reveal significant effects of the number of movement directions and knowledge of the target direction (including an interaction between these variables), which are not easily accommodated by the original motion-filter account. Taken together, these effects suggest that direction tuning of the motion system can facilitate search for motion–form conjunction targets.

Alternative Framework

Von Mühlenen and Müller (in press; Müller & von Mühlenen, in press) have recently argued that visual search for motion–form conjunction targets is best explained within a GS framework (e.g., Wolfe, 1994). Within this framework, discrimination of the moving items (always) involves the interaction between the motion and form systems, with the role of the motion system limited to guiding (restricting) the search to the moving items. By this account, target selection operates from an overall-saliency, or master, map of locations (e.g., Cave & Wolfe, 1990; Koch & Ullman, 1985; Treisman & Sato, 1990). The master map units integrate, in parallel, the output of dimension-specific feature analyzers (via spatiotopic connections between feature analyzer and master map units). Selection can be top-down controlled by enhancing the saliency of display items sharing target features, at the feature map level (e.g., Cave & Wolfe, 1990; Treisman & Sato, 1990; Wolfe, 1994). In conjunction search for a moving X, moving items will be activated through the motion system, and Xs through the form system. The moving X will achieve a higher saliency than will moving-O and stationary-X distractors at the master map level, because it is the only item receiving activation from both the motion and X-form detectors (distractors are supported by only one detector). Thus, search can be efficiently guided to the moving target even when there are stationary items in the display sharing the target form.

The main effect of direction cuing (knowledge of target direction) established in the present experiments can be easily accommodated within this framework by making the following assumption:

Assumption 1: The top-down enhancement can be distributed nonspecifically over all movement directions or directed selectively to items moving in the target direction (under the assumption that all detectors coding movement in target direction are enhanced, whether or not there is an appropriate moving stimulus within their receptive fields). When enhancement is directed to the target direction (direction tuning), the appropriate items, including the target item, achieve a greater saliency at the master map level than items moving in other directions. As a consequence, there is a reduced likelihood that one of the moving items (i.e., an item moving in a nontarget direction) will gain a greater saliency than the target, because of noise in the saliency computation (Cave & Wolfe, 1990; Wolfe, 1994), and target detection is expedited.

According to this account, enhanced target detection will result both when moving items move in one direction only and when they move in multiple directions. (In the former case, if the target direction is unknown, enhancement will also be distributed across multiple directions, reducing the saliency of items moving in the only—target—direction. This will be the case—at least initially. Some direction tuning may occur, though, during the course of a trial.[5])

However, that account does not explain (a) why search was more efficient when there was only one movement direction, rather than multiple movement directions (the main effect of number of movement directions); and (b) why the cuing effect was more pronounced with multiple movement directions (the interaction between the cuing and number of movement directions effects). To explain these two effects, two additional assumptions are necessary:

Assumption 2: Items moving in multiple directions (crossing each other's paths) interfere with the computation of motion-direction signals. In extreme instances of interference, the motion signal for an item moving in a particular direction may be annihilated temporarily— that is, the item is not represented as moving and, thus, receives no top-down enhancement. Assumption 2 would explain why search was easier with only one movement direction but not why the cuing effects (i.e., the cost of not knowing the target direction) were greater with multiple movement directions. To explain the latter interaction effect, we introduced the third added assumption:

Assumption 3: Direction tuning of the motion system not only enhances the saliency of the items moving in target direction but also reduces the interference from items moving in nontarget direction(s). When items move in one direction

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[5] An alternative account for this interaction emphasizes the reduced direction-cuing effect with unidirectional-movement displays (rather than the increased effect with multidirectional-movement displays). It may be that, when there is only one, initially unknown, movement direction, the motion system is automatically tuned to that direction during the course of the trial. Although this tuning is delayed (relative to when target direction is known in advance), it may facilitate target detection in comparison with the multidirectional-movement condition in which the target direction is unknown and stimulus-driven tuning is not possible. Our data do not permit a decision between the alternative accounts of the interaction, which are not necessarily mutually exclusive. Stimulus-driven tuning could affect target detection only if it is achieved rapidly after display onset (i.e., within a time shorter than the normal positive reaction time). We are currently examining whether this is at all feasible.

only, there can be no interference, by definition (on the assumption that only moving items, but not stationary items, generate interference). Consequently, reduced interference would facilitate search only when items move in multiple directions, explaining the interaction.

Table 5 summarizes the combined effects of direction tuning (knowledge of target direction) and of multiple-direction interference. We assigned a plus sign to effects facilitating search performance in a given search condition and a minus sign to effects impairing performance. Under multiple-movement-direction conditions, (a) when the target direction is known, facilitation from direction tuning is counteracted by weak impairment from multiple-direction interference (net effect: 0); and (b) when the target direction is unknown, there is no facilitation from direction tuning but strong impairment from multiple-direction interference (net effect: –2). In the case of one-direction-only conditions, (a) when the target direction is known, there is facilitation from direction tuning but no impairment from multiple-direction interference (net effect: +1); and (b) when the target direction is unknown, there is neither facilitation from direction tuning nor impairment from multiple-direction interference (net effect: 0). Consequently, the cuing effect is greater with multiple movement directions than with one direction only.

Neurophysiological Plausibility

The foregoing account provides a feasible conceptual scheme for explaining the present results. However, the two added assumptions to accommodate the full pattern of effects require further justification to be considered plausible. There is neurophysiological evidence that color-selective and motion direction-selective cells in the primate visual cortex exhibit properties consistent with the foregoing assumptions. The first stage at which neurons show a differential response to

TABLE 5
Facilitating Effects of Target-Direction Tuning (+) and Impairing Effects of Multiple-Direction Interference (–) Depending on the Knowledge of the Target Direction (Unknown or Known) and the Number of Movement Directions (1 or > 1)

	Target direction	
MD	Unknown	Known
= 1	0 = direction tuning 0 = multiple-direction interference	+ = direction tuning 0 = multiple-direction interference
> 1	0 = direction tuning – – = multiple-direction interference	+ = direction tuning – = multiple-direction interference

Note. MD = number of movement directions. + = facilitating effect; – = impairing effect; 0 = no effect.

movements in different directions is the striate cortex, area V1 (e.g., Hubel & Wiesel, 1968). Around one third of V1 cells, particularly cells concentrated in the upper sublayers of layer 4 and layer 6, have a directional response. A strong projection leads from layers 4B and 6 to area MT (e.g., Shipp & Zeki, 1985), whose neurons are almost exclusively directional (e.g., Zeki, 1974, 1993).

Direction Tuning

The cuing is assumed to lead to the direction tuning of the motion filter, facilitating search. Direction tuning of the filter might work by the receptive fields of appropriate direction-selective motion cells (e.g., in area MT) being "contracted" around items moving in the cued direction. Such a contraction has been demonstrated by Moran and Desimone (1985) for color-selective cells in cortical area V4 of the monkey. If, for example, a color-selective cell responded to red, but not to green, stimuli, Moran and Desimone placed both a red and a green stimulus simultaneously inside the cell's receptive field. When the animal was made to attend to the (location of the) red stimulus, which had to be matched with the preceding or subsequent stimulus at that location, the cell gave a good response. In contrast, when the animal attended to the (location of the) green stimulus, the cell gave only a small response, even though the two stimuli on the retina were identical in the two conditions. "In each case, the neuron responded as if the receptive field had contracted around the attended stimulus . . . , suggesting that attention serves not only to filter out unwanted information, but also to increase the spatial resolution of neurons with large receptive fields" (Desimone, 1992, p. 347).

By analogy, attending to a stimulus moving in a particular direction might contract the receptive field of an MT cell tuned to that direction around that stimulus. Consistent with this suggestion is a report by Treue and Maunsell (1996), who recorded the responses of direction-selective neurons in macaque monkey cortical areas MT (and MST) under two different attention conditions. In their Experiment 1, the monkeys were presented with displays of two moving-dot stimuli. One dot moved back and forth through the receptive field of a given cell, along the cell's preferred and null directions, whereas the other dot moved (not necessarily parallel to the first stimulus) outside the cell's receptive field. Most cells responded more strongly to the dot inside their receptive fields when the monkey was instructed to attend to (i.e., respond to a velocity change of) that dot than when the monkey attended to the dot outside the receptive field. In a second experiment, an additional dot was presented inside the cell's receptive field, moving parallel to the other dot, but always in the opposite direction. "When the animal was instructed to attend to either of the dots in the receptive field, the neuron responded most strongly when that dot moved in the cell's preferred direction . . . When the other dot in the receptive field was the target, the phase of the response changed so that the neuron now responded most strongly when that other dot was moving in the preferred direction" (p. 540)—that is, the neuron was tuned to respond to the movement of the target, even if a more powerful stimulus moved through its receptive field in the preferred direction.

The neuron responded as if its receptive field had contracted along the track of the target stimulus movement. Such a contraction would have the effect of increasing the spatial resolution of the cell—that is, by effectively sampling across a reduced receptive field, the cell's ability to discriminate target signals from spurious signals (its signal-to-noise ratio) would be improved and its response rate increased. Within the GS framework outlined earlier, that mechanism has been referred to as direction-specific saliency enhancement.

Multiple-Direction Interference

Snowden et al. (1991) recorded the response of neurons from both area V1 and area MT in the alert monkey to unidirectional motion and to transparent motion of dot stimuli moving in one or two, opposite or orthogonal, directions. Snowden et al. found that "the cells in area V1 . . . respond[ed] well to their preferred direction of motion even in the transparent condition, whereas area MT neurons were substantially inhibited under the same transparent conditions" (p. 2789). The researchers proposed that the suppressive effect exhibited by MT neurons "stems from competitive interactions between neurons with different preferred directions of motion" (p. 2782). In area V1, different neurons are tuned to different directions of motion at the same retinal location, so that more than one motion vector is represented at each local image region. MT neurons, which have relatively large receptive fields (e.g., 6–10° in the study of Qian & Andersen, 1994), then combine these estimates through inhibitory interactions. Those interactions would serve to reduce noise in the motion system, permitting true motion signals to be distinguished from spatio-temporal energies generated by noise inputs to the system such as flicker.

Qian and Andersen (1994) proposed that "the receptive field of an MT cell is composed of many small subunits of size about 0.4°" (subunits correspond to V1 inputs to MT, so their sizes should be comparable to V1 receptive-field sizes), "directional suppression is performed within each subunit," and "the response of an MT cell is determined by the sum of the thresholded outputs of all its subunits" (p. 7378). To generate the percept of motion transparency, the motion vectors in different directions must not be too close to each other—otherwise, they will cancel each other out. (For a further elaboration of this notion, see also Qian, Andersen, & Adelson, 1994a, 1994b.)

In summary, the foregoing work on transparent-motion perception provides direct support for the assumption of multiple-direction interference.

Interaction Between Direction Tuning and Multiple-Direction Interference

The third assumption—that direction tuning of the motion system not only enhances the saliency of the items moving in the target direction but also reduces the interference from items moving in nontarget direction(s)—follows directly from the proposal that direction tuning involves a contraction of the receptive fields of cells sensitive to a particular motion direction. By contracting its field, such a cell would minimize the suppressive effect of nearby stimuli moving in other, nonpreferred directions (i.e., the suppressive effect of stimuli that would have moved through the cell's uncontracted receptive field). Thus, in addition to improving the cell's signal-to-noise ratio, the receptive-field contraction would automatically reduce the interference from items moving in nonpreferred directions.

The study of Treue and Maunsell (1996) provides some evidence for this proposal. In their Experiment 2, when the monkey was instructed to attend to the dot outside the recorded cell's receptive field, its response to the two dots moving in opposite directions inside its receptive field was reduced to a level intermediate between the levels of preferred and null motion directions alone. Treue and Maunsell took "this intermediate level of activity [to] reflect . . . the response suppression in MT using transparent motion displays" (p. 540; cf. Snowden et al., 1991). By implication, attending to one or the other dot inside the cell's receptive field reduces the suppressive effect of the other stimulus moving in the opposite direction.

Conclusions

In conclusion, a relatively simple model derived from the GS theory provides a satisfactory account for the effects of direction cuing and number of movement directions in motion–form conjunction search. However, the GS model, as a general theory of visual search, would not have been able to account for the full pattern of results without specifying the mechanisms responsible for multiple-direction interference and how these mechanisms are modulated by direction tuning. In this sense, Driver and McLeod (1992) were right in arguing that for a full understanding of visual search performance, "General theories . . . will have to take the specific properties of different visual subsystems into account" (p. 32).

REFERENCES

Berger, R. C., & McLeod, P. (1996). Display density influences visual search for conjunctions of movement and orientation. *Journal of Experimental Psychology: Human Perception and Performance, 22,* 114–121.

Cave, K. R., & Wolfe, J. M. (1990). Modeling the role of parallel processing in visual search. *Cognitive Psychology, 22,* 225–271.

Desimone, R. (1992). Neural circuits for visual attention in the primate brain. In G. A. Carpenter & S. Grossberg (Eds.), *Neural networks for vision and image processing* (pp. 343–364). Cambridge, MA: MIT Press.

Driver, J., & McLeod, P. (1992). Reversing visual search asymmetries with conjunctions of movement and orientation. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 22–33.

Finley, G. (1985). A high-speed point plotter for vision research. *Vision Research, 25,* 1993–1997.

Horowitz, T. S., & Wolfe, J. M. (1998). Visual search has no memory. *Nature, 357,* 575–577.

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, 195,* 215–243.

Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: Towards the underlying neural circuitry. *Human Neurobiology, 4,* 219–227.

Marr, D. (1982). *Vision.* San Francisco: Freeman.

McLeod, P., Driver, J., & Crisp, J. (1988). Visual search for a conjunction of movement and form is parallel. *Nature, 332,* 154–155.

McLeod, P., Driver, J., Dienes, Z., & Crisp, J. (1991). Filtering by movement in visual search. *Journal of Experimental Psychology: Human Perception and Performance, 17,* 55–64.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229,* 782–784.

Müller, H. J., & Found, A. (1996). Visual search for conjunctions of motion and form: Display density and asymmetry reversal. *Journal of Experimental Psychology: Human Perception and Performance, 22,* 122–132.

Müller, H. J., & von Mühlenen, A. (in press). Visual search for conjunctions of motion and form: The asymmetry for easy-to-discriminate targets depends on practice. *Visual Cognition.*

Pashler, H. (1987). Detecting conjunctions of color and form: Reassessing the serial search hypothesis. *Perception & Psychophysics, 41,* 191–201.

Qian, N., & Andersen, R. A. (1994). Transparent motion perception as detection of unbalanced motion signals: II. Physiology. *Journal of Neuroscience, 14,* 7367–7380.

Qian, N., Andersen, R. A., & Adelson, E. H. (1994a). Transparent motion perception as detection of unbalanced motion signals: III. Modeling. *Journal of Neuroscience, 14,* 7381–7392.

Qian, N., Andersen, R. A., & Adelson, E. H. (1994b). Transparent motion perception as detection of unbalanced motion signals: I. Psychophysics. *Journal of Neuroscience, 14,* 7357–7366.

Raymond, J. E., O'Donnell, H. L., & Tipper, S. P. (1998). Priming reveals attentional modulation of human motion sensitivity. *Vision Research, 38*(19), 2863–2867.

Segalowitz, S. J., & Graves, R. E. (1990). Suitability of the IBM XT, AT, and PS/2 keyboard, mouse, and game port as response devices in reaction time paradigms. *Behavior Research Methods, Instruments, and Computers, 22,* 283–289.

Shepherd, M. (1984). EMDISP: A visual display system with digital and analogue sampling. *Behavior Research Methods, Instruments, & Computers, 16,* 297–302.

Shipp, S., & Zeki, S. (1985). Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. *Nature, 315,* 322–325.

Snowden, R. J., Treue, S., Erickson, R. G., & Andersen, R. A. (1991). The response of area MT and V1 neurons to transparent motion. *Journal of Neuroscience, 11,* 2768–2785.

Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12,* 97–136.

Treisman, A., & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception and Performance, 16,* 459–478.

Treue, S., & Maunsell, J. H. R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature, 382,* 539–541.

von Mühlenen, A., & Müller, H. J. (in press). Perceptual integration of motion and form information: Evidence of parallel-continuous processing. *Perception & Psychophysics.*

Wolfe, J. M. (1994). Guided Search 2.0. A revised model of visual search. *Psychonomic Bulletin and Review, 1,* 202–238.

Wolfe, J. M. (1998). Visual search. In H. Pashler (Ed.), *Attention* (pp. 13–73). Hove, UK: Psychology Press.
Zeki, S. (1974). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *Journal of Physiology, 236,* 549–573.
Zeki, S. (1993). *A vision of the brain.* Oxford, UK: Blackwell Scientific Publications.

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