



Visual Search of Expansion and Contraction

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The perception of expansion/contraction in human subjects was examined with a visual search paradigm. When searching for a target defined by two-dimensional expansion among distractors defined by two-dimensional contraction, the time needed to find the target did not vary as the number of distractors was increased. However, for a target defined by two-dimensional contraction among distractors defined by two-dimensional expansion, the search time increased as a function of the number of distractors in the display. A similar search asymmetry remained between one-dimensional expansion and one-dimensional contraction, even though one-dimensional expansion was searched in a serial manner. This asymmetry between expansion and contraction reflects a basic characteristic of higher-order motion information processing. © 1997 Elsevier Science Ltd.

Visual motion Visual search Expansion/contraction Search asymmetry

INTRODUCTION

A formal analysis of optical flow shows that each point in the flow field can be decomposed into the invariant properties of translation, expansion/contraction, rotation, and shearing (e.g. Koenderink, 1986; Longuet-Higgins & Prazdny, 1985; Harris, 1994). How these relative motions are processed is an important question in the study of the visual system (e.g. Cavanagh & Favreau, 1980; Duffy & Wurtz, 1991; Freeman & Harris, 1992; Hershenson, 1987; Nakayama *et al.*, 1984; Regan & Beverley, 1978b; Sekuler, 1992; Tanaka & Saito, 1989; Werkhoven & Koenderink, 1991). In this study, the perception of expansion/contraction in human subjects was examined with a visual search paradigm.

A typical visual search experiment measures how fast observers can find a visual target among a variable number of distracting items. The time required to find a target has been assumed to reflect how the target is represented in the visual system (Treisman & Gelade, 1980; Treisman & Gormican, 1988). If the target is represented as a single feature or an element in a stage where information is processed preattentively and in parallel, then the time required to find the target will be independent of the number of distractors. If the target is represented as a conjunction of single features, then the search time is influenced by the number of distractors.

Based upon the visual search paradigm, we can make two assumptions about how expansion/contraction is represented in the visual system. If expansion/contraction is represented as a single feature, then the time needed to detect expansion/contraction will not vary as the number

of distractors in the display (set size) increases. However, if expansion/contraction is represented as a conjunction of local translations and their specific spatial positions, the time needed to detect expansion/contraction will increase as a function of set size. Braddick and Holliday (1991) examined these two hypotheses, and showed that the characteristics of the slope of the reaction time-set size function mirrored those of a serial search. They concluded that local expansion/contraction is not represented as a single feature, but as a conjunction of local translations in the visual system.

Regan and his colleagues, however, have demonstrated through the use of various psychophysical methods that expansion/contraction is represented as a specialized feature, and not as a conjunction of translations (Beverley & Regan, 1979, 1983; Regan, 1986, 1993; Regan & Beverley, 1978a,b; Regan *et al.*, 1979). Regan and Beverley (1978b) found that the adaptation to expansion selectively depresses visual sensitivity to expansion. In another study, Beverley and Regan (1979) observed that the decay time constants of the motion aftereffect induced by expansion/contraction (MAE in depth), and that induced by translation (linear MAE) are different. From these results, they suggested that a looming or changing size detector, which selectively responds to expansion (or contraction), be implemented in the human visual system.

Regan and Beverley's hypothesis seems to be inconsistent with the findings of Braddick and Holliday (1991) in that no "pop-out" phenomena occurred during expansion/contraction (Regan, 1993; Braddick, 1993). Although the discrepancy between Regan and Beverley (1978b) and Braddick and Holliday (1991) could be attributed to differences in the respective tasks they used, it is possible that some factor deteriorated the search performance in Braddick and Holliday's results. One

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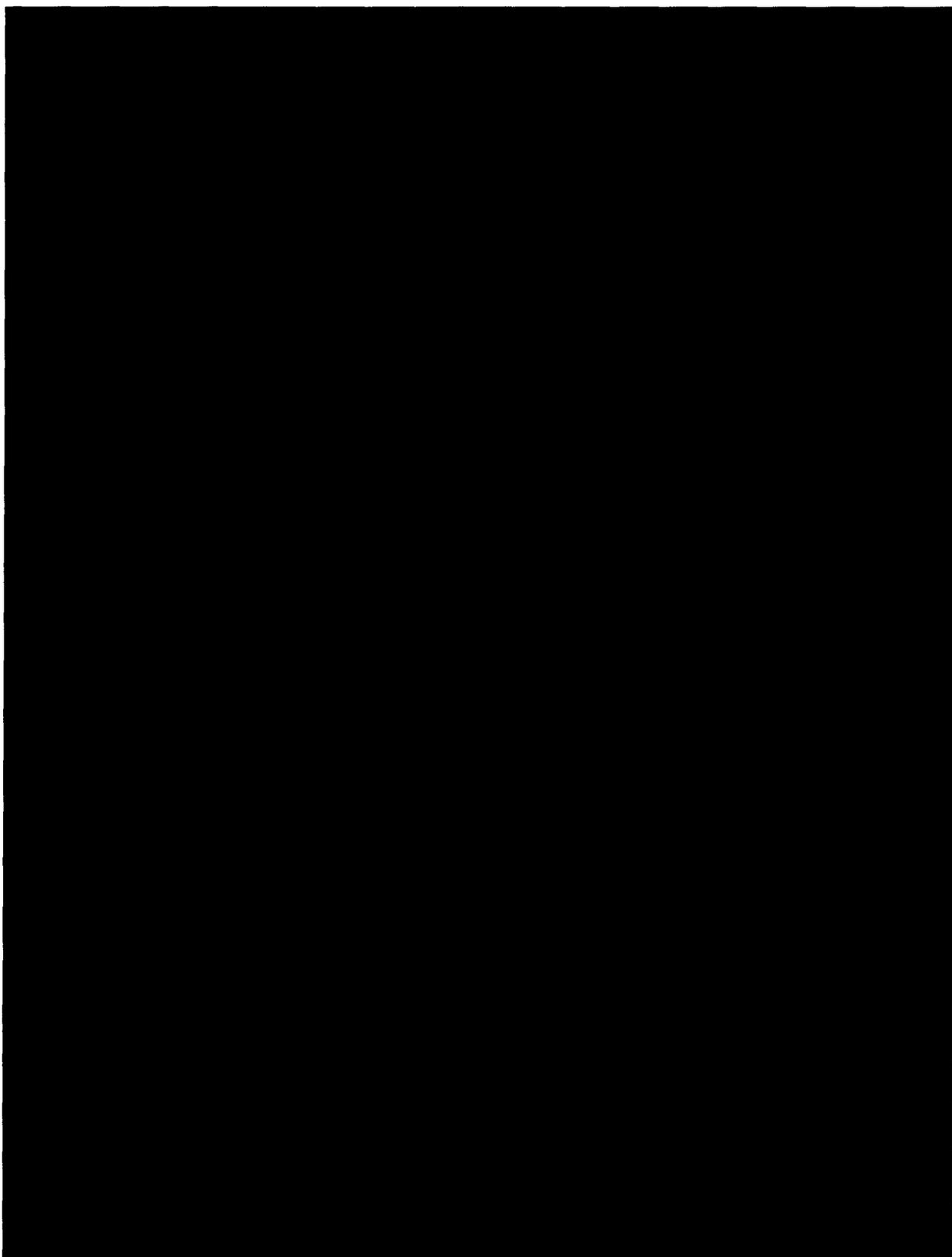


FIGURE 1. Snapshot of one frame of the two-dimensional expansion/contraction display. Set size is 25.

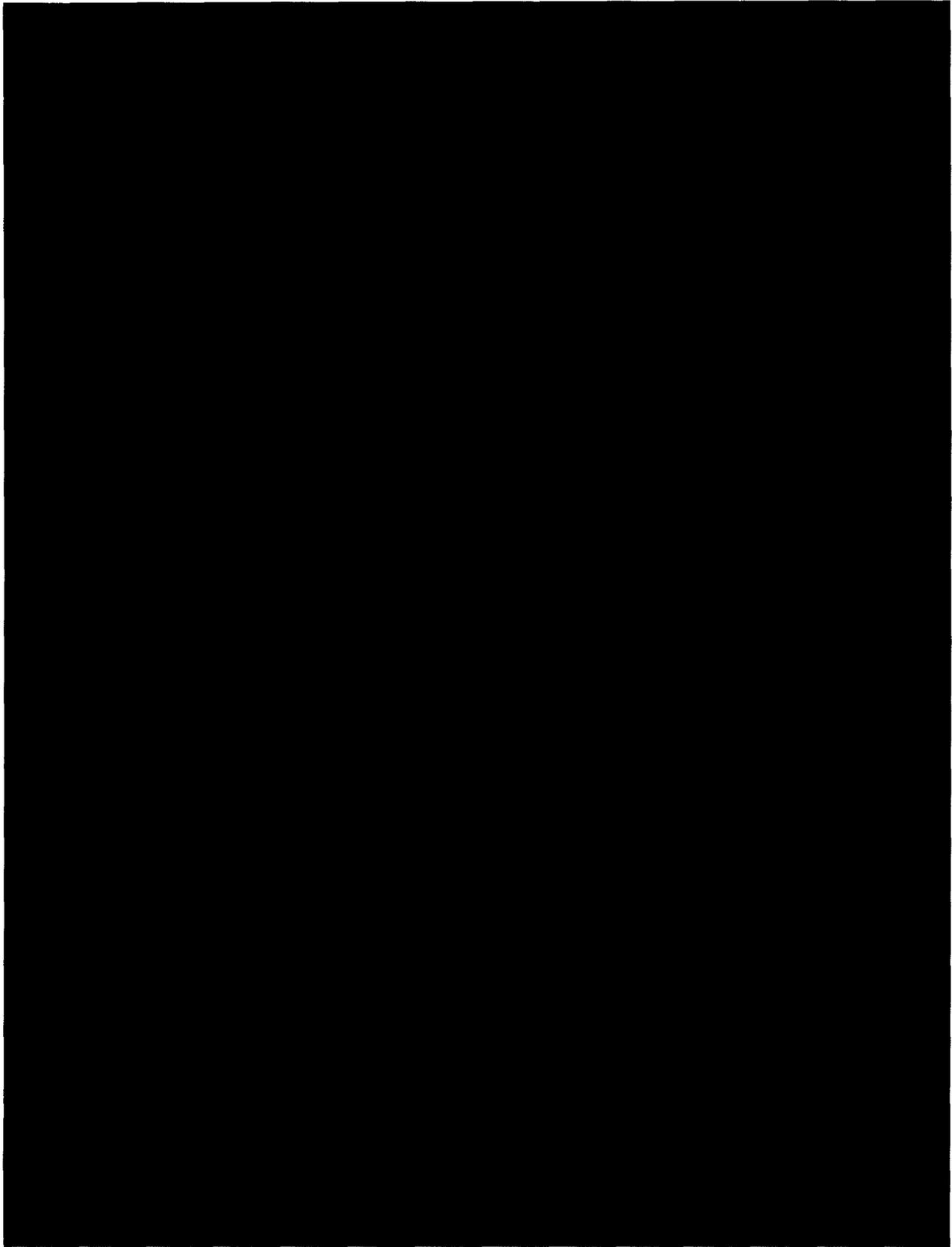


FIGURE 2. Snapshot of one frame of the one-dimensional expansion/contraction display. Set size is 18.

plausible factor is a special characteristic of the stimulus they used. Because the movement of expansion or contraction was generated by the cyclical presentation of the outline of a square in the display, the outline made sudden jumps in the opposite direction when it reached the last part of the cycle, thereby bringing about a contraction in an expansion and vice versa. Braddick and Holliday (1991) maintained that this should not affect the search performance because the targets defined by the direction of translation showed clear pop-out in spite of the cyclical presentation which produced jumps in the opposite direction to the smooth translation (p. 351). This reasoning is based on the assumption that the sensitivity to expansion/contraction and translation are the same when some noise component is added to each stimulus. De Bruyn and Orban (1990), however, found that many more signal dots were needed to detect expansion or contraction than to detect translation in a noisy field. On the contrary, Freeman and Harris (1992) found that the minimum motion threshold of expansion was lower than that of translation. Though these two results are inconsistent and further studies are needed to solve the matter, we can assume that the visual system might have different signal-to-noise ratios (SNRs) for translation and expansion/contraction. Considering the difference in SNRs, it is possible that the addition of irrelevant direction components generated by the sudden jumps affected Braddick and Holliday's results.

In this study, the visual search performance of human subjects to expansion/contraction was examined. The noise generated by sudden jumps was eliminated by using a periodic stimulus. To examine the perception of expansion/contraction, a two-dimensional stimulus, in which both the vertical and horizontal components expand or contract, has frequently been used. Beverley and Regan (1979), however, showed that a square-shaped one-dimensional adapting stimulus whose two vertical edges only expand or contract while its horizontal edges remain stationary elicits MAE in depth. Therefore, both two-dimensional and one-dimensional expansion/contraction were used in this study.

METHODS

Subject

Four subjects aged between 21 and 39 yr participated in the experiment. They had normal or corrected-to-normal vision. They were well-practiced in psychophysical experiments involving visual search tasks and were not informed of the exact purpose of the experiment.

Apparatus

The stimuli were displayed on a 21" color display (Sony GDM-2036S) controlled by a computer (Apple Macintosh IIci). The frame rate of the CRT was 66.7 Hz with a gray-level resolution of 8 bits. The monitor was calibrated with a Minolta Color TV Analyzer, and its output was gamma-corrected under software control.

Moving patterns were generated using look-up table animation (Baro & Hughes, 1991).

Stimuli

Figure 1 shows a snapshot of one frame of the two-dimensional expansion/contraction display. Each stimulus was a square filled with periodic gratings within which luminance varied as a sine function. The spatial frequency of the moving stimulus was 0.48 c/deg. The direction of the motion of the stimulus is shown by the arrows in the upper-right portion of Fig. 3. The orientation of the gratings was orthogonal to the direction of motion. Figure 2 shows a snapshot of one frame of the one-dimensional expansion/contraction display. In this case, each stimulus was divided into two regions, and two vertical sinusoidal gratings moved in the opposite directions in each region (see also Fig. 4).

The Michelson contrast was 80% and the average luminance was 10.5 cd/m². The background luminance of the display was also set to 10.5 cd/m². Only the green gun of the CRT was used. The size of each stimulus was held constant during each moving sequence to avoid generating noise from sudden jumps. The starting phase was randomly selected for each stimulus (see Figs 1 and 2) so that the motion information was the only source for discriminating the expansion and contraction. Each stimulus was drawn on an imaginary matrix of 5 × 5 cells in the display. The size of each cell was set to 6.0 deg (horizontal) × 4.0 deg (vertical). Therefore, the whole display size subtended 30.0 deg (horizontal) × 20.0 deg (vertical). In order to avoid the effects of spatial alignment, the position of each stimulus was jittered from the center of its cell. The size of the jitter was randomly chosen from 0.0 deg to 1.0 deg, in a random direction distributed about 360 deg. The inner periodic gratings moved at a constant speed of 11.1 deg/sec. Viewing was monocular from a distance of 57 cm. The viewing distance and the position of the subjects was maintained by a chin rest and a head rest.

Ramachandran and Anstis (1990) reported that the size of an annulus whose inner component expands looks subjectively larger than one whose inner component contracts even though both annuli are physically the same size. To avoid this effect, the size of each stimulus was randomly varied in each trial from 1.0 × 1.0 deg to 3.0 deg × 3.0 deg (see Figs 1 and 2). The average size of all stimuli in one trial was set to 2.0 × 2.0 deg.

Procedure

Each block of the experiment consisted of 100 trials: 10 trials for each of 10 conditions (1, 6, 12, 18, or 24 total items with the target item either present or absent) presented in random order. Half of the trials in a block contained targets and the other half did not. In target-present trials, only one target stimulus expanded (or contracted) while all other distractors contracted (or expanded). In target-absent trials, all of the stimuli contracted or expanded uniformly. The experimental blocks were preceded by four practice blocks of 100 trials

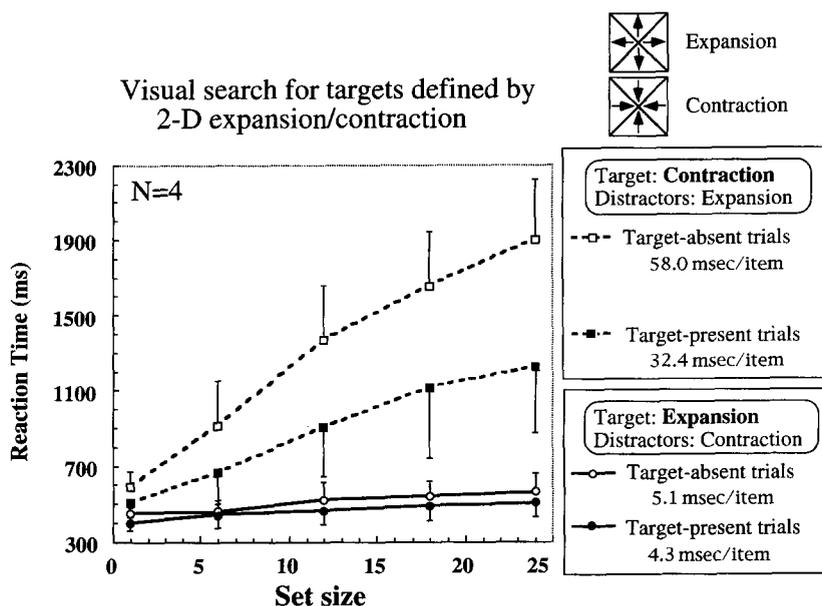


FIGURE 3. The average result across four subjects of visual search for targets defined by two-dimensional expansion or contraction. Mean reaction times as a function of set size. Error bars show ± 1 SD. The moving stimuli are schematically shown in the upper right corner of the figure. The solid lines show the search performance when two-dimensional expansion was the target. The dashed lines show the search performance when two-dimensional contraction was the target.

for each target type (two-dimensional and one-dimensional expansion/contraction). Then, each subject completed three experimental blocks for each target type. The blocks for each target type were presented in random order for each subject. The task was to indicate whether the target was present or absent in the display by pushing one of two keys on a keyboard. When the subject made a correct response, the reaction time was recorded. When the subject made a mistake, feedback (a buzzing sound) was given and recorded as an error. Reaction times for incorrect responses were discarded. In addition, reaction times < 150 msec or > 5 sec were discarded, and any trials exceeding those time limits were repeated after the remaining trials of that block were done. Only 1.0% of the total number of trials were repeated. Each trial began with the presentation of a small black fixation cross in the center of the display. After 500 msec, the cross disappeared, and the stimulus appeared 100 msec later. The stimulus then remained visible until the subject responded. The inter-trial interval was 5 sec. To motivate the subject, the mean reaction time and error rate of each 20 trials were presented at the inter-trial interval. Each subject was instructed before the experiment to try to maintain an error rate within 5%. They were also instructed that a block in which the error rate exceeded 10% would be repeated. No blocks were repeated throughout the experiment.

Results

The mean correct reaction times for two-dimensional stimuli are shown in Fig. 3. Each data point here was calculated from 120 trials, combined across all subjects. Figure 3 also shows the mean regression slopes for reaction times against set size obtained by the least square method. The slopes were determined from the

combined data of all subjects. There were two main findings in this experiment. First, the time required to find each expansion was almost independent of the number of distractors (4.3 msec/item in target-present trials). Also, the slope ratio for target-absent trials (5.1 msec/item) and target-present trials was $5.1/4.3 = 1.2$, which departed from the typical ratio (2.0) of a self-terminating serial search (Treisman & Gelade, 1980). Thus, the search of the target defined by two-dimensional expansion was done in a parallel way. Second, search asymmetry of reaction times between expansion and contraction was found. The reaction times varied more or less linearly with the number of distractors displayed when the targets were defined by two-dimensional contraction. Also, the search rate for target-absent trials was almost twice that for target-present trials (32.4 msec/item in target-present trials; 58.0 msec/item in target-absent trials). This suggests that the target defined by two-dimensional contraction was searched serially.

Figure 4 shows the results of the experiment using one-dimensional expansion/contraction. The overall search rate increased largely compared to that for the two-dimensional expansion/contraction (Fig. 3), and it can be said that both one-dimensional expansion and contraction were searched serially. The results also clearly show search asymmetry between one-dimensional expansion and one-dimensional contraction. The search rate for one-dimensional expansion (23.2 msec/item) was nearly three times faster than that for one-dimensional contraction (67.7 msec/item).

DISCUSSION

The results can be summarized as follows. First, under the appropriate conditions, expansion is searched paral-

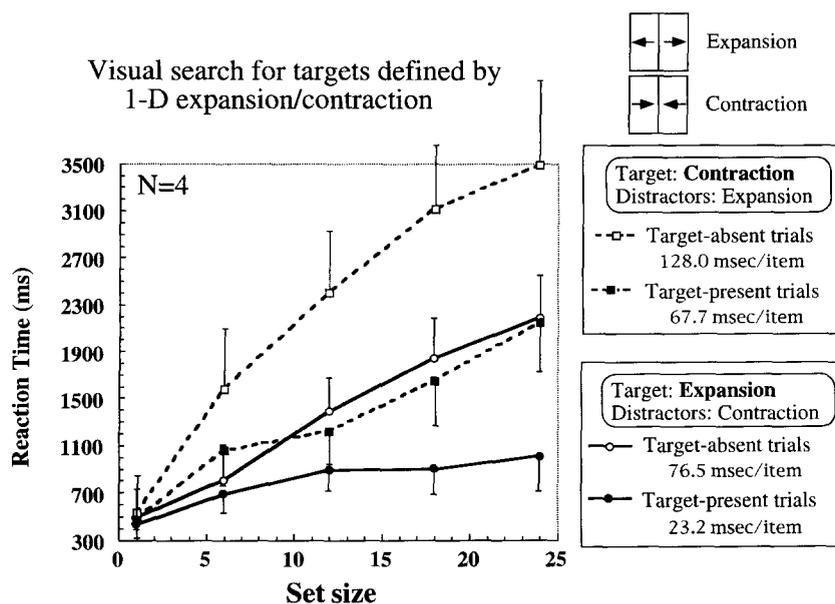


FIGURE 4. The average result across four subjects of visual search for targets defined by one-dimensional expansion or contraction. Mean reaction times as a function of set size. Error bars show +1 or -1 SD. The moving stimuli is schematically shown in the upper right corner of the figure. The solid lines show the search performance when one-dimensional expansion was the target. The dashed lines show the search performance when one-dimensional contraction was the target.

iel. Second, a search asymmetry was observed between expansion and contraction. Third, two-dimensional expansion/contraction is found faster than one-dimensional expansion/contraction.

These three points were not reported by Braddick and Holliday (1991). They used only the two-dimensional stimulus, and concluded that expansion/contraction is searched serially. It should be noted that Braddick and Holliday did not show their data for expansion and contraction separately. If our results for both types of targets in Fig. 3 or Fig. 4 are averaged, then a qualitatively similar result to that of Braddick and Holliday's is obtained. A search asymmetry may appear if their data expansion and contraction data are replotted in separate figures. The overall reaction times for two-dimensional stimuli, however, were faster in this study than in Braddick and Holliday's. The absence of the noise component in our display seems to have decreased the reaction times, especially for two-dimensional expansion.

Except under the condition where the target was two-dimensional expansion, the subjects searched the targets (two-dimensional contraction, one-dimensional expansion/contraction) in a serial manner. However, this does not lead to the conclusion that expansion/contraction is represented as a conjunction of local translation elements, and not as a single feature. The search asymmetry found in our study is not predicted if expansion/contraction is represented as a conjunction of local translations because the local elements that constitute expansion/contraction are the same except for their spatial positions. Rather, it is more plausible to postulate the existence of a specialized motion unit that detects expansion/contraction, and to regard the search asym-

metry observed as an emerging property of this hypothesized detector.

It has been shown that many visual stimuli elicit search asymmetries (e.g. Cohen, 1993; Ivry & Cohen, 1992; Kleffner & Ramachandran, 1992; Treisman & Gormican, 1988; Treisman & Souther, 1985; von Grünau & Dubé, 1994). Treisman and Gormican (1988) suggested that search asymmetries arise because the presence of a "feature" is easier to discern than its absence. A tilted line pops-out from a background of vertical lines because the tilted line has the special feature of "tilt". In this case, vertical is the standard, and tilt is the deviation from the standard. A purple object pops-out from a background of red objects because the purple object contains the feature "blue" in it. However, in the case of expansion/contraction, there is no a priori reason to assume that expansion is a deviation and contraction is a standard. Rather, as suggested by von Grünau and Dubé (1994), it is more plausible to assume an ecological explanation for the search asymmetry between expansion and contraction. Assuming a motion detecting unit that responds to objects moving toward a subject with higher sensitivity than to objects moving away from a subject might be a valid explanation for the present results.

Morrone *et al.* (1995) have proposed a two-stage model in which local motions are processed first, and expansion/contraction is processed in a secondary stage. They showed that different directions of local motion signals are integrated in a way that can be predicted with an ideal integrator model. Sekuler (1992) showed that the speed discrimination threshold of expansion was predicted from the simple linear combination of local translations, and referred to the hypothesis that the outputs of local sensors are combined in a higher-order looming detector. Braddick (1993) suggested in the

course of a discussion with Regan (1993) that the inconsistency between Braddick and Holliday's result and Regan's conclusion could be reconciled if a specialized motion detecting unit for expansion/contraction were implemented at a higher stage of visual motion processing than where simple translation is represented.

We can make two suggestions about the characteristics of these hypothesized motion detectors from our experimental results. First, these hypothetical detectors show an asymmetric response between expansion and contraction. In addition, the overall search rate for two-dimensional expansion/contraction was faster than that for one-dimensional expansion/contraction in our experiment. This suggests that the hypothesized detector for expansion and contraction has a receptive field that integrates local motion signals not only from a pair of 180 deg separated directions, but also from all directions that expand from or contract to a single point. The results of Sekuler (1992) and Morrone *et al.* (1995), in which the observers' performance improves with additional directions, further support this conjecture.

In the above discussion, the search asymmetry is considered as a basic characteristic of the hypothesized expansion/contraction detectors. The anisotropic responses between expansion (centrifugal motion) and contraction (centripetal motion) have been reported in studies using other psychophysical methods. The strength of MAE (Harris *et al.*, 1981; Reinhardt-Rutland, 1994; Scott *et al.*, 1966, Wohlgenuth, 1911), the simple reaction time to motion onset (Ball & Sekuler, 1980; Mateeff & Hohsbein, 1988; Mateeff *et al.*, 1991), the perceived direction of ambiguous motion (Georgeson & Harris, 1978), the perception of three-dimensional motion (Perrone, 1986), and the threshold of global-dot-motion (Edwards & Badcock, 1993) have been examined, and both centrifugal and centripetal biases have been observed. For example, Ball & Sekuler (1980) found that response latencies were shorter for motion away from the fovea than for motion towards it. Mateeff *et al.* (1991), however, found both centrifugal and centripetal biases, depending on the type of stimulus used. Edwards and Badcock (1993) found that sensitivity to centripetal motion was greater than to centrifugal motion when the threshold of global-motion was measured.

Apparently, some results are consistent (for example, Ball and Sekuler), and some are inconsistent (for example, Edwards and Badcock) with our results showing that expansion is detected faster than contraction. However, in the display we used, most of the individual moving targets were located in the periphery (Figs 1 and 2). The expanding stimulus contains only centrifugal motion when it is displayed at the fovea. If it is displayed in the periphery, the motion nearest to the subjects spatially is centripetal when the subjects gaze at the center of the display. In that sense, the asymmetry observed in this study cannot be attributed to previously observed centrifugal or centripetal biases. Our results suggest the existence of position-invariant biases to

expansion in which expansion is detected faster than contraction irrespective of the position where it is displayed.

Recent studies have shown strong effects of learning in which some visual searches can progress from serial to parallel through practice (Heathcote & Mewhort, 1993; Sireteanu & Rettenbach, 1995). Sireteanu and Rettenbach (1995) found that learning in visual search is not specific to the task involved and claimed that learning takes place at a higher level in the visual pathway. Therefore, we calculated the search rate on the practice blocks to examine whether learning makes the search rate of expansion faster. The average search rate of four subjects for two-dimensional expansion on the first practice block was 4.9 msec/item in target-present trials and 6.0 msec/item in target-absent trials. These results are comparable to those obtained in the experimental sessions shown in Fig. 3. Subjects, however, were well-trained for visual search tasks before they participated in this experiment. Therefore, there remains the possibility that they already completed nonspecific learning and this was transferred to the current task, as suggested by Sireteanu and Rettenbach (1995). Further study is needed to clarify the mechanisms of perceptual learning and its transfer. We can, however, conclude that expansion is searched in parallel without specific learning.

Physiological studies have also shown an asymmetry between expansion and contraction. Tanaka and Saito (1989) reported that the number of cells that selectively respond to expansion is seven times greater than those that respond to contraction in the dorsal part of the MST of macaque monkeys. Albright (1989) also reported the centrifugal directional biases in the neurons of MT with peripherally located receptive fields. Graziano *et al.* (1994) found neurons of MSTd show strong biases towards expansion. Although most of these reported MSTd cells have extremely large receptive fields, Duffy and Wurtz (1991) used small-field stimuli (down to 6 deg). They found that some groups of MSTd neurons maintain their activity and selectivity even when stimuli are displaced at different locations in their large receptive fields. Our results predict that the neurons that respond to small-field stimuli also show an anisotropic response to expansion/contraction, like the neurons that respond well to large-field stimuli.

REFERENCES

- Albright, T. D. (1989). Centrifugal directional bias in the middle temporal visual area (MT) of the macaque. *Visual Neuroscience*, 2, 177-188.
- Ball, K. & Sekuler, R. (1980). Human vision favors centrifugal motion. *Perception*, 9, 317-325.
- Baro, J. A. & Hughes, H. C. (1991). The display and animation of full-color images in real time on the Macintosh computer. *Behavior Research Methods, Instruments and Computers*, 23, 537-545.
- Beverley, K. I. & Regan, D. (1979). Separable aftereffects of changing-size and motion in depth: Different neural mechanisms? *Vision Research*, 19, 727-732.
- Beverley, K. I. & Regan, D. (1983). Texture changes versus size changes as stimuli for motion in depth. *Vision Research*, 23, 1387-1400.

- Braddick, O. J. & Holliday, I. E. (1991). Serial search for targets defined by divergence or deformation of optic flow. *Perception*, *20*, 345–354.
- Braddick, O. J. (1993). Adaptation and “pop-out” in the analysis of divergence-sensitive mechanisms. *Perception*, *22*, 500.
- Cavanagh, P. & Favreau, O. E. (1980). Motion aftereffect: A global mechanism for the perception of rotation. *Perception*, *9*, 175–182.
- Cohen, A. (1993). Asymmetries in visual search for conjunctive targets. *Journal of Experimental Psychology: Human Perception and Performance*, *19*, 775–797.
- De Bruyn, B. & Orban, G. A. (1990). The role of direction information in the perception of geometric optic flow components. *Perception and Psychophysics*, *47*, 433–438.
- Duffy, C. J. & Wurtz, R. H. (1991). Sensitivity of MST neurons of optic flow stimuli. II. Mechanisms of response selectivity revealed by small-field stimuli. *Journal of Neurophysiology*, *65*, 1346–1359.
- Edwards, M. & Badcock, D. R. (1993). Asymmetries in the sensitivity to motion in depth: A centripetal bias. *Perception*, *22*, 1013–1023.
- Freeman, T. C. & Harris, M. G. (1992). Human sensitivity to expanding and rotating motion: Effects of complementary masking and directional structures. *Vision Research*, *22*, 81–87.
- Georgeson, M. A. & Harris, M. G. (1978). Apparent foveofugal drift of counterphase gratings. *Perception*, *7*, 527–536.
- Graziano, M. S. A., Anderson, R. A. & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *The Journal of Neuroscience*, *14*, 54–67.
- von Grünau, M. & Dubé, S. (1994). Visual search asymmetry for viewing direction. *Perception and Psychophysics*, *56*, 211–220.
- Harris, L. R., Morgan, M. J. & Still, A. W. (1981). Moving and the motion after-effect. *Nature*, *293*, 139–141.
- Harris, M. G. (1994). Optic and retinal flow. In Smith, A. T. & Snowden, R. (Eds), *Visual detection of motion* (pp. 307–332). London: Academic Press.
- Heathcote, A. & Mewhort, D. J. K. (1993). Representation and selection of relative position. *Journal of Experimental Psychology: Human Perception and Performance*, *19*, 488–516.
- Hershenson, M. (1987). Visual system responds to rotational and size-change components of complex proximal motion patterns. *Perception and Psychophysics*, *42*, 60–64.
- Ivry, R. B. & Cohen, A. (1992). Asymmetry in visual search for targets defined by differences in movement speed. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1045–1057.
- Kleffner, D. A. & Ramachandran, V. S. (1992). On the perception of shape from shading. *Perception and Psychophysics*, *52*, 18–36.
- Koenderink, J. J. (1986). Optic flow. *Vision Research*, *26*, 161–180.
- Longuet-Higgins, H. C. & Prazdny, K. (1985). The interpretation of a moving retinal image. *Proceedings of the Royal Society of London*, *208B*, 385–397.
- Mateeff, S. & Hohnsbein, J. (1988). Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Research*, *28*, 711–719.
- Mateeff, S., Yakimoff, N., Hohnsbein, J., Ehrenstein, W. H., Bohdanecy, Z. & Radil, T. (1991). Selective directional sensitivity in visual motion perception. *Vision Research*, *31*, 131–138.
- Morrone, M. C., Burr, D. C. & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature*, *376*, 507–509.
- Nakayama, K., Silverman, G., MacLeod, D. I. A. & Mulligan, J. (1984). Sensitivity to shearing and compressive motion in random dots. *Perception*, *13*, 229–243.
- Perrone, J. A. (1986). Anisotropic responses to motion toward and away from the eye. *Perception and Psychophysics*, *39*, 1–8.
- Ramachandran, V. S. & Anstis, S. M. (1990). Illusory displacement of equilluminous kinetic edges. *Perception*, *19*, 611–616.
- Regan, D. (1986). Visual processing of four kinds of relative motion. *Vision Research*, *26*, 127–145.
- Regan, D. (1993). The divergence of velocity and visual processing. *Perception*, *22*, 497–499.
- Regan, D. & Beverley, K. I. (1978a). Illusory motion in depth: Aftereffect of adaptation to changing size. *Vision Research*, *18*, 209–212.
- Regan, D. & Beverley, K. I. (1978b). Looming detectors in the human visual pathway. *Vision Research*, *18*, 415–421.
- Regan, D., Beverley, K. I. & Cynader, M. (1979). The visual perception of motion in depth. *Scientific American*, *241*, 136–151.
- Reinhardt-Rutland, A. H. (1994). Perception of motion in depth from luminous rotating spirals: Directional asymmetries during and after rotation. *Perception*, *23*, 763–769.
- Scott, T. R., Lavender, A. D., McWhirt, R. A. & Powell, D. A. (1966). Directional asymmetry of motion aftereffect. *Journal of Experimental Psychology*, *71*, 806–815.
- Sekuler, A. (1992). Simple-pooling of unidirectional motion predicts speed discrimination for looming stimuli. *Vision Research*, *32*, 2277–2288.
- Sireteanu, R. & Rettenbach, R. (1995). Perceptual learning in visual search: Fast, enduring, but non-specific. *Vision Research*, *35*, 2037–2043.
- Tanaka, K. & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, *62*, 626–641.
- Treisman, A. & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*, 97–136.
- Treisman, A. & Gormican, S. (1988). Feature analysis in early vision: Evidence from search asymmetries. *Psychological Review*, *95*, 15–48.
- Treisman, A. & Souther, J. (1985). Search asymmetry: A diagnostic for preattentive processing of separable features. *Journal of Experimental Psychology: General*, *114*, 285–310.
- Werkhoven, P. & Koenderink, J. J. (1991). Visual processing of rotary motion. *Perception and Psychophysics*, *49*, 73–82.
- Wohlgemuth, A. (1911). On the after effect of seen movement. *British Journal of Psychology: Monograph*, Supplement 1.

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