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The Hierarchical Nature of Perceiving Direction of Motion in Depth from Optic Flow

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Monocular adaptation to flow fields of optic expansion and contraction juxtaposed on either side of fixation influenced subsequently perceived rotation direction of a figure rotating in depth (kinetic depth effect) about its vertical axis with a normally ambiguous direction. This influence was shown to be asymmetric since adapting to optic expansion produced significantly more aftereffects of translation in depth than did adapting to perceived rotation in depth when viewing a neutral test stimulus. The results are evidence for a hierarchical processing model for the perception of motion in depth from optic flow. Serendipitously, we discovered a new aftereffect from viewing kinetic depth rotation with direction specified by proximity–luminance covariation (PLC). The results and other research are discussed in terms of neural network models with synergistic interactions between levels.

Aftereffects Depth perception Motion adaptation Optic flow Vection

INTRODUCTION

Depth perception is most often associated with binocular vision. However, retinal projections of moving patterns of light from object boundaries and surface markings and textures, or patterns of *optic flow*, have been shown to be compelling *monocular* sources of information for depth and motion in depth (Gibson, 1950, 1979; Lee, 1980; Koenderink, 1986; Simpson, 1992; Warren & Kurtz, 1992; Ziegler, 1993). A classic example of this was provided by von Helmholtz (1962): though a forest looks flat when viewed monocularly when one is still, "everything disentangles itself" like "a good stereoscopic view" (pp. 295–296) when one moves.

Optic flow similar to that in Helmholtz's example can be made as if from an object rotating on an axis perpendicular to the line of sight§ and creates a compelling illusion of depth, named *the kinetic depth effect* (KDE) by Wallach and O'Connell (1953). One can create KDE by projecting element coordinates from virtual three-dimensional space to a two-dimensional computer screen with two basic types of projections (Braunstein, 1976; Fig. 1). Polar projections provide perspective information specifying direction of rotation synonymous with a front–back ordering of the two groups of oppositely moving elements. Parallel projections on the other hand, provide two alternative interpretations of rotation direction. Continuous viewing of a parallel-projected KDE stimulus results in random and spontaneous reversals of perceived direction of rotation (Toppino & Long, 1987). Simultaneous with those reversals are front–back reversals similar to those of static figures of perspective ambiguity (Virsu, 1975) such as the Necker cube.

Such a reversible KDE figure was used by Petersik, Shepard and Malsch (1984) to demonstrate a rotation-in-depth aftereffect. Subjects adapted to viewing a nonambiguous KDE figure that had its rotation direction specified by polar projection. Four dots moved as if at the corners of an invisible, 14-deg square rotating in depth around its central vertical axis. After 9 min subjects immediately viewed the same pattern but with parallel projection (normally ambiguous for rotation direction). Subjects reported a negative aftereffect. That is, significantly more rotation (over 90%) was perceived in the opposite direction to that specified by the adapting figure.

From those results, Petersik *et al.* (1984) suggested that the monocular perception of the direction of rotation in depth may be considered a higher-level process fed by a lower stage consisting of pairs of "approaching" and "receding" detectors. They reasoned that this was so because polar-projected KDE contains patterns of *optic expansion* (or OE¶) (Braunstein, 1977) which is produced, for example, during the approach of an object to the eye (Swanston & Gogel, 1986). However, their experiment

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§Identical to the optic flow from walking around a fixated object.

¶The term OE will be used here as positive or negative.

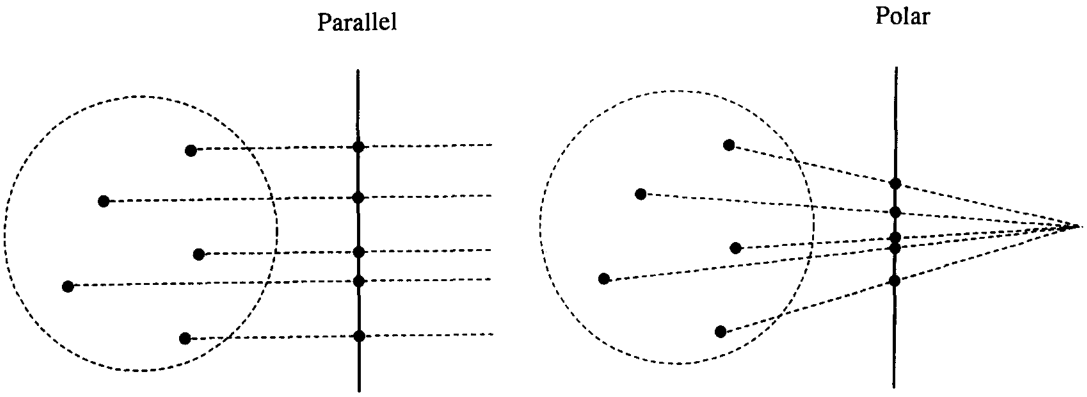

FIGURE 1. Parallel and polar projections from virtual space to the computer screen. Parallel-projected kinetic depth figures are ambiguous for rotation direction. Polar-projected figures contain perspective information specifying direction.

did not test that theory. This conjecture can only be truly tested if the influence on rotation occurs after adaptation to a pattern where rotation itself is not seen. Otherwise a single level could have been adapted.

This is not to imply that the speculations of Petersik *et al.* (1984) were without foundation. A compelling aftereffect from OE, explicitly perceptible for 10–20 sec or so, has a history starting with Plateau in 1849,* and was examined in a series of studies (Beverley & Regan, 1979a, b; Regan & Beverley, 1978a, b, 1979a, b). In those experiments subjects adapted to OE patterns on a monitor for 10–20 min, then the subjects adjusted test patterns to null the aftereffect. The aftereffect was found specific to the retinal location of the center or focus of expansion (FOE) within a few degrees (Regan & Beverley, 1979a). It resulted only from elements moving together or apart within a range of about 1.5 deg or less of visual angle, and occurred even at eccentricities of over 3 deg (Beverley & Regan, 1979b).

Regan and Beverley (1979b) provided a computational model with detectors of monocular OE operating in parallel and providing inputs to the same motion-in-depth stage as dynamic stereopsis (changing retinal disparities) (Rogers & Graham, 1982). Furthermore, Nawrot and Blake (1991) found that the aftereffect of dynamic stereopsis disambiguates the direction of rotation of parallel-projected KDE. To complement those studies and provide modeling constraints, we sought evidence for the hierarchy suggested by Petersik *et al.* (1984), that OE detection at one level provides inputs to rotation in depth at a higher stage. Therefore, we chose to adapt subjects to OE flow fields and then test for an aftereffect on perceived rotation direction using an ambiguous KDE globe.

However, when testing with such a reversible figure, perhaps especially with the highly reduced stimuli in a laboratory experiment, the system may be far from delicately balanced at the border between the two percepts (Girgus, Rock & Egatz, 1977; Rock & Mitchener, 1992). Rather, subjects may have a pre-existing bias. Our experience with pilot studies suggested that even after familiarity with both rotation directions of our reversible KDE figure, and even after frequent reversals, after a period of not seeing the figure subjects would often return to their favored interpretation. We thus adapted each subject to two separate treatments with expansion on either side of fixation. An influence on rotation direction from the treatments would be in opposite directions, while any pre-existing bias would be expected to remain in the same direction.

EXPERIMENT 1: OPTIC EXPANSION AFTEREFFECTS ON ROTATION DIRECTION

We tested the hypothesis that the aftereffect of OE, as juxtaposed expansion and contraction on either side of fixation (JOE/C), influences perceived direction of rotation in kinetic depth. Since it has been shown that direction of expansion (whether elements move apart horizontally or vertically) is significant in directly perceiving rotation direction (Braunstein, 1977) we adapted each subject to treatments for vertical, horizontal, or their combination, full two-dimensional or radial flow. Each treatment was immediately followed by the same ambiguous KDE figure and reported rotation directions were recorded continuously.

Since the aftereffect of OE is negative, adaptation to expanding flow results in the perception of motion away from the observer in depth, and the opposite occurs for contracting flow (Gates, 1934). Therefore the specific experimental prediction was that the patterns with expansion on the right side of fixation would result in an increased likelihood, immediately after adaptation, of what we termed "right rotation" or the nearer surface moving rightward. The opposite prediction held for expansion on the left.

Method

Subjects. Subjects were 32 undergraduate volunteers (22 females and 10 males) who earned partial course credit for participating and were unaware of the purpose of the experiment.

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*OE is the radial component of the spiral aftereffect investigated *ca* 1911 by Wohlgemuth, among others. A review of early work is found in Holland (1965).

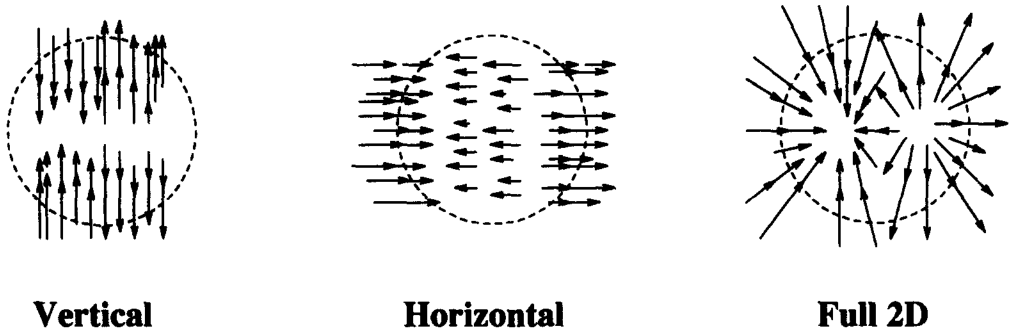

FIGURE 2. Schematic of the three types of juxtaposed OE and contraction stimuli (JOE/C) used in Expt 1 (only right expansion treatments shown). Arrows represent velocities of the random dots. The circles represent locations of the subsequently-presented KDE test globe. Balancing for side of expansion gave six treatments.

Stimuli. All cinematograms (movies) had a white "X" (about 0.6 deg tall) in the middle of a dark screen. Otherwise all stimuli consisted only of 0.05 × 0.05 deg white dots. Each of the six adaptation movies was immediately followed by the identical test movie.

Adaptation stimuli. We used three types with dots moving horizontally, vertically, or with full two-dimensional or radial motion (Fig. 2). Each type consisted of expansion and contraction patterns juxtaposed left and right of fixation. Balancing for side resulted in six adapting treatments per subject. The foci of expansion or contraction of all flow fields were offset laterally from the fixation point by 3 deg so that aftereffects would occur in the middle of each half of the subsequently presented test figure. Adaptation movies cycled through a set of 18 frames at about 12 Hz.

Although a single OE or KDE stimulus can represent an infinite combination of real object sizes and ranges of movement, in this experiment accommodation or context may have provided a distance cue. Along with the retinal size of the test figure this could have resulted in the perception of a specific object size (Swanston & Gogel, 1986). Since the object appeared to be rotating, it would thus have a perceived range of movement in depth. So the OE patterns were made to match the test figure's range of virtual movement (see Fig. 3). At most, this perceived distance would be one diameter. Since the dot planes at mid-range matched in size the test figure, we made the range of simulated movement for each plane equal to the perceived range of movement of the dots in the test figure. With that set of assumptions, each plane was simulated to moved between one radius on either side of the location in actual depth of the fixation point on the screen.

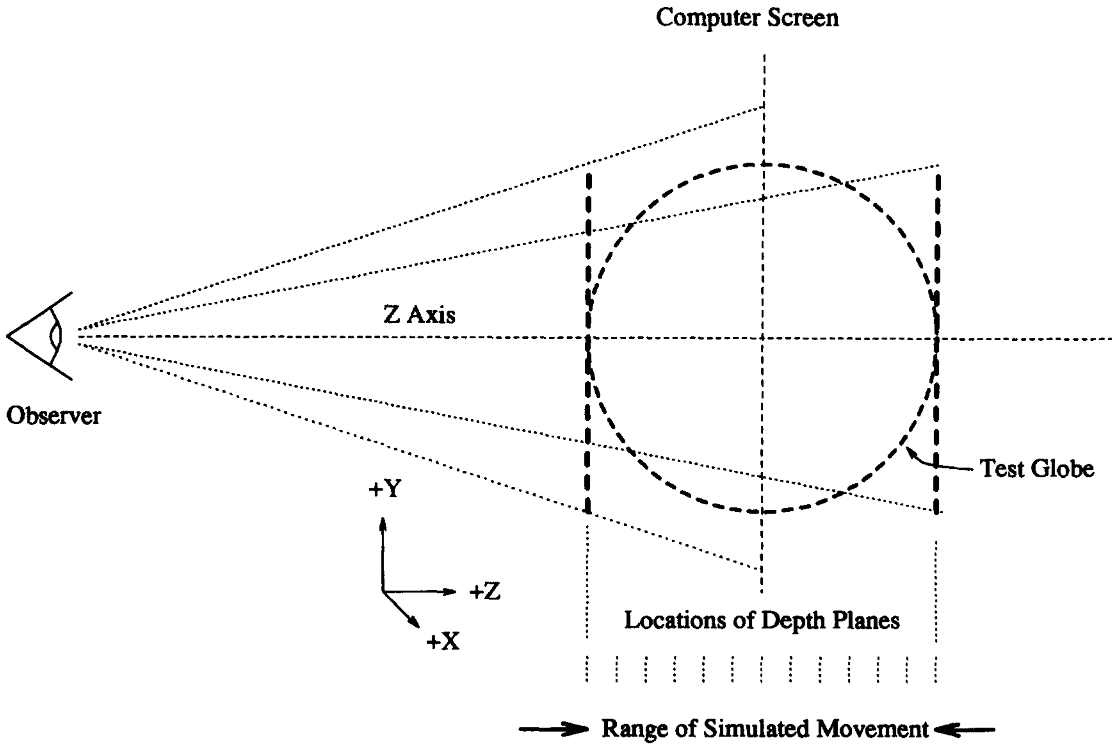

FIGURE 3. The layout of virtual space used in programming the cinematograms (side view). The vertical dashed lines represent the arrays of random dots at their near and far limits of movement. The circle is at the location of the kinetic depth globe following adaptation.

This stimulus-generation algorithm produced smooth and continuous JOE/C. It included scintillation (72% on-time) that prevented apparent motion in the unwanted direction (flyback). Dots were only plotted that remained within their respective side of the screen. Each half of a JOE/C pattern using this algorithm produced a compelling perception of translation in depth.

Horizontal and vertical treatments were constructed using the same dot coordinates and subroutine except that one perspective transformation, and thus movement in that dimension, was bypassed. The only other difference was a compensation for the loss of a dimension so that the average speeds were the same in all treatments. This was done by increasing the frame rate by a factor of approx. $2^{1/2}$ (1.4).

Test stimulus. To construct the test movie, a set of 100 dots were programmed to move in the same directions and speeds as those of a real rotating dot-filled globe (Braunstein, 1976) seen as about 12 deg in diameter. The 35 frames cycled continuously with a stimulus onset asynchrony (SOA) of 166 msec or about 6 Hz,* for a rotation period of 6 sec. A compelling impression of a transparent, smoothly rotating globe that spontaneously reversed its rotation direction was consistently produced.

Apparatus. Subjects viewed the computer screen through a 3.2 cm hole centered horizontally on one side of a box with side lengths of 61 cm (2.0 ft). Monocular viewing eliminated potential confounds with the Pulfrich effect, an illusion of rotation in depth in a particular direction that may be caused by unequal exposure of the two eyes to ambient light (Burr & Ross, 1979; Ono & Steinbach, 1983). The hole was 40 cm above the table to align with the center of the screen of a monitor facing the subject at the opposite, open end of the box and sitting on a stand about 16 cm in height. The box had a black interior and baffle so all was dark except a central area of the screen large enough for the stimuli. Black shroud cloth at the rear of the box blocked ambient light. The computer, a Sun 4 SparcStation SLC, was programmed to provide all movies, timing, prompting, and data collection tasks in an integrated manner. Subjects pressed the left and right mouse buttons to indicate their perceptions of direction of rotation.

Viewing conditions. Viewing distance was approx. 56 cm. The monitor was adjusted at medium brightness so the stimuli produced no "comet tails". A subject chose either eye and used that same eye for all trials. Subjects were instructed to keep their eye on the fixation character and to minimize body movements during both phases. The experimenter sat about 3 m to the subject's right and a small night-light to his left allowed continuous monitoring to detect any small head motions.

Procedure. Before a session began each subject viewed the test figure until able to experience at least one reversal. A few minutes later the control (unadapted) test was followed by a treatment. Treatment orders were by a Latin-square design with the pairs of each stimulus type always contiguous. The presentation order of both the pairs within each type and the stimulus types themselves were random and counterbalanced across subjects. The experimenter was blind to the treatment order.

Talking was not permitted during trials because it appeared to interfere with the effect in the pilot studies.† Adaptation time was 2 min followed immediately and without warning by testing for 1 min with the ambiguous rotating globe. During adaptation, subjects kept their hand ready on the mouse. They had been instructed that when the globe first appeared they were to press the right or left mouse button corresponding to the direction of motion of the front surface, and to do so after every reversal. The end of a trial was indicated by a beep and a screen message. Then two subjects swapped, or a single subject took a 4-min break to allow aftereffects to decay.

Results

Of the 32 subjects participating, 26 completed all trials successfully. Although eye movements were not explicitly monitored, those subjects appeared very cooperative with respect to the task demands. Few head movements were detected.

Analyses began by dividing the 1-min test phases into four 15-sec periods. In each period, the average times the globe was perceived rotating to the right (arbitrarily chosen) for the six adaptation treatments are plotted in Fig. 4. The control plot shows a rightward bias that was not significant at the $P = 0.05$ level using a binomial test.

In Fig. 4(B, C), the adaptation curves are shifted in the directions consistent with negative aftereffects. So we proceeded with our planned comparisons between the results of the adapting treatments and the control condition. A full-factorial analysis of variance (ANOVA) was made on the balanced data using the SAS procedure GLM for Type III sums-of-squares. The dependent variable was the average change per subject, due to the type of adaptation, in the time the globe was perceived turning in a particular direction within the time bins. That is, we computed the average shift in seconds between the control level and the two adapting treatments of each stimulus type, collapsed by the attempted direction of adaptation. The means and SDs of those values are shown in Table 1. Significant effects were found for period [$F(2,311) = 8.27$, $P < 0.0001$] and the interaction of condition with period [$F(2,311) = 8.27$, $P < 0.015$]. Condition approached reliability [$F(2,311) = 3.12$, $P < 0.06$] but this test was relatively insensitive since it included periods when the aftereffects could have already ended.

Therefore, another ANOVA was performed restricted to the results in the first period alone with condition and subjects as independent variables. Here the effect of condition was found significant [$F(2,77) = 74.1$, $P < 0.01$]. The most sensitive tests, pairwise contrast

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*Even at low frame rates, continuous motion and direction of rotation is easily perceived (Petersik, 1980; Petersik *et al*., 1984, p. 490).

†Attention has been shown to influence motion aftereffects (Chaudhuri, 1990), the detection of OE (Braddick & Holliday, 1991), adaptation to direction of rotation in kinetic depth (Shulman, 1991), and the reversal rate of ambiguous figures (Reisberg & O'Shaughnessy, 1984).

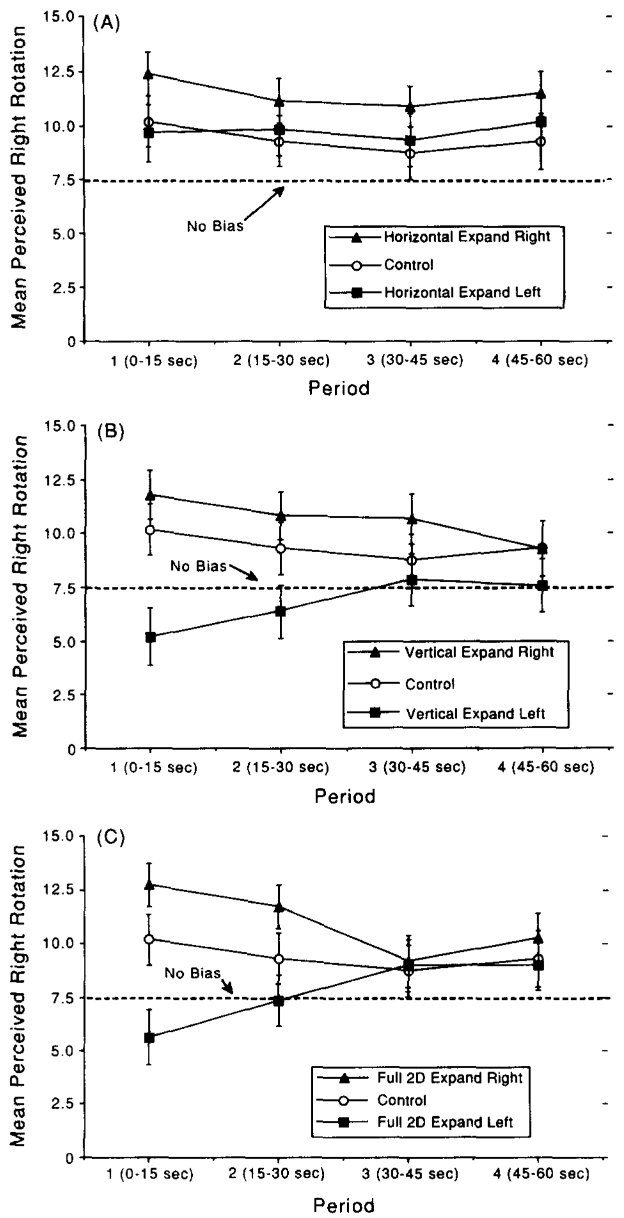

FIGURE 4. Perceived rotation direction of kinetic depth globe after adapting to (A) horizontal-only, (B) vertical-only, and (C) two-dimensional JOE/C. Average number of seconds of perceived right rotation in 15-sec periods following adaptation. ▲ Right expansion, left contraction. ■ Vice versa. Bars signify SEMs. Dashed line represents chance level. The control data were collected before any adaptation and are the same in each plot.

comparisons, were performed between each of the three treatment types. Horizontal was significantly different from both vertical [$F(1,77) = 6.73$, $P < 0.013$] and two-dimensional [$F(1,77) = 8.65$, $P < 0.005$]. However, vertical and two-dimensional were not significantly different from each other [$F(1,77) = 0.12$, $P > 0.70$].

Individual ANOVAs were then performed for each period. Periods 1 and 2 each showed significant main effects of condition [$F(2,27) = 5.17$ and 5.65 respectively, both $P < 0.01$]. In contrast, condition was not significant in periods 3 and 4 [$F(2,27) = 1.83$, $P > 0.17$, and 0.06, $P > 0.94$ respectively].

Another statistical approach to the data analysis was also used. Here the dependent variable was the proportion of time in each period of perceived rightward-rotation, but without collapsing. Thus the control was one of seven separate treatments. This allowed for more sensitive contrast comparisons between the results of adapting to the two different sides of expansion for each treatment type. In the first period these contrasts were all significant, $F(1,181) = 4.85$ ($P < 0.03$), 28.0 ($P < 0.001$), and 32.5 ($P < 0.001$) for the horizontal, vertical, and two-dimensional conditions respectively. In the second period, only the vertical and full treatments were significant [$F(1,181) = 17.92$ and 17.34 respectively, both $P < 0.001$]. Only vertical was significant in period 3 [$F(1,181) = 6.97$, $P < 0.01$]. None of these contrasts were significant in period 4.

Next we performed a linear regression analysis in order to best estimate the durations of the influences of the aftereffects. We first divided the time line of the test data for each trial into an arbitrary bin size of 5 sec. For each trial we computed the total time in each bin that right rotation (chosen arbitrarily*) was reported. Next we computed the difference in each bin between a subject's control condition value and the values in each of that subject's adaptation trials, respective of attempted adaptation direction, to obtain the possible shift due to adaptation. These shift or delta values were averaged over all subjects. Dividing by the bin size produced, as an average for each bin, the change in the probability of perceiving a given rotation direction in the direction of the aftereffects. Plots of these values appear in Fig. 5. The total durations were estimated as the intercepts of the regression lines for the vertical (62 sec) and the two-dimensional stimulus types (40 sec).

Discussion

We have demonstrated that adapting to juxtaposed OE and contraction flow fields biases the subsequently perceived direction of rotation in depth. We suggest that this influence is due to changes at the same level that produces the phenomenal experience of the translation-in-depth aftereffect of OE.

An interpretation that does not include a level of OE detection is that subjects had adapted somehow to the spatial structure of the velocity field. Such variations do allow for the perception of structure and motion in depth (Treue, Husain & Andersen, 1991). However, our horizontal-motion stimuli provided abundant second-order changes in the velocity field yet nonetheless this had a weak if any effect.

Perhaps our most significant evidence that we adapted at a higher level than that at which local motion is processed, is that the influence on rotation resulted from adapting to vertical-only motion whereas the test stimulus elements moved only horizontally. However, an alternative is that adaptation to frontoparallel motion in the four quadrifields, which produces the classical or linear motion aftereffect (MAE) (Hershenson, 1989),

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*Choosing left rotation as the measure in our analyses would have produced the same results since the two values for each bin were always complementary.

TABLE 1. Shifts in total seconds the globe was perceived rotating in the adapted direction from control levels following the three types of adapting stimuli in Expt 1

Adapting stimulus type		Post-adaptation time period 1 (0–15 sec)	2 (15–30 sec)	3 (30–45 sec)	4 (45–60 sec)
Horizontal-only	Mean	1.4	0.7	0.8	0.6
	SD	3.2	2.0	2.2	2.0
Vertical-only	Mean	3.3	2.2	1.4	0.9
	SD	3.4	2.8	3.2	3.5
Full two-dimensional	Mean	3.6	2.2	0.1	0.7
	SD	3.5	2.9	1.6	2.8

could have later influenced the higher level, where signals were integrated during the test phase, to influence rotation direction (cf. Simpson, 1992). Although adaptation could occur at many levels, this explanation seems less likely. It appears more reasonable that aftereffects of OE reflect modifications at the level that correlates with what people most commonly experience, translation in depth (85% of the time in (Gates, 1934; also Regan & Beverley, 1979a, p. 731; Braunstein, 1976). To our knowledge no one ever saw parts of the test globe moving vertically or changing in size. Furthermore, the durations we found are similar to the duration of the phenomenal experience of the motion-in-depth aftereffect of OE.

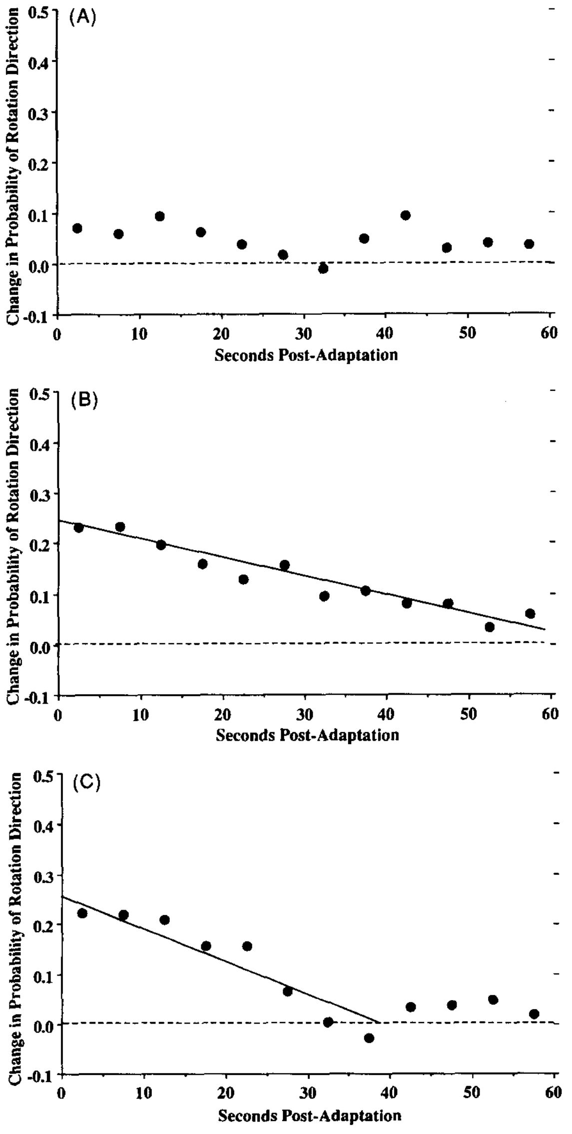

FIGURE 5. Average change in probability of perceiving a given rotation direction following adaptation to (A) horizontal-only, (B) vertical-only, and (C) full two-dimensional JOE/C in Expt 1. (See text for details.)

We now turn to the other question of which component of element motion, vertical or horizontal, was responsible for the results. At first sight our results imply only the aftereffects of vertical OE influence KDE rotation. This does not contradict the findings of Regan and Beverley that adaptation to both horizontal and vertical OE occurs; perhaps only the vertical aftereffect is utilized by the visual system when rotation is perceived about the vertical axis. This is not difficult to accept on ecological grounds, since vertical expansion is invariant. That is, for a single rotation direction about the vertical axis, both horizontal expansion and contraction take place on both sides of fixation, whereas vertical expansion takes place only on one side and contraction takes place only on the other. Using real-time displays Braunstein (1977) found that vertical OE determines monocularly-perceived rotation direction about the vertical axis.

Nevertheless it may be questioned whether the asymmetry we found between horizontal and vertical expansion was due to our adapting stimuli layout. The two OE patterns on either side of fixation were taller than they were wide, so the vertical case contained a larger proportion of faster dots than the horizontal. Higher velocities do produce stronger classical MAE (Thompson, 1981). On the other hand, Beverley and Regan (1979b) found no OE aftereffects for elements farther apart than 1.5 deg. If their conclusion holds in our situation, since the additional vertical extents in our layout were well beyond this range, the movement there would not have contributed. Furthermore, horizontal motion appears to have provided no additional influence whatsoever to the two-dimensional results, and the increase in the recovery time of the vertical over the two-dimensional case can be totally accounted for by the average speed difference in the two conditions. However, considering the asymmetry of the experiment, more tests will be necessary to support that vertical motion alone is responsible for the effects.

Another asymmetry was that our test stimulus had only horizontally moving elements. This suggests that a useful complement to this experiment would be to use a KDE test figure rotating about its *horizontal* axis after adaptation to OE above and below fixation. Such an experiment might show if an anisotropy exists in the perception of rotation in depth, i.e. if the aftereffects shown are tied ecologically to the vertical (Shiffrar & Shepard, 1991) or merely contingent on the perceived rotation axis of the test figure. We were hesitant to include this test since Eby, Loomis and Solomon (1989, p. 431) used such a figure but abandoned their data when they found a bias (71%) in seeing roll toward the observer. Our subsequent experience suggests such bias may have been circumstantial and might not be an obstacle to testing with horizontal-axis KDE.

We return to our main goal of providing psychophysical evidence for a hierarchical level of processing of the optic flow as speculated by Petersik *et al.* (1984). Although OE aftereffects influence rotation direction in KDE, what is the nature of this relationship? If rotation in depth in a particular direction as well as translation in depth were due simply to changes in the pattern of distribution among the identical set of units, we may have gotten the same results. In order to establish a hierarchy, by definition, a processing asymmetry must exist. Could there be an effect exactly opposite to that shown in our first experiment? That is, does adapting to viewing rotation in depth in a particular direction result in an aftereffect of perceiving translation in depth, like the aftereffect from OE? If a hierarchical model with levels [stages, modules (Marr, 1982)] for processing optic flow is to be more than speculation, experimental evidence is required.

EXPERIMENT 2: HIERARCHICAL PROCESSING OF OPTIC FLOW

We tested the hypothesis that adapting to OE results in significantly more aftereffects of perceiving translation in depth, using a neutral test stimulus, than does adapting to a rotation in depth (KDE) in a particular direction. Although it was not intuitively obvious that KDE would produce an aftereffect of perceived motion along the line of sight, to our knowledge this question had not been tested in earlier experiments.

Adapting subjects to KDE rotation in a specific direction, however, presented an obstacle. Unambiguous polar-projected KDE could not be used to specify rotation direction since those stimuli contain motion components of expansion and contraction (Braunstein, 1977). We were able to overcome this problem with the technique, traditionally used by artists' to specify depth relations, of making nearer objects brighter. Proximity–luminance covariation (PLC) in KDE stimuli has been demonstrated to robustly specify rotation direction (Schwartz & Sperling, 1983; Dosher, Sperling & Wurst, 1986). We thus adapted subjects to a *PLC-KDE* figure, then had them report verbally their perceptions of three-dimensional motion in a neutral stimulus, a field of scintillating (limited lifetime), statically positioned dots.

A control was required to insure that PLC-KDE was indeed an effective adapting stimulus. Therefore, additional trials were included where subjects adapted to viewing the same PLC-KDE globe as in the main hypothesis but were then tested for perceived rotation direction of the same direction-ambiguous globe test stimulus as in Expt 1.

In addition, a second set of control trials was included to demonstrate that our neutral test stimulus actually would allow aftereffects of translation in depth to be perceived. Since OE was known to produce those aftereffects, subjects were tested after adapting to viewing OE on one side of fixation and contraction on the other (the same two-dimensional JOE/C as in Expt 1). They then viewed the field of scintillating dots and provided verbal reports.

Method

Subjects. Undergraduate volunteers (18 females and 12 males).

Stimuli. There were three types of adapt–test pairs (see Fig. 6). Balancing for side of expansion resulted in six adapting trials per subject. Adaptation movies cycled through a set of 18 frames at about 12/sec. Elements were the same as in the first experiment, except for the PLC-KDE adapting stimulus which had dots on the front surface twice the size (0.1 × 0.1 deg) and thus greater in total luminance than those on the far surface. The PLC-KDE was hollow to eliminate blooming of elements that might specify OE, and the same size as the ambiguous KDE test globe.

Apparatus and viewing conditions. These were the same as for Expt 1.

Procedure. The same as Expt 1 except that verbal reports were made instead of button-pressing in four of the six adapting trials. Each subject began with a control phase consisting of the same two test stimuli used in the subsequent trials but without prior adaptation. That is, the scintillating dot field was presented for 30 sec and subjects explained verbally what they saw. Then subjects registered the perceived rotation direction of the ambiguous KDE globe as in Expt 1.

The experimenter did not know the treatment orders other than what was implied from the subjects' reports. Subjects were prompted on-screen to notify the experimenter at the beginning of each adaptation trial whether it was a "button-pressing" or a "talking" trial so that the experimenter would know to prompt the subject for a report in the latter. Each adaptation lasted 2 min. Button-pressing trials were identical to Expt 1. In the talking trials subjects reported perceptions of motion sideways or in depth and categorization was recorded by the experimenter.

Results

Data from one subject was rejected because of failure to follow instructions. Subjects made no reports of motion in depth from viewing the control test of scintillating dots.

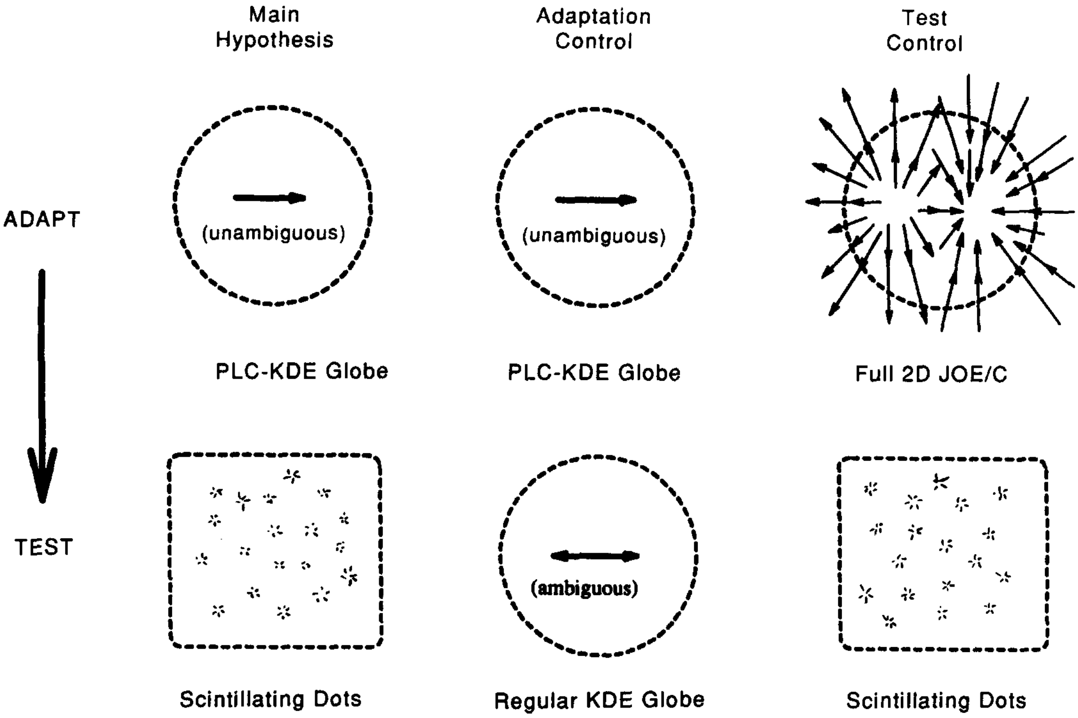

FIGURE 6. Schematic of half of the adapt–test stimulus pairs in Expt 2. Six adapting trials per subject resulted from balancing for side of expansion or rotation direction.

An informal sample of the subjects had been questioned as to whether they saw reversals of the PLC-KDE adapting globe. Some reversals did occur but subjects reporting them almost all remarked that they were rare and the figure was perceived most of the time as rotating in the direction of the more luminant dots, as in Dosher *et al.* (1986).

The results of the control condition to test for adapting to PLC-KDE were analyzed as in the first experiment, the dependent variable being the number of seconds that each subject reported the globe turning to the right. The results are given in Fig. 7. A plot of the average change in probability of the right-rotation percept (calculated as in Expt 1) is shown in Fig. 8 with aftereffect duration estimated by linear regression at 3.8 min.

An ANOVA on the data from period 1 showed significant main effects of treatment [$F(2,31) = 10.45$, $P < 0.001$]. The shifts from the control levels after adaptation were also collapsed by attempted adapted direction as in Expt 1. The means and SDs are listed in Table 2. An ANOVA using average shift as the dependent variable and period as the independent variable found period, unlike Expt 1, not significant.

The control condition for the effectiveness of the scintillating dot field as a neutral test stimulus after adapting to JOE/C resulted in reports of translation in depth in 50% of the trials. The test of the main hypothesis, that adapting to the KDE globe made unambiguous for rotation direction with PLC would result in perceived translation in depth while viewing the neutral test stimulus, resulted in such reports in 15% of the trials. This

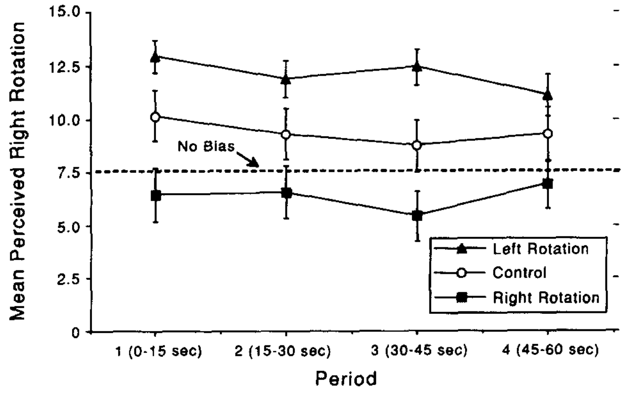

FIGURE 7. Perceived rotation direction after adapting to KDE rotation made unambiguous for direction by proximity–luminance covariation (KDE-PLC) in Expt 2. ▲ After left rotation; ■ after right rotation.

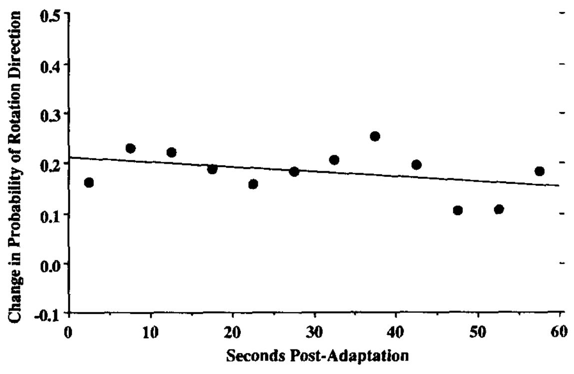

FIGURE 8. Average change in probability of perceived a given rotation direction following adaptation to PLC-KDE in Expt 2 (as in Fig. 5). Note the apparent oscillatory component.

TABLE 2. Shifts in total seconds the globe was perceived rotating in the adapted direction from control levels following adaptation to PLC-KDE in Expt 2

Period	Mean	SD
1 (0–15 sec)	3.2	3.5
2 (15–30 sec)	2.7	3.4
3 (30–45 sec)	3.5	3.3
4 (45–60 sec)	2.1	3.5

was significantly different from the result of adapting to JOE/C [$\chi^2(1,14) = 11.3$ ($P < 0.005$)].*

The shape of the curve in Fig. 8 implied to us that the aftereffects of PLC-KDE adaptation follow a much longer time-course than those from adapting to two-dimensional JOE/C in Expt 1 [Fig. 5(C)]. To test this difference we extended our statistical comparisons between experiments. Between-subjects comparisons are valid because sufficient subjects were used in each experiment for sampling errors to be insignificant. In addition, the same test stimulus was used in both experiments. The two unadapted control curves are also nearly identical, indicating that the difference in pre-existing bias between the two groups of subjects was minor.

The means in the first period after adapting to unambiguous KDE in Expt 2 (Fig. 7) appear equal to those produced in the first period of the two-dimensional JOE/C trials of Expt 1 [Fig. 4(C)]. We tested this difference using an ANOVA and found that the two-way interaction of experiment and side in this period not significant [$F(1,3) = 0.07$, $P > 0.79$] indicating effects of the two treatments were statistically indistinguishable initially. However, this interaction became significant in the third period [$F(1,3) = 9.41$, $P < 0.003$] supporting the intuitive impression from the plots that the two aftereffects have different durations.

Discussion

We demonstrated that adaptation to OE has a significantly stronger aftereffect of perceived translation in depth using a neutral test stimulus than adaptation to patterns specifying a particular direction of rotation in depth.

This result is not because our KDE stimulus, with rotation direction specified by PLC, did not adapt subjects for rotation in depth. On the contrary, we found our PLC-KDE to be a potent adapting stimulus, resulting in the same level of influence on ambiguous-rotation-direction KDE as OE (JOE/C). This serendipitous result is at odds with the findings from an experiment using a similar paradigm, where aftereffects of PLC-disambiguated KDE were reported not to influence rotation direction (Nawrot & Blake, 1991, pp. 238–239). We cannot say with certainty why the effect was not observed in that experiment. However, those researchers seem to have used only two observers. Our experience with this paradigm indicates the value of a larger sample size to control for the possibility of pre-existing bias.

Furthermore, that adapting to PLC-KDE has an effect on ambiguous KDE on a different time scale, about 6 times longer, than that from adapting to OE alone further supports a processing hierarchy. Considering the difference in adaptation times, the time to recovery with our PLC-KDE is like that in the Petersik *et al.* (1984) experiment (over 15 min) where rotation in depth was also perceived in the adapting stimulus. Although in their case rotation direction seems to have been specified by the OE components, our findings and theirs together support that translation and rotation in depth are processed at different levels.

In this light, the results of our first experiment in comparison to Petersik *et al.* suggest an interaction between real-time perceptions of rotation in kinetic depth and cues for direction (OE) that is nonlinear or synergistic. That is, adding rotation in depth to the direction cue in an adapting stimulus can be expected to dramatically increase the rotation-in-depth aftereffect duration over that from adapting to the low-level cue alone.

GENERAL DISCUSSION

A hierarchy for processing motion in depth

We have shown that not only does adaptation to OE result in motion in depth using a neutral test stimulus, but also that the same adaptation also influences perceived direction of rotation in depth. Furthermore, continuously viewing a pattern specifying rotation in depth in a particular direction has little if any aftereffect of perceiving translation in depth. This asymmetry implies the processing of optic flow patterns for translation and rotation in depth is hierarchical.

However, there is an alternative model. Our results could also be explained if a single lower level for linear flow had been adapted to the parts of the OE fields. That level's aftereffect could then influenced two independent modules, one for rotation and one for translation in depth. Independent modules would not adapt each other and so we would have gotten no aftereffect of rotation on translation. We could even imagine modules with different time-courses for recovery.

Although our results do not directly falsify such a theory, it is certainly less than parsimonious. If we assume two independent modules, one for rotation and the other for translation in depth, then the rotation module would have to repeat the expansion detector function already inherent in the translation module. Furthermore, it seems not coincidental that the duration of the JOE/C aftereffect on rotation direction is similar to that of the phenomenal experience of the motion-in-depth aftereffect from OE. A hierarchical model, with distributed representations, would more likely represent the continuum we experience of motion in depth.

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*Using odd–even pairing to satisfy the independence assumption of the test. The value for the other set was almost identical.

A connectionist model for motion-in-depth aftereffects

A connectionist (Hebb, 1949) model of visual aftereffects has been proposed by Barlow (1990a, b). Since multiple units with only slightly different selectivities may each respond to the same stimulus (course coding), their continuous activation could increase the strength of their mutually inhibitory connections [GABAergic neurons (Vidyasagar, 1990)] and lower their activity. The resulting shift in the activity distribution in the network (Mather, 1980) during presentation of a neutral or ambiguous sensory input could correlate with the experience of a visual aftereffect.

Such network models of interconnected, cooperative/competitive units used to explain the reversibility of static ambiguous figures (McClelland & Rumelhart, 1984, p. 10) can also explain KDE reversibility, as well as the influence of the OE aftereffects. Connections between sets of internal units could constrained the interpretation of ambiguous KDE to only one rotation direction (winner-take-all). If the activity of the dominant units were to diminish with continuous activity, a spontaneously switch to the competing set would occur whether or not there were any bottom-up inputs. That is, since rotation direction is not actually specified in the stimulus, the portion of the network signalling a particular rotation direction undergoes *self-adaptation* that allows the internal state to reverse. The relative advantage of one set over its opposite (one rotation direction over another) is a function of any combination of sensory inputs, aftereffects of sensory input, and intrinsic activity.

Although speculative, such a model with sparser representations at the higher level of rotation direction might explain the tendency to assign the same direction to multiple objects rotating in depth (Gillam, 1981) despite perspective cues to the contrary (Eby *et al.*, 1989). It might also explain the apparent periodicity in Figs 5 and 8. The self-adaptation cycles of the subjects could have begun in-phase at the end of adaptation, resulting in a periodic component in the average.

The cortical motion area and depth from optic flow

The anatomical locus for these effects is suggested by a recent positron-emission tomography experiment in which subjects viewed continuous frontoparallel motion of a checkerboard pattern (Watson, Myers, Frackowiak, Hajnal, Woods, Mazziotta, Shipp & Zeki, 1993). The key areas for which neural activity appeared to correlate with motion perception were located bilaterally near the junction of the occipital and temporal lobes. That finding is supported by human lesion studies (Regan, Giaschi, Sharpe & Hong, 1992; Vaina, Grzywacz & LeMay, 1990; Zihl, Von Cranon & Mai, 1983). That region is considered the homolog of the motion area in the superior temporal sulcus of the macaque monkey* cortex (Zeki, 1994) which includes area MT (V5). There, cellular activity has been shown to correlate with the perception of motion direction as implied by behavior (Britten, Shadlen, Newsome & Movshon, 1992). Cells in MT are tuned to velocity (Allman, Miezin & McGuinness, 1985) and respond to transparent motion (Snowden, Treue, Erickson & Andersen, 1991). A study in adapting cells to planar flow in MT of the owl monkey (Petersen, Baker & Allman, 1985) concluded that network changes were responsible. Similar conclusions from studies in other cortical areas that adaptation is due to mutual inhibition are found in Movshon and Lennie (1979) and Vidyasagar (1990).

The integration of more complex optic flow may first occur in neighboring area MST which receives its main inputs from MT. There, cells have receptive fields often covering over half the visual field. The directional selectivity of some of these cells has been found to be a function of disparity, a feature useful to disambiguate kinetic depth information and thus the direction of motion of an animal through its environment (Roy, Komatsu & Wurtz, 1992). Cells have also been found selective along a continuum of relative combinations of OE frontoparallel rotation, and translational flow (Duffy & Wurtz, 1991). As we have discussed, such a continuum is required by a network model of adaptation.

All areas provided signals from MST have yet to be completely characterized (Felleman & Van Essen, 1991). Furthermore, although Duffy and Wurtz (1991) did not report finding any cells in MST selective for rotation in depth, such selectivity has been reported in the motion area (Saito, Yukie, Tanaka, Hikosaka, Fukada & Iwai, 1986; Sakata, Shibutani, Ito & Tsurugai, 1986).

That the homologous motion area in humans is the site of the aftereffects reported here is also supported from another psychophysics experiment. Subjects were shown to adapt in the direction of the two-dimensional motion of plaid patterns but not in the direction of their component gratings (von Grunau & Dube, 1992). It was concluded that adaptation must have occurred at the higher levels, since cells in striate cortex (V1) appear incapable of integrating component motion (Movshon, Adelson, Gizzi & Newsome, 1985). A similar argument could be made that neural changes correlating to the aftereffect of motion in depth from OE occurs only where those signals are integrated in the motion area.

The function of adaptation to optic flow

The two classes of optic flow used here, the stimuli for translation and rotation in depth, have in general been treated separately in past research. In terms of self-motion (vection),* these two pure examples actually exist at the ends of a continuum and arise from viewing directions (relative to movement direction) that are 90 deg apart. But everyday visual experience may include any angle, and the resulting optic flow also depends on the observer's

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*Although KDE is usually discussed in terms of an object itself rotating, if one maintains fixation upon and walks around an object (e.g. a bush or small tree) the resulting optic flow is identical.

path in relation to the object(s) viewed. Furthermore, both flows can specify a moving observer, a moving object, or both, and to some extent the system appears not to have discriminated between these situations at the levels we adapted.

The human motion system analyzes these flows to maintain the association between visual and proprioceptive inputs for, among other functions, the timing of interception or avoidance of impact (Lee, 1980), the control of posture (Andersen & Dyre, 1989) and the determination of heading (Warren & Kurtz, 1992). A related though more complex function is to maintain a spatial reference despite body movements (space constancy). The brief adaptations reported here may be related to longer-lasting neural changes (Barlow, 1990b) needed to maintain the robustness of these motion associations as the body changes with age or due to illness or injury.

While it may not be surprising that adapting to these flow patterns briefly biased the motion system, a remarkable consistency remains to be explained. In all of our pilot studies as well as the experiments reported here, that used different stimuli and different sets of subjects months apart, the average level immediately after adaptation ended was always about halfway between chance and a total influence. While this level might be raised by stronger stimuli, it may also reflect the inherent stability of direction percepts from large ambiguous motion patterns (Hock, Kelso & Schoner, 1993, Expt 7) that resisted the influence of the aftereffects. Also, in terms of self-motion perception, if the aftereffects had functioned as visual vection signals, they would have been in conflict with proprioceptive inputs specifying the absence of self-motion.*

CONCLUSION

Our results and those of other researchers appear best explained by a hierarchical model for perceiving translation and rotation in depth from optic flow. Such a model could provide for the continuum we experience of motion in depth. It is hoped that our results suggest new psychophysical and physiological experiments that will provide more constraints for developing network models of these phenomena. This may lead to an understanding not only of this fundamental type of visual experience. It may also help us understand a presumably newer phylogenetic development, stereopsis, with which, as Helmholtz noted, it is naturally related.

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*More dramatic examples of interactions between vision and proprioception have certainly been reported (Lackner & Levine, 1978).

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