We examined whether a negative motion aftereffect occurs in the depth direction following adaptation to motion in depth based on changing disparity and/or interocular velocity differences. To dissociate these cues, we used three types of adapters: random-element stereograms that were correlated (1) temporally and binocularly, (2) temporally but not binocularly, and (3) binocularly but not temporally. Only the temporally correlated adapters contained coherent interocular velocity differences while only the binocularly correlated adapters contained coherent changing disparity. A motion aftereffect in depth occurred after adaptation to the temporally correlated stereograms while little or no aftereffect occurred following adaptation to the temporally uncorrelated stereograms. Interestingly, a monocular test pattern also showed a comparable motion aftereffect in a diagonal direction in depth after adaptation to the temporally correlated stereograms. The lack of the aftereffect following adaptation to pure changing disparity was also confirmed using spatially separated random-dot patterns. These results are consistent with the existence of a mechanism sensitive to interocular velocity differences, which is adaptable (at least in part) at binocular stages of motion-in-depth processing. We did not find any evidence for the existence of an “adaptable” mechanism specialized to see motion in depth based on changing disparity.

Keywords: motion in depth, stereomotion, interocular velocity difference, motion—3D, binocular vision, depth


Introduction

Physiological and psychophysical evidence suggests that cats and primates, including humans, have visual mechanisms “specialized” to detect motion in depth based on binocular information (Beverley & Regan, 1973; Cynader & Regan, 1978, 1982; Hong & Regan, 1989; Pettigrew, 1973; Poggio & Talbot, 1981; Regan & Beverley, 1973; Spileers, Orban, Gulyas, & Maes, 1990; Toyama, Fujii, & Umetani, 1990; Toyama, Komatsu, Kasai, Fuji, & Umetani, 1985; Toyama & Kozasa, 1982; for a review, see Howard & Rogers, 2002). Specialized mechanisms imply that motion in depth is processed by dedicated low-level detector networks rather than by a succession of static depth percepts derived from binocular disparity (i.e., tracking of position in depth; Patterson, 1999). Theoretically, there are at least two binocular cues to motion in depth (Cumming & Parker, 1994; Regan, 1993). The first is changing binocular disparity over time (CD). The second is interocular velocity difference (IOVD), namely, velocity difference between corresponding elements in the monocular images on the two eyes (Figure 1A).

Although the existence of an IOVD mechanism has been suggested by some psychophysical studies (Allison, Howard, & Howard, 1998; Brooks, 2001; Brooks & Mather, 2000; Brooks, 2002a, 2002b; Brooks & Stone, 2004, 2006; Czuba, Rokers, Huk, & Cormack, 2010; Fernandez & Farrell, 2005, 2006; Harris & Watamaniuk, 1995; Shioiri, Kakehi, Tashiro, & Yaguchi, 2003, 2009; Shioiri, Nakajima, Kakehi, & Yaguchi, 2008; Shioiri, Saisho, & Yaguchi, 2000), other studies found evidence against the existence of such a mechanism (Cumming & Parker, 1994; Harris, McKee, & Watamaniuk, 1998; Portforts-Yeomans & Regan, 1996). As for CD, several studies have shown that perception of motion in depth can be elicited in dynamic random-dot stereograms, where CD is the only coherent cue to motion in depth (Cumming & Parker, 1994; Harris & Watamaniuk, 1995; Regan, 1993; Shioiri et al., 2008). There are at least three possible mechanisms that could extract motion in depth from CD (Figures 1B–1D): (1) the detection of a succession of disparity-defined static depths (Figure 1B), (2) initial...
detection of disparity followed by detection of the temporal derivative of disparity (Figure 1C), and (3) direct detection of the temporal derivative of disparity (Figure 1D). The first mechanism (Figure 1B) is not specialized for motion in depth but rather assumes a sequence of depth percepts, while the second (Figure 1C) and the third mechanisms (Figure 1D) are specialized for motion in depth. Although some psychophysical studies have suggested the existence of a CD mechanism specialized for detection of motion in depth (Brooks, 2002a; Portfors & Regan, 1997; Portfors-Yeomans & Regan, 1996; Regan, Portfors, & Hong, 1997; see also Regan & Gray, 2009; Regan et al., 1998), others have argued against a specialized mechanism (Harris & Watamaniuk, 1995). Thus, there is little consensus on the existence of a mechanism specialized for motion in depth based on CD, which could be modeled as Figure 1C or 1D.

To clarify whether mechanisms specialized to see motion in depth based on IOVD and on CD exist, we adopted the technique of selective adaptation. If adaptation to motion in depth based solely on a particular binocular cue induces a directional (negative) motion aftereffect (MAE) in depth, a mechanism specialized to detect motion in depth based on that binocular cue is indicated.

**Experiment 1: Adaptation to motion in depth based on CD and/or IOVD**

**Subjects**

Four (three males and one female) volunteers naive to the purpose of the study and one male author took part in both Experiments 1 and 2. The ages ranged from late 20s to early 30s. All were previously screened for normal or corrected-to-normal acuity and normal binocular vision.

**Apparatus**

All the experiments were conducted in a darkened room. The stimuli were generated using Vision Egg software (Straw, 2008). They were presented on a 20-inch monochrome CRT monitor (Monoray Model M20ECD5RE, Clinton Electronics) refreshed at 120 Hz and viewed dichoptically from a distance of 120 cm through ferroelectric shutter goggles in order to produce separate left and right eye images (FE-1 Goggles, Cambridge Research Systems). The cross talk (i.e., the luminance of “ghost” images of bright objects seen by the fellow eye expressed as a percentage of the luminance of the object as seen by the intended eye) was less than 0.2%. A chin rest was used to stabilize head position.

**Stimuli**

The adaptation stimulus consisted of two frontoparallel planes (each subtending 17.4° × 2.91°) depicted by dichoptic random elements, one above and one below the fixation point (Figure 2). Each element was square and subtended 17.4° × 17.4 arcmin (16 × 16 pixels). The elements in each plane were horizontally and vertically aligned. In a monocular half-image, the luminance value (bright or dark) of each element was pseudorandomly determined so that the element density was 50%.

The two planes repeatedly moved in depth in opposite directions for 2 min (Figure 3). To obtain a unidirectional...
motion-in-depth signal for each plane, following each disparity ramp the stimulus was reset to its initial position and the ramp repeated (sawtooth disparity profile). The disparity in one dichoptic plane changed from $-17.4$ arcmin to $+17.4$ arcmin, while, simultaneously, the disparity in the other plane changed from $+17.4$ arcmin to $-17.4$ arcmin (where positive and negative values indicate crossed and uncrossed disparity, respectively). The successive disparity ramps were interleaved with a blank of 16.7 ms.

The motion in depth was specified by (1) both IOVD and CD by using random elements that were binocularly and temporally correlated (random-element stereograms, RESs), (2) IOVD alone by using binocularly uncorrelated but temporally correlated elements (uncorrelated random-element stereograms, URESs), and (3) CD alone by using binocularly correlated but temporally uncorrelated elements (dynamic random-element stereograms, DRESs), respectively.

In RES adaptation, identical element patterns were presented to the two eyes to form the top and bottom planes. In each monocular half-image, the top and bottom planes were moved laterally in opposite directions. Furthermore, each plane moved in opposite directions in the two eyes so that one dichoptic plane appeared to recede while the other approached at any given instant with the motion in depth specified by both coherent CD and coherent IOVD.

In URES adaptation, different random-element patterns were presented to each eye and were thus spatially uncorrelated between the eyes. As in the RES adaptation, the top and bottom planes were moved laterally in opposite directions in each monocular half-image and in opposite directions in the two eyes. This stimulus specified motion in depth by coherent IOVD but not by any coherent CD.

Both in RES and URES adaptation, the luminance values of the elements were changed pseudorandomly at the beginning of every disparity ramp to avoid local light adaptation (i.e., afterimage).

In DRES adaptation, the element patterns were binocularly correlated. Although in each monocular half-image the top and bottom planes moved laterally in opposite directions as in the RES adaptation, the luminance value of each (binocularly correlated) element was pseudorandomly determined every frame to eliminate coherent IOVD. Thus, the disparity of each plane changed over time to simulate smooth motion in depth without coherent IOVD.

During adaptation, the positions of the left and right edges of the planes were fixed. This was important because it ensured that the DRES adaptation stimulus did not contain global motion of the planes or motion of the texture-defined edges, which would have allowed adaptation to be attributed to CD of the texture elements. The rate of change of disparity of RES and DRES adaptation stimuli, and equivalently the differential lateral motion of RES and URES adaptation stimuli, was constant throughout a trial at either 2.18 (fast condition) or 0.545 (slow condition) deg/s, which corresponds to an average motion-in-depth speed of 84.1 or 21.0 cm/s, respectively. We changed the frame rate (not CRT refresh rate) to alter the rate of disparity change and the lateral motion.

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Figure 2. A monocular half-image of the stimulus used in Experiment 1. White features in the stimulus were presented at 10.0 cd/m$^2$ on a dark background ($<0.01$ cd/m$^2$) when viewed through shutter goggles. Each square element subtended 17.4 $\times$ 17.4 arcmin (16 $\times$ 16 pixels). The element density was 50%. The fixation point subtended 4.36 $\times$ 4.36 arcmin. Vertical and horizontal lines beside the fixation point subtended 6.54 $\times$ 52.3 and 17.4 $\times$ 4.36 arcmin. Nonius lines subtended 4.36 $\times$ 17.4 arcmin. The distances from the fixation point both to the nonius and horizontal lines were 4.36 arcmin. The distance between the horizontal and vertical lines was 2.18 arcmin. Figure not to scale.

Figure 3. The sequence of one trial of Experiment 1. During adaptation, disparity was repetitively ramped (sawtooth function) from $-17.4$ to $+17.4$ arcmin in one plane and from $+17.4$ to $-17.4$ arcmin in the other, where positive and negative values indicate crossed and uncrossed disparity, respectively. The disparity of the test stimulus was fixed to zero.
motion of the adaptation stimuli. The frame rates of the fast and slow conditions were 60 Hz and 15 Hz, respectively.

The test stimulus consisted of RES or DRES with constant zero disparity, or URES or monocularly viewed random elements with no objective motion. Note that these test stimuli were all stationary in depth rather than moving in depth. Thus, we examined a “static ” MAE in depth—where the static refers to the lack of test stimulus motion in depth. In the case of the DRES test stimulus, there was dynamic change in the cyclopean image as dots refreshed, but it remained (objectively) stationary in depth. Hence, with the DRES test stimulus, we examined a “static in depth” but “dynamic in 2D” MAE in depth.

Vertical and horizontal lines were presented with zero disparity just beside the fixation point to help the subjects lock the vergence of their eyes at zero disparity (Figure 2). Nonius lines were also presented just above and below the fixation point to confirm that there was little or no vergence eye movement.

Procedure and tasks

For each trial, a 2-min adaptation period was followed by the test period (Figure 3). In the test period, if the subjects saw opposing motion in depth of the planes, then they pressed a key when the apparent motion in depth ceased. Following the test, subjects verbally reported the apparent directions of the motion in depth of the test planes. If the subjects did not see such opposite motion in depth of the test stimulus, they verbally reported so. When MAE occurred in diagonal directions (i.e., apparent lateral motion in addition to motion in depth), the subjects pressed a key when the depth component of the apparent motion ceased. Diagonal MAE occurred only when the test stimulus was monocularly presented. During each trial, the subjects fixated the fixation point.

There were twelve adaptation conditions (three kinds of cue combination, two levels of speed of motion in depth, and two directions of motion in depth) and four test conditions as described above. Each subject participated in one trial for each of the 48 adaptation—test combinations. The order of the conditions was randomized for each subject except that the direction of the motion in depth of the adaptation stimulus alternated every trial between “top-approaching, bottom-receding” and “top-receding, bottom-approaching.” Successive trials were interleaved with a rest of at least 3 min.

Results and discussion

Frequency of MAE in depth data (i.e., proportion of trials in which MAE in depth occurred; Figure 4A) was analyzed by 4-way ANOVA (adapt cue, adapt speed, adapt direction, and test condition), followed by Tukey’s HSD post-hoc test, with α set at P < 0.05. The ANOVA shows that only the adaptation cue significantly affected the aftereffect frequency (F_{2,47} = 136.91, P < 0.0001). The post-hoc test showed that DRES adaptation produced an aftereffect less frequently than RES and URES adaptation. There was no significant difference in aftereffect frequency between the RES and URES adaptation.

When an MAE was reported, it was almost always a negative MAE, with motion in the test stimulus opposite to that in the adaptation stimulus. Only in a very tiny fraction of trials was an aftereffect other than a negative MAE reported; an aftereffect in the same direction as the adapter for one or both of the planes was noted on two trials, and an overall, as opposed to differential, aftereffect was reported on four trials. In all these cases except for one, these reports occurred following the DRES adaptation. Note that these trials were not counted as those in which MAE in depth occurred. As we will see in Experiment 2, these reports are likely due to disparity adaptation rather than motion adaptation.

Interestingly, the test condition did not significantly affect the aftereffect frequency (F_{3,47} = 2.141, P < 0.110, Figure 4A). This result implies two intriguing points.

First, the finding of substantial MAE in depth for URES test stimuli suggests that binocular correlation is not required for the perception of motion in depth based only on binocular information. This conclusion, however, appears rather inconsistent with the subjects’ introspective reports that the directions of motion in depth were harder to discern during adaptation to the binocularly uncorrelated URES stimulus than during adaptation to correlated adapters, particularly during the fast adaptation condition. This apparent inconsistency will be discussed in the General discussion section.

Second, even a monocular test stimulus showed a substantial MAE in a diagonal direction in depth. The depth component of the MAE under monocular test conditions suggests that binocular processes are involved in generating MAE in depth, because adaptation of only monocular processes should result solely in lateral MAE in this case.

ANOVA for the aftereffect duration data for the RES and URES adaptation (Figure 4B) found no significant main effects or interaction. Importantly, the RES and URES adaptation produced very similar aftereffect duration (F_{1,128} = 0.330, P = 0.567). Although not statistically significant, the faster adaptation stimulus tends to show a slightly longer aftereffect (ANOVA, F_{1,128} = 2.273, P = 0.135).

While it had no significant effect on aftereffect frequency, the test condition tended to affect the aftereffect duration although this effect was not statistically significant (F_{3,128} = 2.087, P = 0.107). Specifically, as can be seen in Figure 4B, the DRES test tended to show shorter aftereffect duration than the other test conditions. This result is consistent with previous reports that adaptation to moderate speed lateral motion produces lateral MAE of shorter duration for dynamic compared to
static noise test patterns (Van de Grind, Van Hof, Van der Smagt, & Verstraten, 2001; Verstraten, Van der Smagt, & Van de Grind, 1998). Note that although the DRES test tended to show a shorter aftereffect duration, this does not logically imply a lower frequency of MAE or deny the existence of CD mechanisms. The subjects reported that the aftereffect in the DRES test was about as strong as for the other test conditions at the onset of the test stimulus but weakened and ceased quickly.

In summary, the RES and the URES adaptation produced MAEs with very similar frequencies and durations (Figure 4). These results suggest that generation of MAE in depth does not depend on disparity coherency of the adaptation stimulus. Moreover, the fact that the DRES adaptation produced an aftereffect less frequently than the RES and URES adaptation suggests that generation of MAE in depth depends on IOVD coherency of the adaptation stimulus.

Figure 4. Results of Experiment 1. The numbers at the top of the figure indicate the rates of disparity change and/or differential lateral speeds of the adaptation stimuli. (A) The proportion of trials in which differential MAE in depth was observed between the upper and lower planes, each test plane appearing to move in a direction opposite to the adaptation stimulus. Note that only the trials in which both the top and bottom test planes appeared to move in depth in the directions opposite to those of the adaptation stimulus were counted as the trials in which MAE in depth occurred. (B) The duration of MAE in depth averaged across the trials in which the aftereffect occurred (±1 SEM). (C) The duration of MAE in depth averaged across all the trials (±1 SEM). In trials in which the aftereffect did not occur, the duration was dealt with as zero.
After the experiment, some subjects reported that, during some adaptation conditions, the average depth of each moving plane appeared biased toward its direction of motion in depth despite the disparity range being symmetric about zero screen disparity. Thus, MAE in depth reported in the experiment could (partially) be due to adaptation to this perceived biased “depth” rather than to “motion in depth,” or the subjects’ responses could be based on the buildup of a depth aftereffect that subsequently decays during test rather than MAE in depth.

**Experiment 2: Control of potential adaptation to apparent depth**

To clarify the cause of the aftereffect, in Experiment 2, we shifted the depth range of the DRES or RES adapting stimuli opposite to their directions of motion in depth (Figure 5). Note that the URES adaptation stimulus was not included, as it cannot be shifted in depth because it does not contain coherent disparity. The results of Experiment 2 should be the same as those from Experiment 1 if the visual system adapted to motion in depth because the direction of motion in depth of the adaptation stimulus was the same in both experiments. Conversely, if the visual system adapted to perceived depth, the aftereffect in Experiment 2 should be eliminated or in the opposite direction to that of Experiment 1, because the perceived depth range of the adaptation stimulus should be opposite to that of Experiment 1 or close to zero (i.e., the bias due to motion could be canceled).

**Methods**

During adaptation, disparity was repetitively ramped (sawtooth function) from $-34.8$ to 0 arcmin in the approaching plane and from $+34.8$ to 0 arcmin in the receding plane, where positive and negative values indicate crossed and uncrossed disparity, respectively. The configuration (top-receding and bottom-approaching vs. bottom-receding and top-approaching) chosen for each subject was the one that produced the longest duration of aftereffect in Experiment 1. Three adapting stimuli were used: RES adaptation at 2.18 deg/s (fast condition in Experiment 1) and DRES adaptation at either 2.18 deg/s or 0.545 deg/s. The test stimuli were identical to those used in Experiment 1 (i.e., zero disparity and/or no objective coherent motion).

**Results and discussion**

Adaptation to RES produced negative MAE in depth on every trial with an average duration similar to that in Experiment 1 (Figure 6). There were no statistically significant differences between Experiments 1 and 2 in the aftereffect duration for RES fast adaptation (two-tailed paired $t$-test, $t < 0.98$, $P > 0.39$ for each test condition, compare Figures 4B and 6B). On the other hand, adaptation to DRES did not produce MAE in depth on...
any trial for both fast adaptation (Figure 6A) and slow adaptation (not shown).

These results suggest that the MAE in depth produced by adaptation to RES in Experiment 1 was due to adaptation to motion in depth. On the other hand, the response to adaptation to DRES in Experiment 1 was probably due to a depth aftereffect produced by adaptation to biased perceived “depth” rather than to MAE in depth.

As mentioned in Experiment 1, only in a small fraction of the trials of Experiment 1 were the reported directions of the aftereffect not in the directions opposite to that of the adapter. The fact that these reports only occurred in conditions that were subject to depth adaptation effects rather than MAE suggests that they might have arisen due to variation in the perceived depth bias during these trials.

In Experiment 1, the DRES adaptation produced MAE in depth only in a small proportion of trials. Moreover, in Experiment 2, the DRES adaptation produced no MAE in depth. These results suggest that adaptation to motion in depth based solely on CD does not produce MAE in depth. However, this suggestion appears to contradict two previous reports. First, Regan et al. (1997) reported that adaptation to dynamic random-dot stereograms (DRDSs) simulating back-and-forth motion in depth decreases the sensitivity of such motion (see also Regan et al., 1998). Second, Brooks (2002a) in his Experiment 2 reported that adaptation to binocularly and temporally correlated random-dot stereograms (RDSs) simulating a receding surface affects perceived velocity of the following receding stimulus (velocity aftereffect) more than adaptation to binocularly uncorrelated and temporally correlated random-dot stereograms (uncorrelated random-dot stereograms, URDSs). These two reports suggest that the mechanism for motion in depth based on CD is adaptable.

However, these previous studies did not investigate whether an MAE could be induced after adaptation to these stimuli. Effects of adaptation on suprathreshold speed estimates or sensitivity to oscillation do not necessarily predict that a static MAE will be obtained with similar adapting stimuli. As Regan et al. (1997) used balanced oscillatory motion, no static MAE would be expected. In Brooks (2002a), the URDS and RDS adapting stimuli would have differed in the quality of the stereoscopic percepts produced (noisier for the URDS), even when the stimuli were not moving, and this might partially explain their relative effectiveness. In any case, evidence for an effect of CD in the velocity adaptation was only for RDS adaptation stimuli presented at an uncrossed disparity pedestal. Regan et al. also presented their adapting stimuli on a disparity pedestal. Given our finding in Experiment 2 that exposure to DRES stimuli can produce depth aftereffects, it is possible that depth aftereffects may have influenced the velocity judgments in the disparity pedestal case of Brooks. Nevertheless, it is important to ensure that our findings of no appreciable MAE to CD stimuli did not result from the particular choice of stimulus used in our experiments. Thus, we ran a series of experiments (collectively grouped here as Experiment 3) to investigate whether our findings generalize to other stimulus patterns, particularly patterns that have previously been used to provide evidence for the adaptability of CD mechanisms. More specifically, whereas we used randomly colored black or white elements that were aligned horizontally and vertically (Figure 2), the two previous studies used random dots that were randomly distributed in each monocular half-image.

In Experiment 3, we used randomly distributed dots in the adaptation and test stimuli and examined whether adaptation to binocularly correlated but temporally uncorrelated stimulus (DRDS) produces MAE in depth.

### Methods

One author (Subject 1) and two naive volunteers (Subjects 2 and 3) took part in Experiment 3. All subjects were previously screened for normal or corrected-to-normal acuity and normal binocular vision. Subjects 1 and 2 participated in Experiments 1 and 2.

**Case 1:** All the stimuli were depicted by dichoptically presented random dots (Figure 7A) presented in an arrangement similar to Experiment 1. In each monocular half-image, all the dots were separated and randomly distributed. The disparity range of the adaptation stimuli, motion profile, and adapting speeds were identical to those of Experiment 1.

**Case 2:** After Regan et al. (1997), the adaptation stimulus was either an RDS or a DRDS in which dots in a windowed portion of the display changed disparity (and appeared to move in depth). The optical arrangements of the half-images were based on Portfors-Yeomans and Regan (1996), which provided a more complete description (Figure 7B). During adaptation, disparity in a portion of the display was repetitively ramped (sawtooth) within crossed disparity either from +15.2 to +2.2 arcmin or from +2.2 to +15.2 arcmin (mean 8.7 arcmin) depending on whether the trial involved adapting to receding or approaching motion. Each cycle of the disparity ramp lasted 0.72 s including a 16.7-ms blank interval at the end of the ramp.

**Case 3:** The optical arrangement of each monocular half-image of the stimulus (Figure 7C) followed that of Brooks (2002a). The adaptation stimulus was an RDS, a URDS, or a DRDS while the test stimulus was an RDS.
During adaptation, disparity was repetitively ramped from 0.0 to −26.1 arcmin (uncrossed disparity), simulating a receding surface. The disparity of the test stimulus was fixed to −13.1 arcmin. We did not interleave the successive disparity ramps with a blank, as Brooks did not. The duration of each disparity ramp was 0.43 s, and for DRDS adaptation, we used this rate and also used a slower adaptation stimulus where the duration of each disparity ramp was 1.3 s. The speed of this slower adaptation was identical to that of Case 2.

The adaptation stimulus was binocularly and temporally correlated (RDS) or binocularly correlated but temporally uncorrelated (DRDS). For Case 3, we additionally used a URDS adapting stimulus similar to Brooks (2002a). In RDS adaptation, relative positions of the dots within each half-image remained unchanged (except for the changing disparity). In DRDS adaptation, on the other hand, the dot positions were randomly determined every frame to eliminate any coherent IOVD. The test stimulus was a static RDS with zero disparity (Case 1) or the mean disparity of the adapting stimulus (Cases 2 and 3).

Each adaptation period lasted for 2 min in the RDS adaptation and for either 2 min (Cases 1 and 3) or 10 min (Cases 1 and 2 based on Beverley & Regan, 1973) in the DRDS adaptation. All combinations of motion direction, adaptation stimulus, adaptation duration, and adapter speed were presented to each observer in repeated measures designs (for each subject, once in each of twelve conditions.

Figure 7. Stimuli used in Experiment 3. (A) A monocular half-image of the stimulus used in Case 1. Each square dot subtended 13.1 × 13.1 arcmin (12 × 12 pixels). There were 400 dots in each plane. In the RDS adaptation conditions, the dots were randomly redistributed every time the new disparity ramp started in order to achieve spatially uniform adaptation. In the DRDS adaptation conditions, the dots were randomly redistributed every frame. (B) A monocular half-image of the stimulus used in Case 2. Each square dot subtended 4.4 × 4.4 arcmin (4 × 4 pixels). There were 770 dots in the black circle. During the adaptation period, only 8 dots presented in the center of a square section of the dot pattern (45.7 × 45.7 arcmin), highlighted here by a red square, simulated movement in depth. The disparity of the remaining dots, the bright square, and the fixation point presented between the nonius lines was fixed to zero. In the RDS adaptation condition, all the dots were randomly redistributed every time the new disparity ramp started. In the DRDS adaptation condition, all the dots were randomly redistributed every frame, so that the plane of dynamic dots inside the red square simulated cyclopean motion in depth. The red square is for illustration only and was not presented in the experiment. (C) A monocular half-image of the stimulus used in Case 3. In all the adaptation conditions, only the texture elements inside the square area highlighted in red (the red boundary is for illustration only and was not presented) simulated movement in depth, while the other elements were stationary and fixed at zero disparity. Each texture element subtended 4.4 × 4.4 arcmin (4 × 4 pixels). The luminance of the bright and dark elements was 10.0 cd/m² and 1.11 cd/m², respectively, so that the Michelson contrast was 0.80, as in Brooks (2002a). Both the luminance of the lower gray rectangle and that of the center gray rectangle containing the fixation cross were 5.56 cd/m², which was the mean of those of the bright and dark elements. Two pairs of nonius lines were presented, one on either side of fixation, and one at 10.0 cd/m² (bright) and the other at less than 0.01 cd/m² (dark).
in Case 1, twice in each of four conditions in Case 2, eight times in the RDS and URDS adaptation conditions and twice in the DRDS adaptation conditions in Case 3. Successive trials were interleaved with a rest of at least 3 min. The session for 10-min adaptation was conducted on a different day from the 2-min trials to avoid fatigue.

Results and discussion

For the Case 1 and Case 2 stimulus arrangements, MAE in depth occurred after every RDS adaptation period for Subjects 1 and 2, but for Subject 3, the aftereffect frequency was lower (Figure 8A). For Case 3, MAE in depth occurred frequently after the RDS adaptation in every subject; an MAE in depth also followed URDS adaptation in Subjects 1 and 3, although not for Subject 2. The aftereffect duration was comparable for the three subjects when the aftereffect occurred (Figure 8B).

In contrast, DRDS adaptation did not produce any MAE in depth in any subject for any of the 3 different stimulus arrangements (Figure 8A). These results suggest that adaptation solely to CD does not produce MAE in depth and, conversely, that coherent IOVD is involved in producing MAE in depth. These results are consistent with the results of Experiments 1 and 2, indicating that our failure to find an MAE in depth after adaptation to CD alone cannot be explained by the use of stimulus that differs markedly from those used by Brooks (2002a) or Regan et al. (1997).

Note that while the optical arrangements of the stimuli in this experiment were designed to mimic those in earlier experiments there are important differences in the motion profiles and tasks used. Our adaptation stimuli moved
unidirectionally in depth (with periodic resets) and our test stimulus was stationary in depth; in contrast, Brooks (2002a) and Regan et al. (1997) used stimuli that moved in depth both in the adaptation and test phases. The findings of an influence of adaptation to CD on perceived speed and threshold for detecting oscillation in the earlier studies is not necessarily at odds with our findings of a lack of an MAE; it is possible that adaptation to CD only affects test stimuli moving in depth, and as with the lateral MAE, there may be a distinction between the MAE and velocity aftereffects (for a review, see Thompson, 1998).

Unlike Experiment 1, MAE in depth did not occur after adaptation to DRDS in the Case 1 arrangement even though there was no compensation for depth aftereffect as in Experiment 2. This could be due to the fact that in a monocular half-image of the DRES adaptation stimulus used in Experiment 1, the element edges (i.e., positions of luminance changes), which are second-order features, moved smoothly. This could have, in turn, produced a second-order IOVD that could have contributed to producing an MAE in depth in the DRES adaptation conditions in Experiment 1.

### General discussion

#### Summary

MAE in depth occurred frequently after adaptation to motion in depth depicted by RES and URES. In contrast, MAE after DRES adaptation was not obtained when depth bias (Experiment 2) and second-order motion (Experiment 3) were controlled. These results suggest that RES adaptation produces a robust MAE in depth while DRDS adaptation does not. The weak aftereffect reported after the DRES adaptation in Experiment 1 was likely due to adaptation to apparent depth, not to motion in depth. Brooks (2002a) and Regan et al. (1997) have reported reduced sensitivity following adaptation to DRDS, but we found that no negative MAE in depth could be obtained following DRDS adaptation using similar stimuli. Since the RDS and the URDS contained coherent IOVD while the DRDS did not, the results of all our experiments suggest that the human visual system has a mechanism specialized to see motion in depth based on IOVD. On the other hand, we did not find any evidence for the existence of a mechanism specialized to see motion in depth based on CD.

### IOVD mechanisms

As described in the Introduction section, there has been significant controversy about whether IOVD is used to see motion in depth. We found that MAE in depth occurs after adaptation to RDS and URDS (as well as RES and URES) but not after adaptation to DRES or DRDS (Figures 4, 6, and 8). These results strongly support the idea that the human visual system has a mechanism for detection of motion in depth based on IOVD and that this mechanism is adaptable.

One model for an IOVD mechanism has independent monocular motion detectors detecting motion in each eye and feeding into a subsequent binocular stage (Figure 1A). In such a model, adaptation of the initial motion detection stages to motion in each eye could predict an MAE in depth without adaptation of binocular processes. Previous research has suggested that monocular motion mechanisms can be adapted and have an influence on subsequent estimates of motion in depth (Brooks, 2002b; Shioiri et al., 2009). We suspect that similar processes are responsible for at least part of the IOVD adaptation reported here. However, this cannot be the whole story.

The monocular test stimulus in Experiments 1 and 2 produced an MAE in a diagonal direction in depth (Figures 4 and 6). If the IOVD-produced MAE in depth were due only to adaptation of separate left and right eye monocular motion detectors feeding into a later binocular stage that did not adapt, then only a lateral MAE should have been obtained with a monocular test stimulus. The depth component of the MAE under monocular test conditions indicates that the binocular processes are adaptable and involved in generating MAEs in depth.

Interestingly, in Experiments 1 and 2, the URES “test” stimulus also showed substantial MAE in depth (Figures 4 and 6). These results suggest that perception of stereoscopic motion in depth does not require a spatial correlation between the two eyes. This conclusion is consistent with the finding that motion-in-depth percepts can be generated by URDS stimuli (Allison et al., 1998; Shioiri et al., 2000) and the results of Rokers, Cormack, and Huk (2008; see also Allison & Howard, 2011), who found that the subjects can judge substantially the direction of motion in depth depicted by binocularly anti-correlated dots, in which depth could not be seen.

However, our subjects reported that the directions of motion in depth of the URES adaptation stimulus used in Experiment 1 were not seen clearly, even in trials in which it was clear that the subsequent URES test stimulus appeared to move in depth. This phenomenon was more conspicuous in the fast adaptation conditions, in which binocular random matching could be more difficult because of the shorter duration of the ramp of motion in depth. Since the URES adaptation and the URES test stimulus were both binocularly uncorrelated, this phenomenon is puzzling. One possible reason for the clear perception of motion in depth only in the test stimulus could be the longer presentation duration with the unchanged element patterns, which enabled the visual system to make binocular matches between the random elements. However, to clarify the mechanism of this phenomenon, further study would be required.
CD mechanisms

Why did our DRES and DRDS adaptation stimuli fail to produce MAE in depth? There are at least four possible reasons. First, the mechanism to see motion in depth based on CD could simply rely on a succession of depth percepts based on binocular disparity, which can be modeled as Figure 1B. In this case, there would simply be no mechanism to adapt. Second, the CD mechanism could be specialized to see motion in depth as described in Figure 1C or 1D, but the mechanism may not be adaptable. Third, our adaptation stimulus could be inappropriate to produce MAE in depth from CD adaptation. For instance, DRDS displays do not eliminate motion energy but make it incoherent. Thus, IOVD signals were incoherent but still present and could have adapted IOVD mechanisms in both directions in depth, possibly disturbing MAE in depth from CD adaptation. Alternatively, in the DRES and DRDS adaptation, owing to the short duration of each element or dot, possible false matches could have occurred and disturbed MAE in depth from CD adaptation. However, the DRES and DRDS adaptation stimuli produced strong percepts of motion in depth. Fourth, our test stimulus could be inappropriate to show MAE in depth from CD adaptation. For instance, a zero disparity test pattern might probe adaptation of different mechanisms than a test pattern moving or alternating in depth. In the case of lateral MAE, after adaptation to lateral motion defined only by a modulation of stereoscopic depth, not by luminance, a counterphasing test pattern shows a negative MAE while a static test pattern shows little or no MAE (Nishida & Sato, 1995) although it has been reported that a static test pattern also shows reliable MAE if adaptation lasts longer than 30 s (Bowd, Rose, Phinney, & Patterson, 1996; Patterson et al., 1994).

The first reason is consistent with Harris and Watamaniuk (1995), who found that speed discrimination for motion in depth depicted by a DRDS was poor compared with that depicted by an RDS. However, the first, second, and third reasons are inconsistent with Regan et al. (1997), who found that adaptation to oscillation in depth depicted by a DRDS decreases sensitivity to subsequent oscillation in depth, and with Brooks (2002a), who found velocity aftereffect in depth after adaptation to DRDS, with both studies suggesting adaptability of motion-in-depth mechanism based on CD. It is possible that CD adaptation affects the sensitivity of the mechanism without any rebalancing of neural activity usually associated with negative aftereffects. A possible foundation for the fourth reason is that our test stimuli were physically all stationary in depth while the test stimuli used in Regan et al. and Brooks moved in depth. Thus, it is possible that there is distinction between static and dynamic tests analogous to that found for lateral MAE. In the latter case, it was argued that the MAE in a counterphasing test pattern reflects relatively fast motion mechanisms while that in a static test pattern reflects slow motion mechanisms (Shioiri & Matsumiya, 2009). A possible mechanism for this fourth reason could be that adaptation to motion in depth based on CD might only decrease the gain of motion in depth. If so, after adaptation solely to CD, the speed of motion in depth and sensitivity to motion in depth could decrease without producing any apparent motion in a stationary test stimulus. Although the fourth reason may explain why our DRES and DRDS adaptation stimulus failed to produce MAE in depth, further study is required.

What cues and stages can be involved in generating MAE in depth?

If adaptation to a single cue to motion in depth produces an MAE in depth, it can be inferred that the mechanism to see motion in depth based on the cue is adaptable and “specialized” to detect motion in depth, not just a succession of depth percepts. In addition, if a monocular test stimulus shows an MAE with a depth component following binocular adaptation, it can be inferred that processes beyond binocular combination are adaptable and responsible for depth component of the MAE.

So far, adaptation to the monocular changing-size cue has been shown to produce MAE in depth (Beverley & Regan, 1979; Harris, Morgan, & Still, 1981; Regan & Beverley, 1978, 1979).

In terms of binocular cues, Kitagawa and Ichihara (2002) found that adaptation to stereoscopic motion in depth of a square that contains both coherent CD and coherent IOVD produces an auditory changing-loudness aftereffect. More recently, Rokers, Cormack, and Huk (2009) found that after adaptation to dots moving in depth, which contain both coherent CD and coherent IOVD, dots stereoscopically moving in depth in random directions (random walks through depth) appear biased to move in the opposite direction to the preceding adapting direction. Although these two reports suggest that motion-in-depth mechanisms based on binocular cues are adaptable, they tell us nothing about whether the CD or IOVD cue is responsible for the aftereffects.

Shioiri et al. (2003, 2009) found that after adaptation to monocular lateral motion, a binocularly viewed test pattern appeared to move in a diagonal direction in depth. These results suggest that monocular processes for motion in depth based on IOVD are adaptable and responsible, at least in part, for the depth component of the MAE.

Here, we found that MAE in depth occurs after adaptation to RDS and URDS, but not after DRDS. Our results suggest that IOVD, not CD, is responsible for the MAE in depth. Moreover, we also found that following RDS or URDS adaptation a monocular test pattern showed MAE in a diagonal direction in depth. These results suggest that binocular processes for motion in depth based on IOVD are adaptable and involved in generating MAEs in depth.
Can the MAEs in depth be explained by vergence eye movements?

It has been suggested that registration of vergence eye movements can be used to see motion in depth (Howard, 2008; Welchman, Harris, & Brenner, 2009). However, it is unlikely that the MAEs in depth in the experiments reported in the present paper were caused by vergence eye movement during “adaptation” because of the following reasons. First, the directions of the MAEs in depth were opposite in the top and bottom planes in Experiments 1, 2, and 3. Second, the well-trained subjects reported that nonius lines remained aligned during the experiments.

One might also suppose that the MAEs in depth were induced by potential vergence eye movements in the “test” period, which could have, in turn, caused coherent CD and/or coherent IOVD depending on the kind of the test stimulus. An analogous effect has been reported in which adaptation to lateral motion induces smooth pursuit eye movement (Braun, Pracejus, & Gegenfurtner, 2006). However, it is unlikely that the MAEs in depth were caused by vergence eye movements in the test phase, because during the test period, the nonius lines remained aligned and the configuration requires opposite MAE in the top and bottom planes. Furthermore, even if vergence eye movements did occur in the test phase, they would have produced uniform CD and IOVD of the whole test stimulus. It has been reported that uniform CD and IOVD in isolated random-dot patterns produce almost no sensation of motion in depth (Allison & Howard, 2011; González, Allison, Ono, & Vinnikov, 2010; Howard, 2008; Regan, Erkelens, & Collewijn, 1986). Therefore, it is very unlikely that MAEs in depth found in the present study were caused by vergence eye movement in the adaptation and/or the test period.

Can the MAEs in depth be explained by attentive tracking?

One might suppose that the MAEs in depth observed in the present study were induced by attentive tracking of the adapter’s position in depth, because in the case of lateral MAE, it has been suggested that attention to the adapter’s motion affects MAE (aftereffect strength: Culham, Verstraten, Ashida, & Cavanagh, 2000; Mukai & Watanabe, 2001; aftereffect duration: Nishida & Ashida, 2000). However, it is unlikely that the observed MAEs in depth can be explained (at least wholly) by attentive tracking because of the following reason. During the URES and the URDS adaptation, position in depth was not clearly perceived, making attentive tracking of the position in depth of the planes difficult. On the other hand, in the RES, RDS, DRES, and DRDS adaptation conditions, position in depth was both clearly perceived and easily trackable. If the MAEs originated from attentive tracking of the adapter’s position in depth, the RES, RDS, DRES, and DRDS adaptation should have produced MAEs in depth, while the URES and the URDS adaptation should not. However, our results show that the RES, RDS, URES, and URDS adaptation produced MAEs in depth with similar frequencies and durations, while the DRES and DRDS did not, opposite to the expectations based on attentive tracking. Thus, it is unlikely that attentive tracking (at least wholly) produced the MAEs in depth in the present study.

On individual differences

Nefs, O’Hare, and Harris (2010) have reported that a certain fraction of the population is blind (or has large thresholds) to either CD or IOVD. In our sample, all subjects experienced motion in depth during the adaptation phase for both CD- and IOVD-based adapters. While we cannot conclude that “all” people experience the MAEs in depth found in the present study, the effects were robust and reliable for all observers tested (i.e., for at least 6 subjects as 5 subjects participated in Experiments 1 and 2, and 2 subjects and a new one in Experiment 3). The results were very consistent in terms of whether MAEs in depth occurred after different kinds of adapting cues, namely, MAEs in depth occurred after adaptation to coherent IOVD but not solely to coherent CD. In addition, a number of others were shown demos and reported percepts consistent with the experimental data as did observers in the pilot experiments. Thus, we are confident that at least in our observers, and presumably in a certain percentage of people if not in all people, IOVD is used to detect motion in depth and that the IOVD mechanisms are adaptable.

Conclusion

We found that a movement aftereffect in depth occurs after adaptation to motion in depth based on binocular information, specifically coherent interocular velocity differences without dependence on coherent changing disparity. Our findings suggest the existence of a mechanism specialized to detect motion in depth based on interocular velocity differences. Although many previous studies have reported that motion in depth can be seen based on coherent changing disparity only, in our study, we did not find any evidence for the existence of an “adaptable” mechanism specialized to detect motion in depth based on changing disparity. In order to clarify whether such a mechanism exists, further study is required.
Acknowledgments

This work was supported in part by grants from Province of Ontario (Premier’s Research Excellence Award), the Canadian Foundation for Innovation, and NSERC (Canada). Portions of this study have been previously reported in abstract form (Sakano, Allison, & Howard, 2005).

Commercial relationships: none.
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