Unconscious adaptation: a new illusion of depth induced by stimulus features without depth

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Abstract

Here, we show a new illusion of depth induced by psychophysical adaptation to dynamic random-dot stereograms (RDS) that are interocularly *anticorrelated* (i.e., in which the images for the two eyes have reversed contrast polarity with each other). After prolonged viewing of anticorrelated RDS, the presentation of uncorrelated RDS (i.e., in which two images are mutually independent random-dot patterns) produces the sensation of depth, although both anticorrelated and uncorrelated RDSs are perceptually rivalrous with no consistent depth by themselves. Contrary to other aftereffects demonstrated in a number of visual dimensions, including motion, orientation, and disparity, this illusion results from *unconscious adaptation*; observers are not aware of what they are being adapted to during the process of adaptation. We further demonstrate that this illusion can be predicted from the simulated responses of disparity-selective neurons based on a local filtering model. Model simulations indicate that the inspection of anticorrelated RDS causes the adaptation of all disparity detectors except one sensitive to its disparity; therefore, those selectively unadapted detectors show relatively strong activation in response to the subsequent presentation of uncorrelated RDS and produce depth perception.
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1. Introduction

When similar images fall on the two retinas with slight displacement (known as binocular disparity), we can fuse them and perceive a sensation of depth (called stereopsis). This process requires the extraction of disparity information by establishing a correspondence between image features in two images, even though there are a multitude of false matches. Overall image correlation between two images is thought to be substantial for solving this correspondence problem. If the two retinal images differ widely in configuration, they compete with one another rather than fuse and do not produce consistent depth perception because the matching process does not find a globally consistent solution (Howard & Roggers, 1995).

Random-dot stereograms (RDS), images comprising patterns of random dots that are interocularly correlated (identical) but laterally displaced, provide a way to exclusively investigate the stereoscopic process because they can produce depth perception devoid of all monocular depth and familiarity cues (Julesz, 1964). We can examine the role of image correlation on stereopsis by using variants of RDS whose dot patterns are interocularly different (not correlated), such as anticorrelated RDS (A-RDS) and uncorrelated RDS (U-RDS) (Julesz & Tyler, 1976).

An A-RDS is produced by replacing one random-dot pattern (left or right) with its complement (negative correlation) so that each black dot in one eye is geometrically matched with a white dot in the other eye and vice versa (see Fig. 1a). Throughout this paper, we will refer to the lateral displacement between anticorrelated areas as "disparity" although, strictly speaking, this term is a misnomer (Cumming & Parker, 1997). On the other hand, binocular images of an U-RDS are generated by independent random-dot sequences so that the

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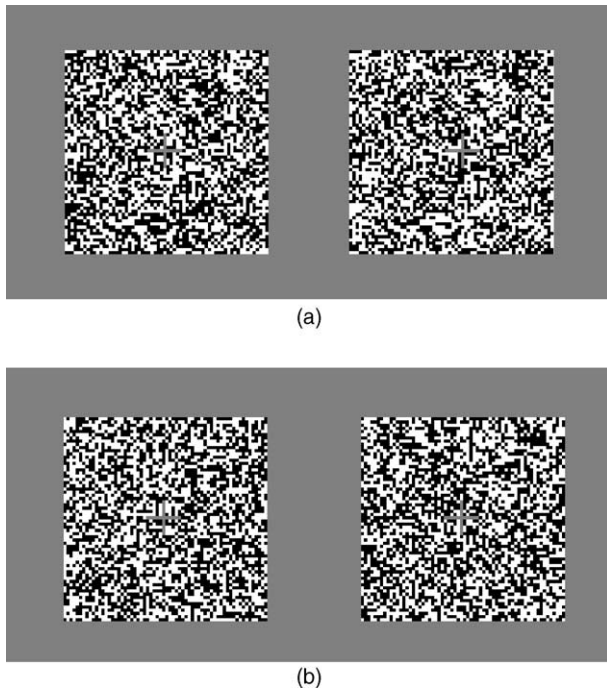*E-mail address:* hayashi@caltech.edu (R. Hayashi).

Fig. 1. Examples of RDSs. (a) A-RDS and (b) U-RDS.

pattern for one eye has no (zero) correlation with the other eye (see Fig. 1b). Since the patterns of both A-RDS and U-RDS lack globally consistent matching, they are visually rivalrous with fluctuating depth either in front of or beyond their surroundings (Julesz & Tyler, 1976) except at low dot densities (Cogan, Lomakin, & Rossi, 1993).

Neurons that modulate their firing rate in response to disparity have been observed in many visual areas of the primate brain and are thought to form the neural substrate for stereopsis (DeAngelis, Cumming, & Newsome, 1998; Poggio & Fisher, 1977; Poggio, Gonzalez, & Krause, 1988). The studies on disparity-selective neurons in area V1 have indicated that the neurons that respond to correlated RDS (C-RDS) are also sensitive to the disparity of A-RDS and often show an inversion of disparity tuning with A-RDS (Cumming & Parker, 1997). Since the local filtering models (known as binocular energy models (Ohzawa, DeAngelis, & Freeman, 1990)) can predict the profile of such responses, it is thought that V1 neurons merely respond to simple local matches between the two eyes regardless of overall image correlation. However, for all these physiological and model studies, the way that image correlation affects the human stereo-systems is still unclear.

The subject of this paper is to analyze computationally the neural responses that underlie the perception of C-RDS, A-RDS, and U-RDS and predict a new illusion from the analysis. We then demonstrated the existence of the illusion in human subjects and examined some aspects of the illusion by psychophysical experiments.

2. Simulation study

As mentioned above, the binocular energy model is known as a computational model that fits the response-profiles of disparity-selective neurons in physiological data. Furthermore, theoretical studies indicate that the model can code the disparity information regardless of Fourier phases of input patterns (Qian, 1994). Fleet, Wagner, and Heeger (1996) demonstrate that pooled responses of binocular energy neurons across orientations, phases, and spatial frequencies can produce an unambiguous representation of disparity for RDSs and solve the corresponding problem effectively. Thus, it has been shown that the model not only capture many aspects of cell's behavior in visual cortex but also provide a computational framework for computing disparity map from stereograms.

Based on this currently accepted model of disparity processing, we investigated the underlying process during the presentation of dynamic RDSs (patterns of random-dot change with every frame) that varied in image correlation.

2.1. Method

The model used here to study the responses of disparity detectors to dynamic RDSs is our own implementation of the model described in Ohzawa et al. (1990), and Fleet et al. (1996). In the model, each input from the two eyes is convolved with the Gabor function, and the binocular sum for each subunit is then squared and summed to generate the output of disparity-selective neurons (complex cells) in area V1. Here, disparity preferences are introduced by the positional shift between receptive fields in the two eyes. For simplification, we only consider a one-dimensional input pattern, and orientation-selectivity of the neurons is thus not considered. By pooling the binocular energy responses (output of complex cells) across two phases (0 and $\pi/2$) and five spatial frequencies (1/4, 1/8, 1/16, 1/32, and 1/64 cycle/pixel), we simulate the activity of disparity detectors, which produces an unambiguous representation of disparity. The variances of the Gaussian windows of Gabor functions are inversely proportional to the spatial frequency (1, 2, 4, 8, 16 pixel). The average response across 100 trials is calculated to predict the responses of detectors to dynamically presented stimuli. In order to detect disparity information regardless of Fourier phases of input images, we have to choose at least 2 orthogonal phases and adequate number of spatial frequencies that can cover the spatial frequency band of input images. However specific numbers and parameters of filters mentioned above are not critical in the results. Parameters used in this paper were selected arbitrarily based on previous studies (Gray, Pouget, Zemel, Nowlan, & Sejnowski, 1998; Jain & Farrokhnia, 1991).

2.2. Results

Simulation results are shown in Fig. 2. The model simulations indicate that both A-RDS and U-RDS have an effect to excite various types of disparity detectors broadly. However, there is a crucial difference between two stimuli; while A-RDS selectively inactivates the detectors tuned to its disparity, U-RDS has no such selectivity (Fig. 2b and c, respectively).

It has been reported that adaptation to a particular stimulus causes a change in sensitivity of the underlying perceptual mechanism and distorts perceptual judgment on subsequently presented stimuli (Gibson, 1937; Grunewald & Lankheet, 1996). Regarding the adaptation of the disparity-tuned mechanism, prolonged inspection of a C-RDS produces a shift in the apparent depth of subsequently viewed C-RDSs (Blakemore & Julesz, 1971; Long & Over, 1973). If the model simulates the processing of disparity detection in the human visual system, the results lead to the prediction that prolonged observation of A-RDS causes adaptation of all disparity detectors except for one that is sensitive to the disparity
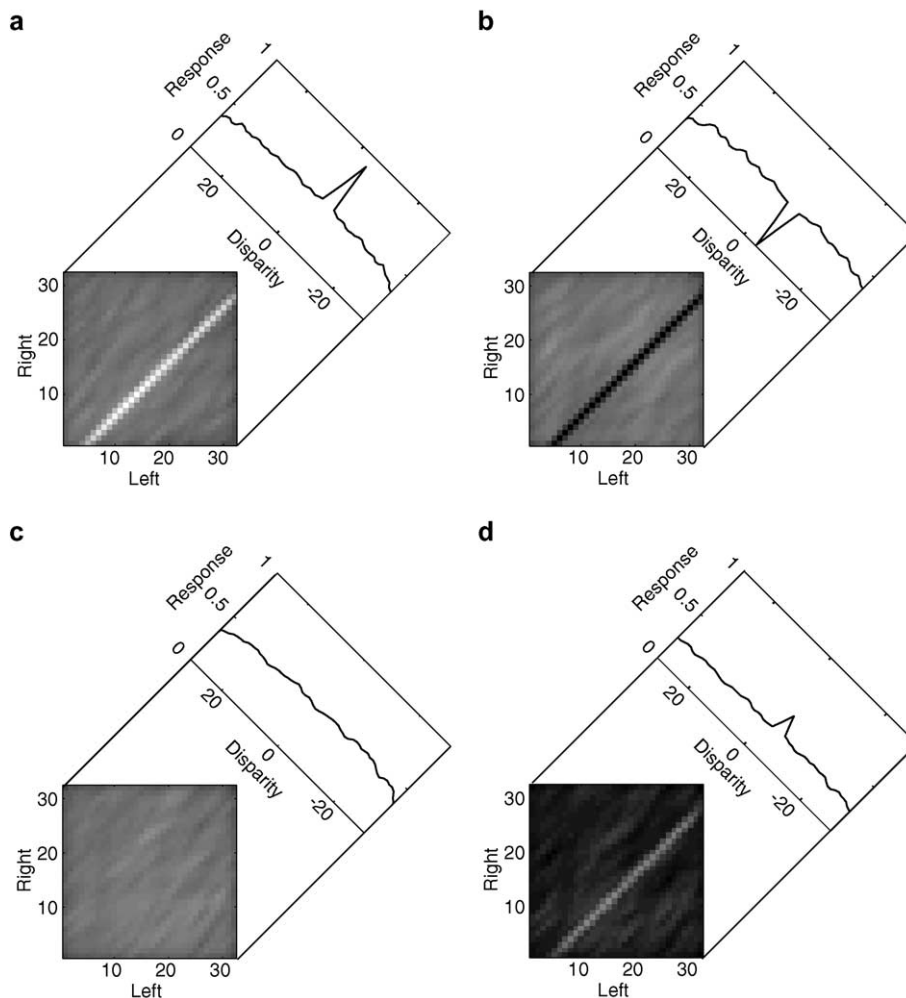

Fig. 2. Simulated responses of disparity detectors (pooled responses of binocular energy neurons) to several types of dynamic RDS. The horizontal axis indicates the receptive field (RF) position of disparity detectors in the left eye, and the vertical axis shows the RF position in the right eye. Each pixel represents the activity of the disparity detectors (increasing from black to white). Therefore, detectors located along a diagonal line are tuned to the same disparity, and line graphs indicate the averaged response across these detectors (normalized by the maximum activity of a detector in response to C-RDS). Input images consist of 32 pixels, and disparate areas are extended to the whole images. Each dot of RDSs has an equal probability of being black or white. The disparity of both C-RDS and A-RDS is −4 dots (crossed/near disparity). (a) Responses to C-RDS. Detectors tuned to the disparity of C-RDS are selectively activated and succeed in representing the disparity of C-RDS unambiguously. (b) Responses to A-RDS. Contrary to C-RDS, detectors tuned to the disparity of A-RDS are selectively inactivated, and the excitation of the other detectors is broadly distributed. (c) Responses to U-RDS. There is neither a selective excitation nor inactivation of detectors. Rather, various detectors are evenly activated. (d) Responses to U-RDS after adaptation to A-RDS of crossed disparity (−4 dots). The depressive effect of adaptation on the sensitivity of an individual detector is assumed to be proportional to its activity in response to the adapting stimulus. We do not consider any time factor and chose a suitable value of decrement rate (0.9) so as to depict the aftereffect qualitatively. As can be observed, the detectors tuned to the disparity of adapting A-RDS are strongly activated relative to the others after adaptation as if the detectors responded to the C-RDS of the same disparity without adaptation (Fig. 2a) in spite of the degraded amplitude, suggesting the emergence of depth sensation.

of A-RDS. Thus, even though U-RDS could activate all detectors evenly in an unadapted state, the subsequent presentation of U-RDS is expected to strongly excite the formerly inactivated detectors relative to the others and produce an illusory sensation of depth (see Fig. 2d).

3. Psychophysical experiments

We tested the prediction of simulation results in the following psychophysical experiments.

3.1. Experiment 1

3.1.1. Method
3.1.1.1. Subjects.
Four expert and 13 naïve subjects whose stereo acuity was normal (more than $40''$ in Randot Stereotests, Stereo Optical, Co.) participated in the experiment.

3.1.1.2. Apparatus.
RDS stimuli were generated by a VSG graphics card (CRS, Rochester, UK) and presented dynamically on a CRT monitor (FlexScan T760, 19 in., EIZO) at a viewing distance of 70 cm. For the dichoptical presentation, ferroelectric stereo-goggles were synchronized with the refresh rate of a CRT monitor (Crystal eyes for PC, Stereographics Co.) at 120 Hz (60 Hz for each eye).

3.1.1.3. Stimulus.
Subjects fixated a central black cross (on the screen plane, subtending $29.6' \times 44.3'$, presented to both eyes) against a background (mean luminance was 5.54 cd/m² with goggles). Disparate areas of RDSs covered the whole screen, subtending $20.8° \times 21.2°$. The dots were each $2.0' \times 3.0'$, colored black or white with equal probability.

3.1.1.4. Procedure.
We adapted subjects to dynamic A-RDS for 1 min and asked them to report the direction of depth they perceived after viewing dynamic U-RDS (with reduction of Michelson contrast to 40%) for 5 s (see Fig. 3). Subjects were instructed to gaze at the fixation point throughout each trial. During the adaptation phase, an A-RDS of either crossed or uncrossed disparity ($\pm 5.9'$) was chosen at random and displayed on the screen. The disparity values of adapting A-RDSs were selected from the fact that the stereoscopic after-effect reached a maximum when the adapting C-RDS had between $4'$ and $8'$ of either crossed or uncrossed disparity (Long & Over, 1973). At the end of each presentation, subjects made a two-forced-choice decision about whether a test stimulus (U-RDS) was perceived at 'near' or 'far' depth relative to the fixation point. The trial was repeated until each condition was presented 20 times (40 times in total). Before every 10 trials, the two conditions were presented once to remind the observer of their different appearance and to help him maintain vigilance. No feedback about the accuracy of responses was given. Subjects pushed one of two key pad buttons to make a two-forced-choice decision at the end of a trial, and this response triggered the next trial after a 30 s delay. Responses for the direction of depth conducive to the model prediction (adaptation to an A-RDS of crossed disparity produces near depth perception and vice versa) were regarded as "correct," and the rate of correct identification was calculated.

3.1.1.5. Results.
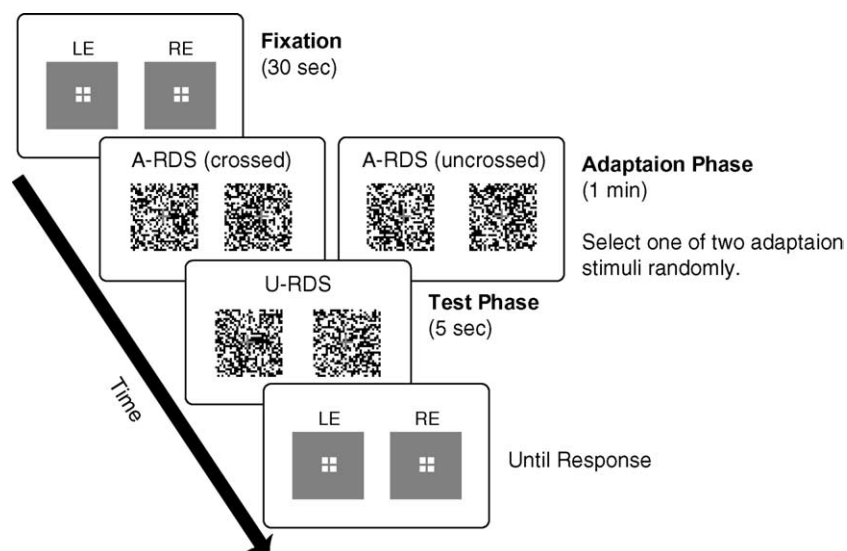Fig. 4a shows the result of the adaptation experiment. About 70% of the subjects were able to dis-

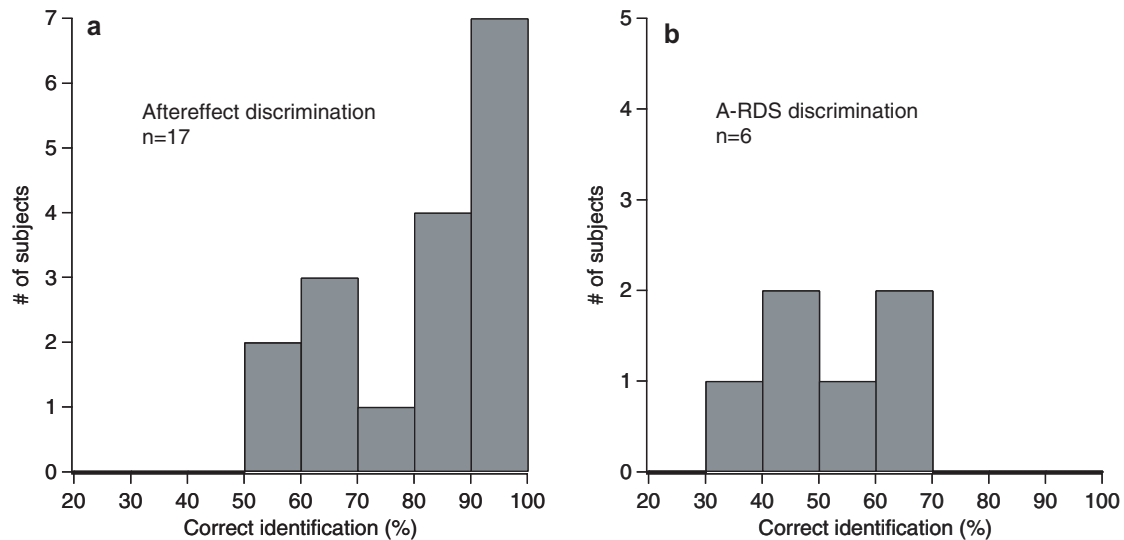Fig. 3. Sequence of events on each trial in the adaptation experiment.

Fig. 4. Histograms on performance of discrimination tasks. (a) Discrimination between two depth aftereffects. About 70% of the subjects were able to discriminate between two aftereffects with more than 75% accuracy, and about one half of the subjects showed a good performance of more than 87.5%. The average rate of correct identification across all subjects was 81.2% ± 15.3 std. (b) Discrimination between two A-RDSs (crossed and uncrossed, ±5.9′) in an unadapted condition. All naïve subjects participating in the task showed reduced performance of discrimination toward chance level. The average rate of correct identification across all subjects was 49.2% ± 12.9 std.

criminate between the two conditions at high probability (more than 75%) and about one half of the subjects showed good performance (more than 87.5%), supporting the hypothesis of the presence of predicted depth illusion. The subjective impression of depth sensation induced by this illusion was vague compared with the depth sensation of C-RDS. Most of the subjects did not perceive a crisp surface at a distinct depth but rather a lacy surface covering the fixation point for the 'near' condition or the fixation point floating in air for the 'far' condition. Nevertheless, the illusory depth was more consistent around a certain depth than the fluctuating depth of U-RDS in an unadapted state and some subjects reported that they were able to see a surface. Subjects also verbally reported that they perceived one of the two directions of depth more strongly. Such preferred depth was not biased toward one particular direction across subjects; across subjects, preference for near depth was just as common as far depth. These results are reminiscent of the findings that individual subjects generally preferred one direction of depth to the other (Richards, 1971). We could not see depth aftereffects when A-RDS and U-RDS were presented statically (see Section 4).

3.2. Experiment 2

It is conceivable that the subjects gave their answers based on the visual difference between the two adapting stimuli. Indeed, expert subjects could discriminate between the two adapting stimuli accurately with the clue that the apparent depth of the dots in A-RDSs was slightly biased in the direction opposite to its disparity. However, naïve subjects could not discriminate two adapting stimuli as accurately as they could discriminate illusory depth aftereffect. We tested the performance of a discrimination task between two A-RDSs of crossed and uncrossed disparities without adaptation. Naïve subjects who showed high performance (more than 80%) in the adaptation experiment participated in this task ($n = 6$). At the beginning of every 10 trials, two A-RDSs, the same as in the above adaptation experiment (experiment 1), were presented one at a time as reference stimuli. Then, one of the two A-RDSs was chosen at random and displayed on the screen for 5 s. After each presentation, subjects were asked to answer which of two reference stimuli had been presented (a two-forced-choice decision). For all subjects, the performance of discriminating between two A-RDSs was severely reduced to a chance level (see Fig. 4b). Consequently, it seems most unlikely that the good performance of many naïve subjects on the aftereffect discrimination could be explained by their ability to discriminate the adapting stimuli. We can conclude that, in the adaptation experiment, the naïve subjects were not certain of the visual difference between adapting A-RDSs but were indeed able to provide the perceived depth in U-RDS after adaptation. Even expert subjects commented that they did not notice the difference between the adapting A-RDSs unless they were asked to discriminate among them. All of the subjects except for the authors ($n = 15$) thought that the two identical test stimuli were different to give different depth impressions.

3.3. Experiment 3

We further examined some factors concerned with this illusion by additional experiments. Hereafter, one expert (subject RH) and one naïve subject who demonstrated high performance (more than 87.5%) in the first experiment participated in the following experiments. The total number of trials was reduced to 20 times. The experimental procedure was essentially unchanged.

First, taking into account the fact that the direction of perceived depth in U-RDS is negatively related to fixation disparity (divergences with respect to the surroundings are associated with near depth, and convergences are associated with far depth) (O'Shea & Blake, 1987) and that A-RDS gives rise to vergence eye movement in the opposite direction to its disparity (Masson, Busettini, & Miles, 1997), it may be argued that misalignment of vergence induced by A-RDS caused the perception of depth in the direction corresponding to the disparity of A-RDS when viewing U-RDS.

As evidence against the vergence hypothesis, we found depth corrugation aftereffects induced by anticorrelated images of RDS that portray a sinusoidally corrugated surface with vertical ridges (depicted in Fig. 5). Following inspection of the adapting A-RDS, U-RDS appears to be corrugated sinusoidally. If vergence were responsible for the illusory depth, the perceived depth in U-RDS would be homogeneous, and the corrugated surface or disparity gradient would not be seen.

We confirmed the corrugation aftereffect by testing whether subjects can discriminate the aftereffects of two A-RDSs of sinusoidal gratings that are mutually antiphased in depth. The fixation point was located midway between a peak and a trough of the corrugations, and subjects were required to report which side of the fixation point (left or right) was perceived at near depth. The purpose of this was to make subjects answer the perceived disparity gradient. The corrugation frequency used in the experiment was 0.15 cycle/deg and the peak-to-trough amplitude of disparity was ±7.9′.
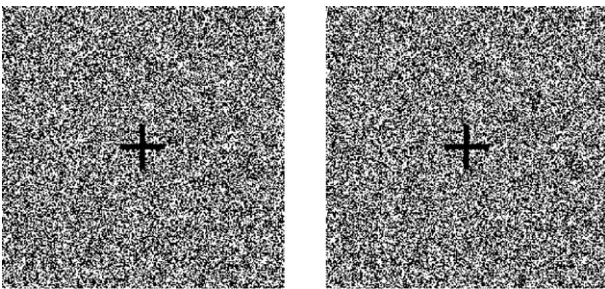

Fig. 5. An example of C-RDS that depicts vertically oriented sinusoidal corrugation.

Both subjects reported seeing the corrugated surface and the discrimination between two conditions was almost perfect (RH: 100%, IT: 90%), suggesting that vergence is not fundamental for depth perception in the illusion. Additionally, performance of subject RH (expert) to discriminate the two adaptation stimuli used in this experiment without adaptation became worse (65%), compared with 100% correct responses on aftereffect discrimination, which implies that even expert subjects do not respond to the adapting stimuli but to the apparent depth of test stimulus.

3.4. Experiment 4

As mentioned above, individual subjects reported a clearer perception for one direction of depth (near or far depth). Therefore, it is also possible that the subjects perceived the mere direction of depth rather than the amplitude of depth from the fixation disparity. In order to investigate the extent to which perceived depth is separable, we used two A-RDSs whose disparities were different in magnitude (−7.9′ and −2.0′) but the same in the direction of depth (crossed disparity) as adaptation stimuli. The difference of the two disparity values was comparable to the separation of the distinct disparity-detection channel (between 5′ and 10′) elucidated by a study of stereoscopic aftereffect (Stevenson, Cormack, Schor, & Tyler, 1992). Subjects were asked to discriminate between two samples with near depth. All subjects perceived the different amount of depth between two conditions; the rate of correct identification was almost perfect (subject RH: 100%, subject ND: 90%) as it was when the adaptation stimuli were A-RDSs of uncrossed disparity (7.9′ and 2.0′) (subject RH: 100%, subject KH: 95%). These results indicate that the depth sensation of this illusion is more than near or far impression.

3.5. Experiment 5

If the illusory depth results from relatively strong activations of disparity detectors that are not adapted during the inspection of A-RDS, we can consider that, besides U-RDS, any test stimulus that excites the previously unadapted detectors also produces similar depth sensation.

Since model simulations suggest that an A-RDS excites detectors that are not tuned to its disparity (see Fig. 2b), an A-RDS whose disparity is different from the disparity of adapting A-RDS is expected to activate the unadapted detectors as the test stimulus and induce the perception of depth.

In order to test this prediction, we modified the procedure of the above experiments as follows (see Fig. 6); the adaptation stimulus was settled to an A-RDS of crossed disparity (−5.9′), and an A-RDS whose disparity was either crossed or uncrossed (±5.9′) was then dis-
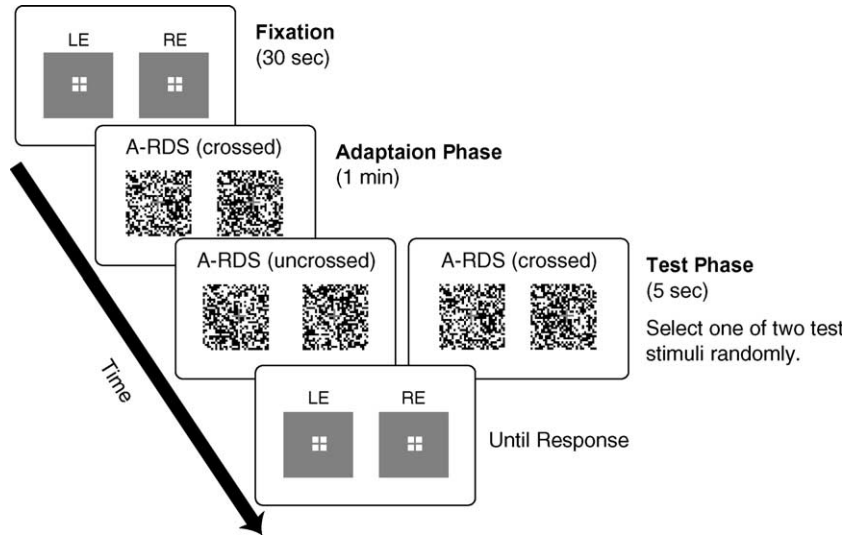
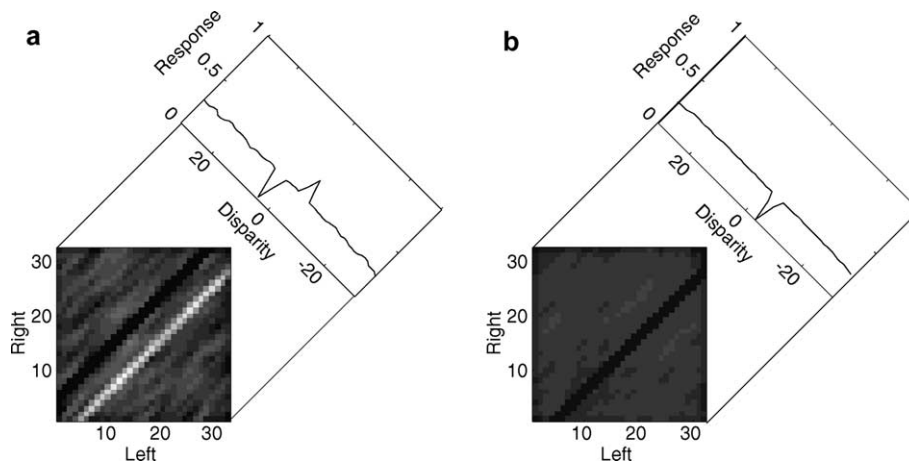Fig. 6. Sequence of events on each trial in experiment 5.

Fig. 7. The simulated responses of disparity detectors to A-RDSs after adaptation to an A-RDS of crossed disparity (−4 dots). The results are derived from the same calculation described in Fig. 1d. (a) Responses to an A-RDS of uncrossed disparity (4 dots). Though the detectors tuned to the disparity of the test stimulus are inactivated, formally unadapted detectors tuned to the disparity of adaptation stimulus provide strong excitation relative to the other, predicting the emergence of depth sensation. (b) Responses to an A-RDS of crossed disparity (−4 dots). Unadapted detectors are still inactivated in response to the test stimulus, suggesting that consistent depth will not be perceived.

played as a test stimulus. Subjects were instructed to respond whether they perceived near depth or not.

The hypothesis predicts that an A-RDS of uncrossed disparity (different from adapting A-RDS) will be perceived in 'near' depth (see Fig. 7a) but an A-RDS of crossed disparity (same as adapting A-RDS) will not be perceived as having a constant depth (see Fig. 7b) as in the case without adaptation. The results proved the prediction almost perfectly (subject RH: 100%, subject IT: 95%). The converse is true when the disparity of the adaptation stimulus was uncrossed (subject RH: 100%, subject YZ: 100%), indicating that the depth aftereffect is perceived whenever a test stimulus excites the unadapted disparity detectors.

4. Discussion

We found that our illusion is perceived when A-RDS and U-RDS are presented dynamically but not when they are presented statically. Even though our energy model does not include temporal factor to investigate the difference between dynamic and static presentation in detail, we show that our simple model explains the phenomena qualitatively. As described in Fleet et al. (1996) and Read and Eagle (2000), when input images are correlated, binocular energy neurons (or cross-correlation functions) have its central peak at the true displacement of input images for all different filters irrespective of the preferred orientation, phase and

spatial frequency of the channel (see Fig. 1 in Read & Eagle, 2000). Thus, simply picking the common largest peak provides the correct displacement of images. One of the simplest methods to do this is to summate energy model responses across all different filters (Fleet et al., 1996). On the other hand, when the images are anti-correlated, energy neurons have its central trough at the displacement, but false peaks occur at different positions for the different filters (see Fig. 1 in Read & Eagle, 2000). Since amplitude of the response of respective filters depends on the configuration of images, the positions of the largest false peaks vary with input patterns.

Therefore, if we assume that human stereo-system is very sensitive to the large peak among filters, the system can detect correct disparity from C-RDS (Fig. 8a) but detect distributed false disparities from A-RDS (Fig. 8b) when input images are presented statically. Responses to a static U-RDS are similar as the result of a static A-RDS (Fig. 8c). In this way, static A-RDS and U-RDS
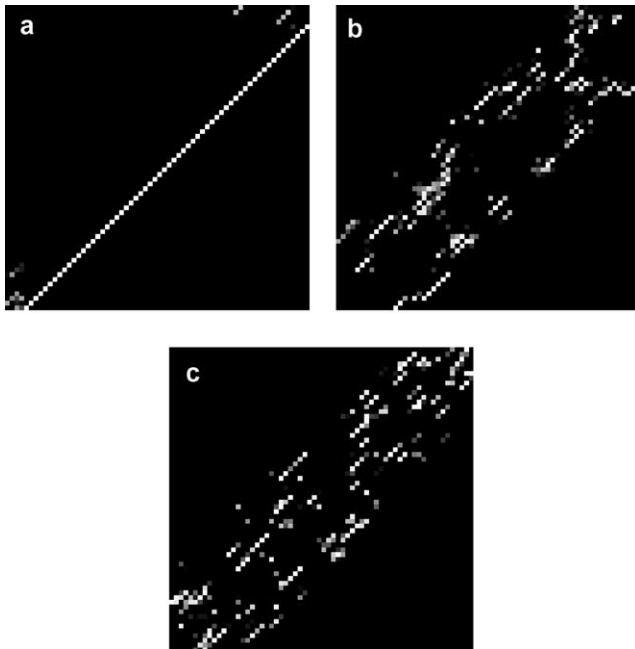

Fig. 8. The simulated responses of disparity detectors to several types of static RDS. We use 2D images (64 × 64 pixels) for input and include orientation selectivity in binocular energy neurons. Parameters of each filter are followings: phase = (0, pi/4, pi/2, 3*pi/4), orientation = (0°, 45°, 90°, 135°), (spatial frq., size of Gaussian window) = ((1, 1/2), (2, 1/4), (4, 1/8), (8, 1/16)). Disparities depicted in these maps are limited within ±16 pixels. In order to describe sharp peak sensitivity, disparity maps are normalized by maximum responses at each column and row. (a) Responses to static C-RDS. Detectors tuned to the disparity of C-RDS are selectively activated regardless of static and dynamic presentation. (b) Responses to static A-RDS. Although there are multiple excitations of disparity detectors except for one sensitive to the disparity of A-RDS, whole excitations are sparse, compared with the responses to dynamic A-RDS. (c) Responses to static U-RDS. Disparity detectors are sparsely activated depending on input images.

activate particular disparity detectors depending on input image patterns.

On the other hand, when A-RDS patterns are presented dynamically, the positions of false peaks change among all disparity detectors except for one sensitive to a true displacement of images. Therefore, if we plot averaged responses of disparity detectors to dynamically changed A-RDS images, we will get a pattern depicted in Fig. 2b. Since responses of binocular energy neurons to U-RDS have neither its central peak nor trough, all disparity detectors are activated equally to dynamic U-RDS (see Fig. 2c).

If we assume that selective unadaptation of disparity detectors during the inspection of A-RDS and their subsequent excitation in response to U-RDS causes our depth aftereffect, we can understand why static presentation does not induce the illusion. Since static A-RDS and static U-RDS have strong localized false peaks, they fail to selectively unadapt disparity detectors sensitive to the displacement of an A-RDS during adaptation and fail to activate those detectors selectively stronger than others at test phase.

It has been shown that static A-RDSs with interocular delay induce depth perception (optimal delay for depth is around 80 ms) (Cogan et al., 1993). Since we used ferroelectric stereo-goggles for the display, the right and left eyes' images were delayed with respect to each other by one frame (16.7 ms). Though Cogan et al. reported that delays 15–30 ms do not induce depth in static A-RDS, one would suspect that the sensitivity to interocular delay with dynamic A-RDS may be greater than with static A-RDS. Therefore, it may be possible that the interocular delay in our stimuli is responsible for generating the weak sensation of depth (as visible to expert subjects) and induces the aftereffect illusions reported here. We replicated experiment 1 and used dynamic RDS stimuli that were generated by a method that does not introduce an interocular delay. Subjects observed the left and right eyes' images drawn simultaneously on a monitor through mirror stereoscope. Stimulus size was 12.5° by 12.3° and dots were each 3.8′ by 3.7′. Disparities of A-RDSs used here were ±11.1′. We ran four subjects and found that all subjects saw the depth illusion induced by the aftereffect of A-RDS and their discrimination performance was very good (100%, 90%, 90% and 85%, respectively). From these results, we can conclude that the phenomenon of depth-by-interocular delay do not play a crucial role in our aftereffect illusion.

Contrary to previous studies using static A-RDSs (Cumming, Shapiro, & Parker, 1998; Read & Eagle, 2000), depth cues in dynamic A-RDSs used in our study are detectable if observers are trained or strongly attend to detect them. Even discrimination performance of naïve observers depicted in Fig. 4b is unlikely to be statistically at chance level. However, depth cues in dynamic

A-RDSs is still hard to detect and high performance of naïve subjects on detecting depth aftereffect cannot be explained merely by their ability to discriminate A-RDSs. In addition, all subjects, except for authors, who did not know exact stimulus configurations reported that they thought depth impression was induced by test stimuli, and adapting stimuli were identical. Since depth cues in dynamic A-RDSs are very weak and ambiguous, depth perception does not become consciously aware during adaptation of A-RDSs, unless subjects are instructed to attend to it. Nevertheless, subjects report a consistent depth perception in test stimulus (U-RDS) after adaptation and discrimination performance is very good. Therefore, our depth aftereffects are induced regardless of conscious awareness of depth perception during the adaptation phase. Whether conscious depth perception is involved during the adaptation of an A-RDS or not, observation of an A-RDS is considered to cause selective unadaptation of disparity detectors at low-level processing as described by our energy models. Consequently, following presentation of an U-RDS excites these unadapted disparity detectors selectively and induces conscious depth perception.

5. Conclusion

In conclusion, we found that the aftereffect of A-RDS produces depth perception in U-RDS. According to our simulation studies and psychophysical experiments, this illusion can be explained by the selective unadaptation of disparity detectors during the inspection of A-RDS and their subsequent excitation in response to U-RDS.

The finding of this illusion has several implications. First, our results indicate that the perception of both A-RDS and U-RDS (interocularly not correlated input images) involve multiple excitations over various disparity detectors in common. Such excitations of disparity detectors are likely to cause a multistable state on the neural machinery subserving stereopsis and produce rivalrous and fluctuating depth perception.

Note that the viewing of artificial stimulus such as A-RDS and U-RDS is not the only situation in which images are not correlated between the two eyes. Even in a normal three-dimensional scene, the situation when a surface occludes a more distant surface gives rise to regions that are partially hidden by the foreground and visible to only one eye. Since these interocularly unpaired regions are found at every vertical boundary between two surfaces, such regions could be used by the visual system to indicate the presence of a depth discontinuity that is a fundamental clue for recovering contour as well as depth (Nakayama & Shimojo, 1990). It might be considered that interocularly unpaired images are actively detected by monitoring concerted activations of multiple disparity detectors.

Second, since our illusion is sufficiently predictable from binocular energy neuron responses, this illusion provides psychophysical evidences supporting that computational framework of the binocular energy model is plausible as disparity processing in human visual system. We show that the binocular energy model, though originally proposed for depicting the response profiles of disparity-selective neurons in area V1, is applicable to explain some aspects of human stereopsis. This idea has been also supported by studies using psychophysical technique of reverse correlation (Neri, Parker, & Blakemore, 1999).

Finally, the most interesting aspect of this illusion is that, although both A-RDS and U-RDS are perceptually rivalrous with no consistent depth, subjects can perceive a consistent depth in U-RDS after viewing A-RDS. Note that most of the previously reported aftereffects are attributed to the selective adaptation of neural detectors tuned to a particular range of a visual dimension and have a negative effect on the perception of a subsequent stimulus (Blakemore & Julesz, 1971; Gibson, 1937; Grunewald & Lankheet, 1996; Long & Over, 1973). However, the illusion demonstrated here is novel in that selective *unadaptation* causes a *positive* aftereffect; it is based on broad-band adapting effects that has a narrow notch in energy at a specific value of disparity, thus an A-RDS of crossed disparity produces a near depth, and vice versa. In other words, this illusion is an inside-out stereoscopic aftereffect. Since viewing of A-RDS excites multiple disparity detectors and perturbs a consistent depth perception, subjects are not aware of what they are being adapted to (or not) during the adaptation phase. Therefore, we suggest that this illusion results from *unconscious adaptation*.

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