in the conditioning of CS approach and contact behaviors such as those observed in the initial experiment.

Six control chicks were trained similarly to paired subjects in the first experiment. On each of three consecutive days, these subjects received 40 CS-US conditioning trials with the chamber temperature set at 15°C, 10°C, and 5°C on days 1, 2, and 3, respectively. To assess the possible contribution of accidental peck-heat pairings, six other subjects were given omission training (O) in which the heat lamp was activated provided that subjects did not peck the key light stimulus; one or more pecks to the key light caused omission of the 4-second heat lamp presentation at the termination of the 8-second trial stimulus.

Within 70 trials, all 12 chicks began pecking the key light. Cumulative response records of four subjects in the paired condition and four subjects in the omission condition are shown in Fig. 2 (*12*). Omission subjects all acquired the key pecking response and persisted despite response-dependent nonreinforcement, although they responded with a generally lower rate than did paired subjects. Over the course of the 90 trials beginning with the first CR, the four omission subjects in Fig. 2 responded on 25 to 55 percent of the trials. Under similar experimental conditions, even higher response frequencies have been observed in additional subjects (data not included in this report). As in the first experiment, the change in topography from pecking to snuggling was observed in both paired and omission subjects.

The present data support the following conclusions: (i) Approach and contact of conditioned stimuli is under the control of Pavlovian reinforcement contingencies. Only paired (but not random) presentations of the key light and the heat lamp were effective in producing and sustaining key responding (experiment 1). Furthermore, key responding emerged and persisted even when contacts of the key actually prevented the heat lamp from being activated (experiment 2). (ii) Instrumental approach and contact of US's are unnecessary for the emergence of CS approach and contact. The chicks approached and contacted the lighted key even though no instrumental behaviors were required to receive the heat lamp stimulation. (iii) Approach and contact of CS's does not depend on similar or compatible CS- and US-controlled responses. The chicks approached and pecked or snuggled with the lighted key even though the heat stimulus evoked none of these behaviors. (iv) The topography of the conditioned response is not immutable and may undergo transformation during the course of conditioning. The pecking of paired and omission chicks tended to evolve into snuggling on successive days of training.

The form of the conditioned behaviors observed in these experiments raises an important issue concerning CR determination in Pavlovian conditioning. Here the chicks engaged in energetic approach, pecking, and snuggling activities toward the key light CS even though the heat lamp US elicited generally unenergetic and undirected postures and movements. If the topography of the conditioned response were primarily determined by the reinforcing stimulus and if the CS were merely a substitute or surrogate for the US (*1–3*), then the CS should have evoked the latter behaviors rather than the former ones. That this did not occur points to conditioned stimuli as potentially important determinants of conditioned response form and direction in conditioning studies (*13*).

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2. G. B. Peterson, J. E. Ackil, G. P. Frommer, E. S. Hearst, *Science* **177**, 1009 (1972).
3. H. M. Jenkins and B. R. Moore, in preparation.
4. Peterson *et al.* (*2*) used electrical stimulation of the rat brain as US, which also required no instrumental approach or contact behaviors. The functional similarity between electrical stimulation of the brain and more "natural" reinforcers is presently a controversial issue [J. A. Trowill, J. Panksepp, R. Gandleman, *Psychol. Rev.* **76**, 264 (1969)].
5. A possible exception was reported by H. Rachlin [*J. Exp. Anal. Behav.* **12**, 521 (1969)] who followed key light presentations with electric shock reduction and observed some increase in pigeon's key pecks and wing flaps.
6. The chamber temperature was set at 15°C on days 1, 2, and 3; 10°C on day 4; and 5°C on days 5 and 6. The chamber temperature was reduced in an attempt to maintain the effectiveness of the heat reinforcer because the subjects appeared to be adapting to the cold chamber by day 3 and would occasionally "nap" during experimental sessions. The reductions in chamber temperature did not entirely eliminate cold adaptation, however.
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9. Interpretation of these data as well as the lowered pecking probability for P-R animals in phase 2 (Fig. 1) is complicated somewhat by the decline in responsiveness to cold (*6*). Therefore, (i) as far as the present data are concerned, only trials with at least one peck were considered, and (ii) R-P animals actually increased their response frequencies in phase 2.
10. Baby chicks will also peck a key when pecks immediately produce heat and light stimulation [J. F. Zolman, S. D. Chandler, D. Black, *Develop. Psychobiol.* **5**, 181 (1972)].
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12. The two other paired subjects responded at rates intermediate to those of subjects 3P and 1P. The two other omission subjects responded at rates intermediate to those of subjects 7P and 4O; however, neither subject responded within the first 30 trials and so their data were not included in Fig. 2.
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14. Supported by NSF postdoctoral fellowship 41105. I acknowledge the aid of my supervisor, N. S. Sutherland, and the valuable advice and assistance of R. J. Andrew and D. Clayton.

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Disparity Detectors in Human Depth Perception: Evidence for Directional Selectivity

Abstract. *Viewing a target moving in depth depresses visual sensitivity to depth when test and adapting stimuli simulate motion along closed paths with the same directions of rotation. However, for opposite directions of rotation, sensitivity is either unaffected or increased. This points to two classes of disparity detectors. Either eye's input to a single class of disparity detector consists of the physiological responses to a single direction of horizontal movement.*

Stationary objects appear to be in motion if objects moving in one direction are first viewed for some time. The direction of the illusory motion is opposite to the direction of movement of the first-viewed objects. This aftereffect of seen motion has been cited as evidence for the presence of directionally selective motion detectors in the human visual system (*1*). According to this explanation, the human visual system contains motion detectors that respond preferentially to a retinal image that is moving in a specific direction. The "preferred" direction differs for different motion detectors. The particular detectors that are excited by a moving stimulus provide a physiological representation of the direction of movement. The balance between the

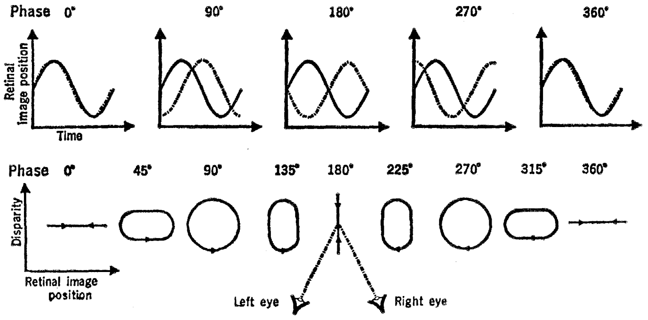

Fig. 1. (Top) Position of retinal image as a function of time for left eye stimulus target (dotted line) and right eye stimulus target (solid line). The position of each target was varied sinusoidally. The phase difference between the two sinusoidal oscillations was then changed. (Bottom) The apparent movements in depth of the binocularly fused target for each phase setting. The plots are of retinal disparity as a function of retinal image position.

outputs of detectors with different "preferred" directions is upset when all detectors with the same "preferred" direction are selectively fatigued, and this imbalance produces an illusion of movement. Motion-sensitive neurons of a type that could be responsible for this effect have been found in rabbits (*2*).

We report a new aftereffect of seen motion. The aftereffect cannot be observed monocularly. It provides a clue to the way in which the signals from the left and right eyes are combined so as to produce the sensation of depth.

When suitable static two-dimensional patterns are viewed by the left and right eyes, the binocularly fused image appears to be extended in the third dimension, as in the familiar stereoscope. If suitable moving two-dimensional patterns are viewed by the left and right eyes, then the binocularly fused image appears to move in the third dimension. In our experiments, both left and right eyes viewed separate patterns of small, irregularly spaced black dots (*3, 4*). Each pattern subtended an angle of 5°. The central 2° of each pattern could be oscillated from side to side while the outer parts of the pattern remained stationary. The patterns viewed by the left and right eyes were identical except that the central areas (that is, the targets) could be oscillated independently. The targets did not leave a blank space when they moved.

Both targets oscillated from side to side at a rate of 0.8 hertz. We had found that this frequency was sufficiently low to avoid confounding the threshold for movement in depth with the threshold for sideways movement (*5*). Both targets moved in simple harmonic motion with peak-to-peak amplitudes set at ratios of either 1:1, 1.5:1 or 2:1. Figure 1 shows a ratio of 1:1. In our experiments we varied the phase relation (that is, the relative timing) of the sideways oscillations presented to the left and right eyes. Figure 1, top, illustrates how the retinal image positions for the left eye target (dotted line) and right eye target (solid line) varied as a function of time.

Figure 1, bottom, gives an impression of how the apparent motion of the binocularly fused target changed when we altered relative phase. When the phase difference was 0°, the central target appeared to oscillate from side to side and did not move in depth at all. When the phase difference was increased to 45°, the target pursued an elliptical orbit in depth. The sense of rotation around the orbit meant that the target was moving from left to right when it appeared nearest to the eye (largest crossed disparity) and from right to left when it appeared furthest from the eye (largest uncrossed disparity). As we progressively increased the phase difference, the orbit grew more elongated in depth until, at a phase angle of 180°, the target appeared to oscillate along a straight line directed at a point midway between the eyes. Further increases in phase angle caused the orbit first to open out and then flatten until, for a phase of 360°, the situation was the same as for 0°. These illusions are just what would be expected from the known facts of binocular disparity. Figure 1 also illustrates the central point that the sense of rotation of the orbit was opposite for phase angles less than 180° than for phase angles greater than 180°.

In experiment 1 we set the phase to some fixed value and adjusted a control knob that varied the amplitudes of the target oscillations until movements in depth could just be seen (*6*). An adjustment of the single control knob produced the same fractional change in the oscillation amplitudes of the left and right targets. The peak-to-peak amplitude through which retinal disparity oscillated was then calculated and plotted as the depth threshold as a function of phase (solid lines, Fig. 2). These plots are baseline measures for the unadapted situation (*7*).

We found that sensitivity to depth oscillations was markedly reduced by steadily viewing the target for a period as short as 20 seconds. In order to minimize effects due to adaptation, we made threshold settings during 10-second viewings of the stimulus (*8*).

In experiment 2 we first adapted to a stimulus phase angle less than 180° (174° in Fig. 2A) by steadily viewing for 10 minutes a suprathreshold stimulus that had a peak-to-peak disparity excursion of 9.6′. At first the target appeared to execute large movements in depth, pursuing an anticlockwise orbit (if viewed from above). After 10 minutes of viewing, depth perception had collapsed so that the target appeared to oscillate from side to side. We then repeated our measurements of depth threshold over a range of test phases between 0° and 360° (dotted line, Fig. 2A). Each setting was made within 10 seconds of viewing time and was followed by 30 seconds of adaptation to a stimulus phase of 174°.

A clear elevation of threshold was produced for test phases less than 180°. In contrast, threshold was not elevated for test phases greater than 180°. Indeed, for one subject out of the three studied, a decrease in threshold was produced when the test phase was just greater than 180° (Fig. 2A).

In experiment 3 we first adapted to a stimulus phase angle greater than 180° (186° in Fig. 2B). Otherwise experiments 3 and 2 were similar. When the adapting phase was greater than 180°, depth threshold was clearly elevated for test phases greater than 180° but was not elevated for those less than 180°. Again, the same subject as before showed a reduction in threshold for phases just less than 180° (Fig. 2B). Identical test stimuli were used to obtain the quite different plots of Fig. 2A and Fig. 2B.

Experiments 1 through 3 were repeated for three different ratios of A_L to A_R (where A_L was the peak-to-peak amplitude of oscillation of the left eye stimulus and A_R was that of the right eye stimulus). The effects of adaptation shown in Fig. 2 held for ratios of 1.0 : 1, 1.5 : 1, and 2.0 : 1, though they were most marked for a ratio of 1.5 : 1.

The other subjects, one of whom was naive as to our hypothesis, confirmed the asymmetric threshold elevations of Fig. 2. We used adapting phases of 90° and 270° and an $A_L : A_R$ of 2.0 : 1. The asymmetry was also confirmed with a black bar target of 2° by 9′ at an amplitude ratio of 1.5:1.

Adaptation determined at a site peripheral to binocular convergence cannot explain the selective changes that we have found in the ability to see depth. At all times the left eye viewed a sinusoidally oscillating target, so that there was always an exact balance between movements in different directions. The same was true for the right eye. Phase, which alone distinguishes test and adapting stimuli, is meaningless if only one eye is used. Therefore, adaptation of monocular, directionally specific motion detectors cannot account for our observations in the way that it can account for classical aftereffects of seen motion such as the waterfall effect (*1, 2*).

However, our findings can be explained in terms of adaptation at, or central to, the site of binocular convergence. Suppose that for every point on the left retina there is a group of motion detectors that are most sensitive to stimuli moving from left to right (positive velocity for left eye, that is, v_L + ve), and a second group of motion detectors that are most sensitive to stimuli moving from right to left (negative velocity for left eye, that is, v_L − ve). Suppose also that for every point on the right retina there are similarly two groups of motion detectors. This means that for each value of retinal disparity there could be four classes of disparity detectors. These classes would be A (excited v_L + ve and v_R + ve); B (excited v_L − ve and v_R − ve); C (excited v_L + ve and v_R − ve); and D (excited v_L − ve and v_R + ve). The four classes would therefore exist only if the directionally sensitive outputs from both eyes are kept separate up to the level at which retinal disparity is computed.

Now consider the stimulus situation shown in Fig. 1 for phases less than 180°. When crossed disparity is greatest (that is, when the target appears to be nearest the eye), both left and right targets are moving from left to right so that class A disparity detectors are excited. We suggest that prolonged viewing will produce appreciable adaptation of class A disparity detectors but little adaptation of class B disparity detectors. This would explain our finding that depth thresholds were elevated for test phases of less than 180° but not for test phases of more than 180°.

A similar argument suggests that prolonged viewing of a stimulus with phase greater than 180° would produce appreciable adaptation of class B disparity detectors but little adaptation of class A disparity detectors. This could account for our finding that the asymmetry of the threshold elevation curve reverses when the adapting phase crosses 180° (Fig. 2, A and B) (*9*).

The small, localized reduction in depth threshold that we observed for one subject (Fig. 2) could be explained in terms of antagonism or mutual inhibition between class A and class B disparity detectors. Such a "sharpening-up" process might also account for our subjects' sensitivity to small changes in phase angle around 180°.

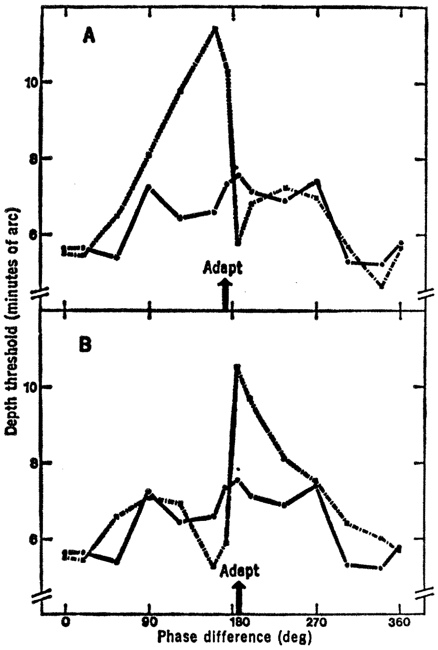

Fig. 2. Depth threshold (reciprocal of sensitivity) as function of phase difference between the target oscillations presented to the left and right eyes. The solid lines are control baselines measured with no adaptation. The dotted line in (A) shows thresholds measured after adaptation at a phase of 174° (arrow). The dotted line in (B) shows thresholds measured after adaptation at a phase of 186° (arrow). The left eye stimulus was a pattern of random black dots that subtended 5° and had mean luminance of 110 cd/m². The dots subtended 2′ and occupied about 10 percent of the total area. A 2° circular target area at the center of the stimulus was oscillated from side to side at a rate of 0.8 hertz; $A_L : A_R$ was 1.5 : 1. Each point is the mean of four settings.

In terms of biological usefulness, the ability to make acute discriminations between the inputs to class A and class B disparity detectors would give the ability to judge precisely whether an object approaching from a distance will pass just to the right or just to the left side of the head.

Our explanation for the findings of Fig. 2 has been qualitative, and entirely in terms of two of four possible classes of disparity detectors. A more quantitative explanation might involve an additional neuronal organization based on the relative amplitudes of oscillation of the targets in the left and right eyes ($A_L : A_R$) (*10*).

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5. D. Regan and K. I. Beverley, *Vision Res.*, in press; *ibid.*, in press.
6. The control knob did not give the subject a cue to the disparity setting since (i) the knob was circular, and (ii) from time to time the experimenter altered the relation between its position and stimulus amplitude.
7. Since $A_L : A_R$ was 1.5 : 1 in Fig. 2, depth oscillations could be seen even when the phase was 0° or 360°.
8. There have been reports of cyclopean adaptation, although these were for static disparities rather than for movement in depth. B. Julesz and C. Blakemore [*Science* **171**, 286 (1971)] reported that random dot stereograms used as adaptation stimuli can influence the perceived depth of similar test stimuli. Also, Julesz (*4*), published an ambiguous stereogram for which the direction of perceived depth is determined by prior exposure to an unambiguous stereogram.
9. Because the mean position of our target was in the plane of fixation, our argument has been framed in terms of crossed and uncrossed disparity detectors and would fit with W. Richards' suggestion [*Exp. Brain Res.* **10**, 380 (1970)] that detectors of crossed and uncrossed disparities are organized into separate pools. However, the existence of separate pools is not necessary for our argument. As an example, for targets whose mean position is off the fixation plane the argument could equally well be framed in terms of larger and smaller disparities.
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