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PERCEPTUAL ADAPTATION TO INVERTED, REVERSED, AND DISPLACED VISION [1]

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Recent research has shown that a simple form of adaptation to prism-produced displacement of the visual field consists primarily of a proprioceptive change—a change in the felt position of the arm seen through prisms—rather than a visual, motor, or visuomotor change. More complex sorts of adaptation (to inversion, reversal, and other optical transformations) can also be understood as resulting from changes in the felt locations of parts of the body relative to other parts. Contrary to the usual empiricist assumption, vision seems to be very stable, whereas the position sense is remarkably flexible. When the 2 senses provide discrepant information, it is the position sense that changes.

For over a century, psychologists have been experimenting with optical devices that displace, reverse, or invert the retinal image. When a person first puts on such a device, he misses things he reaches for and bumps into things he is trying to walk around. But after a while he adapts. He ends up behaving normally despite the optical distortion.

Typically, experimenters have accepted this adaptation as evidence for or against various theories about the origin of visual space perception in the infant. But even if one hesitates to generalize from adult behavior to infant development, adaptation to optical distortions is of interest in revealing how perceptual-motor systems work and how they can be modified.

Recently there has been much concern with the mechanisms for adapting to optical distortions and with the conditions that are necessary for such adaptation to take place. Less attention has been given to the *end product* of adaptation. What change does the adaptation procedure produce in the subject? How does the adapted subject differ from one who has not adapted?

Previous investigators have offered diverse answers to this question. For example, Kohler (1964) and Taylor (1962) believe that adaptation results in a change in visual perception. Smith and Smith (1962), on the other hand, claim that it consists mainly of learning specific motor responses. Held and Freedman (1963) say that adaptation "represents a change in state of the relevant sensorimotor control system" based on the storage of "newly correlated information" derived from "the one-to-one relation between movement and its sensory feedback [p. 457]."

This paper proposes another interpretation of adaptation: that it consists of changes in the position sense for various parts of the body. A

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change in position sense has been clearly demonstrated in one form of adaptation to displaced vision. The extension of this interpretation to other forms of adaptation is more speculative but seems to make sense out of a mass of otherwise perplexing data. (For summaries of earlier experimental work on adaptation see Held & Freedman, 1963; Kohler, 1964; Smith & Smith, 1962; Taylor, 1962.)

The Position Sense

Even in the dark we can perceive the relative locations of the various parts of our bodies. The sense that enables us to do this will be referred to as the *position sense,* and the perception of the position will be called a *felt position.* Changes in the position sense will be called, for want of a better adjective, *proprioceptive* changes. (The term *kinesthesis* will be restricted to the perception of movements of parts of the body.)

The position sense is a psychological phenomenon; its physiological basis has not yet been conclusively established. Receptors in the joints seem to play the major role (Rose & Mountcastle, 1960); however, efferent activity may enhance the responses of these receptors, making the position sense more accurate during active movement (Lloyd & Caldwell, 1965). The fact that monkeys can perform acts with a deafferented limb (Taub, Elman, & Berman, 1964) suggests that a "sense of innervation," registering the motor outflow to the limb, may be able to take over the functions of sensory inflow. Indeed, motor outflow seems to be the sole basis for registering the position of the eyes (Brindley & Merton, 1960; Helmholtz, 1962b; Ludvigh, 1952). If motor signals do play this role, though, the nervous system must somehow register the *positions* called for, not the *movements;* otherwise we would lose track of body parts whenever they were moved (or kept from moving) by an outside force.

Although information registered by the position sense is usually available to introspection, we are not constantly aware of the locations of all of our body parts. And sometimes a subject's conscious perception of the positions of some body parts (especially his eyes) is vague and variable, even though there is abundant behavioral evidence that these positions are being "taken into account" accurately. In general, the hypotheses presented in this paper apply whether the position information is conscious, potentially conscious, or not available to consciousness.

ADAPTATION TO DISPLACED RETINAL IMAGES

Arm Adaptation

Adaptation to inversion or reversal of the visual field may take many days or even weeks. However, as Helmholtz reported in 1866, a person can adapt to sideways displacement of the visual field in just a few minutes (Helmholtz, 1962b, p. 246).

If you look through prisms that displace the apparent locations of seen objects to the right, for example, and try to reach quickly for something, you will miss it by reaching too far to the right. But after just a few more attempts, your aim will improve considerably. When the prisms are then removed, however, you will reach too far to the left. For convenience, both the improved reaching while wearing prisms and the aftereffect when they are removed will be referred to as *adaptation* (i.e., adjustment to new conditions), since they are presumably manifestations of a single underlying change. The amount of adaptation (the *adaptive shift*) is indicated by the difference between a subject's responses on pre- and postadaptation tests. (During these tests the subject must not be allowed to see his hand; otherwise, by moving it slowly and guiding it visually, he would always be able to point correctly.)

Proprioceptive Changes. If a person's eyes are closed when he first puts on displacing prisms, he is surprised when he opens his eyes and looks at his hand. Because the prisms shift its visual image, his hand does not appear to be where he felt it was. If the discrepancy between the seen and felt locations of the hand is to be eliminated, either the person's visual perception or his position sense (or both) must shift.

According to the proprioceptive-change hypothesis, the subject comes to feel that his arm is where he saw it through prisms—even though this makes that arm's position sense erroneous (nonveridical). That is, after such a change, the subject's judgment of that arm's position relative to any other part of the body will be incorrect. If the prisms are removed and the subject tries (without seeing his hand) to reach for a target that he sees in a certain place, he will move his hand until he feels that it is in that place—but it will actually be off to one side of it. The same thing will happen if he tries to point at a sound or simply to point straight ahead. Only when judging the whereabouts of his hand relative to objects seen through prisms will he be accurate.

It is not clear a priori whether a proprioceptive shift would make a subject misperceive arm positions other than those he saw while adapting. Since neurons in the proprioceptive system have rather large receptive angles (Mountcastle, Poggio, & Werner, 1963), a change in the operating level of proprioceptive neurons in the central nervous system might exert an effect over a wide range of arm positions. At any rate, the presence or absence of such a shift should depend mainly on the actual position of the arm, not on the movements by which the position was reached.

Other Interpretations. Five other simple, plausible conceptions of the nature of adaptation can also account for the rapid improvement in reaching for objects seen through prisms. Each, however, suggests a different set of predictions about other behavior. These five conceptions, which are often implicit rather than explicit in previous investigators' writings, have been presented in greater detail elsewhere (Harris, 1963a). They are described briefly below, together with some of their predictions about a subject who adapts by pointing with one arm, using a stereotyped arm movement, at a single target seen through prisms.

1. *Conscious correction of one's aim.* When the subject misses the target, he realizes that the prisms are deceiving him about the target's location and so deliberately aims to one side of visual targets; when the prisms are removed, he goes back to pointing normally.

2. *Altered visual perception.* A changed translation from retinal image to perception makes a target which at first looked off to the side appear to be straight ahead. This new perception can be demonstrated by any appropriate judgment of, or response to, a visual target seen with or without prisms.

3. *Reorientation of the perceptual frame of reference.* Perception of all external stimuli, visual or auditory, is shifted to one side; perception of the arms, however, is unaffected (if perception of the arm shifted too, the

TABLE 1

TEST PERFORMANCE PREDICTED BY SIX INTERPRETATIONS OF ADAPTATION TO DISPLACED VISION

Test task	Proprioceptive change in the arm	Conscious correction	Visual perception	Frame of reference	Visuomotor recorrelation	Motor learning
Same as during adaptation[a]	+	+	+	+	+	+
Pointing at visual target without prisms	+		+	+	+	+
Pointing at visual target with unexposed hand		+	+	+		?
Verbal judgment of location of visual target		?	+	+		
Pointing at auditory target[b]	+			+		+
Verbal judgment of location of auditory target[b]				+		
Pointing straight ahead[b]	+					+
Pointing at visual target with different arm movements	+	+	+	+	?	
Pointing at visual targets in different locations	?	+	+	+	?	
Judgment of distance between hands[b]	+					
Judgment of location of passively moved adapted arm relative to visual target	+	+	+	+		
Pointing with adapted hand at unexposed hand[b]	+					+
Pointing with unexposed hand at adapted hand[b]	+					

Note.—The subject adapts by pointing with one arm, using a stereotyped arm movement, at a single target seen through prisms. A + indicates the prediction of an adaptive shift as large as that obtained with the task used during adaptation.

[a] Except that (as with all the other tests) the subject cannot see his hand and receives no information about his accuracy.

[b] While blindfolded.

subject would show no adaptive shift in pointing at targets).

4. *Visuomotor recorrelation.* Visual perception does not change, but a given visual input is paired with a different motor output. Since only the visuomotor system used during adaptation is altered, the unexposed arm and all nonvisual targets are unaffected.

5. *Motor-response learning.* The practiced arm acquires a new motor response to stimuli from a given spatial location regardless of their modality. There is a generalization de-

crement when the subject uses arm movements that differ from the practiced one.

Table 1 summarizes the predictions of the proprioceptive-change hypothesis and the other five conceptions. Several other, more sophisticated theories are discussed briefly at the end of this paper. Unfortunately, these theories often make equivocal predictions, or none whatever, about many of the tests listed in Table 1.

Experimental Findings. Harris (1963a, 1963b) carried out six of the tests listed in Table 1. The subjects, whose heads were held stationary by a bite board, adapted by pointing for 3 minutes at a visual target seen through prisms that displaced its image 11° to the right or left. Adaptation was found to produce sizable and significant adaptive shifts, which were virtually identical whether measured by pointing at visual targets, at auditory targets, or "straight ahead." The shift was no smaller when subjects pointed at targets several inches from the one they had practiced on, even though the arm movements used then differed from the practiced one. However, adaptation had little or no effect on pointing with the unexposed hand. Nor did it affect judgments of whether a given auditory target sounded straight ahead. (Hein & Held, 1960, had previously reported that, with a similar adaptation procedure, there was no change in judged location of visual targets.) Others have independently demonstrated the adaptive shift with auditory test targets and with pointing straight ahead (Pick, Hay, & Pabst, 1963) and the absence of any shift in pointing with the unexposed hand (H. B. Cohen, 1963; Hamilton, 1964a; Mikaelian, 1963; Scholl, 1926). Subsequent studies have also confirmed these three findings (Goldstein[2]; Hay & Pick, in press; McLaughlin & Bower, 1965; McLaughlin & Rifkin, 1965).

On the basis of these results, five of the notions listed in Table 1 may be ruled out. The data can be accounted for only by the first interpretation: that adaptation consists of a change in the felt position of the adapted arm relative to the rest of the body.

Further Tests. The proprioceptive-change interpretation implies that a subject should make errors in judging how far his adapted hand is from other parts of his body—for example, his other hand. This prediction was tested by having subjects (who had adapted their right arms by pointing at a target seen through prisms) move their unexposed hands to specified subjective distances from their adapted hands while blindfolded (Harris, 1963a). After seeing their right hands shifted to the right by base-left prisms, subjects felt their hands to be farther apart, at a given physical distance, than when their hands were not adapted. Subjects who wore base-right prisms felt their hands to be closer together. These results demonstrate that there is in fact a change in the felt location of the adapted hand relative to the other hand.

During these tests, the subject was not allowed to make any active movements with his adapted arm. Thus, a simple motor-learning or conditioned-response theory of adaptation is inadequate: Although self-produced movements may be an essential precondition for adaptation, they are not a necessary part of the end product. The adaptive shift is evident whether the subject actively points at a target during the test or a luminous target is moved until he says it is right over his

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[2] Donald Goldstein, personal communication, June 1964.

stationary hand (Hamilton & Hillyard[3]). A change in the position sense will indeed *affect* motor responses of the adapted arm, but the change does not itself *consist* of newly acquired motor habits. On the contrary, it is a *perceptual change* (in the felt position of the adapted arm).

The most direct evidence for the hypothesized change in position sense is obtained when the subject points with his unexposed arm (which points correctly at all other targets) at his stationary adapted arm. Harris' (1964) results fell just short of significance, but more recently Efstathiou and Held (1964) and Goldstein[2] have found large and significant shifts on this test, as well as on pointing with the adapted hand at the unexposed hand. Both findings were anticipated by Scholl (1926).

Related Findings. Several other recent studies fit in well with the proprioceptive-change hypothesis. Bossom and Hamilton (1963) and Hamilton (1964b) found that adaptation to displaced vision—in contrast to visual discrimination learning—shows complete interocular transfer and no intermanual transfer in split-brain monkeys; the adaptation is specific to the arm, not the eye. Nielsen (1963), Hay, Pick, and Ikeda (1965), Rock and Victor (1964), and Wertheimer and Arena (1959) have demonstrated that vision may immediately and completely dominate the position sense when the two disagree, a finding analogous to the smaller but longer lasting adaptive shifts discussed above.

All in all, it seems reasonable to conclude that, when a person watches one hand through prisms with little head movement, the adaptation is mainly a change in the felt position of that arm relative to the rest of his body. Although their own data did not rule out all alternative hypotheses, other investigators have independently, at about the same time, reached similar conclusions: that such adaptation takes place in the "kinesthetic spatial system" (Hochberg, 1963; Pick et al., 1963) or, more specifically, in the adapted arm's position sense (Hamilton, 1964a, 1964b). A similar hypothesis was proposed earlier by Scholl (1926).

Head-Body Adaptation

Another way to adapt to displaced vision is simply to walk around while wearing prisms (Hay & Pick, in press; Held & Bossom, 1961; Kohler, 1951, 1964; Taylor, 1962). The results are quite different from those of arm adaptation. When presented with a visual target after the prisms are removed, the subject points incorrectly with *both* arms, even if he saw neither one through prisms (Bossom & Held, 1957), and says the target *looks* straight ahead of him when it is actually somewhat off to one side (Held & Bossom, 1961; Kohler, 1964).

Is this type of adaptation, then, completely unlike arm adaptation? Probably not. Just as the felt relationship between arm and body is altered by moving the arm while wearing prisms, so perhaps the felt relationship between head and body is altered by moving the head while wearing prisms.[4] The three investigators who independently proposed this hypothesis

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[3] Charles R. Hamilton and S. A. Hillyard, personal communication, August 1964.

[4] It is convenient to think of arm adaptation as a change in the felt position of the adapted arm, with that of the rest of the body remaining unchanged. However, the same phenomena would be observed if the perception of the arm stayed the same and that of all of the rest of the body changed. Strictly speaking, we can detect only a changed relationship between the two. This is even clearer in the case of head-body adaptation.

—Hamilton (1964a), Harris (1963a, 1963c), and Mittelstaedt (1964)—were unaware that Kohler (1951, p. 23) had already observed just such a phenomenon: A subject who wore prisms developed the "habit" of holding his head turned 6°–9° to the right of his body midline but was "completely unaware" of the deviation.[5] He felt that his head was pointing straight ahead.

It is the unawareness, not the turning, that is crucial. Contrary to Smith and Smith's claim (1962, pp. 92, 116–117), a "compensatory reaction" of turning the head cannot in itself counteract the prism-produced visual displacement: The perceived location of an object (relative to one's body) does not normally change when one turns one's head, because the new position of the head is taken into account. Perception of the object changes only if a subject misperceives the orientation of his head.

Whereas misperception of just one arm affects only tests that involve that arm, virtually any test will show the effects of misperceived head orientation. If a subject feels his head to be pointing straight ahead of his body when it is really somewhat turned, then when he sees an object directly in front of his nose he will incorrectly (if he is not wearing prisms) perceive that object to be straight ahead of his body. If he tries to point at it with either hand, he will point straight ahead of his body and thus point incorrectly. (Such misperception of head position would, of course, lead to improved accuracy of performance while the prisms are on.) Similar results will occur even if the test apparatus constrains the subject to hold his head straight relative to his body, as in Held and Bossom's (1961) procedure. When Kohler forced his subject to point his head straight ahead, the subject felt that it was turned several degrees to the left (1951, pp. 23–24).

A change in the felt relationship between head and body necessarily entails a change in the perceived direction of visual targets relative to the body. But it would be inaccurate to describe such adaptation as solely a change in visual perception, since, for example, altered perception of head orientation would also result in altered auditory localization.

Intermanual Transfer. A number of investigators have found that if a subject watches one hand through prisms, with little head movement, the adaptation is completely or almost completely confined to the exposed hand. Helmholtz (1962a, p. 157), however, reported considerable adaptation of the unexposed hand as well. How can these findings be reconciled?

A plausible answer was suggested independently by Hamilton (1964b) and Harris (1963a, 1963c). They both noted (as did H. B. Cohen, 1963) that subjects whose heads were immobilized while they adapted showed

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[5] "*Als Prismenträger ist man ständig gezwungen, Auge und Kopf gegenüber der Greifrichtung etwas verdreht zu halten. Und in der Tat liess sich als Nachwirkung dieser aufgezwungenen 'Lebensgewohnheit' eine merkbare Verdrehung zwischen Kopf und Rumpf nachweisen, welche aber der Aufmerksamkeit der Vp. vollkommen entging. Sie meinte gerade und unverdreht zu stehen, während sie in Wirklichkeit den Kopf nach rechts gedreht hielt (6–9 Grad von der Körpermediane abweichend). Korrigierte man aber die Rechtslage des Kopfes, so entstand im Erleben der Vp. der Eindruck einer Linksverdrehung* [cf. Kohler, 1964, p. 38]."

The Fiss and Gleitman translation (Kohler, 1964) differs, in many places, from the German papers on which it is based (Kohler, 1951, 1953). Though usually slight, the discrepancies are sometimes misleading at crucial points. Therefore, the present writer's translations are occasionally given instead.

little intermanual transfer, whereas those who were free to move their heads, as Helmholtz was, exhibited considerable transfer to the unexposed hand. Hamilton and Harris concluded that moving the head while wearing prisms leads to a change in the felt position of the head relative to the body, which would make the subject mispoint with both hands even if he never saw them through prisms. If he did see one arm through prisms, he would show a larger aftereffect with that arm than with the unexposed arm (since, in addition to the error caused by misperceiving the orientation of his head, there would also be a misperception of the exposed arm's orientation), thus manifesting "partial intermanual transfer."

If this analysis is correct, the term intermanual transfer is, in this context, something of a misnomer. Transfer implies that the adaptive change in one arm (or relevant parts of the nervous system) somehow spreads to or induces a similar change in the other arm (or contralateral part of the nervous system). Although this possibility has not been definitely ruled out (as Hamilton, 1964b, noted), it is simpler to assume that the measured adaptation in the unexposed arm results wholly from head-body adaptation, which affects both arms equally, and that there is in addition some arm adaptation of the exposed arm.

Wooster's Experiment. The concept of altered position sense of the head removes much of the mystery from a phenomenon reported by Wooster (1923). Her subjects reached beneath an opaque board to point at targets that were visible, through prisms, above the board. Surprisingly, even subjects who never saw their hands through prisms and so had no "knowledge of error" gradually became more accurate. Wooster considered a number of possible reasons for the improvement, tested them in further experiments, and found that none fitted all of her data.

Although Wooster's subjects did not walk around while wearing prisms, they were free to move their heads and so could have undergone head-body adaptation. Had Wooster tested the unpracticed arm, she might have been even more surprised to find that it had improved just as much as the practiced one.

A change in the proprioceptively perceived relationship between head and body could also account for many of the findings reported by Wallach, Kravitz, and Lindauer (1963), by Bossom (1964), and by McLaughlin and Rifkin (1965), as well as for the aftereffects of the incidental vertical displacements produced by Stratton's (1897, p. 471) and Kohler's (1964, p. 32) inverting goggles.

Eye-Head Adaptation

All of the phenomena ascribed above to head-body adaptation (except for Kohler's direct observation of a change in felt head position) might equally well be due to a change in the registered relationship between the eyes and the head (Harris, 1963a)—a modification of the "judgment of the direction of the gaze," as Helmholtz (1962b, p. 246) put it. Indeed, Kohler (1964, p. 32) says that in his experiments alterations in "kinesthetic sensations" from the eyes were often encountered.

Unlike head-body adaptation, eye-head adaptation would not affect auditory localization. Thus, a subject who misperceived the orientation of his eyes should misperceive the location of a visual target relative to that of a sound from an unseen source (Harris, 1963a). Recent studies have demonstrated just such an auditory-visual mismatch. After certain adaptation procedures, a subject errs in judging where on a luminous visual scale a sound is coming from (Hay & Pick, in press; Wallach & Bernheim [6]). He points in one direction at a light and in another at a sound which is actually in the same place (Hay & Pick, in press; McLaughlin & Bower, 1965).

These and other findings reported by Hay and Pick (in press), McLaughlin and Rifkin (1965), and McLaughlin and Bower (1965), as they acknowledge in their later papers, are all attributable to a change in registered eye position plus a change in the exposed arm's position sense, with the amounts of the two changes varying during the course of adaptation.[7]

Because incorrect registration of eye position would entail incorrect localization of all seen objects, one can say that eye-head adaptation alters visual perception. But this alteration is fundamentally different from purely visual modifications such as dark adaptation and localized figural aftereffects. It is more akin to altered position sense in the arm or head. Thus it seems inadvisable to make a sharp distinction between "proprioceptive adaptation" (of the arm) and "visual adaptation." Such a distinction might, for example, lead to a fruitless search for modifications in the pathways connecting the retina to the visual cortex.

Half Prisms. Prisms that cover only the upper half of the eye displace the upper half of the visual field relative to the lower half, making a straight vertical line look discontinuous. Kohler (1964) reported that subjects who adapt to half prisms say that the line eventually looks straight and unbroken most of the time despite the discontinuous retinal image.

Although this adaptation sounds like a purely visual change—a change in perceived relationships *within* the visual field—Kohler's other observations indicate otherwise. When an adapted subject was asked to move his eyes straight up and down in the dark, Kohler says, the subject actually moved them in a jagged line, with a sideways jump approximately in the middle of the movement (*"einen seitlichen Sprung ungefähr in der Mitte der Bewegung"*—Kohler, 1951, p. 73; cf. 1964, p. 93). With more rapid eye movements, the path became diagonal. But the subject "always thought that his eyes moved vertically and without sudden deflections [1964, p. 94]." Apparently, the subject perceived a broken line as straight only because he felt that the jagged eye movement he made in scanning it was straight. What happened when the subject *fixated* the dividing line between the prism and nonprism areas? Kohler (1964, p. 83) says explicitly that, when fixated, vertical lines looked just as discontinuous after many days of adaptation as they had at first. Clearly, there was no change in the purely "pictorial" aspect of visual perception, but only in those perceptions of visual location that depend on the registration of positions and movements of the eyes. Note that the adaptation did not entail any change in scanning *behavior:* When scanning the discontinuous line, the subject made essentially the same eye movements after adapting as he had before. The only change was that a jagged eye movement was interpreted as straight. This is a perceptual change, not the acquisition of new motor responses.

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[6] Hans Wallach and Joseph Bernheim, personal communication, December 1963.

[7] Part of the shift that Hay and Pick (in press) attributed to arm adaptation may actually be due to head-body adaptation; Hay and Pick's tests do not distinguish between the two.

Curvature. Straight vertical lines look curved when viewed through a sideways-displacing prism because the prism displaces the top and bottom of the visual field more than the middle. The curvature is a set of relative displacements of the same sort as produced by a half prism. So perhaps adaptation to curvature also involves altered registration of eye movements without any change in scanning behavior. After adapting, the subject may feel that his eyes are moving in a straight line when they are actually tracing out a curve.[8] Perhaps the "unstable aftereffect" experienced by one of Kohler's subjects ("straight objects—for example, long and heavy steel pipes—curved and straightened out while the amazed subject was in the very act of looking at them"—1964, pp. 37–38) was due to alternate scanning and fixation.

An analogous case of curvature adaptation, resulting from altered kinesthetic perception of movements of the arm, was recently studied in collaboration with Judith R. Harris (Harris, 1964). Subjects moved one hand back and forth along a horizontal straight line while looking through prisms that made the line look curved upwards or downwards. Before this practice and again afterwards, they were asked to draw straight horizontal lines while blindfolded. The prediction was that if a subject ran his hand along a straight line that looked curved upward, for example, a straight horizontal arm movement would come to *feel* curved upward, so the subject would compensate and draw a *downward* curve in order to feel that his arm was moving in a straight line. A significant shift, in the predicted direction, was found. Note that this shift cannot be due to an intermodal figural aftereffect, because the shift is in the wrong direction; it cannot be motor learning, because the arm movements made during practice were actually straight.

ADAPTATION TO INVERTED RETINAL IMAGES

Is a proprioceptive-change interpretation appropriate when subjects adapt to optical transformations more drastic than displacement? Stratton's (1896, 1897) reports on his adaptation to "reinversion" of the retinal image indicate that the answer is yes.

Stratton's Experiments

Proprioceptive Changes. Stratton's reports are indeed difficult to comprehend—at times they sound bizarre, at times, self-contradictory. But it is clear that Stratton experienced proprioceptive changes similar to those considered above, though far more extensive and less stable.

When he first looked through inverting lenses, Stratton (1896) says,

> . . . the parts of my body were *felt* to lie where they would have appeared had the instrument been removed; they were *seen* to be in another position. But the older tactual . . . localization was still the *real* localization [p. 614].

Soon, however,

> . . . the limbs began actually to feel in the place where the new visual perception reported them to be. . . . The seen images thus became *real things* just as in normal sight. I could at length *feel* my feet strike against the *seen* floor, although the floor was seen on the opposite side of the field of vision from that to which at the beginning of the experiment I had referred these tactual sensations. I could likewise at times feel that my arms lay between my head and this new position of the feet; shoulders and head, however, which under the circumstances could never be directly seen, kept the old

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[8] This idea was developed in conversations with Julian Hochberg. Experiments by M. M. Cohen (1963) and Held and Rekosh (1963) suggest that there are at least two kinds of curve adaptation; the registered eye-movement explanation applies to only one kind.

> localization they had had in normal vision, in spite of the logical difficulty that the shape of the body and the localization of hands and feet just mentioned made such a localization of the shoulders absurd [p. 615].

Proprioceptive changes such as these account for the behavioral aspects of Stratton's adjustment to inverted vision.[9] If the felt locations and movements of his hands and feet came to agree with their seen locations and movements, he would have no trouble reaching for or kicking things, whereas before adapting he had to move the limb in a direction that felt wrong. When the new proprioceptive perceptions became stable enough to persist even when the limb was out of sight, responses with that limb would be completely normal with no need for conscious deliberation.

These proprioceptive changes also explain Stratton's feeling that he had achieved a "reharmonization" of touch and sight: Whenever he touched an object with an adapted limb, he felt it to be where he saw it, because he felt the limb to be in a new location that agreed with its visual location.

Upright Vision. Stratton was not primarily interested in behavioral adjustments nor in proprioceptive or intersensory alterations. He wanted to find out whether the usual (inverted) orientation of the retinal image is necessary for seeing things as upright. If so, Stratton (1896) said, "it is certainly difficult to understand how the scene as a whole could even temporarily have appeared upright when the retinal image was *not* inverted [p. 616]." Yet, he claimed, this was precisely what happened. After several days of adaptation, the world seen through inverting lenses sometimes appeared to be "in normal position" (1896, p. 616), "right side up" (1897, pp. 358, 469), "rather upright than inverted" (1897, p. 354). Some psychologists have taken these statements as conclusive evidence of a change in Stratton's visual system. Others have maintained that Stratton's assertions mean nothing at all. Walls (1951), for example, insisted that Stratton's descriptions of the scene as "upright" were "entirely metaphorical" (p. 191) and that actually all that Stratton achieved was a harmony between current perceptions and inverted eidetic imagery of objects outside the field of view (p. 200).

Stratton himself, on the other hand, thought it was quite natural for things to come to look upright again since he believed that "harmony between touch and sight, . . . in the final analysis, is the real meaning of upright vision [1897, p. 475]." But although "harmony between touch and sight" might indeed make the perceived orientation of the body and of the seen world agree, both body and world might still be perceived as *inverted* rather than upright. Perceived uprightness must depend on some other factor. That factor, as many investigators have pointed out, is the sensations of pressure and tension in the feet, legs, and body produced by the pull of gravity. Recently, experiments on subjects with labyrinthine defects led Clark and Graybiel (1963) to suggest that such pressure cues, rather than labyrinthine cues, may in fact be the major determinants of the perceived direction of gravity. Under zero-gravity conditions, for instance, subjects perceive the direction of the surface that their feet are touching as downward (Simons, 1959).

When Stratton first put on invert-

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[9] Since Stratton's lens system rotated the retinal image through 180°, he actually adapted both to inversion and to reversal. Kohler's (1951, 1964) experiments, using mirrors that inverted the retinal image without reversing it, generally support Stratton's observations.

ing lenses, he felt gravity pulling *away* from the seen location of the floor; "the general feeling was that the seen room was upside down; the body of the observer . . . was felt as standard and as having an upright position [1897, p. 348]." But gradually he began to feel that his feet, then his legs and arms, then most of his body were all in "the place where the new visual perception reported them to be [1896, p. 615]." The new proprioceptive localization was not stable—sometimes he even seemed to feel his limbs in both the normal and the new locations at once (1897, pp. 345–346, 465)—but when his legs and body were clearly felt to be in the new place, so, of necessity, were the gravitational pulls. Because the direction of the pull of gravity is, by definition, *down,* objects seen to lie in the same direction from the head as the legs were felt to be were perceived as down. So the floor looked "down," making the room look "right side up."

Since Stratton's head and shoulders "kept the old localization they had had in normal vision," he should then have felt that his legs and body were not on the same side of his eyes as his chin and shoulders. In other words, his head should have felt inverted! This is evidently just what happened:

> Outer objects . . . frequently seemed to be in normal position, and whatever there was of abnormality seemed to lie in myself, as if head and shoulders were inverted and I were viewing objects from that position, as boys sometimes do from between their legs [1896, p. 616].[10]

Stratton's simile conveys exactly the sense in which things seen through inverting lenses looked upright. They did *not* look the same as they did before the goggles were put on. Rather, they looked upright relative to the felt direction of gravity, the way things look when seen from between the legs. If you set a book upright on the floor and look at it from between your legs, you will see the bottom of the book as "down" and the top as "up." You will see the pointed part of a capital A above the open part. In this sense, everything will look upright. And yet, you will have trouble reading the book—the letters will look rather like upside-down print.

Kohler's Experiments

Kohler's accounts (1951, 1964) of adaptation to inversion help clarify the role of gravitational pulls on proprioceptively adapted body parts. When a partly adapted subject, who still saw the world as inverted, took hold of a string with a weight attached to the other end, he suddenly *saw* the weight as hanging from the string instead of floating upward like a balloon. The explanation may be that the hands and arms are often the first parts of the body to adapt (Taylor, 1962). So, when the weight pulled on the subject's arm and attracted his attention to it, he felt it pulling toward where he saw the floor and therefore perceived that direction as "down."

Several writers (e.g., Klein, 1960, p. 103) have assumed that gravitational cues provide a direct access to reality—a veridical standard to which visual perception, when shown the error of its ways, conforms. According to the present interpretation, however, gravitational cues will make the inverted scene look upright only if they are felt by some proprioceptively adapted body part. Prominent gravitational cues in an *unadapted* area (produced, for instance, by a weight hanging from the subject's chin) might

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[10] "At other times," Stratton (1896) noted, "the inversion seemed confined to the face or eyes alone [p. 616]."

make the scene look even more clearly inverted.

If we assume that the adaptive change is in the felt direction of gravity, not in the visual system, we can make sense of Kohler's (1964) report that one subject, who had been wearing inverting goggles for several days, said that "two adjacent heads, one upright, the other inverted, were *both* perceived as upright [p. 32]." Apparently, one head (the physically erect one) looked upright in that its chin was seen below its forehead; the other one (normally oriented on the retina) looked more natural, more recognizable as a normal face.

Illusory Movements of the Visual Field

Ordinarily, when you move your head downward, objects enter your field of view from below and travel to the top. You perceive the external world as stationary. If you move your head downward while wearing inverting goggles, though, objects enter the visual field from the top and travel downward. As a result, the world appears to be moving rapidly downward. (With reversing goggles, sideways movements produce a similar illusion.) After a few days the illusory swinging diminishes, until eventually the world appears stationary during head movements (Kohler, 1964; Stratton, 1897; Taylor, 1962).

This sort of adaptation may also be more closely related to proprioceptive arm adaptation than to purely intravisual phenomena. Stratton (1897, p. 358) noted that he saw the world as stationary only when he misperceived the direction in which *he* was moving: "Movements of the head or of the body . . . seemed to be toward that side on which objects entered the visual field, and not toward the opposite side," as they had felt when he first put on inverting lenses. This sounds like a kinesthetic change, which would stabilize visual perception without any change in the neural mechanism that normally takes head movements into account to yield a stationary visual world; only the felt movement of the head, the input to this mechanism, changes.

ADAPTATION TO REVERSED RETINAL IMAGES

Kohler (1953, 1964) has described in detail how subjects who wear right-angle prisms, which reverse their retinal images right for left, eventually achieve normal behavior and what he calls "correct seeing" (1964, p. 140). At first reading, his account is as bewildering as Stratton's.

"Piecemeal" Adaptation

When a person puts on reversing prisms, Kohler says, he initially reaches in the wrong direction for things, makes wrong turns, and sees all writing as mirror writing. In attempting to cope with reversed vision, the subject tries out various tactics, such as deliberately heading left when his goal appears to be on his right. As the subject adapts behaviorally, during the course of several weeks, he becomes able to walk, reach, and turn correctly without resorting to such "tricks." Concurrently, Kohler claims, his visual perception changes in a peculiar piecemeal fashion: Some parts of the visual field are perceived correctly while other parts remain reversed. For example, after 18 days:

> Inscriptions on buildings, or advertisements, were still seen in mirror writing, but the objects containing them were seen in the correct location. Vehicles driving on the "right" . . . carried license numbers in mirror writing . . . the subject is capable of localizing both sides of, say, a "3" correctly (open to the left, the curves to the right) and still see it mirrorwise [1964, p. 155]!

At this stage, even though the subject's spontaneous behavior is usually correct, he often becomes confused and makes "errors" when asked to attend to his "immediate visual experience."

After many weeks, Kohler says, the subject's behavior and vision are both reoriented. He achieves "almost completely correct impressions, even where letters and numbers were involved [1964, p. 160]."

When one thinks of adaptation as a change in visual perception, these observations are incomprehensible. How can vision ever be partly right way round, partly reversed?

Determinants of Judgments

In attempting to make sense of Kohler's puzzling observations, it is helpful to bear in mind four different determinants of what a subject says when the experimenter tries to find out whether he sees things right way round. The first two determinants are distinguishable aspects of perception, whereas the other two are essentially irrelevant to spatial perception. Doubtless, people differ in which of these factors enter into their judgments in a given situation, and a given person may judge differently at different times. But it is often possible to find out operationally which factors the subject's report is based on and to design experiments that avoid the ambiguities of previous reports.

1. *Directional perception.* When asked "Does that object appear to be on your right or on your left?," many people probably make a directional judgment relative to their dominant hand. If the object is seen to lie on the same side of the body as the right hand, the subject says: "It's on my right" or "on my right-hand side." The same kind of judgment can be elicited whether or not the words right and left are used, whether or not the subject has a dominant hand, and whether or not he refers the judgment to his hand: The experimenter can simply touch any spot on the subject's body and ask whether an object appears to be on the same side of his body as the touched spot.

Such a judgment is based on one aspect of spatial perception—perception of the location of an object relative to some part of the body. This is the sort of perception that usually guides motor behavior such as reaching for an object or walking toward it (cf. the concept of "manipulable regions," Kohler, 1964, p. 163).

2. *Pictorial perception.* Most of the debate on adaptation to distorted vision has concerned this aspect of visual perception, though it has not been clearly differentiated from other determinants of subjects' judgments. Pictorial perception consists of "looking at" the "picture" received by the visual system (cf. Gibson's, 1950, concept of "the visual field"). It is most obvious in successive comparisons: For example, we can ask a subject whether an arrow he is looking at is pointing the same way as the locomotive in a painting he saw before the experiment began.

The perception of "clockwise" or "counterclockwise" motion and "east" or "west" on a map are probably pictorial perceptions for most people, based on purely visual memories. Thus, to test for changes in pictorial perception, we can keep a subject from seeing any clocks or maps during the experiment and then ask him whether something appears to be moving clockwise or counterclockwise, or whether it is on the same side as the 9 on a clock or the east coast on a map. As long as the subject has a visual image of a clock or a map, he need not even think about the labels "right" and "left," nor about any part of his body, when making his judgment. (Occasionally a subject may make a directional judgment when asked to make a pictorial one—for example, if he remembers that the locomotive in the painting was "going toward my right" —that is, toward his right hand. But such exceptions have no theoretical importance once recognized for what they are.) Even when he uses the terms right and left, which are often characteristic of directional judgments, the subject may be making a pictorial judgment: Some people habitually think of a certain part of the visual field as "the lower left corner" without referring at all to any part of the body.

3. *Familiarity.* A subject often describes his first perceptions through reversing goggles as "strange," "unusual," "unfamiliar," "new," or "mirror imaged." Later he describes them as "normal," "natural," "all right," "usual," "familiar," "right way round" (see Kohler, 1964, p. 142). Such descriptions are based almost entirely on past experience with particular stimuli or classes of stimuli and can be changed through repeated visual observation, even without distorting spectacles. For example, a person (perhaps an apprentice typesetter) who practices reading mirror writing may soon say that it is beginning to look "natural" or "all right." But neither his directional nor his pictorial perception has changed. If asked to judge the location of part of a letter (relative to part of the body or to visual memories), a person gives the same answer whether the letter looks "familiar" or "strange."

4. *Labels.* It is risky to let a subject use the words right and left. First, the same word may be used to label two quite different sorts of perception, pictorial and directional. Second, a subject wearing reversing prisms could decide to start calling everything right that he formerly called left, even if he had not adapted at all. And third, he may be inconsistent or hesitant about which word to use even when his perception is completely determinate, stable, and clearcut; as Kohler (1964) put it, "there are people who always have trouble when asked to tell quickly where right or left is, but who never have difficulty in reaching for seen objects [p. 153]." Labels like right and left do not affect perception; it is irrelevant that the subject has learned to call a certain direction left and another direction right.[11]

Proprioceptive Changes

With these distinctions in mind, it is possible to reexamine Kohler's observations and conclude that adaptation to reversed vision can be ascribed to a radical change in the felt location of the arms, legs, and body relative to the head and eyes, without any change in pictorial visual perception.

Kohler (1953, p. 110; cf. 1964, p. 153), in fact, did observe some proprioceptive and kinesthetic changes during the course of adaptation to reversal. After several days of wearing the goggles, he reported, there was:

> . . . a weakening of the right-left orientation of the body image, which becomes uncertain, especially in connection with movements that have been deliberately practiced in reverse. The subject may even turn left, with full

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[11] Terms like "upright" and "inverted" are even more ambiguous. Saying that an object looks upright may mean that it appears to be in its usual position, that it looks the same as it did before inverting goggles were put on, that it looks the same as it feels, that its top is perceived to be pointing away from the direction of gravitational pulls, that its bottom appears to be near where one's feet are, or that it is oriented appropriately to the rest of the visual scene.

> confidence, when he does a "right face" with his eyes closed. When he moves his head and hands, the kinesthetic position- and movement-sensations are completely in accord with the (reversed) visual field. Yet ultimately this leads to a "dead end" (two errors that cancel each other!).[12]

In a footnote, Kohler added:

> . . . by touch, doors, for example, seem to open in a reversed direction (as compared with earlier), as if they had been turned around in the meantime. However, the pre-experimental "right-left" of the body image remains unchanged in the shoulder and upper-arm region, and from there it undertakes its new conquest. When the attention is concentrated on this region, there is almost never any error.[13]

Clearly, Kohler regarded these kinesthetic and proprioceptive changes as temporary aberrations of no theoretical importance, leading only to a "dead end." Since proprioception and vision were *both* reversed, Kohler thought that both must proceed to a further, "correct" stage before adaptation could be complete. Stratton's reports, however, suggest that proprioceptive and kinesthetic changes, far from being temporary and trivial, become more and more extensive as adaptation progresses and are directly responsible for the "correct" perceptual judgments that ultimately emerge.

In order to clarify this interpretation of adaptation to reversal, let us consider a hypothetical experiment in which we test the subject's perception by having him look at a blackboard bearing an L on his left and an R on his right (Figure 1A). Immediately after putting on reversing spectacles, the subject says that he feels that his right hand (the one he writes with) and the right side of his body are near the same end of the blackboard—namely (since he is looking at it through reversing prisms), the end with a backwards L on it (Figure 1B). But when he holds up his writing hand and looks at it, he sees it nearer to the backwards R.

Now he starts adapting. If the proprioceptive-change hypothesis is correct, there is a change in the felt locations of his hands relative to his body. That is, his writing hand not only *looks* as if it is nearer to the backwards R, it now *feels* nearer as well (Figure 1C). Thus the subject feels his right hand to be near the (physically) left side of his body.

Suppose we ask the subject to turn right. He most likely assumes we mean toward the hand he writes with. Accordingly, he turns toward where he feels that hand to be, and the experimenter writes down that the subject turned left when told to turn right. The error is not due to uncertainty or "weakening of the right-left orientation of the body image"; if, instead of asking the subject to turn right, we touched his right hand and asked him to turn toward it, he would make the same error. If we

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[12] *"Aber auch umgekehrt schwächt sich das Rechts-Links der Körperfühlsphäre und wird unsicher, besonders im Zusammenhang mit jenen Bewegungen, die man absichtlich verkehrt eingeübt hat. Die Vp. kann mit voller Evidenz sogar bei geschlossenen Augen 'rechts um' machen und dreht sich dabei in Wirklichkeit nach links. Sie macht Kopfwendungen und Handbewegungen, deren kinästhetische Lage- und Bewegungsempfindung ganz mit der (verdrehten) visuellen Welt übereinstimmt. Was dabei letzten Endes herauskommt, führt aber in eine 'Sackgasse' (zwei Fehler, die sich gegenseitig aufheben!)."*

[13] *"Das führt so weit, dass sogar im Tasten z. B. Türen (gegenüber früher) verkehrt aufzugehen scheinen, als wären sie inzwischen versetzt worden. Worauf sich das vorexperimentelle 'Rechts-Links' im Körpergefühl aber versteift und von wo es dann seinen neuen Vorstoss unternimmt, ist die Schulter- und Oberarmpartie. Wenn man darauf die Aufmerksamkeit konzentriert, gibt es kaum jemals eine Verwechslung."*

(This footnote refers to the sentence that ends with *"übereinstimmt."*)

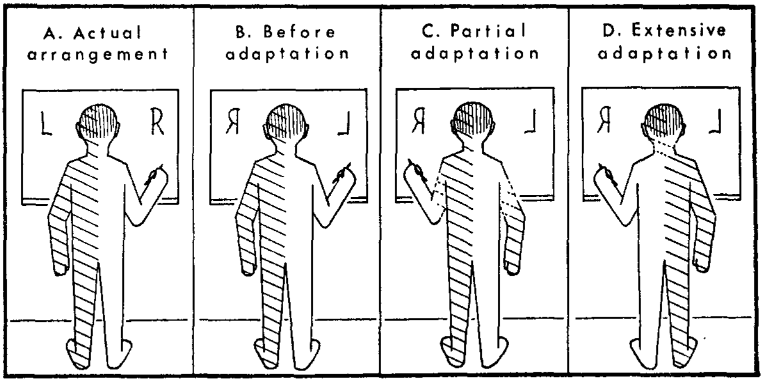

FIG. 1. A subject's perceptions during the course of adaptation to reversed vision, according to the proprioceptive-change hypothesis. (In all cases perception of the letters is visual; perception of the subject's head and body is proprioceptive. A: The actual physical arrangement. B: The subject's perceptions when he first puts on reversing goggles. C: The subject's perceptions at an intermediate stage of adaptation, with only his arms adapted. D: The subject's perceptions at an advanced stage of adaptation.)

touched his (unadapted) right shoulder, however, or if the subject focused his attention there, he would turn correctly to the right.

When we now ask the subject which end of the blackboard appears to be on his right, he may fall into the state of indecision that is so characteristic of Kohler's partly adapted subjects. His right hand feels closer to the letter R, whereas his right shoulder feels closer to the L. Depending on which region of his body he concentrates on, he can consider either the L or the R as being on his right. Thus he may switch his judgment back and forth from "right" to "left" without the slightest change in visual perception. Moreover, Stratton's reports indicate that the partly adapted subject sometimes feels his hand to be in two different places at once, with fluctuations in which of the localizations seems most "real." So even if the subject keeps judging relative to his hand, his judgments may waver. And, of course, he may switch back and forth from directional to pictorial judgments.

With further adaptation, according to the proprioceptive-change hypothesis, the felt locations of the subject's legs, torso, and perhaps even his shoulders and most of his head, change. He again feels, as he felt before the experiment started, that the (physically) right half of his body is near the hand he writes with. Now he can reach accurately for objects seen through the reversing goggles, turn correctly, and correctly judge the directions of objects relative to his body.

Pictorial Perception

But still his pictorial visual perception remains unchanged. The letters on the blackboard and the license plates on cars look just the same as they did when he first put on reversing goggles. The only difference is that he now feels the right side of his body to be on the same side as the curve of the backwards R that he sees (Figure 1D), so he says the curve is "on my right."

Why, then, does writing eventually come to look "normal" through reversing goggles? Because, with practice, mirror writing becomes familiar and easy to read, whether the letters are actually printed in reverse or simply look reversed because one is wearing special goggles. Indeed, Kohler's (1964, p. 160) subject reported that "the first words to rectify themselves were the common ones," which were seen most often through the reversing goggles. But it is a mistake to conclude that pictorial perception reversed and "mirrorwise seeing" (*"spiegelbildliche Sehen"*—Kohler, 1953, p. 113) became established. We would not say that about someone who learned to read mirror writing without wearing reversing spectacles.

Given this interpretation of adaptation, it is not surprising to hear that one stubborn subject (Taylor, 1962, p. 180) "achieved satisfactory behavioral adjustment" but "denied that he ever perceived the world the right way round through his spectacles," even after 71 days of wearing them. When questioned closely, this subject said that all of his "incorrect" judgments were made by deciding whether his right temple or his left temple was closer to the part of the visual field he was judging. Stratton's reports suggest that even after the felt location of the rest of the body has changed, the area around the eyes does not, so judgments made relative to the temples would remain unchanged. Or, the subject may have been trying to tell the experimenter that he was making a pictorial judgment, based on an unaltered visual memory of right and left. In either case, this subject's perceptions—visual and proprioceptive—were probably just the same as those of subjects who, according to Taylor, managed to "perceive the world the right way round."

Aftereffects

The "peculiar experiences" (Kohler, 1964, p. 158) that the adapted subject encounters when he takes off the experimental spectacles are just what one would expect if the subject has undergone proprioceptive changes, has become accustomed to the reversed appearance of particular stimuli, but has experienced no change in pictorial perception.

When Kohler (1964, p. 158) removed his reversing goggles, after weeks of adaptation, and looked at a picture which he had seen before but not during the experiment, the picture immediately looked familiar. The person in it appeared (pictorially) to be running, as before, from left to right. Nevertheless, the person was seen as running toward the *left* edge of the page; that is (as Kohler makes clear), toward where Kohler felt his (adapted) left shoulder to be.

Kohler (1964, p. 160) does report that another subject, the one who "achieved almost completely correct impressions" while wearing reversing goggles, *saw* the whole room mirrorwise when the spectacles were removed. But the evidence for this statement is that the subject read p's as q's, b's as d's, and 10:30 on a clock as 1:30—which is just what would happen, without any perceptual change, if one read nothing but mirror writing and saw nothing but backwards clocks for 37 days.

LIMITATIONS OF THE PROPRIOCEPTIVE-CHANGE HYPOTHESIS

Although changes in the position sense may underlie most of the phenomena of adaptation to optical distortions, there are some kinds of adaptation that cannot be so interpreted. For example, adaptation to the chromatic dispersion produced by prisms ("color fringes"—Kohler, 1964) seems to depend on changes in "contour detectors" within the visual system (Hay, Pick, & Rosser, 1963; McCollough, 1965a). Adaptation to bicolored spectacles (Kohler, 1964) has been shown to depend on retinal color adaptation and simultaneous contrast (McCollough, 1965b). There appear to be several forms of adaptation to tilting, curvature, and other optical distortions (see, e.g., M. M. Cohen, 1963; Held & Rekosh, 1963; Kohler, 1964; Mikaelian & Held, 1964; Morant & Harris, 1965; Ohwaki, 1961). Some of these appear to be purely visual changes; others may be based on changed registration of head or eye positions and movements.

Many adaptation situations probably include some motor-skill learning. This component may sometimes be even larger than that due to proprioceptive changes (as, perhaps, in Smith & Smith's, 1962, studies) or it may be much smaller but still considerable. For example, Hall (1964) and Harris (unpublished data) both found that when the arm movement used during adaptation differed grossly from that used in the tests, there was some decrement in the measured adaptive shift. (Hall's data have been published by Freedman, Hall, & Rekosh, 1965.)

In some cases, a proprioceptive-change interpretation requires additional assumptions similar to those made by other theories. For instance, the increased variability of responses that follows watching one's hand through a variable prism whose amount of displacement keeps changing (Cohen & Held, 1960; summarized by Held & Freedman, 1963) could be due to increased uncertainty about arm position. Many of the "conditional aftereffects," which others ascribe to the conditioning of visual perceptions to nonvisual cues (Kohler, 1964; Taylor, 1962), can be attributed to the conditioning of altered position sense to these same cues.

Recently, several experimental findings have been cited as directly ruling out a proprioceptive change in adaptation to displacement. Efstathiou and Held (1964) reported that adapting one hand to displacing prisms had no effect on blindfolded subjects' reaching for the remembered locations of targets they had previously felt. They also found that the measured adaptive shift was smaller when the unexposed hand served as test target than when the target was a visually perceived object. Bauer and Efstathiou (1965) found an adaptive shift in pointing "straight ahead" only if subjects were first tested on pointing at visual targets; if tested on straight ahead first, the shift was sizable, but in the wrong direction. And H. B. Cohen (1963) reported that adaptation with the target in the retinal periphery does not transfer completely to test targets on the fovea. It is difficult to assess these findings since each is contradicted, directly or indirectly, by other findings (e.g., Goldstein[14]; Hamilton & Hillyard[15]; Harris, 1963a). The reasons for the empirical disagreements have not been satisfactorily worked out.

In the reports of Stratton (1897), Kohler (1964), and Taylor (1962), several passages seem to describe perceptual changes that cannot be attributed to altered position sense. Further work is needed to determine whether these statements are based on confusions about the various determinants of subjects' verbal reports or result from some complicated alterations in position sense or do in fact represent other sorts of adaptive change.

OTHER THEORIES OF ADAPTATION

Stratton

After reading Stratton's striking descriptions of the proprioceptive changes

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[14] Donald Goldstein, personal communication, June 1964, May 1965.

[15] Charles R. Hamilton and S. A. Hillyard, personal communication, July 1964, August 1964.

he underwent, one is surprised to find him saying in his theoretical discussion that "the tactual perceptions, as such, never changed their place," and "the restoration of harmony between the perceptions of sight and those of touch was in no wise a process of changing the absolute position of tactual objects so as to make it identical with the place of the visual objects [1897, p. 476]." He seems to be ignoring his own introspections when he claims that there is neither a change in proprioceptive localization nor a change in visual localization, but only a change in the relationship between the two. This noncommittal idea has proven quite appealing to many present-day psychologists.

Clearly a change either in vision or in the position sense would result in a changed relationship between the two. But saying that only the relationship between the two modalities changes is ignoring information about the changes *within* one (and only one) of the modalities.

Stratton's own reports make it clear that the first step in his adapting to inverted vision was to feel that his feet were in a new location relative to the rest of his body—a change within the position sense. Gradually, the felt locations of more and more of his body swung into line with that of his feet, that is, into line with the inverted visual scene. True, the final result was a new relationship between the position sense and visual perception, but this new relationship was brought about entirely by changes in the position sense, with no changes in vision.

In 1897, Stratton (pp. 472-475) theorized that adaptation is the attachment of new visual imagery to tactual sensations and, concurrently, the attachment of new tactual imagery to visual sensations. If we ignore the second half of this formulation and just postulate that adaptation consists of associating new visual imagery of parts of the body with proprioceptive stimuli from those parts, we can deal with much of the relevant data, provided we make one additional assumption: that the felt position of a limb is not directly connected with proprioceptive stimuli, but is a byproduct of where the limb is mentally pictured. The visual imagery notion, then, would make the same predictions as the proprioceptive-change hypothesis, but requires an extra step—a step that some subjects' introspections deny.[16]

Taylor

Taylor (1962, 1964) attempts to explain all perception, from depth perception to color vision, with a single hypothetico-deductive theory. According to this theory, visual perception of an object is determined by the "activation" of stimulus-response engrams—neural traces of the responses (especially walking, reaching, and verbal responses) that have been conditioned to similar stimuli. Taylor apparently believes that adaptation to displacement, inversion, or reversal of the retinal images leads to changes in directional perception and perhaps to pictorial changes as well (1964, p. 73). However, he thinks that these perceptual changes, though genuine, are largely

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[16] In a later paper, Stratton (1899) did state, contradicting his earlier theoretical views, that "the place in which any part of the body is persistently seen influences the localisation of the dermal and kindred sensations arising in that part. If one were to see his feet, for instance, in some direction different from their present visual position, he would in the end refer thither their kinaesthetic impressions also [p. 463]." But only a few subsequent writers (notably Walls, 1951; Smith & Smith, 1962) have paid much attention to Stratton's later interpretation or even to his original detailed descriptions of proprioceptive changes.

the result of changes in verbal labeling (1962, pp. 179–181, 185). He expects adaptation to progress in piecemeal fashion with visual perception becoming more and more veridical as the subject acquires a larger number of appropriate responses (1962, pp. 188, 197, 207).

Beyond this, it is difficult to derive unequivocal predictions. For example, Taylor's theory could predict either way about transfer to most of the tasks in Table 1, depending on what assumptions are made about steepness of generalization gradients, breadth of "equivalence classes," degree of "interpenetration" of sensory modalities, and relative importance of motor behavior and implicit verbal responses.

Kohler

Kohler's (1964) studies of adaptation to a wide variety of visual distortions have provided the inspiration, directly or indirectly, for much of the research in this field. He has concentrated on setting down his observations rather than on providing a detailed theory. It is clear that he agrees with Taylor that adaptation involves changes in directional perception, based on the acquisition of new behavioral responses to transformed retinal images (see, e.g., pp. 163–164). With prolonged exposure to reversing spectacles, Kohler says, there are eventually pictorial changes, with more and more stimuli "seen correctly" (pp. 140, 163–164). Unlike Taylor, however, Kohler thinks that verbal labeling is of no great significance in adaptation.

Although Kohler did mention (in a footnote) that "alterations in kinesthetic sensitivity" may be "of crucial importance" (p. 32) in adapting to displacement, he did not make much use of these alterations in explaining other aspects of adaptation. In fact, in his discussions of reversed vision, he regards such alterations as transitory—normal proprioception and kinesthesis are soon reinstated, and form the basis for the "correct" visual perception that ultimately emerges. In his theoretical discussions, Kohler did not attempt to explain the simpler phenomena of adaptation to displacement, inversion, and reversal of retinal images, but rather dealt with the complex "situational aftereffects."

Held

In an extensive series of carefully controlled experiments, Held and his co-workers have demonstrated the importance of active movement and movement-produced visual feedback ("reafference") in producing adaptation. These experiments set the pattern for most of the recent work in the area: brief adaptation periods with quantitative before-after measurements.

Held has been primarily concerned with the necessary preconditions for adaptation; he has said little about the nature of the adaptive change (see, e.g., Held, 1961). It is not clear whether Held believes that adaptation involves any perceptual changes, visual or proprioceptive. For instance, Held and Freedman (1963) say that adaptation "represents a change in state of the relevant sensorimotor control system, such that [after complete adaptation] the input-output or stimulus-response relation becomes identical to that which existed prior to rearrangement [p. 457]." Recently Efstathiou and Held (1964) proposed a tentative theory of arm adaptation to displacement, according to which "the change responsible for the shifts occurs in a representation, within the nervous system, of the spatial relation between the exposed arm and directions that are defined independently of that arm." Further elaboration of this model is necessary to determine how it differs from the proprioceptive-change interpretation.

Smith and Smith

Smith and Smith (1962) claim that adaptation consists of acquiring highly specific perceptual-motor skills. They seem to deny that there is any general reorientation of perception, whether directional or pictorial (1962, pp. 83, 311). Their research and theory supplement the proprioceptive-change interpretation by dealing with situations in which proprioceptive changes probably are minimized because there is a large spatial separation between the felt location of the hand and its televised visual feedback. The acquisition of highly specific perceptual-motor skills is facilitated by Smith and Smith's tasks, which permit continuous visual feedback and stress speed of execution. Indeed, their usual measure (speed of performance) is sensitive only to the development of highly practiced motor skills. However, it is possible that adaptation of Smith and Smith's three movement systems—locomotion, transport, and manipulation—may in part represent, respectively, proprioceptive head or eye adaptation, arm adaptation, and acquisition of manipulatory skills.

Werner and Wapner

Werner and Wapner (1955) have discussed some of Kohler's findings in terms of their organismic sensory-tonic field theory, attributing adaptation to changes in the subject's "organismic state (sensory-tonic distribution)." Basically, though, their account simply restates Kohler's observations. Some of their statements would match the present author's if the words "felt position" of certain body parts were substituted for such abstract terms as "organismic state" or "equilibrial axis." But Werner and Wapner consider the organismic state to be only one part of the process that determines body perception, not the perception itself. Moreover, the organismic state is assumed to include "not only postural, but emotive, motivational factors, etc. [p. 133]," which are clearly beyond the scope of the present formulation.

PRECONDITIONS AND MECHANISM FOR ADAPTATION

Visual Proprioceptive Discrepancy

Although the proprioceptive-change interpretation of adaptation does not specify any particular process or precondition for the change, it is tempting to assume that adaptation results from a discrepancy between proprioceptive and visual information. One effective way to produce such a discrepancy is to look at some part of one's body through distorting goggles, but it is not the only way. For instance, when a subject walks while wearing displacing prisms, his position sense may indicate that his head is turned to one side of the direction of movement, whereas the retinal flow pattern (Gibson, 1950; Held & Freedman, 1963) may indicate that the head is pointing right along the axis of movement.

On the other hand, there is no logical necessity that proprioceptive inputs be used at all by the mechanism that recalibrates the position sense. It could be, as Helmholtz (1962b) suggested, that adaptation is based on the changes in the retinal image that result from a given "effort of the will," or, in Held and Freedman's (1963) terminology, on motor corollary discharges and visual reafference contingent upon active movement. Or the proprioceptive change could be due to the laying down of engrams of conditioned responses, like those postulated by Taylor (1962).

Some proprioceptive changes may

arise from something like "sensory fatigue," without any direct participation by vision. Hein (1965) has found that after simply holding their heads turned to one side for 10 minutes, even with their eyes closed, subjects point incorrectly at visual targets. This "postural after-effect," as Hein called it, probably was due to a change in felt head orientation. Similarly, Kohler (1951, p. 18) reports that subjects who wear displacing prisms tend to hold their eyes in an abnormal position that eventually comes to feel normal once more. Such a "fatigue" effect could indeed produce some of the phenomena of adaptation to displacement, but it can underlie neither adaptation to inversion or reversal nor arm adaptation to displacement.

Active Movement

A number of experiments by Held and his colleagues have shown that active movements by the subject play an important role in adaptation to several optical distortions (Held & Freedman, 1963). Although some recent investigators have claimed to find extensive adaptation with passive exposure (e.g., Wallach et al., 1963; Weinstein, Sersen, Fisher, & Weisinger, 1964), active movement does seem greatly to facilitate adaptation.

Theories that consider the end product of adaptation to consist of new motor responses or new visuomotor correlations (e.g., Held, 1961; Smith & Smith, 1962; Taylor, 1962) also assume that active movement is a crucial precondition for adaptation. On the other hand, Hamilton (1964a) has listed several ways to account for the importance of active movement without postulating any motoric component in the end product. For example, the position sense during active movement may differ from (and be more precise than) that during passive movement. Or motor discharges may act as a "catalyst" that permits a joint's position sense to change.

IMPLICATIONS FOR PERCEPTUAL DEVELOPMENT

Psychologists have traditionally looked to studies of adaptation to distorted vision for clues about the development of visual perception in the infant. The usual, empiricist assumption (outlined by Berkeley in 1709 in his *New Theory of Vision;* see Berkeley, 1910) is that visual space perception is "secondary": It is based on the spatial sensations given by touch, kinesthesis, and position sense. As Dewey (1898) put it: "Ultimately visual perception rests on tactual. . . . Spatial relations are not originally perceived by the eye, but are the result of the association of visual sensations with previous muscular and tactual experiences [p. 165]."

This belief in the primacy of touch is so ingrained that experimental results are sometimes flagrantly misinterpreted in order to support it. Carr (1925), for instance, concluded: "It is thus obvious that the Stratton experiment involves no reconstruction or alteration of tactual . . . space. It is the visual system that is disrupted and then reorganized so as to conform to touch . . . [p. 141]." Stratton's, Kohler's, and Held's findings have been cited over and over as evidence that visual space perception is flexible and therefore must have been acquired through tactile-proprioceptive and motor experience. The reinterpretation of these findings that has been presented here suggests the opposite conclusion. Vision seems to be largely inflexible, whereas the position sense is remarkably labile.

The implication, if one dare draw any, is that the Berkeleyan notion should be turned around. It seems more plausible to assume that proprioceptive perception of parts of the body (and therefore of the locations of touched objects) develops with the help of innate visual perception rather than vice versa.[17] A growing number of recent studies support the view that many aspects of visual perception are not influenced by experience and are largely innate (e.g., Bower, 1964; Fantz, 1965; Gibson & Walk, 1960; Hubel & Wiesel, 1963; Robinson, Brown, & Hayes, 1964). Furthermore, if the position sense were innate—if each spot on the skin were proprioceptively "preaddressed"—the local sign lodged in a baby's fingertip might go on forever signaling that his arm is 10 inches long.

So, when a baby stares raptly at his outstretched hand, he is probably findout where his hand is, not what his visual sensations mean. He is making use of an adaptive mechanism that keeps his position sense accurate despite extensive and uneven growth of his body. This mechanism enables us to use the precise, detailed information that vision provides, as a means of continually readjusting our vaguer and more variable position sense.

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[17] Clearly vision is not the *only* basis for acquiring and maintaining the position sense or blind people would have no idea where their arms and legs were. Vision may, however, provide the quickest and most exact recalibration.

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