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*Theoretical article*

# REORGANIZATION OF PERCEPTION: A KONORSKIAN INTERPRETATION OF THE INNSBRUCK EXPERIMENTS

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*Abstract.* This paper discusses the close fit of Konorski's model to the data of Kohler's Innsbruck experiments and also to more recent neurophysiological studies of environmental surgery or sensory disturbances. The dramatic Innsbruck research using special goggles or prismatic glasses that reversed or distorted the visual field confirmed and extended Stratton's earlier use of the substitution method. The subjects had at first insuperable difficulties in their locomotor behavior if it was guided by vision. After practice guided by certain rules, they were able to perform and eventually to "see" correctly in the strange environment. These studies demonstrate the plasticity of the nervous system, even in the adult. The problem for the field is to determine how these new associations, antagonistic to long established conditioned reflexes (CRs), become functional. The particular questions arise: what rules impede, what rules facilitate the transformation of CRs, and what physiological mechanism is responsible for the changed relations between the organism and the external world? Konorski's remarkable theory is that *no* transformations of connections occurs in the reversal training. Instead, what actually happens is the formation of a connection between the original instrumental CR and non-reinforcement, and actualization of excitatory connections between the CS units and the kinesthetic units of the antagonistic movement. If correct, this motor act marks the termination of the eliciting drive and is reinforced. The original CR is readily re-established by restitution of its reinforcement.

> Alice looked round eagerly and found that it was the Red Queen. She's grown a good deal, was her first remark. She had indeed: when Alice first found her in the ashes, she had been only three inches high — and here she was, half a head taller than Alice herself...
>
> "I think I'll go and meet her", said Alice, for though the flowers were interesting enough, she felt that it would be far grander to have a talk with a real Queen.
>
> "You cant possibly do that," said the Rose. "I should advise you to walk the other way."
>
> This sounded nonsense to Alice, so she said nothing, but set off at once towards the Red Queen. To her surprise she lost sight of her in a moment, and found herself walking in at the front door again.
>
> A little provoked, she drew back, and after looking everywhere for the Queen (whom she spied out at last, a long way off) she thought she would try to plan this time, of walking in the opposite direction.
>
> It succeeded beautifully. She had not been walking a minute before she found herself face to face with the Red Queen, and full in sight of the hill she had been so long aiming at.
> (2, p. 191–2)

Lewis Carroll (2) might have been a subject in one of the Innsbruck experiments with goggles (18). These subjects wore reversing mirrors, prismatic and half-prism spectacles, even split-color goggles to study the effects of these experimental disturbances on behavior and perception. Forward and back are reversed in a mirror, as are left and right; objects are simultaneously enlarged and reduced — in a mirror all asymmetrical objects (objects not superposable on their mirror images) "go the other way".

The prism goggles reverse right and left, and near and far. They also change the sizes of things in a surprising way, depending upon the direction of gaze.

Kohler (28) and the subjects of the Innsbruck experiments survived long periods of wearing these goggles and overcame the disturbances with new habits of both behavior and perception — habits that ran counter to a lifetime of previous experience and activity.

The Innsbruck experiments uncovered an adaptive process of general validity. The most remarkable finding was Kohler's discovery that stimulation of the same retinal area led not only to a variety of visual aftereffects but that these aftereffects were contingent upon the presence or absence of certain conditions of stimulation. These "situational aftereffects" challenge traditional theories and require explanations in terms of physiological processes.

Konorski's (19) approach to the problem of the mechanisms of transformation of associations offers an attractive framework for organizing the experimental findings. The present paper is an examination of Kohler's and more recent studies of sensory disturbance in the light of Konorski's general theory.

The central finding of the Innsbruck studies was the differential adaptation that occurred in one and the same area of the retina. "It is as though", Kohler wrote, "the particular retinal area had not one but a whole series of subjective standards of reaction for the same visual stimulation (18, p. 26)".

The problem is to explain the occurrence of variable aftereffects; variable degrees of resistance to the transformation of old habits and the formation of new habits; the lead role of motor behavior and only secondarily, of vision; and the complete failure of certain visual phenomena, e.g., the color-stereo effects, to show any adaptation, whatsoever.

Konorski's (19) insight into the value of the "substitution method" and aftereffects experiments as probes to discover the genesis of correct perception and coordinated visual-motor behavior in normal human development is now confirmed by new discoveries of the activity and organization of the cerebral cortex.

## RECEPTIVE FIELD STUDIES

In the mammalian visual system, the important discovery is that any given retinal area transmits information to the brain in a hierarchy of stages of neural activity, corresponding to increasingly higher orders of abstraction of specific features of stimulation. Especially significant is the finding that single cells in the eye and brain are organized into receptive fields of mutually antagonistic activity. In consequence, the visual system tends to dichotomize perception not only into such opposites as light and dark, black and white, red and green, but also into such spatial opposites as left and right, near and far, above and below, and concave and convex. This opponent organization is maintained by a functional architecture that enables us to respond selectively not to absolute properties of stimulation but to the relations between them.

We find selectivity at every stage. A particular retinal area gives different reactions to the same total stimulation at different times and under different conditions because cells farther upstream select the features to which they will respond and reject the others. Some regions react to the onset; others to the offset of stimulation. Individual neurons react to lines, bars or gratings with specific sizes, shapes, orientations, directions of movement, and contrasts, dark against light, or light against dark backgrounds. This selective processing is repeated again and again at progressively higher levels. In this processing, the neural activity sharpens gradations and turns them into contours.

Direction is an important factor in the perception of form since the same contour will look different according as it is attached to the right or to the left, above or below the figure it outlines. The receptive field studies show clearly that both the direction of movement and the brightness gradient or spatial phase (light to dark, or dark to light) is critical for the response of a single cortical cell in cat or monkey. Human perception emphasizes this feature of contour also; the one-sided action of contour is fundamental to the discrimination of objects and the segregation of figure and ground.

The apparent paradox of opposite aftereffects arising from one retinal area is no longer bewildering. Having available the data derived from Hubel and Wiesel's (13–16) experiments, we know that the same retinal area sends convergent and divergent impulses to many cells of different receptive field types. Single cell studies using microelectrodes have examined and compared the effective stimuli for cells at successive levels of the visual pathway from the retina to the striate cortex in cat and monkey. Their results provide a physiological and anatomical basis for understanding the deprivation and relearning experiments in animals and human beings.

The striate cortex of cats and monkeys contain sets of neurons that receive information from lower levels of the visual pathways and are either excited or inhibited by slits of light or gratings selectively oriented and placed in the visual field. Within the cortex each region of visual space is "...represented over and over again in column after column, first for one receptive field organization and then another (13, p. 106)".

Since the same receptors and the same units of the lower levels take part in different combinations in various neuronal circuits, the number of these circuits exceeds the number of units at the lower levels. Although there appears to be an initially organized functional architecture ready to work soon after birth, the details of these connections depend strikingly on the previous experience of the individual.

Most neurons in the visual cortex of normal cats and monkeys respond selectively to moving contrasts, lines or gratings presented to one eye alone or both eyes together. Some cortical cells react preferentially to vertical, some to horizontal, and some to oblique orientations of lines or gratings with all orientations being represented. Cells with similar characteristics are grouped together; their receptive fields are close together also; usually they overlap but each group includes various sizes and some scatter. The important point is that each small region of the retina has input to many cells with different response characteristics and different stimulus requirements. The cell soon habituates to continued or repeated stimulation and ceases to respond, although the termination of a stimulus may evoke a burst of excited activity.

## SENSORY DISTURBANCE EXPERIMENTS

The Innsbruck experiments on the transformation of human perception fit hand in glove with the recent neurophysiological studies of the effects of early distortion of sensory input on the visual system of kittens and monkeys.

Taken together with the research on single cells of the nervous system in various species, these different lines of investigation enable us better to understand how the structure and function of the brain are affected by the history of the organism. The ability to undergo long term alterations as a result of experience is a remarkable property of the nervous system. The factors that influence this relearning or reconditioning are presumably no different than those involved in the initial formation of the perceptual world.

Yet there is one important exception. A brief early experience during a *critical period* of development may cause irreversible aftereffects. In newborn animals the closure of one eye may result in permanent damage even though the neuronal circuits required for vision were already present and ready to work at birth. Kittens are born with the basic wiring already established. Both eyes drive cortical neurons and these cells have receptive fields like those in the adult cat. Some cells are driven better by one eye, some by the other and some are driven equally well by both eyes. What happens when one eye is deprived of all visual experience?

Hubel and Wiesel (14) tried the experiment on a newborn kitten by sewing the lid of one eye closed for three months and then recorded the activity of the cortical cells. The effect in the kitten's visual cortex was extraordinary. Not a single cell could be influenced by the eye that had been closed.

When the previously deprived eye was opened and the experienced eye closed (*reverse suturing*) the kittens were practically blind. They would bump into objects and fall off tables even though no gross defect could be found in the operated eye. But electrical recordings of the responses of cortical cells showed striking changes. Very few cells showed any response to the stimulation of that eye. In short, deprivation of the use of one eye at a critical period of development leads to permanent loss of function in that eye. As little as a day of deprivation at about four weeks of age (the height of a "sensitive period") can provoke the permanent reorganization of the visual cortex in the kitten (21, 22).

In the monkey, Blakemore and Van Sluyters (1) have shown that if the originally experienced eye is closed at the time that the deprived one is reopened there can be virtually total capture of neurons by the newly opened eye. This reverse suturing procedure is more effective the earlier in the sensitive period it is done; at 4 or 5 wk of age it causes total re-invasion of input from the deprived eye.

## EFFECTS OF ABNORMAL VISUAL EXPOSURE

If young kittens are raised during the critical period (3–14 wk) in a visual environment consisting only of stripes of one orientation, most cortical neurons will be maximally sensitive to orientations within ±30° of the one to which they had been exposed. That may sound like a wide range until you consider that the hands of the clock between 12 and 1 o'clock are 30° apart.

What are the effects of selective exposure to tilt on *mature* animals? Creutzfeldt and Heggelund (3) exposed seven adult cats to vertical stripes for one hour a day and for the rest of the time kept them in darkness over a period of 2wk.

The surprising result was that cells selectively sensitive to the vertical were *less* frequently found than cells sensitive to horizontal or near horizontal orientations. Unlike newborn kittens, in the adult cats, prolonged exposure to a specific orientation *decreased* sensitivity to the stimulus to which they had been exposed — a finding that supports the idea of neural plasticity in the cortex of the adult animal.

These results are remarkably similar to the orientation-specific effects on adaptation or habituation found in experiments in human perception (7–9). The negative visual aftereffects of tilt, direction of movement, curvature, and color found in the Innsbruck experiments and the many different McCollough effects (20, 23) may have a common basis in the underlying neural mechanisms.

In humans, Fiorentini, Ghez and Maffei (5) found physiological correlates of adaptation to a rotated visual field. Subjects wore prismatic spectacles that tilted the visual field by 30° or 45° for 5–7 days and all reported progressive diminution of apparent tilt. When the relative contrast thresholds and amplitudes of evoked potentials to vertical and oblique gratings were studied, the adapted subjects showed a surprising departure from the normally greater sensitivity to vertical contours compared with oblique contours. What was especially interesting was the finding of a decrease in the usual difference between the contrast threshold for vertical and for oblique orientations. Most measures of acuity show that human beings are far better at detecting vertical and horizontal contours than oblique ones. Presumably it is the relative paucity of oblique contours in the environments of individuals raised in technological societies filled with artifacts that emphasize the horizontal and vertical outlines of objects. Following removal of such prisms the expected aftereffect occurs — the world is now distorted in a direction opposite to that of the adaptation prisms.

## SQUINT (STRABISMUS)

The most interesting neurophysiological experiment and the one most closely related to the Innsbruck research was on squint (strabismus). An adult who develops squint sees double; an infant or child with squint suppresses vision in one eye. If the squint persists the eye may deteriorate and produce severe loss of vision or blindness (24).

Hubel and Wiesel (15) produced a squint in newborn kittens by cutting the medial rectus muscle. The optical axis of the eyes are thereby deflected from normal. Three months later they tested the kittens' vision. Curiously, the cats had perfectly normal pattern vision in both eyes. But the investigators went ahead to record from the cortex of these animals. To their astonishment they found that few cells could be driven by both eyes; 80% were completely monocular. Squint causes the dominant eye to take over, leading to a complete loss of control from the other eye.

Why should this be? Is it the lack of synergism between the 2 eyes, or some kind of active antagonism or competition? To answer the question it is necessary to allow both eyes to be used but to prevent their working together.

When the kittens are raised normally but allowed to use only one eye at a time, alternating monocular closure, the same results are found. What is not normal is the time relations between the impulses from the two eyes. The squint result in kittens comes from the eyes not working together (12).

There is a remarkable correspondence between these findings and those of the Innsbruck squint prisms on human adults. The failure of the color-stereo effect to show any adaptation strengthens the conclusion that normal binocular depth perception requires synergistic cooperation between the two eyes.

Once the two eyes have worked together cooperatively to deliver stereoscopic information to the brain, even if only for a short period of time, the binocular function remains. Those born with cataracts may find that surgery fails them, but the removal of cataracts from previously sighted persons does magically restore vision. The magical factor in the latter case is explained by Konorski (12) as the opportunity to form relevant gnostic units in the visual gnostic field. Those born blinded by cataracts never develop the requisite gnostic units.

The child or monkey with amblyopia (squint), unless the amblyopia is overcome early, will rarely recover normal binocular vision. The appropriate gnostic units are lacking.

## PRINCIPLES OF RECONDITIONING

Both Kohler (18) and Konorski (19) make telling use of introspection as a source of information about the processes of conditioning and reconditioning in behavior and perception.

In this reversed world, the use of the eye to guide walking is dangerous, Kohler points out.

> The old habit (of visually guided initiation of movement) continues despite the spectacles but now to the disadvantage of the subject. Subject G. describes his impressions as follows: My feet don't go where I want them to... but I have the feeling that I'm walking straight ahead; only now and then I get grass under my feet, which I'm quite sorry for... His path taken with the intention of 'staying in the middle,' appears as a zigzag line. No wonder: the first little deviation was spontaneously corrected, but since the visual field was reversed, the correction was incorrect — until finally the error was obvious and the game (after reorientation) began once more (p. 147).

Lewis Carroll describes a similar corkscrew path for Alice.

> "I should see the garden far better," said Alice to herself, "if I could get to the top of that hill: and here's a path that leads straight to it — at least, no, it doesn't do *that* —" (after going a few yards along the path, and turning several sharp corners), "but I suppose it will at last. But how curiously it twists. It's more like a corkscrew than a path. Well, *this* turn goes to the hill, I suppose — no, it doesn't. This goes straight back to the house'. Well then I'll try it the other way."

In the unfamiliar world on the other side of the looking glass, Alice found that her old habits were in the way. They had first to be overpowered before new patterns could prevail.

To control the zigzag movements, Kohler explains (18, p. 149), the subject has to say to himself at every opportunity:

> "Always do the opposite, head into danger, walk in the direction that you want to turn away from..." By this process he gradually develops a new set of habits and comes eventually to 'see correctly.'
>
> The overcoming of the disturbance does not begin with vision but rather with touch... (and, one must add, with kinesthesis). Walking, avoiding obstac-

> les, reaching, etc. become better and finally almost faultless after two or three weeks while visual experience — in other words, perception — still remains reversed. In these conditions, one cannot yet speak of perceptual adaptation, but only of a correction of behavior. But it is of greatest interest that the latter becomes a stepping stone for the former. This demonstrates that they are related in some fundamental way. The "how" of this relationship was indeed the primary question of the entire experiment, and the participants always waited expectantly for that moment in the experiment when 'correct seeing' occurred for the first time. And this climax always takes place. But a peculiar route, one might almost say a "detour" is taken to get there (18, p. 149).

False movements cannot be endured; the immediate necessity is correct behavior. Kohler shows us how this happens and then traces the transition from behavior to correct "seeing."

The process of reconditioning may be codified as a set of rules.

> Rule 1. Don't think — *Act!* Conscious reasoning about the reversing spectacles and what was *really* right and *really* left was counterproductive.
>
> Rule 2. Go the *other* way. Your first impulse is wrong. Command yourself to do exactly the opposite of what your eyes, on the basis of pre-experimental experience, direct. Head into obstacles, don't avoid them.
>
> Rule 3. Slow down! An affective tone of "watch out..." does not stop false reactions but it does delay them. From this develops an important area of contact between vision and touch (and *kinesthesis*) which is the basis of the development of a new experience (p. 151).
>
> Rule 4. Revise *expectations*. The only thing of relevance is "correct or incorrect," not "right" or "left" (p. 151). ... Eventually, there develops a kind of premonition, an expectation about this during the moment of reaching which predicts the result... When dealing with corrections of *expectations*, we are nearing the initiation of correct seeing (18, p. 152).

## MECHANISMS OF TRANSFORMATION OF CONDITIONED RESPONSES

On what factors do these rules depend? We are beginning to understand the physiological mechanisms that underlie the transformation of conditioned responses. Of particular interest to an explanation of Kohler's discoveries is Konorski's (19) theory of the formation of separate gnostic fields and their interconnections in the brain.

Konorski's (19) theory of the formation of associations between different analyzers, especially vision and kinesthesis, provides a useful framework for understanding the sensory disturbance experiments. The interplay between our visual and proprioceptive afferent systems controls all our visual orientation in space. Even our mental visual images reflect this pervasive influence of proprioceptive associations. With both your eyes closed, observe how difficult, if not impossible, it is to imagine the right side of your room without turning your eyes to the right.

The kinesthetic eye movements play a decisive role in visual spatial imagery.

Kohler's subjects had to reverse a lifetime of experience with specific visual-kinesthetic, visual-somesthetic and labyrinthine-spatio-visual associations. They had to form new habits antagonistic to the old firmly established associations or conditioned responses.

What appeared to be truly amazing was that the sensory aftereffects of tilt, curvature, size, shape and color following prolonged wearing of the distorting spectacles were contingent upon specific eye movements (looking left or right, up or down) and also on specific conditions of stimulation (the general illumination, and the kinds of objects being observed).

"Again and again," Kohler wrote, "standards of size, angulation and movement within a single retinal area were found to vary, even though the stimulus remained the same (p. 122)." Now the crucial question arises, why should this be so?

Although there was a time in the history of sensory psychology when there was a controversy about the validity of these observations — "How can vision ever be partly right, partly reversed?" (10, p. 432) — we now know enough about the physiological properties of the visual system to describe how the neural network is organized so as to bring about these different situational aftereffects.

Observations that seemed bewildering — the apparently paradoxical split between, on the one hand, small, manipulable objects that normally appear in any position; and on the other hand, printed symbols, asymmetric letters and numerals, that show a greater resistance to rehabituation, are no longer surprising.

According to Konorski's (19) ideas of the functional organization of the brain, we can discriminate between the formation of gnostic fields clustered around projective areas of each analyzer in various parts of the cerebral cortex and the formation of interconnections by long association pathways between these cortical areas. The gnostic areas, unlike the projective areas, have a categorical and not a topographical organization in the brain. All the possible stimulus-patterns impinging upon a given afferent system belong to different categories determined by the elements of which they are composed. Within each category sets of neural units (gnostic units or unitary perceptions) represent the various biologically meaningful objects or patterns that the organism has experienced and recognizes.

The basis for perception is the stored representation of familiar patterns in the brain cells. These gnostic units (or as I call them, *"cognons,"* in order to link *cognition* to the biological units, the *neurons*) are divided into particular categories in the different perceptual systems and subsystems. The sense of sight, hearing, touch and so on, each contain separate categories of unitary perceptions based on differences between their elements.

For instance, the visual pattern system contains categories representing human beings, animals, small manipulable objects, large movable objects, and far-off scenes, mountains, landscapes. The visual space system categorizes spatial relations giving us near-far, above-below, left-right, in front-behind. The auditory system divides heard sounds into categories also — music, voices, spoken words, and noises of the external world.

Within each category there are files containing a number of equivalent functional gnostic units or cognons representing the biologically meaningful stimulus patterns and objects that the individual has experienced and stored in memory. Following damage to the brain, a patient may lose the ability to recognize a whole category, human faces, for example, without impairment of visual recognition of other body parts, and with complete retention of auditory and other sensory capacity.

The visual system concerned with the spatial relations between the organism and the environment, and between various parts of the environment is of central interest to the experiments with goggles.

In the day-to-day world of familiar experience the subjective standards are formed under consistent conditions of eye and body position and movement. For each object: your hand, the face of a friend, a house, there is a certain normal viewing distance; its size at this distance becomes the standard size for this particular object. Not only size, but shape and orientation conform to the normal viewing angle and direction of gaze. When attention is directed to a familiar object, the subjective standard bends the immediate perception to this standard without regard for photographic accuracy. This integrity of the cognon, its ability to deform a stimulus-pattern to a model, is what accounts for the constancies of perception.

Under abnormal conditions of stimulation, the old models no longer fit. All asymmetrical objects: the letter *B*, print in general, faces, feet and shoes — these are firmly associated with the subjective left-right, up-down, and normal viewing angle. Their changed positions confuse and disorient the subject. But small, manipulable objects that ordinarily occur in any position, the cup, the clock hands, the chess piece, etc., have no unique location or orientation. They are movable, and they are ordinarily seen not only from various distances, but also from different sides and in different locations in the visual field.

As the subject adapts, accordingly his visual perception changes in a *piecemeal* fashion. Some parts of the visual field are perceived correctly; others remain reversed. "Vehicles driving on the 'right' (and the noise of the motor agreed) carried license numbers in mirror writing. A strange world indeed (18, p. 155)!"

"Yet Subject Grill went beyond this stage and eventually achieved almost completely correct impressions, even where letters and numbers were involved. Mirror reading became well established. Following removal of the spectacles the mirror world returned; "p's were seen as q's, b's as d's, and on a clock face 10 : 30 was read as 1 : 30 (p. 160)."

This visual-spatial system operates in close correlation with the system of kinesthetic-spatial relations and with the vestibular system. The neurological evidence shows that it is located in the right cerebral hemisphere. Patients with lesions in the right brain lose their spatial images, being unable to locate big cities or familiar landmarks on a contour map, or to sketch their apartments, although the items themselves are well known to them.

The localization of language chiefly in the dominant left hemisphere provides an anatomical separation between verbalization and our visual orientation in space. Here is an explanation of Kohler's finding that words failed to play a helpful role in rehabituation to inverted visual space. Hundreds of times during the day false movements and turns are taken by the subject who naturally seeks methods to control these wrong turns and zigzag paths taken with the intent to walk straight ahead. Like Alice, to succeed, the subject must "influence his initial impulse by saying to himself at every opportunity: Always do the opposite, head into danger, walk in the direction that you want to turn away from..."

Behavior, no more than vision, is not corrected in one simple step, but in stages. The process of rehabituation teaches us that neither behavior nor perception is unitary — recoordination demands the formation of many separate new associations between voluntary movements and visual experience. Much that has been built up in the course of normal development can be discovered through the rehabituation experiment.

Not conscious reasoning, not talking to oneself about the reversed right and left, or the way things really are, (Rule 1) but the method of commanding oneself to go where one does not want to; to raise the wrong foot; to run into obstacles headon — that (Rule 2) led to success.

Although Konorski knew Stratton's experiments and recognized their important value for studying the formation of associations (conditioned responses) it is unlikely that he was acquainted with the Innsbruck research or he certainly would have incorporated these remarkable studies in his 1967 monograph. To Konorski, the "substitution method" as he called it, that Stratton used, was simply to observe the effect of "replacing the expected perception by a quite different one (19, p. 218)."

Some of the *non-verbal* associations that undoubtedly provided the basis for Stratton's and Kohler's adaptation to strange environments include: stereognostic-visual associations; somesthetic-visual limb associations; kinesthetic-visual associations (objects and signs); auditory-visual associations; and labyrinthine-spatio-visual associations (stabilization of the rubber world).

What is particularly impressive is the demonstration that *behavior* is corrected first; movements, reaching, walking, avoiding obstacles are adjusted to the changed world and the new motor adaptation becomes a stepping stone for correct *seeing.*

These prism studies clearly demonstrate the existence of what Kohler describes as "the complex interweaving of habits, built up throughout the course of life and almost inextricably 'boxed into' one another (18, p. 138)."

How do these interconnected habit patterns get disentangled? Kohler's description of the experiment shows us how "complex and variously resistant the components of the habit hierarchy can be; how the "apparently 'simple habit' is built up from a 'network' of components of different 'depths' and how therefore it can never be altered as a whole (18, p. 139)".

Certain new habits are much easier to establish than others. Why is this so? Konorski's (19) theory of the transformation of conditioned responses offers a plausible explanation. According to this view, the ease or difficulty of transformations depends on the strength of previous conditioning or past associations. "...the so-called extinction of a CR (conditioned response) is nothing but the substitution of a new reinforcement for the old one (in that case no–US for US) and thus follows the general rules of transformations of CRs (19, p. 344)." Firmly established associations are nearly indestructible; their susceptibility to suppression by fresher associations depends on the substitution of a new reinforcement antagonistic to the old one.

Conversely, it is relatively easy to reestablish or restore the old conditioned response. The old connections on which this conditioned response is built are already there; reverse training consists only in establishing their relative dominance over the newly formed connections.

In this process, whether reconditioning or reversion to the original conditioning, what chiefly matters in establishing an operant or instrumental conditioned response is the active performance of the movement. Of course it is essential that a drive be present; the conditioned movement must be followed by drive reduction; and the conditioned movement must cease when the drive is satisfied (Rule 3). The formation of an association between two synchronous perceptions may occur only against the background of nonspecific (axodendritic) facilitatory influences exerted upon the neurons receiving the stimuli. As Kohler points out, what is important in the experiments with goggles, is that the hand reaching out to grasp an object gets the object, i.e. that it reaches correctly. If it fails, the subject experiences a strong emotional attitude of annoyance or frustration.

Konorski's ideas about the kinesthetic analyzer are especially relevant here, because this analyzer provides both feedback from self-produced active movements and feed-forward, that is, it plays the role of programming devices for skilled motor acts.

Once the gnostic kinesthetic units for particular acts have been established, these units now begin to function independently of the sensory input to which they owe their function and can mediate higher order habits without sensory feedback from moving parts of the body. Delcomyn (4) summarizes convincing evidence for this principle of central control. The central nervous system is intrinsically capable of providing the proper timing of muscle activation without requiring sensory feedback. A single pacemaker neuron (gnostic unit) or central program generator can produce a repetitive, rhythmic output for such activities as walking, swimming, feeding, etc.

The image of a movement is an agent eliciting that movement. When the image of a movement is not followed by that movement, it must be because at that moment the corresponding projective units are already engaged, being blocked by antagonistic units (Rule 4).

"In the kinesthetic-spatio-visual association the decisive role is played, not by the *feedback* of the eye movement performed, but by the very programming of that movement in the kinesthetic gnostic field (19, p. 222)."

Kohler points to some new habits that are much easier to establish than others. The reason for rapid success in such acts as cutting, filing, and soldering is that the subject has never seen *himself* doing certain things and so does not possess the corresponding images in his visual file. Antagonistic expectations are absent. His locomotor behavior, going down the street, turning the corner, whether on foot, bicycle or skis is controlled, however, by the alternation of visual and kinesthetic images, especially eye movements of his motor acts. These images contradict the required new patterns and Kohler found that it was much easier for his subjects (including himself) to move in a well-known space with his eyes closed than with them open. "There exist movements for which seeing is a luxury (18, p. 144)."

Similarly, when a retinal image is compared to an expectation formed by experience, a deviation from expectation may be interpreted as extraordinary color. Hohmann and van der Malsburg (11) offer this explanation for the vivid prismatic fringes observed by Kohler and also for the McCollough effect (20). They assume that

> ... our central nervous system (CNS) possesses, in every situation, a precise description of the colour fringes produced by chromatic aberration in the eye. Objective colour near the edges can only be perceived as a deviation from this 'expectation.' The chromatic fringes change with certain physical parameters which determine the condition of the eye. The CNS must 'know' the functional dependence of the expected colour fringes on these parameters. If this functional dependence is experimentally manipulated, then the brain can readapt by new learning. Subjects with prisms in front of their eyes report seeing colour fringes in white light, because chromatic aberration is changed and no longer corresponds to the expectation. After a few days of continued exposure to prisms the fringes disappear, showing that the CSN is able to return to changed eye optics (6, 11, p. 551).

## CONCLUSIONS

If we compare Kohler's experimental alterations of the perceptual world with evidence derived from isolation, deafferentation and paralysis of sensory cues and experiments on monocular alternation and sensory deprivation, reverse suturing, exposure to abnormal environments, and artificial squint, we reach the following conclusions:

1. Sensory deprivation or exposure to certain kinds of stimulation can change the organization of the afferent systems.
2. The effects of these experimental alterations may be permanent or reversible, depending upon the age of the subject and the duration of the critical period of susceptibility. A change occurs without obvious deprivation if the two eyes are occluded alternately during the critical period. The two eyes must have the opportunity to work together to insure the connections needed for binocular vision and the formation of unitary stereoscopic perceptions.
3. There are strong associations between motor actions, kinesthetic programs, and visual experiences that may have variable optical consequences (such as alterations in the perceived size, form, spatial direction or color of objects). The conditioned responses established by lifelong experience in the familiar world are more or less resistant, more

or less susceptible to reversal by the substitution of antagonistic unconditioned stimuli or reinforcements. Transformation of conditioned responses can be achieved by the previously conditioned organism in a new situation given the arousal of drive and self-produced activity that satisfies the drive. Changes in preservative and protective motor behavior precede "correct seeing."

4. After removal of the distorting goggles variable aftereffects occur and persist depending on the strength of the newly conditioned responses. Ordinarily, restoration of the original conditioned responses in the mature subject is achieved rapidly relative to the adaptation to the abnormal environment.

5. Situational or conditioned aftereffects do not occur as an all-or-none phenomenon. In both motor activity and visual experience the adaptation to a distorted world is stepwise and complex, just as in the formation of the normal perceptual and behavioral world, "...the apparently simple habit is... built up from a 'network' of components of different 'depths' and therefore can never be altered as a whole (18, p. 139)."

6. The use of Konorski's theory as a framework into which to fit these remarkable studies together with recent electrophysiological work on the transformations of the visual system in cat and monkey further demonstrates the power of his explanatory ideas about the integrative activity of the brain.

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