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## ***The Principle of Reafference: Interactions Between the Central Nervous System and the Peripheral Organs***

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### *INTRODUCTION*

A major question for the physiology of the central nervous system (CNS) has always been this: what lawful relationships hold between impulses which are generated by external stimulation and travel inward into the CNS and those which—either directly or indirectly—reemerge from it; that is, the question of the relations between afference and efference? The CNS has been characterized as a sort of automat, which reflexly delivers a given ticket when a particular coin is inserted in it. For simple protective reflexes—like sneezing and withdrawal from painful stimuli—this idea is easy to accept; for more complicated reactions such as balancing and orienting responses, the same conceptual scheme has been advocated. Even rhythmic locomotor patterns can be understood in these terms, if one assumes that each single movement reflexly evokes its counterpart, that each component sets off its successor in time (reflex chain theory). The higher forms of behavior, which are modifiable through experience, are subsumed under the same rubric by way of "conditioned" reflexes.

This "classical reflex theory" largely still holds sway, although there are many facts which are inconsistent with it. We know that the breathing centre maintains its activity without external rhythmic stimulation, that the central locomotor rhythms of many invertebrates remain intact in the absence of afference (von Holst, 1932, 1933, 1938), that in fish (von Holst, 1935; Lissman, 1946) and amphibians (Weiss, 1941; Gray, 1946, 1950) only a very small part of the afferent innervation is sufficient to ensure that all parts of the body can continue to locomote properly. The reflex chain theory cannot handle such facts. The analysis of relative coordination in anthropods, fish, mammals and humans has taught us to recognize central forces of organization—of coordination and control—whose interplay leads to the establishment of laws which are formally quite similar to those laws of perception which were discovered by Gestalt psychology.

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These newer findings defy description in terms of reflex terminology. It is therefore understandable that they have remained unassimilated to the mainstream of the physiology of the CNS, although they have had a certain influence on research in comparative behavior (Lorenz, 1950; Tinbergen, 1951, for example) and in human psychology (Metzger, 1953). Even recent textbooks are based entirely on the classical reflex theory. For many physiologists the idea that the CNS is an active entity in which orderly occurrences are possible without external stimulation, that rest and sleep are but special forms of CNS activity, seems to be unscientific. The "cause" of every central occurrence is still held to be "the stimulus."~

This position is quite understandable; no one would want to give up a simple theory until he had a better one—especially if on account of its great age that theory has come to be taken as established fact. A new theory must encompass both old and new findings, and allow predictions beyond the areas previously encompassed. Some recent experimental results have led us to develop a conceptual framework which, within specified limits, may satisfy these conditions. This is laid out in the following pages by means of examples, and its viability established in terms of known, but hitherto unexplained, phenomena. The chief characteristic of this new conception is a complete reversal of the usual way of looking at the system. We do not enquire into the relations between a given afference (input) and the efference (output) to which it gives rise (i.e., the reflex arc) but rather start with the efference and ask: what happens after the efference has caused changes in the organism via the effectors, and then is reverberated back into the CNS by way of the receptors, as afference? This type of afference which is caused by the efference itself we shall call refference.

## *REAFFERENCE*

### Introductory Example

Let us start with an example: if a hollow cylinder, the inner surface of which is painted with vertical black and white stripes, is placed over a stationary insect such as the fly *Eristalis*, and rotated, the insect starts to turn in the same direction. It attempts to maintain, or stabilize, its visual field (Fig. 1a). This well-known optomotor reflex is readily elicited at any time. However, if the insect starts to move itself within the (stationary)

<sup>1</sup>This misunderstanding is probably psychologically motivated, in the sense that it reinforces the naive attempt to explain every visible bodily movement in terms of a specifiable environmental event, rather than in terms of invisible transformations within the CNS. The latter seem to have too mystic a quality.

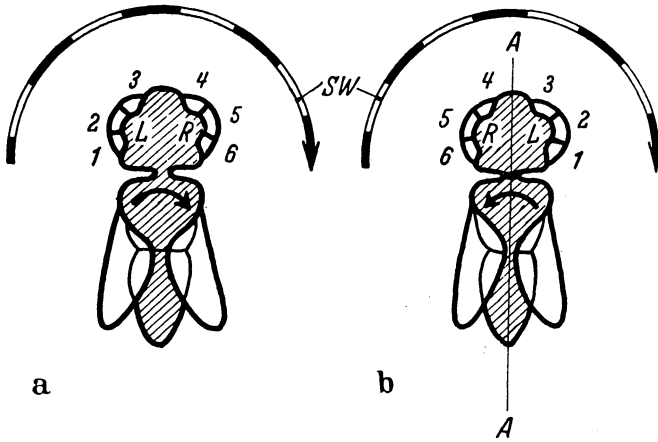


Fig. 1. Behavior of the insect *Eristalis* when a striped cylinder *SW* is rotated past the eyes from left to right. a, Normal insect, b, following rotation of the head by 180° about the axis *A-A*. *R* = right eye, *L* = left eye (each ommatidium is numbered). The arrow on the thorax indicates the direction of active turning.

cylinder, normal voluntary movement occurs just as in an optically unstructured environment. The question now is why the optokinetic reflex does not force the fly back into its starting position, as soon as it begins to turn, since the movement of the image of the cylinder across the retina is the same as in the former case (rotating cylinder, fly stationary). The answer of reflex theory is that during spontaneous locomotion the optokinetic reflex is inhibited. But that answer is wrong! *Eristalis* has a slender and flexible neck which can be rotated through 180° about its longitudinal axis. If this is done, and the head glued to the thorax, the positions of the two eyes are reversed (Fig.-1b; see also Mittelstaedt, 1949). In this way a clockwise rotation of the cylinder produces image movement across the retina which under normal circumstances would be produced by counterclockwise rotation. The stationary fly responds to rightward movement of the cylinder by turning itself promptly to the left. If the optomotor reflex were indeed inhibited during "voluntary" movements, the free movement of the fly within a stationary cylinder should occur normally, as in an intact insect. That only happens, however, in an optically homogeneous environment. In the striped cylinder things are no longer normal; *Eristalis* turns continuously to the left or right in tight circles, or else short sharp turns to the left and right follow one another in rapid succession, until the insect eventually stops, "freezing" in an atypical posture. If the head is returned to its original orientation, behavior is once again restored to normal.

This finding contradicts the reflex inhibition hypothesis; it shows that contour movement across the retina influences locomotion, both when the insect moves itself, as well as when the cylinder moves. As a first formu-

lation we can say: the moving insect "expects" a very specific change in retinal stimulation which, insofar as it occurs, is "neutralized" in some way. But following interchange of the two eyes there is retinal motion opposite to that which is expected, and the optomotor response is immediately evoked. This movement, however, magnifies the unexpected retinal motion, and thus the process is self-reinforcing. Every time the insect starts to turn, it is forced further around in the same direction by the optomotor response. If it attempts to move in the opposite sense, it faces the same dilemma. The result is clearly a central catastrophe!

If this account of things is correct, we must ask ourselves how the CNS "knows" which type of retinal image motion to expect. There are two possibilities; either the CNS retains information for a certain time about the efference which has been sent to the limbs, information which is stored as a central record to be compared to the subsequent retinal changes; or if the CNS does not have this simpler capacity, it must rely on the reafference from the receptors of the moving limbs, calculating the direction and speed of body motion in order to compare them with the retinal reafference. Both alternatives are possible, and we shall leave the question of which one is correct open for the moment, turning our attention instead to another example for clarification.

### SHARPER DEFINITION OF THE PROBLEM

Each labyrinth of the vestibular organs of every vertebrate contains a flat body, the utriculus otolith. When the head is in its normal orientation this body lies horizontally on a sensory surface, and is responsive to gravity. Experiments with fish, recently reported (von Holst, 1949, 1950), show that the adequate stimulus to this receptor is a force parallel to the above-mentioned sensory surface. This shearing force increases sinusoidally as the head tends away from the normal position, and causes a sinusoidally increasing central imbalance in activity, a "central turning tendency" which initiates motor activity to bring the animal back to its normal posture. The system works with great precision without adaptation or fatigue. In the words of reflexology: the organism maintains its normal posture by virtue of its "postural reflex." Now one can readily observe, in all animals and in man, that it is possible to maintain other postures for shorter or longer periods of time. Fish, for example, position themselves practically vertically, facing up or down, turn on their sides, etc., when seeking food, following prey, in fighting, or copulation.

How are these variations in maintained posture possible, in view of the ever-ready "postural reflex"? Reflexology answers as before, that the postural

reflex is wholly or in part inhibited. It is easy to show that this notion is wrong. The "intended" or "goal" postures which differ from the norm are themselves maintained against external perturbations by exactly the same kind of corrective movements which serve to maintain normal posture!

One might suppose that the reflexes are maintained in operation, but shunted through different pathways by a superordinate control mechanism. The higher center merely activates the control points which determine what the route is to be from afference to efference (the "redirected reflex"—*gelenkte Reflexe*—of W. R. Hess). This conception leads to an experimentally testable consequence: simple switching points do the same job, however light or heavy the traffic they bear. In other words, the operation of this reflex governor, or switching mechanism, should be independent of the amount of afference. However, that is simply not the case.

One can magnify the force exerted by the statolith on its receptor surface in a centrifugal field of force. If the weight of the statolith is doubled in this manner, the shearing stimulation produced by departures from the normal posture is also doubled. If the frequent spontaneous deviations (nose up, or down) of a free-swimming fish are recorded, it will be observed that they become smaller, the heavier one makes the statoliths. "Voluntary movements" show themselves to be dependent on the returning stream of afference which they themselves cause!

Another example: fish position the main body axis in the direction of water flow by "latching on" to the optically static environment. This is true in the main also if the current flows at an angle, or vertically from above (or below); the more the fish is able to point its nose into the current, the more easily can it maintain its posture against perturbations without fatigue (von Holst, 1949). Investigating the behavior of a free-swimming fish in a tank subjected to a constant water current, one finds that increasing the weight of the statoliths makes it more and more difficult for the fish to maintain its posture against the current flow as that flow approaches the vertical' (Fig. 2). It now attempts to maintain a dorsal posture to the direction of the current, but can do so only imperfectly, and tires rapidly. This difference-disappears if the statoliths are removed: in that case the proper orientation to the current flow can be maintained, no matter what the mechanical field forces are.

We see, then, that the higher central system which is activated by deviations from the "goal posture" is not simply a switching mechanism, since the reafference caused by its activation has a quantitative influence on the resulting posture itself. Despite this refutation of the concept of "redirected reflex," the following exposition is closely related to the research of W. R. Hess (although his methods are quite different)—both in terms of problem statement and mode of thought. However, this switching (points) system must work harder, the more traffic passes through! How is that to be explained?

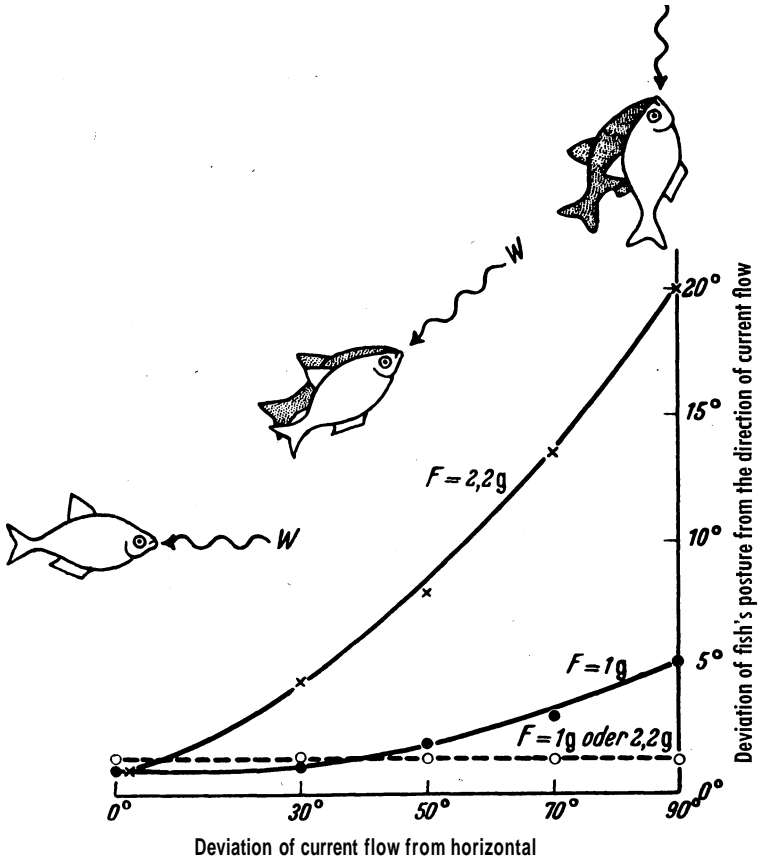


Fig. 2. Postural adjustment of a fish swimming freely in a tank through which water flows with constant velocity. Parameter indicates gravitational field force,  $F$ . ("Vertical" is here the resultant of gravitational and centrifugal forces.) ● and X are for intact fish, O for fish from which the statoliths have been removed. The white fish indicates the behavior of an intact organism under  $F = 1g$ , the grey one under  $F = 2.2g$ .  $W$  = direction of water flow (speed of current approximately one fish length per second). Hydrostatic pressure was held constant. Means for 5 experimental runs each with 3 fish (*Gymnocorymbus* and *Hypsobrycon*).

We can picture the matter quite simply by keeping in mind two well-established and basic physiological facts:

1. The sensory cells of the labyrinth have, like other (and perhaps most) receptors, a basal spontaneous firing rate even in the absence of a shearing stimulus. The shearing stimulation of the statoliths increases or decreases that firing rate, depending on the direction of shear. This automatic response of the receptors has been confirmed both by our own investigation on fish, and by direct electrical recording from the afferent fibers (O Lowenstein, 1950) and from the vestibular nuclei in the brain (Adrian, 1943).

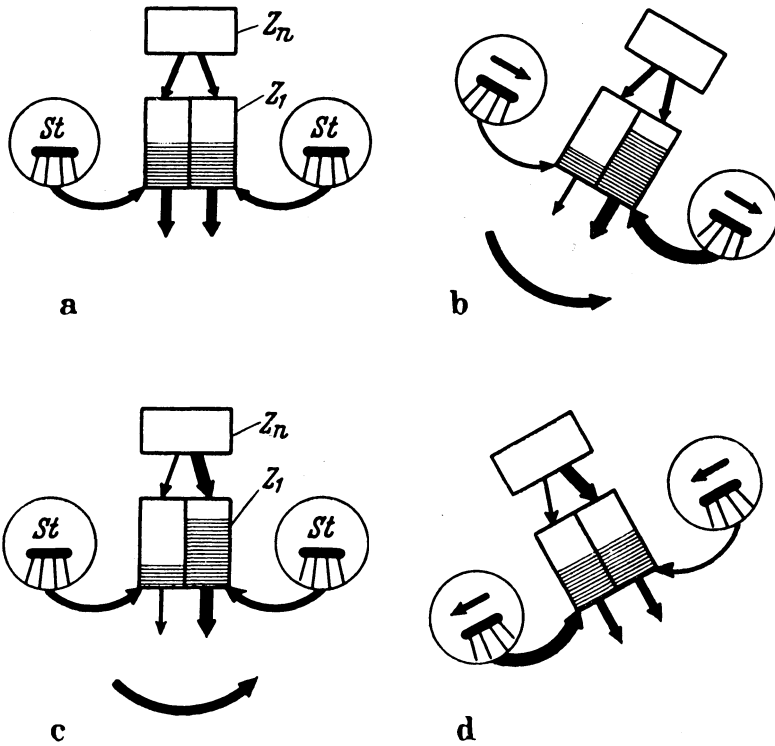


Fig. 3. Schema for the elucidation-of the coordinated activity of higher centres ( $Z_n$ ) with the lower postural centre ( $Z_1$ ) and the Statolith apparatus ( $St$ ) in postural orientation of the fish (about its longitudinal axis). The thickness of the arrows indicates the strength of a stream of impulses (number of impulses per unit time) flowing from one point to another. The shading in  $Z_1$  indicates the strength of activity within its two halves at any given instant.  $St =$  statoliths, the arrows in b and d indicating the direction of shear; the large middle arrows in b and c show the direction of turning. a, Normal situation; b and c show the direction of turning. a, Normal situation; b, tendency to return to the normal posture after the fish has been passively tipped to the side; c, active (spontaneous) turning to the left, d, its result the intended "goal posture."

2. A steady stream of impulses flows between higher and lower centers even in the absence of external motor activity. This also has been established by electrophysiological investigation for many different central areas, and can be inferred from the large and abrupt decline in activity when certain descending central connecting fiber bundles are severed. The "spinal shock" of lower motor centers after destruction of the vestibular-spinal tract corresponds to the "shock" which the left vestibular nucleus suffers on destruction of the left labyrinth. In both cases a steady activating stream of impulses is interrupted.

These two prerequisites are needed to substantiate the model sketched in Figure 3. The "position center," a complex of neural ganglia (whose

spatial distribution is not our present concern) consists of two halves, both of which receive impulses from the statolith epithelium and from higher centers. If both halves are equally "weighted" (both in the same condition of activation) then they send equally strong trains of impulses to the lower motor centers of the spinal cord (Fig. 3a), which result in the well-known "tonus" effect of the labyrinth (Ewald; see also von Holst, 1949). If the fish is tipped passively to the right (Fig. 3b), then, as has been experimentally proven (von Holst), the shearing effect in the right statolith produces an increase in afference, but in the left statolith a decrease. The resulting difference in levels between the right and left "position centers" entails inequality in the trains of impulses to the spinal cord, and this sets in action the motor apparatus to produce a turning movement to the left. This, in the classical terminology, is what is called the "postural reflex."

A corresponding difference in levels can also occur as a result of unequal input from higher centres (Fig. 3c, d); the result is the same motor pattern as before.<sup>2</sup> These occurrences are known as "voluntary movements" in physiology. It appears that the resulting "goal posture" or "intended posture" is just as efficiently maintained in the presence of passive external disturbances as the "normal" posture, and in exactly the same manner in terms of the afference arising from the statolith apparatus; every passive change in position leads to a difference of levels in the postural centres and hence to a "postural reflex" without the involvement of higher centres.

Let us consider some of the testable consequences of this model:

1. Destruction of the left statolith apparatus must result in an immediate fall in the level in the postural center, and hence produce a continuous tendency to turn to the left. And this must reach a maximum when the organism is turned on its right side (strongest afference from the right), a minimum when it is turned on its left side. This turns out to be true for all vertebrates, and has been measured quantitatively in fish (von Holst, 1949). The same is true if the postural center itself is damaged or destroyed, as is already known (Spiegel & Sato, 1927).

2. Once the left postural center has recovered from the immediate post-operative disruptive effects of statolith removal, and is again under normal load or "weight,"<sup>3</sup> the tendency to turn in response to changes of posture only reaches half its former value, since the left-hand input remains constant and only the right-hand input responds to changes of position. This has been confirmed quantitatively in fish (von Holst).

3. Raising of the mechanical field force, and thereby of the afference from the stato-apparatus, must increase the influence of the stato-apparatus on the postural system in comparison to the effects of other processes con-

" The idea that higher centres have the function of controlling the balance of activity in lower antagonistic centres was first developed in connection with the relative coordination of rhythmic locomotor patterns of movement (von Holst, 1936). It has recently been further confirmed by electrophysiological studies (Bernhard and coworkers, 1947).

<sup>3</sup> Our coworker L. Schoen (1949) has studied these central effects quantitatively; we shall not consider them further here.



cerned with posture, such as visual afference in fish. This also has been proven quantitatively (von Holst). Doubling of the mechanical field force, for example, compensates exactly for a missing statolith (point 1).

4. After removal of the higher centers there should be no active deviations from the normal posture. This also is known to be true (Magnus, 1924, among others).

5. The stronger the field forces, and hence the shearing stimulation of the statoliths, the less should spontaneous changes of "goal posture" or those mediated by afference via other higher centers, affect postural adjustments. On this important point, too, as we saw, the prediction is confirmed: the adjustment of the postural centers is mediated by the shearing force; that is, the heavier the statoliths, the smaller the angle of adjustment attained by the organism (see Fig. 2).

6. Conversely, after bilateral interruption of the afferent pathways, small inequalities in the inputs from higher centers will lead to exaggerated movements since, mechanically speaking, if the reafference is removed, the feedback signal, which is used to estimate when movements should be terminated, is destroyed. This phenomenon can readily be observed in free-swimming fish and amphibia, and has often been described. Organisms with bilaterally removed labyrinths exaggerate any intended change of position so strongly that frequently they can do no more than reel and stagger around.<sup>4</sup> In terrestrial animals such behavior is less noticeable, on account of the general lack of tonus which follows loss of the labyrinths and because of the large part the muscle receptors play in movement control (see Fig. 5b,c). Even so, it can be observed after partial loss of the balance receptors; following destruction of both horizontal canals, for instance, horizontal to-and-fro motions of the head can readily be observed during execution of an intentional movement (especially in birds).

A number of the inferences to be drawn from our model thus prove to be correct, and concern matters which, to a degree, cannot be understood in terms of the concepts of reflexology.

## GENERAL EXPOSITION OF THE PRINCIPLE OF REAFFERENCE

The essential point in the examples of the previous section is the role played by reafference, the afference which is itself caused by active movement. The reafference compensates for changes brought about by move-

<sup>4</sup>Schöne (1950) reports a closely analogous observation on insect larvae. The *Dytiscus* larva normally positions itself with its back to the light, but will do backward somersaults in swimming upwards if the backward and forward facing eyes have been blinded. Apparently this happens because the reafferent signal which normally would inhibit its corrective movements (stronger illumination of the anterior eyes) is missing (Schöne's own explanation follows similar lines.)

ment commands from higher centers in such a way that equilibrium is reestablished. If by experimental manipulation this afference is removed, made too great or too small, or reversed in sign (the rotated head of *Eristalis*), predictable changes in motor behavior will result.

We shall first give a general exposition of this principle, and then establish its validity by applying it to a number of different neuromotor systems.

Consider some center  $Z_1$  (Fig. 4) which services an effector EFF, having both sensory and motor connections to it. This effector could be a muscle, a limb, or the whole body. There is a number of superordinate centres  $Z_2 \dots Z_n$  above  $Z_1$ . Some command K from  $Z_n$ , that is, some change in the flow of impulses from  $Z_n$  to  $Z_1$ , produces in  $Z_1$  a sequence of efferent impulses E. In addition to the efference E, however, it causes a strictly correlated neuronal process (e.g., by a change of activity which spreads, after a certain temporal delay, into the neighboring ganglia) called the *efference copy* (EK). The efferent stream of impulses flowing out into the periphery sets its effector in motion, and this gives rise to the afference A. This, in turn, interacts with the efference copy. We shall arbitrarily label the efference and its copy positive (+), the reafference negative (-). The efference copy and reafference compensate for each other exactly in  $Z_1$ . The original command from Z, can therefore flow down without modification as efference. Should the total afference become too great or too small however, as a result of external influences in the effector,  $Z_1$  will show a positive or negative residual bias. This residual is fed back, often—as we shall see—to the highest centers; we shall call this a report, M. This ascending report may—but need not—branch collaterally into  $Z_2$ , where it can again be summated with the descending command. In this case the system consisting of  $Z_2$  and the lower units becomes a feedback control system in the technical sense."

Let us suppose that some influence on the effector EFF causes an increase in afference in  $Z_1$ , and consequently, an increase in the report to  $Z_2$ ; the (negative) report will decrease the positive command output from  $Z_2$  until a balance is again struck. Similarly an externally caused decrease in afference will result in a positive residual bias in  $Z_1$ , a positive report to  $Z_2$ , and consequently an increase in the positive command output from  $Z_2$ . In other words, in both cases the efference is modified until no further report is received from  $Z_1$ .<sup>6</sup> In the example of postural orientation we have already been introduced to such a control system.

<sup>5</sup> We are grateful to Dr. Böhm for pointing out the kinship to control theory (see also Böhm, 1950).

<sup>6</sup> It should be emphasized that this "negative feedback" (negative *Rückkoppelung*) of the Anglo-Saxon literature is not a necessary component of the principle of reafference, and should not be confused with it! The essential point for our principle is the mechanism which distinguishes between reafference and exafference. This distinction plays no part in feedback control technology.

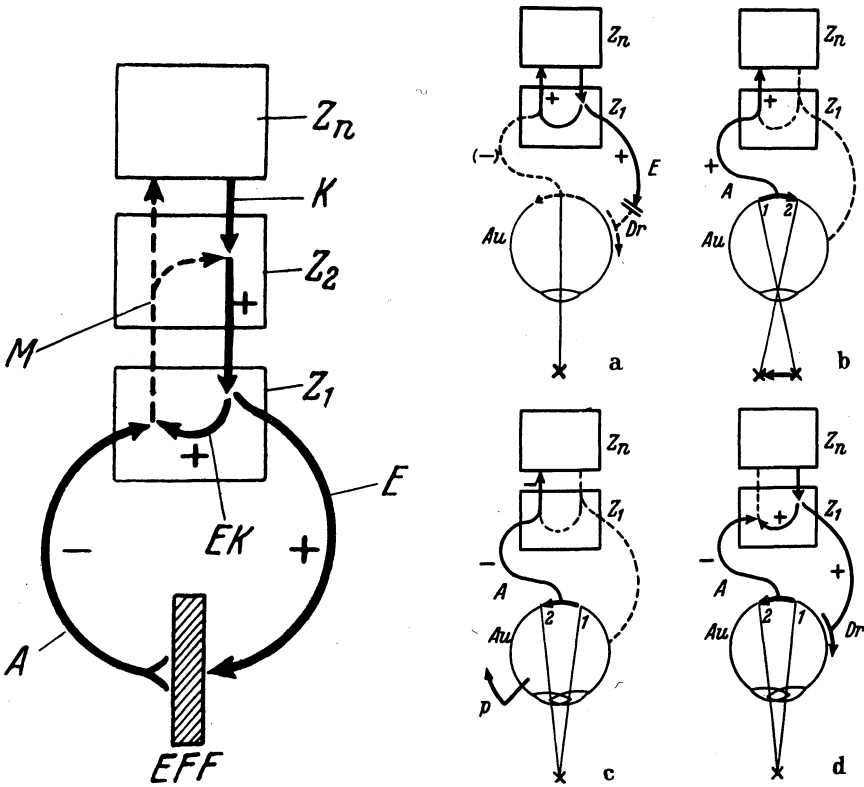


Fig. 4 (left). General schema for the principle of reafference; explanation in text.  
 Fig. 5 (right). Explanation of movement perception by the eye under normal and experimental conditions in terms of the principle of reafference.  $Au$  = eye (in primary position, seen from above),  $Z_1$  lowest,  $Z_n$  highest optical centre. The efference  $E$  which goes to the eye musculature and the afference  $A$  which results from image motion on the retina are labelled analogously to the schema of Fig. 4. In a the paralyzed eye receives the command signal to turn to the right (turning moment  $Dr$  towards the right): in b the observed object  $X$  itself moves to the right, and the retinal image moves from 1 to 2; in c the eye is passively (mechanically) moved, as indicated by the arrow  $P$ , and the retinal image of the stationary  $X$  moves from 1 to 2; in d the eye makes an active (voluntary) movement to the right (turning moment  $Dr$ , as in a), at which the retinal image of the stationary object  $X$  moves from 1 to 2. Further elaboration in text.

We shall define every change in afference which is not a direct consequence of efference, but rather results from external stimulation, as exafference; this exafference occurs in both proprioceptors and exteroceptors. Exafference, then, according to our schema, is that positive or negative residual in  $Z_1$  which ascends from  $Z_1$  to higher centers as a report.

The proposed schema makes two physiological assumptions:

1. The consequences of different impulses (signals) can be mutually (additively) reinforcing or antagonistic. This point is well documented:

for example, in the field of motor behavior the superposition of two motor rhythms of different frequencies in relative coordination (von Holst, 1939) where summation or compensation is possible, according to the phase relations between two rhythms. An example from the field of sensory coordination is the exact linear superposition of statically and optically caused central changes in activity, and similarly, the purely additive positive or negative effect produced by manipulating changes in activity in the postural control center of fish (von Holst, 1949).

2. Efferent output from a lower center leaves behind it a specific change of state, or "copy." This assumption is plausible a priori for the higher centers, and now may be taken as established for lower centers also. Recent work on action currents in the spinal cord using antidromic stimulation (which causes action potentials to propagate in a direction opposite to the normal one) suggests that the normal discharge of a motor ganglion cell is propagated not only over the efferent axons, but also over the small dendrites which interconnect with neighboring internuncial neurons, in which they may cause local changes of state. Tonnie (1949) describes this action as "central feedback" and ascribes great significance to it in the regulation of spinal excitation. For us it is sufficient to see that our assumption is at least plausible physiologically.

#### APPLICATION OF THE PRINCIPLE OF REAFFERENCE TO SEVERAL DIFFERENT NEUROMOTOR SYSTEMS

##### Eye Movements

We shall now try to find out to what extent certain facts that cannot be understood in terms of classical reflexology can be explained by the principle of reafference. In order that we may use perception as a source of evidence, we start with man, and consider the visual system. Here we may expect to find that conditions are simple, since the eye lies within a protective socket in the head, and is not normally subjected to external mechanical disturbance.

Reafference for the active eye can have two sources: (1) movement of the image on the retina and (2) impulses from the receptors in the eye muscles. Only the first of these is available to conscious perception; the part played by the second can at best be inferred. Let us start with a crucial—because unexpected—prediction: if the eye is immobilized and the muscle receptors put out of action (Fig. 5a), then, on the command "look right" (turn the eye: all directions are considered from the subject's point of view), the efference copy will return undiminished from the lowest center as report, in the absence of any reafference from the retina or the eye

muscles. Moreover, this report must be identical with that which, if the eye remained stationary, would normally be caused by a congruent movement of the environment in the same direction (Fig. 5b).<sup>7</sup> "The total visual field 'jumps' to the right." This prediction is correct! It has long been known of patients with paralysis of the eye muscles that intended eye movements give rise in perception to a shift of the visual field in the same direction. Moreover, the extent of the jump appears to be equal in magnitude to the intended eye movement. This point has been carefully confirmed by Kornmiiller (1931) who anaesthetized his own eye muscles to do the experiments. The apparent shift of the visual field cannot be distinguished from a true visual change—understandably so, according to the reafference principle, since in both cases the identical report is fed back. In this experiment, the efference copy itself is, so to speak, made visible.

Since Hering's day (cf. Trendelenberg, 1943, p. 240ff.) this phenomenon has been attributed to "shift of attention" during eye movements. A plausible physiological explanation has been lacking until now. We shall see presently that "attention" has nothing to do with the matter, since the same effect occurs even with eye movements of which the subject is unaware. Perception is here simply a convenient indicator for a physiological process which is otherwise difficult to monitor.

One gets the same experience of movement as above, but in the opposite sense (to the left) if the eyeball is moved passively, by means of forceps, to the right (Fig. 5c). In this case there is no command to move, and the retinal exafference ascends without modification as a report, thereby evoking an "illusory" perception, which is: "the visual world jumped to the left."

Let us now combine the first condition with the second, namely, move a paralyzed eye passively at the very moment when the movement command is given (and in the same direction). Or—obviously, so much easier—let us make a normal eye movement with the intact eye: in either case, there are indeed two complementary trains of impulses (Fig. 5d); an efference copy which on its own makes the visual scene move to the right, and an afference<sup>8</sup> which on its own makes it move to the left. Since, however, these two cancel each other out at the low level of  $Z_1$  no report ascends higher and we see neither movement; as witnessed by our everyday experience, the environment remains stable. And that, in the present instance, is objectively correct. The "right" perception turns out to be the sum of two opposite "false" perceptions.

<sup>7</sup> This is to be expected since in such an environmental shift the opposite displacement of the retinal image occurs to that which would be occasioned by an eye movement to the right. The reversal of direction is represented in our schema by a reversal of the sign of the afference, from negative to positive so that a positive report, that is a report having the same sign as the efference copy, is fed back.

<sup>8</sup> In the first case (forced movement) this afference is, in our terminology, an exafference, in the second case (normal eye movement) a reafference.

This central apparatus has, like all technical structures, definite limits of precision. It works reliably only at mecliusn-sized eye deviations and moderate eye velocities. If one turns the eyes far to the right, for example, and scans rapidly up and down a vertical corner of a room, there is a noticeable "apparent rotation" of the field (Hoffman, 1924). According to our interpretation, this means that the efference copy of the movement (a rotation, according to Listing's law) cannot completely annul the afference which it causes, so that some report is fed back to higher centers. Also, the visual world seems to move to and fro (and in the opposite sense) if the eyes are moved rapidly right and left; in this case, it seems that the efference copy builds up too slowly, so that a small report gets through.

The fact that both passive movements of the normal eye as well as the intention to move a mechanically fixed eyeball can give rise to powerful apparent movements of the visual world (as Helmholtz already knew) demonstrates that the afference of the eye muscle receptors can be of little, if any, significance here. If these receptors signaled the position of the eyeball, in the way that certain receptors monitor limb position (see also the section on limb movements, pp. 58–63), then it should only be possible to get apparent movement of the visual world after they had been eliminated (as in Kornmiiller's experiment). The role of the eye muscle receptors has been much overemphasized up to now—as we shall soon see below—because reflexology took no account of internal feedback processes.

The principle of reafference is valid not only for the so-called "voluntary" movements, but also for those involuntary movements in which the eye "scans" the visual field, fixating first one point and then another, moving rapidly between them. This scanning occurs both in active eye movements, as when reading a book (in which every line requires four or five fixations) as well as when the head and body are turned (labyrinthine nystagmus) or the visual world moves before us (optomotor nystagmus). In all these cases, we normally notice nothing of the to-and-fro movements of the retinal image, but rather see the environment moving steadily in one direction or indeed (as when reading) remaining still. According to orthodox reflex physiology, these phenomena are to be explained as follows: when the visual world passes before our eyes (as in looking out of the window of a train) the eye is "reflexly" driven along with it. The eye muscles therefore move, and their receptors signal the velocity of the moving environment; the movement of the retinal image cannot do so since there is little or no visual movement relative to the retina. When the muscle tension reaches its maximum, there is a "reflex" movement in the opposite direction—the rapid phase of nystagmus. During this rapid phase, the afference resulting from rapid movement of the retinal image is "inhibited," or does not reach consciousness because it is so rapid.

This explanation is contradicted, among other things, by the following observations: Fixation of a bright cross produces a retinal after-image;

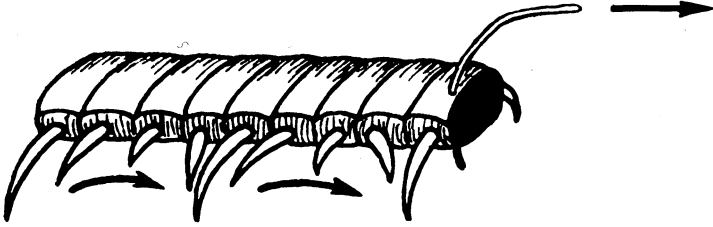


Fig. 6. Short segment of the arthropod *Geophilus* which is pulled forward by means of a hook attached at the anterior end. The legs which are off the ground swing forward actively ( $\rightarrow$ ) in such a manner that each leg lands exactly in the foot-print of its predecessor; the spoor is the same as that of a two-legged organism.

this image remains visible for some time in the dark and when a labyrinthine nystagmus is induced can be observed to move slowly in one direction, and rapidly in the other (some practice in self-observation is needed). That is to say, the image is not eliminated in the rapid phase of nystagmus (Fischer, 1926). However, this behavior is to be expected, as we shall presently see, on the basis of the principle of reafference.

The much-debated mechanism of nystagmus can best be understood by taking quite literally our characterization of it as an "optical pacing" apparatus. Consider by way of comparison the locomotor apparatus of an arthropod, *Geophilus* (von Holst, 1933) following ablation of the higher centers (Fig. 6). The insect can be activated by continuous excitement (e.g., electrical) of the ventral cord, in which case the legs step out in an orderly fashion, just as a steady train of impulses from higher centers sets off nystagmus. But it can also be activated—like nystagmus—by moving the "fixated Visual world," namely by pulling the insect along the ground at a variable speed. The legs then move actively; even those which at any moment are off the ground and thrusting forward at a speed which is determined by the speed of the legs which are on the ground and being driven by the speed of forced motion. The "support" phase corresponds to the slow phase of nystagmus; legs and eyes "fixate" the substrate, and are governed by exafference. The forward thrust phase corresponds to the rapid phase of nystagmus; legs and eyes lose fixation and take a step in the opposite direction. In both instances, higher centers need have no information about the individual steps; the stream of pulses downward is continuous, just as is the ascending report which signals the relative velocities of subject and environment. The pacing apparatus fails to operate if the moving substrate is undifferentiated (*Geophilus*: surface of quicksilver; eye: homogeneous field of view), or if the movement is too rapid. In the latter case, legs and eyes both remain "stuck" in the extreme driven position.

Let us try to understand this central optical pacing system more exactly: the visual world starts to move past the eye, say, to the right, and therefore causes retinal image movement. The image movement generates

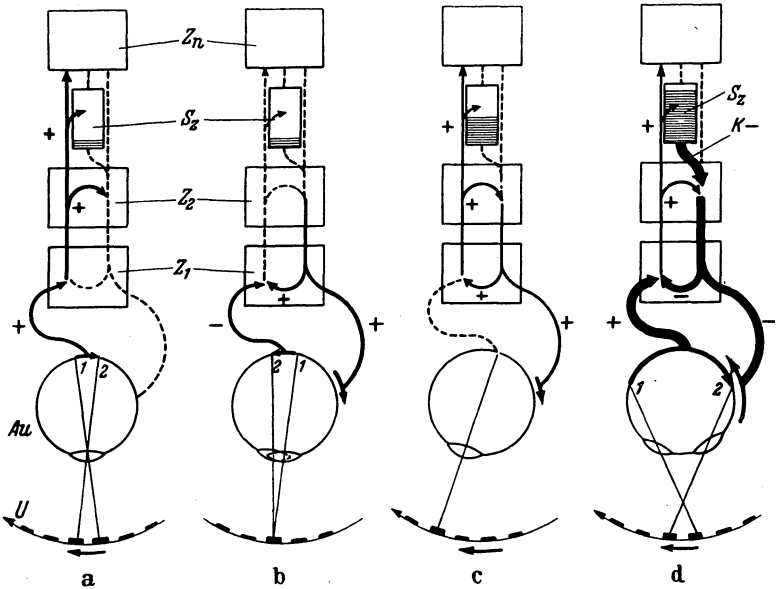


Fig. 7. Explanation of the pacing movements of the eye  $Au$  in the case of optomotor nystagmus as the environment  $u$  moves. The schema follows the pattern of Figs. 4 and 5.  $Z_1$  and  $Z_2$  are lower movement centers,  $SZ$  is the pacing center which is responsible for the rhythmic movements of nystagmus,  $Z_n$  is a higher optical center. In **a** the eye is at rest, the environment moves a bit, and an (arbitrarily chosen) element of the retinal image moves from 1 to 2. In **b** active following has been initiated, and the given element is back at its original retinal position. In **c** the eye moves with the same angular velocity as the environment, and the retinal image remains stationary. In **d** the pacing centre  $SZ$  discharges, causing a powerful movement command  $K$  in the opposite direction; during this rapid movement, the environment continues to move; an arbitrary element of the retinal image moves from 1 to 2. Thickness of the arrows indicates strength of impulse trains. Further elaboration in text.

a positive signal which proceeds to higher centers, including both  $Z_2$  and the "pacing" center  $SZ$  (Fig. 7a). This positive signal returns downwards immediately as efference and initiates eye movement. Thereby the image is restored to its original location on the retina, but at the same time there is a negative efference which cancels the positive efference copy in  $Z_1$ . The eye movement would stop at once (Fig. 7b) were it not for the fact that the process of 7a immediately recurs. The system eventually reaches a state of equilibrium (Fig. 7c); the eye responds so rapidly that no retinal movement (or almost none) is registered, and the whole control system is self-maintaining. As this happens the pacing center  $SZ$  is gradually being "loaded" until eventually it discharges explosively like a relaxation oscillator,<sup>9</sup> and returns the eye to its original position (Fig. 7d); this is the

<sup>9</sup> A. Bethe (1940) in particular has done important experiments on relaxation-oscillators as models for physiological processes.



rapid phase. As it occurs the efference copy and afference cancel each other out, except for the small residual exafference caused by the movement of the visual world; this signal ascends as a report which is thus independent of the change of phase (see Fig. 7c). And now the process recycles.

The reader may convince himself that this whole apparatus is by no means a reflex mechanism, for, in the presence of sufficient self-activation or stimulation from  $Z_n$  it should go into an autorhythmic state, *even in* the absence of all afference (cf. Fig. 7c); such states can in fact be observed under certain experimental and pathological conditions.

## Accommodation

Let us turn from eye movements to another phenomenon: accommodation. The relaxed (single) eye is accommodated to optical infinity, since the elastic lens is flattened by its suspensory ligaments. Near accommodation is achieved by contraction of a sphincter muscle which opposes this tension and allows the lens to bulge, thereby decreasing its focal length. This system mediates perception of the approximate size and distance of visual objects projected on the retina, although it is not their sole determinant. Two equal, and equally sharp, retinal images will be judged as distant and large, or near and small, according to the state of accommodation, or as the usual formulation has it: the "subjective size" depends on the "apparent distance."

Reflexology can only explain this by supposing that receptors in the accommodation system have a ("reflex" effect on the percept which depends on their own state of excitation. This possibility can be discounted by a well-known fact: if the mechanism of accommodation is knocked out with Atropin and one unsuccessfully attempts to accommodate for near vision, everything appears diminished in size (micropsia) although the paralyzed peripheral mechanism cannot produce any "reflex." Conversely, everything appears enlarged if one attempts far vision when the accommodation muscle is fully contracted by application of Eserin (*macropsia*). The reafference principle can explain these relationships.

We start with a simple example, (a): suppose that there is a sharp after-image of a cross on the retina, which was seen in near vision; the eye then focusses on a distant wall. The signal for far accommodation causes a particular efference to the musculature from the lowest center, together with its corresponding efference copy. Since the image of the cross remains as large and as sharp as before on the retina, there is no reafference, the unmodified efference ascends and mediates a distinctive and definite perception: "the cross is now much larger." Consider a second case, (b): the direct observation of a large cross first of all, followed by a smaller one at the same distance from the eye. Here there is no signal to change accom-

modation, and in the absence of an efference copy the exafference ascends simply as a report which again mediates a definite perception: "The (second) cross is smaller." Then (c): we take the larger cross, first observe it in near vision and then move it away until its retinal image is exactly the same size as was that of the small cross in (b) before. Now we have *first* the report [as in (a)] which on its own would mediate the perception "cross is larger" and *secondly* the report [as in (b)] which on its own would mediate "cross is smaller." The efference copy and the exafference cancel each other out in a lower center and no report ascends to higher centers. The perception must therefore be: "the cross remains the same size"—which it does! That is, a "correct" perception is attained as the result of mutual compensation by two "false" perceptions.

This explanation is readily applied to the micropsia and macropsia discussed above: if the peripheral musculature cannot respond to its efference, there can be no retinal reafference, and the efference copy therefore ascends as a report which mediates perception of a change in size.

It is worth noting again that there are limits to the precision with which efference copy and reafference cancel each other out. When accommodation ceases to operate, as in very close or very distant vision, one does indeed see things grow smaller or larger, as is to be expected. Similarly, the mechanism follows rapid changes in distance somewhat sluggishly, so that a rapidly approaching visual object may appear to grow in size.

The principle for monocular distance setting which we have given can also be applied to the binocular distance-measuring function, namely to convergence of the eyes, which increases as a fixated object approaches them. We shall not follow up this example since we do not as yet know whether, or to what degree, reafference from the eye muscles is involved in the process.

## Limb Movements

Consider another system, the moving extremities of the body. Here one may expect to find greater complexities because, in contrast to the well-protected eye, all sorts of passive (mechanical) changes of position occur, about which the CNS must be precisely informed in order to operate properly. We can perceive at least four different types of mechanical influence: touch, pressure, tension ("force"), and position. The first two, as we know from everyday experience, shade into one another. The difference between tension and limb position is vividly experienced under increases in the gravitational field, as in a centrifuge. If one's weight is doubled in this fashion, for example, an amazing effort is required to lift the arms—despite the absence of any external pressure on them—but at the same time one senses correctly their positions. Visual checks of a limb movement that was

not visually guided yields no surprises.<sup>10</sup> The position sense is provided mainly by receptors within connective tissues which are external to the muscles<sup>11</sup>; measurement of tension, on the other hand, is achieved by receptors in the muscle fibers and tendons. Together they mediate the so-called "deep sensibility."

Let us start with a concrete question: how would a muscle which has an external load imposed on it behave, given that the efferent and afferent arrangements between the tension sensors in the tendons and the higher controlling centers are similar to those we have learned about in the postural control of fish? The lightly tensed muscle is stretched so that the tension increases (Fig. 8a). The increased negative afference (exafference) rises to  $Z_2$  and there reduces the magnitude of the previous efference: the muscle relaxes actively. On relaxation flexion the opposite occurs: the positive efference copy rising from  $Z_1$  to  $Z_2$  increases the total efference; the muscle contracts actively (Fig. 8b). However strong the muscle tonus, the

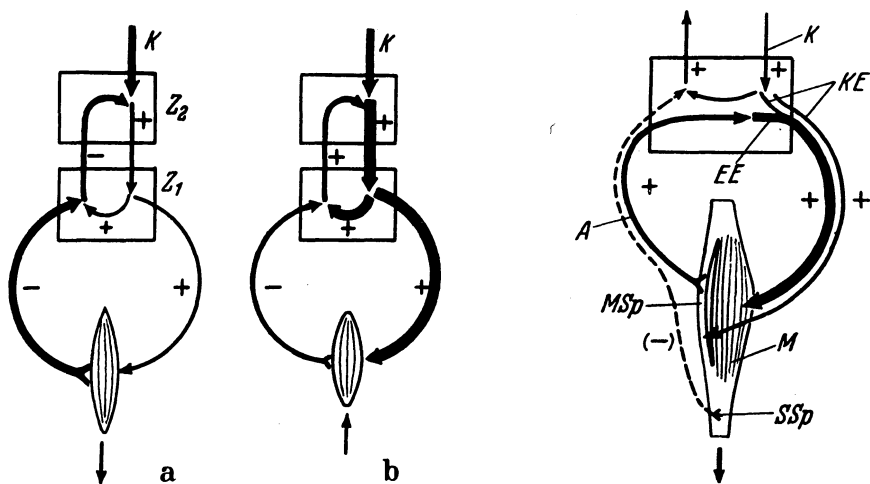


Fig. 8 (left). Explanation of the behavior of a muscle under tension during externally imposed (passive) extension (a) and contraction (b). The muscle actively follows the imposed movement while higher centers maintain tonus by means of the command K. See text for detailed explanation.

Fig. 9 (right). Behavior of a muscle, maintained in slight tension by the higher command K, in response to an externally imposed load. In this case, the central apparatus is so arranged as to oppose actively the external load ( $\downarrow$ ) by contraction. Msp = muscle spindles (tension sensors); KE = efference to the muscle and spindle fibres, determined by command from higher centers; EE = the efference added to KE as a consequence of the afference from the muscle spindles; Ssp = tension sensors in the tendons ("tendon spindles") which have higher thresholds and which switch in the mechanism described in Figure 8.

<sup>10</sup> Personal observation in an enclosed experimental room operated as a centrifuge.

<sup>11</sup> Comment: Subsequent research indicates that the relevant receptors are situated in or at the joints, thus confirming the expectation of finding them outside the musculature (Mittelstaedt).

externally imposed movement is followed "spastically" by the limb. Mechanisms of this sort are common and can be observed in pathological conditions in pure form. An example of this type is the active response of *Geophilus* (Fig. 5a) to imposed movement. The same thing can be observed in vertebrates (dog, toad) following thoracic section of the spinal cord; the hind legs start to walk if the surface supporting them is pulled backwards.<sup>12</sup>

In the actively innervated muscles of intact warm-blooded animals, however, the reaction to an imposed load is normally just the opposite of this: the muscle contracts strongly enough to balance the load. This much-studied "stretch-reflex" (*Eigenreflex*) (cf. P. Hoffmann, among others) is mediated by a direct arc from sensory to motor neuron and works without the intervention of an efference copy or the activity of higher centers. Its receptors are the muscle spindles, delicate contractile fibers which have sensory and motor innervations (and make up about 1 percent of the muscle fibers, the remainder of which have only motor innervation). If we assume that the afference from the muscle spindles is led directly to the motoneurons controlling the rest of the muscle bundle, the behavior of the stretch reflex can be understood (Fig. 9). If the muscle contracts or expands freely without extrinsic load, the spindles remain "silent" so long as their lengths change in the same way as the lengths of the other muscle fibers. If an external load is imposed on the muscle (either when relaxed, or during contraction) the spindles are stretched and "fire" until they are relieved of tension by the contraction of the rest of the muscle fibers.<sup>13</sup> The CNS prescribes the intended position or movement, and the stretch reflex achieves the desired objective, even against external obstacles. We may ascribe to the tension receptors in the tendons, which have a higher threshold, the task of switching off this reflex mechanism in the event of overloading, and switching on the adaptive mechanism described in the previous paragraph, in order to avoid muscle damage.

By this elegant device, Nature achieves maintenance of balance as a self-regulating muscular mechanism. If a stationary animal is pushed from the left, so that it bends over to the right, then—even before the labyrinths can come into play—the extensors of the leg(s) on the right side stiffen as a result of the increased load. The organism gets just the required support at the required time and place, whether standing or walking and remains as well-balanced as if set on delicate springs. The economy in higher control signals and muscle energy which this arrangement affords can well be imagined.

We see, then, that the principle of reafference is replaced by a different,

<sup>12</sup> Of course, some additional locomotor activity must be present to sustain the forward (thrust) phase of leg movement.

<sup>13</sup> We thank Dr. Lissmann of Cambridge and Professor Hoffmann of Freiburg for supplying important data concerning proprioceptor functioning not contained in the literature available to us.

peripheral, mechanism in the case of the stretch reflex, but in other respects still plays a role in limb movement. Let us see to what extent perception—as with the eye—can help us to look further into this.

Section of the afferent pathways (dorsal roots) of a limb, say the arm, does not lead to "apparent movements" when that limb is actively moved, despite the absence of reafference. At first glance, this would seem to argue against the validity of the reafference principle in this case. But the argument does not hold, since any conceivable perception of apparent movement of an object presupposes the perception of a real object, which, in the case of the arm, is probably mediated by touch and pressure afference; in this instance however the afference is also cut off. In a precisely analogous way, the feedback of an efference copy from the actively moving eye in *darkness* naturally does not lead to "apparent movement of unperceived objects." In both cases, the perceptual substrate itself is simply not there. It is certainly true, on the other hand, that a man whose arm has been amputated still has "control" over its central representation, can open and close the "phantom hand," and knows how he moves it.<sup>14</sup> However, as many a witness has stated, these things occur in an "imaginary" space which interpenetrates the "real" space, that is, the one built up by the remaining normal afference.

To avoid these difficulties, let us rather limit our consideration to instances in which we can make concrete predictions for changes of limb perception on the basis of the principle of reafference.

If the deep sensibility of a limb has been impaired, a distinctive sensation should be expected to accompany active movement against a firm substrate or support (apart from extinction of the stretch reflex and the drop in muscle tonus which accompanies it); because there is too little reafference from the tension receptors, each time the limb is moved under tension the efference copy must ascend as a report: "The substrate is moving away." This prediction is confirmed! For example, in polyneuritis the deep sensitivity of the leg extensors is sharply reduced; it appears to the patient as if the floor "sinks down elastically" when he steps down, say, from a bench onto the floor.<sup>15</sup> Analogous reports of *Tabes dorsalis* patients, that the ground is "like rubber" are probably to be explained similarly.

Conversely, from the motor aspect of the matter, one would expect active movements to lead to greater excursion of the limb than was intended. As we already saw in the case of postural orientation, if reafference is reduced there is too little "peripheral feedback" in the lowest centre, normal equilibrium is not achieved so that efference continues, and too great an excursive movement results. The exaggerated ataxic movement of patients suffering from *Tabes dorsalis* demonstrate this very clearly.

<sup>14</sup> Unfortunately, the important question of whether motor impulses proceed into the stump of the limb at such times has apparently not yet been investigated.

<sup>15</sup> Personal communication of K. Lorenz and others.

Another example: according to the reafference principle, the perceptions which arise from a difference in pressure to the soles of the feet should be very different when they are produced by active movement on the one hand, or by passively pressing a surface against the soles on the other. In the first case, one should notice no change in pressure, but in the second case a clear difference should be observed. To a great extent this has been confirmed also. Katz (1948) discovered that the difference threshold is *twenty times higher* if the pressure on the soles is changed through active alternations of weight distribution, as in bending the knees, supporting oneself on one's arms, etc., compared to the threshold found when the subject lies down and the soles of the feet are subjected passively to different pressures.<sup>16</sup>

Thus, again, we see that perception demonstrates the validity of the principle of reafference. In the last example the mechanism should be sought at quite high central levels since it coordinates and controls all four limbs in concert.

### Reafference and Locomotion

We can measure the extent to which reafference is built into a neuromotor system as an *integrative element* by observing how much greater in amplitude and yet much less precise a movement is following destruction of the sensory pathways. In this connection there are some interesting phylogenetic differences: in the lower swimming and crawling species (fish, amphibians) locomotion is still quite normal following deafferentation; in walking mammals it is very ataxic, and the complicated chains of movement of the human hand can only occur in ragged, exaggerated and uncoordinated fragments (Foerster, 1936). From this it follows that in the lower forms the CNS operates in principle independently, and thus is "automatic" in character (von Holst, 1936; Weiss, 1941), whereas higher forms of movement require reafference, although not necessarily reflex-eliciting stimuli. In the series: swim, crawl, walk, climb, grip, touch (hand, tongue), we have first of all movements which require no afference; then types which are mediated and controlled through reafference, and at the end those which depend on exafference!<sup>17</sup>

From this viewpoint the old arguments about whether movements of the limbs are reflexive or automatic can be laid aside; the alternatives were wrong! To put things metaphorically: the fin movements of a swimming fish proceed blindly in the dark, but the moving hand needs an illuminated environment. The deafferented hand is like a blind person who cannot find

<sup>16</sup> The author of these experiments sought to explain the findings in terms of "Gestalt experience of the whole body."

<sup>17</sup> The tongue lacks proprioceptive receptors, as do certain facial muscles; in the fingers, proprioceptors are the most important mediators of exafference.

his way because he does not know where he is. But this hardly means that his readiness to initiate coordinated movement is smaller than is the fish's! And just as the blind help themselves through the sense of touch, so too the eye can come to the aid of the "sensorily crippled" hand. In both cases, the ancillary afference improves matters greatly.

### Interaction of Several Types of Afference

The situation in the CNS is more complicated when afferent streams from different parts of the body work simultaneously to control posture and movement. To take a simple example:

The direction of movement in arthropods is controlled by nerve ganglia in the head. If the right-hand circumoesophageal connections are severed, thereby cutting out operation of the right-hand sensory center (supraoesophageal ganglion), there is a tendency for the organism to turn towards the left (analogous to the tendency produced by unilateral removal of the vestibular nuclei in vertebrates). In attempting to move forward, the insect bends toward the left, and in attempting to move backwards, bends toward the right; that is, in both cases the path of movement is counterclockwise (von Holst, 1934).

If we make the justifiable assumption that the commands which control tonus in the body segments come from a higher center (suboesophageal ganglion) then according to the reafference principle we should expect that reducing the number of segments should lead to more pronounced torsion in the remainder. This is to be expected because, in order to balance out the too great difference in levels in the higher command center, a certain amount of reafference is needed, which following loss of reafference from the severed segments, has to be generated by more vigorous bending of the remaining segments. This expectation is in fact met by the outcome; if a many legged arthropod is shortened (for instance, *Lithobius*) by cutting off a posterior section, the bending becomes progressively greater (Fig. 10 and 11) so that the half-centipede runs in a circle scarcely half the diameter of the circular path of the intact specimen: surely a singular result, so far as reflexology is concerned (von Holst, 1934)!

We should expect, moreover, that passively bending the hind end of the intact insect (in the absence of other disturbance) should lead to an active and opposite bending of the anterior end, because the exafference from the rear must be compensated by an opposing afference from another place in order to maintain the correct summated afference rising to higher centres. This sort of behavior is well known in certain arthropods, and goes by the name "homostrophic reflex" (Fig. 12).

Now let us consider a less straightforward case: the postural orientation of higher vertebrates and man. In the fish, postural orientation is fairly

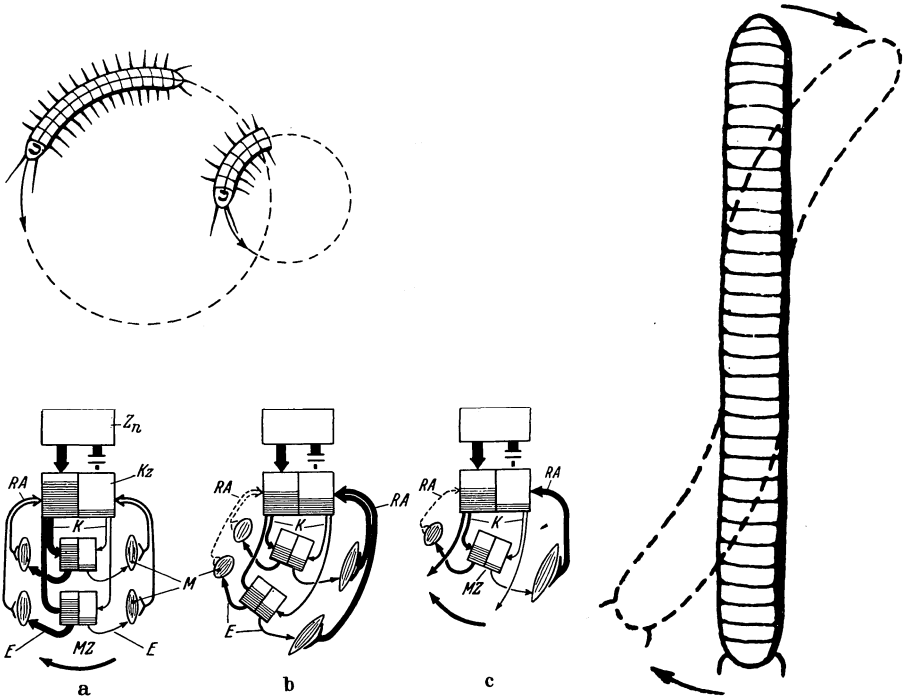


Fig. 10 (upper left). Arthropod (*Lithobius*) runs in circles of a specific diameter following section of the right circumoesophageal connections. a, otherwise intact insect, b, insect with posterior portion removed.

Fig. 11. Schema to explain Fig. 10.  $Z_n$  = higher sensory centre supraoesophageal ganglion;  $K_z$  = command center suboesophageal ganglion;  $K$  = command to the lower motor centers of the body segments  $MZ$  (of which only two are shown);  $E$  = efference to muscles  $M$ ;  $A$  = afference;  $RA$  = reafference from the position sensors in the body joints. The thickness of the arrows indicates the strength of impulse trains. The righthand stream of impulses from  $Z_n$  to  $K_z$  has been interrupted. In Fig. 11a, the asymmetrically innervated command center  $K_z$  causes a similarly asymmetrical input to the motor centers, whose efference leads to a bending (alteration in tonus) to the left (lowest arrow). Fig. 11 b shows how the reafference from this bending stimulates the command center in the opposite sense, so that a balance is struck between asymmetrical innervation from above and reafference from below. If one of the motor centers is removed, as in c, the reafference becomes too small to balance the efference from above, and a further bending, or change in tonus, has to occur (lowest arrow).

Fig. 12 (right). Arthropod (*Julus*) bent passively to the left at the posterior end, responds with active bending of the anterior end to the right ("homostrophic reflex").

easy to comprehend, since the head which carries the otoliths is fairly rigidly connected to the body. Also, the motor system does not have to make permanent active contributions to the *maintenance* of a goal posture once it has been attained, since mechanically, the fish is in a state of indifferent (passive) equilibrium with its supporting medium. Our upright posture, on the other hand, is labile, the maintenance of every goal posture requires



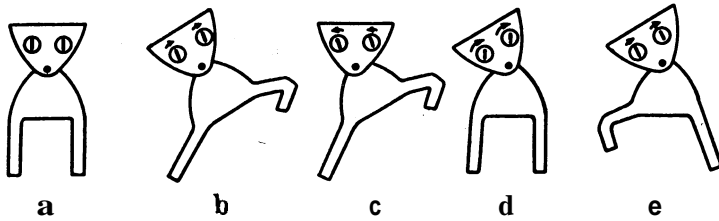


Fig. 13. Schematic indication of the correctional movements of the limbs and eyes in warm-blooded animals (mammals, birds) which are elicited by passive (imposed) changes in position (direction of tipping is labeled from the animals' point of view). a, Normal position; b, body and head tipped to the right; c, body only, d head only turned to the right. In e the same situation is shown as in d, head only turned to the right. In e the same situation is shown as in d, except that in this case the labyrinths have been removed (compare with d and e of Figure 4).

particular active patterns of innervation, and moreover the head, body and extremities are mobile independently of one another. Active or passive movement of the head alone must not be accompanied by reflex movements of the limbs initiated by the labyrinths, since this would only disturb the body's balance! Let us consider the system's actual behavior (compare Fig. 13 a-d).

A stationary animal is turned passively, body and head together, to the right; it makes compensatory righting movements with the limbs (Fig. 13b). If the head is held still and only the body moved, the same movements are elicited (Fig. 13c). If the head is turned by itself, the attempt is made to right it alone, and the rest of the body remains passive (Fig. 13d). These observations are most easily understood by assuming that the positional receptors are in the torso, as has often been postulated (Trendelenberg, 1916, 1907; Fischer, 1926). But the behavior of the eyes is not consistent with this; in condition (b) they rotate slightly to the left, in (c) slightly to the right, and in (d) strongly to the left so that they maintain approximately the same relation to the body as before—which is quite analogous to the behavior of anterior and posterior body segments in the "homostrophic reflex."

The simplest explanation of the whole behavior is that (at least) two afferent inputs are involved in postural control of the torso, head and eyes. One of these stems from the statolith apparatus, in the head, the other from the positional receptors of the neck. The two streams of impulses are mutually subtractive so far as the position of the body is concerned, but are additive with respect to the eyes (Fig. 14a). If this explanation is correct, then the reafference principle predicts a very precise dysfunction as soon as the afference from the two sides of the neck is artificially unequalized. The CNS would have to interpret such an event as "turning of the body, the head remaining upright," and would set in motion a compensatory set of movements in the limbs. This is just what

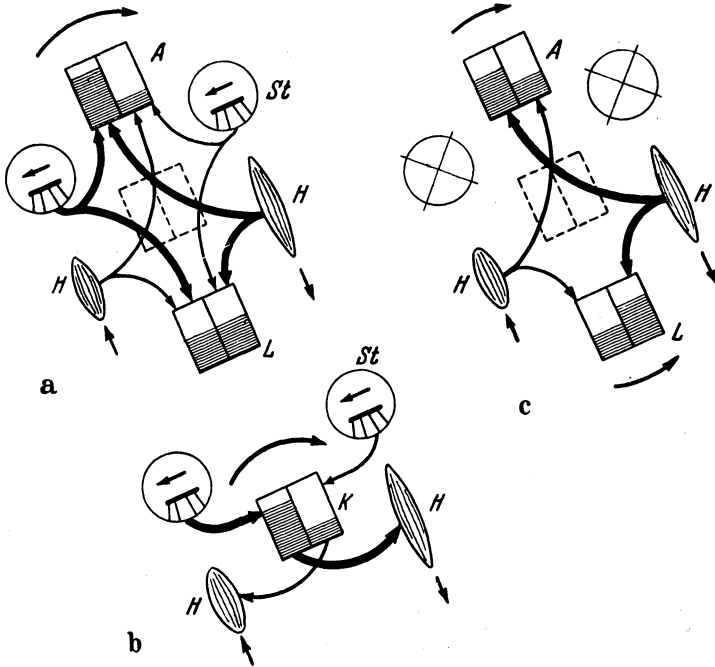


Fig. 14. Schemata (analogous to Fig. 3) to explain the behavior of a warm-blooded animal with statoliths (a, b) and without (c) in the event of passive sideways bending of the head (compare 13 *d, e*—Fig. 14 a and b are also valid for active head movements). L = positional center for the trunk, A for the eyes, K for the head. H = neck muscles. For clarity's sake, K has been omitted from a, but is shown in b (in c it has also been left out). The strength of afference from the statoliths and positional sensors of the neck muscles is indicated by the thickness of arrows, as before. The unequal stimulation of the eye centres (A in a and c), of the head centre (K in b), and of the trunk centre (L in c), cause an impulse to turn as indicated in each case by the curved arrows. Further elaboration in text.

happens: if a cold cloth is held against the left side of the neck below the *os petrosum*, a hot one on the right side (so that the impulse frequency of the assumed neck afference is diminished on the left, increased on the right), the expected limb movements are elicited.<sup>18</sup>

The reafference principle predicts exactly the same misinterpretation if the head is moved, actively or passively, following bilateral removal of the labyrinths. In this case too the CNS must "believe" that the head remains upright and the body is in a rotated position, since no report of head rotation occurs; it therefore should attempt to correct for the rotated position.

<sup>18</sup> This phenomenon was first described by Griesman (1922) and confirmed by Fischer and Wodak (1922). Goldstein (1925) used it as an argument for a general plasticity theory of the CNS. So far as we know no physiological explanation has been given before.

This is precisely what happens, as has long been known (Dusser de Baronne, 1924; Magnus, 1924; cf. Fig. 13a and 14c).

Although these sorts of "neck reflexes" have long been known—they were discovered by Barney (1906)—they were assumed to be absent in normal people, since we can move our heads without eliciting "reflexes" in the body. That this conclusion has been so widely accepted must apparently be held against reflexology, since according to it any stimulus must elicit some response; but in this case the response (movement) does not occur.

The proposed mutual cancellation of afference from the labyrinths and the neck is valid only for control of the trunk and limbs, not for the eye. In that case, the two components are additive. Rotating the head to the left causes an opposite rotation of the eyes to the right—as can readily be observed in a mirror. The amplitude of the eye rotation is equal to the sum of the amplitudes obtained by (1) tipping the whole body while the neck remains motionless and (2) bending the neck as the head remains upright (e.g., turning the body to the right), as Magnus and his co-workers already knew.<sup>19</sup> By means of this summation the eyes tend to maintain their relationship to the vertical, and therefore help to stabilize the visual field when the head moves.

The behavior of the head itself is easy to understand in terms of its afferent-efferent arrangements: the center for "head position" receives afference from the labyrinths and sends efference to the neck muscles. The head, together with the neck muscles, is comparable to the fish and its whole musculature (Fig. 4b). The head rights itself after being passively bent, but can also be actively moved (by command of higher centers). In both cases the reafferent streams which flow from the labyrinths and from the positional receptors of the neck muscles to the centers for head and eye position are equal. Therefore, we see that so far as the trunk and eyes are concerned, active and passive head movements are equivalent. One can now give a plausible account of how the trunk and limbs can be brought actively into any desired posture, while the head maintains its spatial position independently.

## CONCLUSION

The picture here presented is a first crude outline. But even so it has perhaps made clear the ways in which the principle of reafference is an advance on earlier conceptions. Reflexology describes everything which results from stimulation with one and the same word. There would be no objection to this—we too need generalized concepts—if it were not the case that behind

<sup>19</sup> The relative contributions of the two afferences, shown here (Fig. 13) equally big, can be unequal so far as the eyes are concerned.

the word stands the misleading concept of the reflex arc, which nearly always leads to false interpretations. The opposite of reflexology, the doctrine of plasticity (Bethe, 1931) holds that everything is connected to everything else, and excitation in the nervous system spreads out as in a nerve net; it is doubtless correct in its rejection of pure reflex doctrine, but neither one can predict in concrete situations what will actually happen; and that is never "just anything."<sup>20</sup> The reafference principle makes definite predictions by which it is possible to assess the range of its validity. It is one mechanism among several and prejudices nothing with regard to automatism~coordination and spontaneity. It seems rather to have the potential to reconcile various different approaches. Since the reafference principle applies throughout the CNS from the lowest phenomena (internal and external control of the limbs, relations of different parts of the body to each other) to the highest (orientation in space, perception, illusions), it can build a bridge between "low level" nerve physiology, and the "high level" science of behavior.

For example, it has often been asked whether an insect can discriminate between its own movements and movements of its environment. Mathilde Hertz (1934) answered the question positively—with a sure instinct—but could not plausibly explain how it could be so. Other investigators, like von Buddenbrock, have answered in the negative, arguing on the basis that the relative motion of insect and external world are identical in both cases. We recognize now that the eye does not distinguish between the two sorts of movement, but the animal does; for we recognize that the living creature has a CNS which consists of more than simply a set of connecting cables between receptors and muscles! By means of the principle of reafference it achieves a representation of the invariances in its environment.

In human psychology, phenomena relating to invariance play a large role. For instance, the fact that we see a stable environment during eye movements (space constancy), or that an object's size appears to us to be independent of its distance (size constancy), are well known examples. The principle of reafference, as we saw earlier, can explain them both. However, it cannot explain every invariance phenomenon; for example, the color constancy of visual objects, which depends on central processes; this is not a drawback, but rather an advantage of the principle. Because it makes concrete predictions, pseudoexplanations of a heterogeneous collection of different facts can be avoided.

The principle of reafference leads to a precise position on the question of the objectivity of perception. We saw in several instances that the

<sup>20</sup> Bethe is of the same opinion; this is shown in his various attempts to approach an understanding of the actual events by means of physical models. His principle of the mechanical "gliding coordination" (1931) is to our minds a good model; the explanations of Section 5 are indeed the detailed presentation of such a coupling.

"correct" report was the resultant of two "false" reports, and the latter—as we can demonstrate experimentally—each considered on its own have individually the same character as the "correct" report. For a lower center, which receives but one afference, all reports are equally "correct." The question of whether a perception is objectively correct or not can only be asked where several different afferent streams come together. "Objectively correct" then means nothing other than congruence of several reports. A report will only be evaluated as illusory if it is not consistent with other simultaneous reports. The lowest center is in this sense completely stupid, but we should not forget that the highest centers also cannot be more clever than their afferent inputs allow, every one of which can be deceived!

Let us hope that these pages will help to overcome, at long last, the tendency to describe and explain the functions of the most highly developed organ with a few crude notions. Up to now, the barrier between neurophysiology and the study of behavior—consider just terminology alone!—has seemed to be formidable. The sooner we recognize, however, that those complex higher functional entities, before which reflexology stands helpless, have roots in the simplest basic function of the CNS, the sooner will that barrier vanish into oblivion.

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Von *Holst* and *Mittelstaedt* conceive of the reafference principle as applying principally to the rather specific and fixed systems of orientation and balance control, and of the responses of lower organisms to particular environmental events such as predation (*Mittelstaedt*, 1962) types of response which also tend to be rather stereotyped and probably unmodifiable by learning as that process is generally understood by psychologists. It is of some interest to note that the principle has been taken over by psychologists, principally by *Richard Held*, and modified and extended to form the basis for a model of human perceptual lability and adaptation (*Held*, 1962). Also, it should be noted that the reafference principle can only work given that there is also stimulus equivalence; for instance, for the feedback control of a fly-catching mechanism to work, it is necessary that the fly be recog-

nized as such in different positions and at different *times*. *In* a later section a fairly specific neurophysiological basis for such equivalence will be outlined.