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Relations Between the Central Nervous System and the Peripheral Organs*

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The relation of the Central Nervous System (CNS) to the peripheral senses and muscular movement is an old and much discussed problem. Here we are at the heart of the physiology of behaviour, and in comparison to that which is not known, our present knowledge is very meagre and vague! Under these circumstances, our knowledge and conceptions are dependent upon the method which happens to be popular at the moment. In this field, the method which has played the greatest role consists of, first, artificially inactivating the CNS and then, through peripheral stimulation, evoking a particular response. On this basis, the CNS is often held to be only a reflex-mechanism, yet we know today that this view is one-sided. In order to be in co-ordinated activity, the CNS often needs a minimum of stimulation or loading by afferent impulses; the conception of chain-reflex-co-ordination has been recognised almost everywhere as being incorrect. Isolated, that is de-afferented, parts of the nervous system show continued electrical activity. One can therefore say that, as a rule, deafferented ganglion cells, under otherwise normal conditions, possess "automaticity."

These facts allow us to regard the function of the peripheral senses from a new viewpoint. The classical reflex-concept assumes that the peripheral stimulus initiates the central nervous activity. Since we now know that this supposed cause is often unnecessary, it is possible to start from the CNS. We can ask the question, what effect is produced on the sensory-receptors by the motor impulses which initiate a muscular movement? Thus, we look from the opposite direction, not from the outside inward, but from the centre to periphery. You will quickly see that in this manner we shall come upon new problems and experimentally verifiable hypotheses.

In order to make myself clear, I should like first to explain a few terms. The whole of the

impulses which are produced by whatever stimuli in whatever receptors I shall term *afference*, and in contradistinction to this I shall call the whole of the motor impulses *efference*. Efference can only be present when ganglion cells are active; afference, on the contrary, can have two quite different sources: first, stimuli produced by muscular activity, which I shall call *re-afference*; second, stimuli produced by external factors, which I shall call *ex-afference*. Re-afference is the necessary afferent reflexion caused by every motor impulse; ex-afference is independent of motor impulses.

Here are some examples: when I turn my eyes, the image present on the retina moves over the retina. The stimuli so produced in the optic nerve constitute a re-afference, for this is the necessary result of my eye movement. If I shake my head, a re-afference necessarily is produced by the labyrinth. If, on the other hand, I stand on a railway platform looking straight at a train when it starts to move, the moving image on the retina of my unmoving eye produces an ex-afference; likewise, when I lie in a tossing ship, the impulses of my labyrinth will constitute an ex-afference. If I shake the branch of a tree, various receptors of my skin and joints produce a re-afference, but if I place my hand on a branch shaken by the wind, the stimuli of the same receptors produce an ex-afference. We can see that this distinction has nothing to do with the difference between the so called proprio- and extero-receptors. The same receptor can serve both the re- and the ex-afference. The CNS, must, however, possess the ability to distinguish one from the other. This distinction is indispensable for every organism, since it must correctly perceive its environment at rest and in movement, and stimuli resulting from its own movements must not be interpreted as movements of the environment. I want to describe experiments which show how the CNS distinguishes between ex-afference and re-afference.

When one rotates a striped cylinder around a

* Lecture delivered at the Zoological Laboratory, Cambridge, on 30th October, 1953.

quietly sitting insect, for instance the fly *Eristalis*, the animal turns itself in the same sense (Fig. 1a). This is a well-known optomotor—"reflex." As soon as the animal moves itself, for instance, "spontaneously" (or stimulated by a smell), one observes that it turns itself unhindered by the stripes of the stationary cylinder. We must ask ourselves why the animal at every turn is not turned back by his optomotor "reflex," since the movement of the image on the retina is the same as in the first

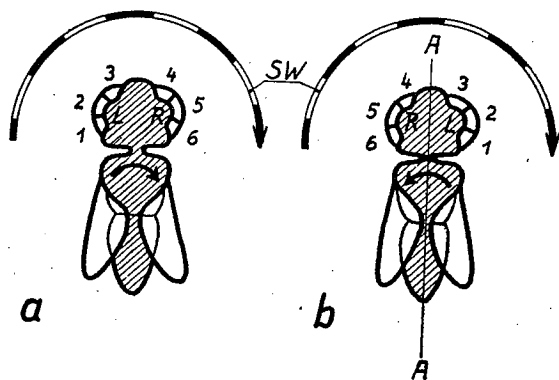


Fig. 1. Insect (*Eristalis*) in striped cylinder (SW), L, R=left, right eyes; a = head in normal, b = in turned position.

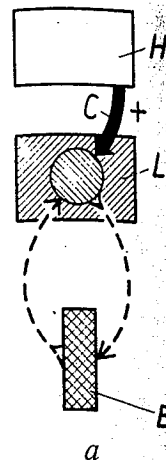
case, when the cylinder moved and the animal was stationary. A possible answer according to the reflex-theory is that in locomotion the optomotor—"reflex" is inhibited or "blocked." But we shall see that this answer is incorrect. It is possible, as has been shown by my colleague Mittelstaedt, to turn the head of the insect through 180° about the long axis (Fig. 1b A-A); then the head is fixed to the thorax, so that the two eyes are effectively interchanged and the order of the visual elements is reversed. The unmoving animal now responds, when the cylinder turns to the right, by turning itself to the left, as is to be expected from the reversed position of the eyes. If it is indeed the case that in spontaneous (or otherwise caused) locomotion the optomotor-reflex is "blocked," the animal should move unhindered in the stationary cylinder. But the opposite is the case; once the insect begins to move, it spins rapidly to right or left in small circles until it is exhausted. We have observed the same behaviour with fishes, whose eyes have been turned 180° about the optic axis. But we have found this behaviour only in patterned optical surround-

ings; in optically homogeneous surroundings the animal moves normally. This indicates that the optomotor—"reflex" is not "blocked" in locomotion, but on the contrary, the associated re-orientation plays an important role. Exactly what that role is will be made clearer by the next example.

If a vertebrate is turned over on its side by external forces, the well-known righting "reflexes" are initiated by the ex-orientation of the labyrinth. But, just as in my first example, every animal is able to take up any position without righting reflexes being produced by the re-orientation of the labyrinth. Again, it has been believed that the reflexes were "blocked" during position changing; and, again, we can show that this is not the case.

The righting reflexes, as is well-known, are released by the statoliths in the labyrinths, which, when the head is tilted, produce a shearing force on the underlying sensory organ, as we have found in fishes. One can increase this mechanical force which the statoliths exert on the sense organs, through the addition of a constant centrifugal force. We have built for this purpose a small revolving laboratory, capable of more than doubling the gravitational force. In this manner the statolith is made heavier, and the corresponding shearing stimuli produced by every tilting of the head are quantitatively increased. If one records the tilting of free swimming fish under these conditions, one finds that the degree of tilting becomes proportionally less, the heavier the statoliths are made. (For the method of measurement see v. Holst u. Mittelstaedt, 1950). If the statoliths are removed, then the behaviour of the fish is the same under normal and centrifugal conditions. We see, therefore, that the re-orientation of the labyrinth is not "blocked", but has a quantitative effect upon the degree of tilting, and, indeed, the greater the re-orientation, the smaller the degree of the movement. One can say that the CNS "measures" the degree of movement by the magnitude of the re-orientation thereby released.

Thus we have learned two facts: if the form of the re-orientation is reversed, as in the first example, than the initiated movement is increased progressively. Secondly, if the re-orientation keeps its normal form but is increased, as in the second example, the initiated movement is correspondingly decreased. These facts allow us to formulate a hypothesis about the



mechanism he that the effect somewhere in of this movement a photograph when superimposed Figure 2 illustrates the subsequent steps. C (Fig. 2a), from specific activation 2b), which is to a specific effect (i.e. a muscle). This central effect, EC. The effect produces a re-orientation of the lower centre, superimposed on the complementary part of this process and the effect coloured). W. re-orientation ex- nothing further re-orientation is difference with is too great, difference with to the particular. The difference itself, or for and produce

Let us first Fig. 2. The

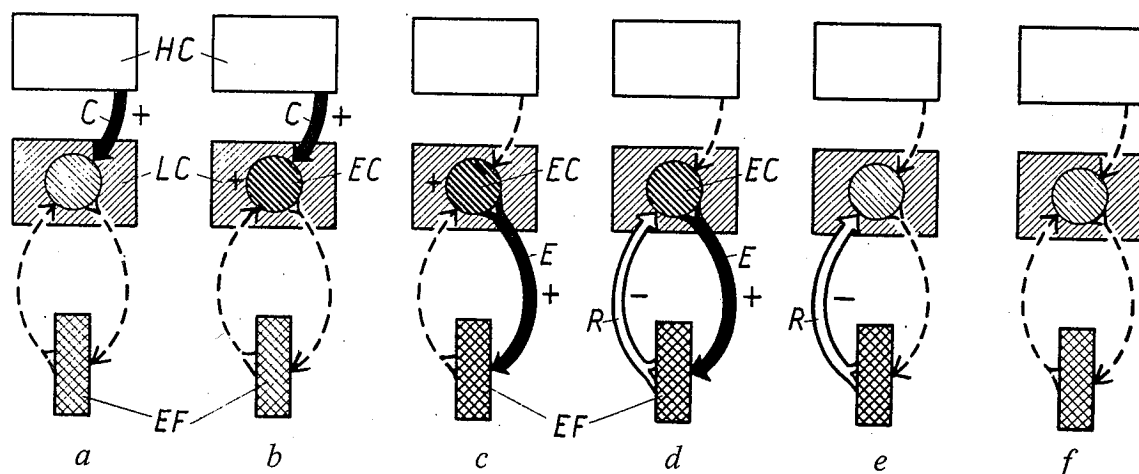


Fig. 2. Illustration of the re-reference principle; see explanation in text.

mechanism here involved. We shall propose that the efference leaves an "image" of itself somewhere in the CNS, to which the re-efference of this movement compares as the negative of a photograph compares to its print; so that, when superimposed, the image disappears. Figure 2 illustrates this in a number of subsequent steps. A motor impulse, a "command" C (Fig. 2a), from a higher centre HC causes a specific activation in a lower centre LC (Fig. 2b), which is the stimulus-situation giving rise to a specific efference E (Fig. 2c) to the effector EF (i.e. a muscle, a joint, or the whole organism). This central stimulus situation, the "image" of the efference, may be called "efference copy," EC. The effector, activated by the efference, produces a re-efference R, which returns to the lower centre, nullifying the efference copy by superposition (Fig. 2d-f). Because of the complementary action of these two components we can arbitrarily designate the whole efferent part of this process as plus (+, dark coloured) and the afferent part as minus (—, white coloured). When the efference copy and the re-efference exactly compensate one another, nothing further happens. When, however, the efference is too small or lacking, then a + difference will remain or when the re-efference is too great, a — difference will remain. This difference will have definite effects, according to the particular organisation of the system. The difference can either influence the movement itself, or for instance, ascend to a higher centre and produce a perception.

Let us first consider the simple situation of Fig. 2. The initiated movement will continue,

until the re-efference exactly nullifies the efference copy. Then we must predict the following: first, if through external influence the re-efference is increased, then the initiated movement will end prematurely. We have already seen that this is the case in the fish labyrinth experiment with the centrifuge. Secondly (Fig. 3a), if the re-efference is inverted, that is changed from — to +, there will be no nullification, but summation (Fig. 3b) and the movement will progressively increase, as we have

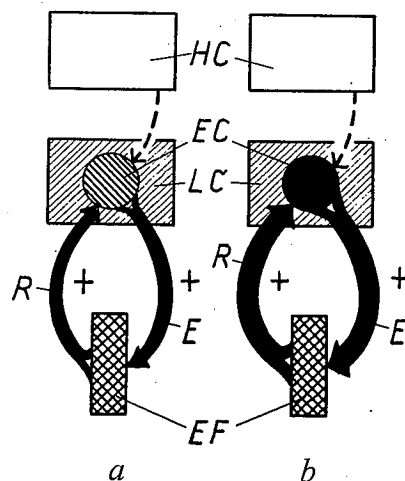


Fig. 3. Illustration of the experiment with the eyes in turned position (Fig. 1); see explanation in text.

already seen in the experiment with the inverted eyes*. Thirdly (Fig. 4), in the case where the re-efference is lacking (for instance, due to the

* This is the so called "positive feed-back."

destruction of the afferent pathways) the initiated movement will not be increased, as in the second case, but will continue until something else limits it. This behaviour occurs widely and

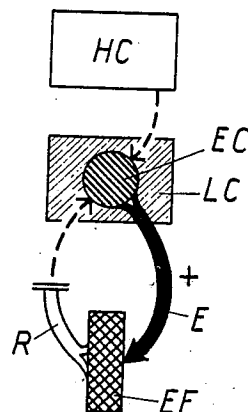


Fig. 4. Illustration of the experiment with interrupted afference; see explanation in text.

can be seen particularly well in fish without labyrinths in optically homogeneous surroundings. Every turning or tilt leads to circling or summersaulting. Also, in the human disease Tabes dorsalis, where the dorsal roots are destroyed, the well known exaggerated, ataxic movements of the limbs indicate that the same mechanism is involved. Therefore, contrary to the chain-reflex theory, the stimulus, originating with every movement, that is the re-afference, produces not an augmenting, excitatory, but a

limiting, effect on the movement. Only those forms of locomotion, such as the swimming of fish, which do not require a constant adjustment to the surrounding medium, proceed just as before after de-afferentation. These movements are automatically co-ordinated in the CNS and therefore require no limiting re-afference (v. Holst, Lissmann).

With this simple scheme we are able to understand a number of previously unexplained types of behaviour. The most hypothetical part of this theory is the postulated efference copy; this "image" in the CNS, produced by the "command" and matched by the re-afference. I am going to present direct proof of the existence of this phenomenon. For this purpose I choose two human examples, in which the difference between the efference copy and re-afference is transmitted to a higher centre and produces a perception. My first example is concerned with the already mentioned human eye movement.

A re-afference from the actively moving eye can have two sources: firstly, movement of the image across the retina and secondly, impulses from the sensory cells of the eye muscles. The former results in a conscious perception; the latter is of no importance for the following consideration. Consider my eye mechanically fixed and the muscle receptors narcotised (Fig. 5a). When I want to turn my eye to the right, an efference E and, according to the theory, an efference-copy EC is produced, but

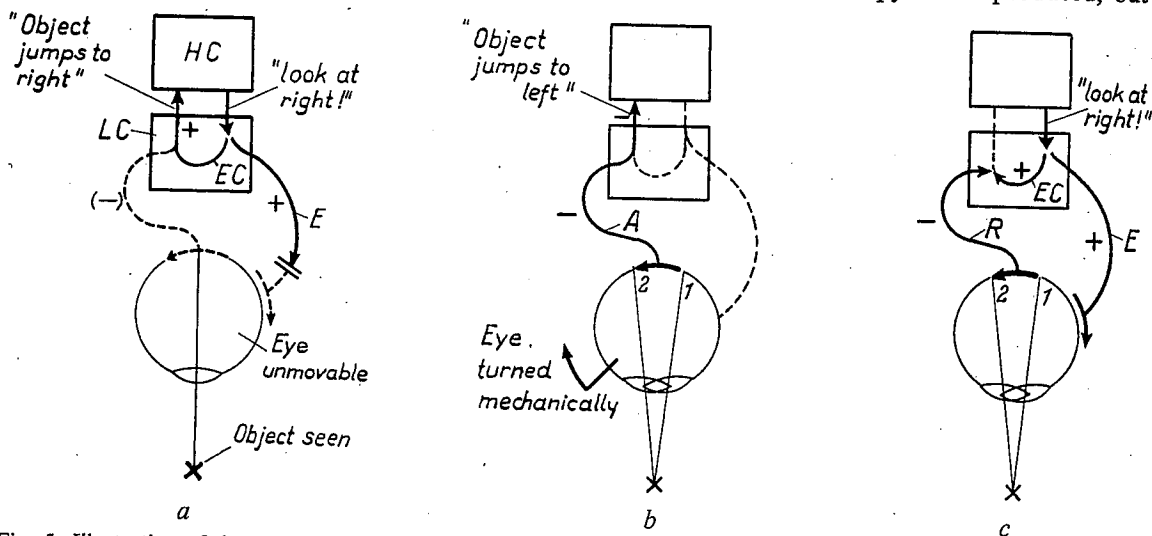


Fig. 5. Illustration of the experiments with human eye; explanation in text (for the letters compare the text of Fig. 2).

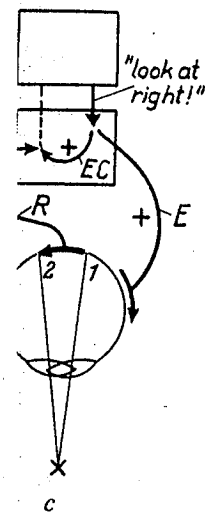
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the immovable eye does not produce any re-afference. The efference-copy will not be nullified, but transmitted to higher centres and could produce a perception. It is possible to predict the exact form of this perception (v. Holst und Mittelstaedt, 1950). The perception, if I want to turn my eye to the right, must be that "the surroundings have jumped to the right." This is indeed the case! It has been known for many years from people with paralysed eye muscles and it has been established exactly from the experiments of Kornmüller on himself that every intended but unfulfilled eye movement results in the perception of a quantitative movement of the surroundings in the same direction. Since here *nothing* happens on the afferent pathways, this false perception *can* only result from the activity, originated by the intention of the eye movement, being returned to higher centres. This is another way of saying that the unmatched efference-copy causes the perception.

Now, we make a simple experiment and turn the paralysed eye mechanically to the right (Fig. 5b). In this case both the motor intention and also the efference-copy are lacking, but the image moves across the retina and afference A is transmitted, unmatched by an efference-copy, to higher centres and produces, as is known, the perception that "the surroundings move to the left." This is also a false perception. If now we combine the first case with the second, that is, if my eye is moved mechanically at the same time I intend this movement—which is the same as *voluntarily* moving a *normal* eye—then in fact these two complementary effects just mentioned are produced: firstly, the perception of the returning "command" causing a jump of the surroundings to the right and, secondly, an image-motion on the retina producing a jump of the surroundings in the opposite direction. These two phenomena, the efference-copy and the re-afference, now compensate each other (Fig. 5c); and as a result *no moving* of the surroundings is perceived. The surroundings appear stationary during this normal eye movement, and *this* perception is *physically correct*. As we have already seen, the correct perception results from two opposite and false perceptions which cancel each other. Thus, we understand a phenomenon with which Psychology has been concerned for many years, that is, the perception of the surroundings as nearly stationary during eye movements ("Raumkonstanz").

Now we come to the second example, visual accommodation. The eye is focussed for distant vision when at rest, since the elastic lens is flattened by its zonal fibres. For near-accommodation a circular muscle, working against these fibres, allows the lens to round up. We should also like to apply our theory to this system. If the accommodation apparatus is narcotised, (for instance by atropine), that is, the eye is permanently accommodated for distant vision, than an intention for near-accommodation will start a motor-impulse, which cannot be nullified by any re-afference and, therefore, must return to a higher centre, where it can produce a perception. This is indeed the case. All objects in the visual field become small, and this false perception is called "micropsia." The same phenomenon must exist with a normal eye, if we imprint an after-image of a distant cross on the retina and then look upon a near surface. Since the after-image remains the same size and sharpness on the retina, it must appear very small on the near surface, because again only the "command" for accommodation returns to the centre of perception. This is also the case, as one can easily convince oneself. These false perceptions appear, although the *peripheral stimulus-situation* is *unaltered*. If, on the contrary, the *accommodation* of a normal eye is *unaltered*, that is, if we look first at a small and then at a large cross at the *same* distance, then naturally the changed afference will be transmitted to the centre of perception and we see the second cross to be larger. Now we combine this last case with the first, that is, we observe with a *normal* eye a cross, moving from a distant point nearer to the eye. This initiates the accommodation-impulse, which returning, tells us "the cross is becoming smaller"; but at the same time the enlargement of the retinal image states, "the cross is becoming larger." The two cancel one another out, with the result that we perceive the cross to be of *constant* size. Again, the correct perception is the result of two opposite false perceptions; and, further, we come to an understanding of a phenomenon, long discussed in Psychology, the "GrößenKonstanz der Seh-Dinge" (Hering), which means that we see the objects to be nearly the same size irrespective of their distance from us.

I could present still further examples from man and from lower and higher animals which would show what role the re-afference plays in general in behaviour. It serves either to limit

the magnitude of movement or to insure the constancy of the perceived surroundings during movement, and so makes possible the distinction between real and apparent motion of objects. The first step in both of these functional mechanisms is the comparison of the re-afference with the efference-copy.

In conclusion, permit me a few general considerations. I have attempted to show through the example of this central nervous mechanism, that it is possible in the field of the Physiology of Behaviour to avoid formulating "theories," which are only generalised descriptions of observations; rather should we follow the example of the exact sciences, namely, that a theory must exactly predict what will happen under defined conditions, so that one can by experiment verify or disprove it. Thus one avoids the error of false generalisation, which often occurs in central nervous physiology. For this reason I would like to emphasize that the principle of re-afference is only *one* of *many* central nervous mechanisms. There exists a large number of other mechanisms with other modes of function, and of these we know as yet very little. We recognise fragments of some of them and call them "reflexes"; but this term denotes fragments of very different mechanisms. I believe the whole Central-Nervous System is a "hierarchical system" of such different func-

tional parts, a concept which you find also in Tinbergen's book "The Study of Instinct."

One final point. I have spoken of neither electrical spikes, nor nerve pathways, nor anatomical centres, in which particular functions might be localised. In the realm of behavioural analysis these things are indeed of secondary interest. The functional schemata, constructed in order to illustrate definite causal relationships, are quite abstract, although the consequences they predict are concrete and experimentally verifiable. The physiologist who fully understands such a causal system is still unable to deduce where the cell elements which perform this function are located, or how they operate. Such questions are dealt with at another level of investigation, where the electrophysiologist works and develops his own terminology. It is useful and justifiable for every level of investigation to have its own language, but we must expect, that, with a greater advancement of our knowledge, it will be easy to translate one such language into another. Until such a time, each field must develop along its own lines, unhindered by the many possibilities for misinterpretation.

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