The case for 'relevance' in sensorimotor physiology

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That the nervous system does not appear to process certain information does not necessarily mean that it is incapable of doing so. If the information is made 'relevant' to the organism, then the 'silent' processing systems can become activated. For example, the 'colour-blind' cat can be trained to respond to different colours provided the reward is suitably appetizing. On the contrary, 'relevance' may often be the best explanation for placing in perspective otherwise-inexplicable physiological phenomena.

When Pavlov gave up his work on the digestive glands that, in 1904, had rendered him the Nobel Prize, he boldly turned to a teleological approach in physiological experimentation. This was based on his well-known method of making a neutral stimulus 'relevant' by rewarding his dogs for taking notice of it. The animals were encouraged to create an internal programme leading to anticipation. It is amusing to recall that Pavlov's friend, the physiologist Robert Tigerstedt, who actively had sponsored his candidacy for the prize, held this new line of study to be an unsound departure from real physiological experimentation and, in conversation, tended to be caustic about it.

Today we may hold Pavlov's term 'conditioned reflex' for a misnomer but the technique of training aided by rewarding (reinforcement) has maintained its place among the leading approaches of behavioural physiology.

In its essence, Pavlov's method was a paraphrase of Nature's own mode of establishing central programmes of behaviour. His way was the way in which natural selection goes about its business, rewarding useful traits, putting a premium on relevance for some biological purpose, and neglecting what deserves to be neglected. This being so, why should it not be possible to make use of the concept of 'relevance' to discover physiological mechanisms, even though it may often be difficult to understand just how to proceed?

Colour-blindness in the cat

I wish to use two illustrations from my personal sphere of interests. Between 1935 and 1945 I spent some time on studying specific responses to the wavelength of light in the retinas of various animals,

among them in the end also the cat, generally regarded as colour-blind. One knew at the time that cones were present in its retina, perhaps in the same proportion as in our own peripheral eye.

In 1943 I published a paper[5] in which single units in the light-adapted eye of the cat were shown to have the same distribution curve of spectral sensitivity as had cone eyes of, for instance, the snake. This curve also agreed with the human spectral luminosity curve of our fovea in which cones alone are present. The energy available in my spectrum was not very high but, nevertheless, it proved possible to obtain evidence against the view that the cat might be merely a cone monochromat. Further work[1,9], as well as experiments with selective adaptation[6], established without doubt that the retina of the cat had cones of different spectra sensitivity. A systematic study[10] of evoked potentials in the visual area of the cerebral cortex confirmed this conclusion, as did the regular increase in rate of rise of spike frequency caused by flashes altered in wavelength from the blue to the red end of the spectrum[3].

The most recent contribution to this problem has been that of Saunders[19] who isolated units in the optic nerve as well as in the lateral geniculate body and presented his coloured stimuli against a background of blue, green, or red, thus producing selective adaptation to these spectral regions. Sinusoidal stimuli divided the units into two populations with respect to a test spot of given intensity. One population had a critical frequency of about 25 Hz, the other at about 35 Hz. This helped to exclude an embarrassing element of chance in hunting for the right kind of units, because specific colour-sensitivity

was found only in the latter group. The former population behaved as if its units had been wholly rod-dominated. The colour sensitive units had maxima around 470, 570, and 600 nm.

The relevance of colour discrimination

For several reasons it seemed likely that the neural mechanisms for discrimination of wavelength in the cat would be poorly developed compared with, for instance, those of birds and monkeys. A discussion of these reasons would fall outside my present aim which is to explain why a number of observers and experimenters constantly have denied the cat colour-sensitivity.

The simple answer is that they did not take the trouble to make colour-discrimination sufficiently relevant for an animal which hunts at dusk. It cannot be easy to eradicate the cat's probable habit of responding chiefly to brightness differences. Those who succeeded in demonstrating colour vision in the cat[1,16,20] realized that a very large number of training experiments would provide a way of making their animals see the point of what was intended.

However, when considering how to make colour-discrimination 'relevant' to an animal for which there is no behavioural motivation to show colour-discrimination, the later experiments of Nancy Mello[15] are of particular interest. The problem of relevance is well illustrated by her reference to the fact that ducklings reared monochromatically do not respond to colours, although, physiologically, they are perfectly capable of doing so. They must somehow be taught to attend to this particular aspect of visual information. Similarly cats have to be taught, and if this is done clear, as did not be necessary to have recourse to an absurd number of trials.

Mello's best results were obtained in her series of "post-discrimination training gradients". The cats had to undertake a differential discrimination training on wavelengths of 450 nm (-) and 550 nm ( ) After some 30 sessions each animal was now able to distinguish 450 nm from 550 nm; generalization gradients obtained for eight colours showed that the cats can respond differentially to wavelengths of equivalent energies as effectively as to achromatic stimuli of different intensities. In fact, for colour-discrimination, fewer training sessions were required for satisfactory performance than for brightness discrimination. Her animals could distinguish red, blue, and green from grey, and also differentiate between blue and green

They did less well with red, which was hardly surprising since from the time of my own early paper of 1943², in which red sensitivity was held to be weak, nearly everyone engaged in electrophysiological work on this problem has made the same observation.

The food used for reinforcement in these studies may have been especially attractive, or at any rate not irrelevant: it was a blend of horsemeat (I can), cod liver oil ($\frac{1}{4}$ cup), milk ($\frac{1}{4}$ cup), and multiple vitamins.

This experiment illustrates the amount of care and thoughtful planning that may be needed to establish 'relevance'. It also shows how creation of a relevant purpose can help the physiologist to discover the existence of a mechanism that has been un-suspected, or has been regarded as im-probable.

With this in mind we now proceed to turn the problem round and ask whether or not 'relevance' often may be the best or sole explanation obtainable for motor or sensory responses that seem to be devoid of meaning and only strike us as 'effects'. Why, if relevance can make an animal do something, can not an observed effect be one that, at times, an animal has developed for a purposive pattern of behaviour? This is but one way of formulating the general problem of the value of teleological explanations in biology. Elsewhere² I have illustrated this point by certain examples, the most striking of which being perhaps von Frisch's well-known studies of the relevance of the dance of the honey bee.

The physiology of servo action

A recent case of interest in this context is an experiment by Marsden, Merton and Morton[11],[12],[13] on 'servo action' in human voluntary movement. They used the long flexor of the thumb and bent the top joint of this digit against a force produced by a torque motor introducing random per-turbations. It is important to realize that the movement involved a tracking experiment which the subject had been practising: he had to follow at a definite speed the move-ment of a spot on a screen through 20° of flexion in 1.0 sec. In the actual experiments the guiding spot was turned off. Contrac-tion was measured by a rectified and inte-grated surface electromyogram, during which the force and displacement generated by the torque motor were being monitored.

When the perturbation was an increase of resistance from the torque motor opposing the thumb's flexion, the 'stretch reflex' of the muscle increased to support the passage of the thumb through the tracking course. This was quite a sensitive

response: its gain, also tended to increase to match the loading as this was augmented by more power from the motor. This is the effect which the authors call 'servo action', the gain control of which takes too long to set in for it to have been handled by the spinal monosynaptic reflex component of the muscle spindles. Furthermore, similar results were also obtained with a subject lacking the monosynaptic reflex. Such people are found from time to time: work by other authors has shown²,¹⁸ that their motor responses are perfectly normal despite the absence of the 'tendon jerk' monosynaptic reflex. Marsden and his colleagues provide some evidence for the suggestion that the delayed servo response has traversed a loop through the cortex and thus cannot be called a reflex in the strict sense of this term. As the experiment is concerned with a voluntary motor act (tracking) a cortical component would hardly be unexpected, the less so as the latencies measured for the servo action are compatible with this alternative.

Relevance of gate opening stimuli

In the present context, however, other aspects of this experiment are of interest: the authors found that if the thumb were anaesthetized, it lost the capacity to compensate for loading. Since the anaes-thesia in the first experiments was pro-duced by pumping up a cuff around the wrist, this meant that the muscle spindles by themselves were incapable of the required servo service: the belly of the long thumb flexor is in the arm, above the site of compression, and so the spindles were not affected by the compression block. The same experiment repeated with the big toe gave a different result¹⁴; servo action proved to be independent of anaesthesia despite profound anaesthesia of the whole foot. Furthermore, when the thumb response was involved in a general movement of the whole arm, it too became independent of anaesthesia¹². Impulses from skin or joint receptors were needed merely for discrete movements of that versatile instrument, our thumb, which has such a large representation in the cortical motor area.

This experiment thus contained an un-expected discovery of 'relevance'. The authors also recognize this by saying that the big toe might have been similarly dependent upon skin or joint facilitation as a gate opener to servo action, if we had learned to use our toes for writing. A teleo-logical interpretation of this kind stimu-lates interest in a finding that otherwise would have been merely an 'effect'. Motor

physiology is loaded with well-established, unexplained, and inexplicable effects, mostly in terms of excitation or inhibition, doomed to be neglected and forgotten for lack of relevance.

The stimulus of teleology

Sometimes a teleological explanation may be the end-point of a piece of research, but more often than not it serves as a real stimulus to continue working and thinking in order to analyse the organization responsible for the findings. Further ex-amples include, for instance, classical prob-lems relating to skin afferents. Long ago Mott and Sherrington, investigating the effects of deafferentation in monkeys, came to the conclusion¹⁷ that skin afferents are essential for delicate motor acts. There are also the findings of Hagbarth⁹ that in the leg of the cat stimulation of the skin over a muscle facilitates its motoneurones and inhibits those of the antagonist muscle.

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