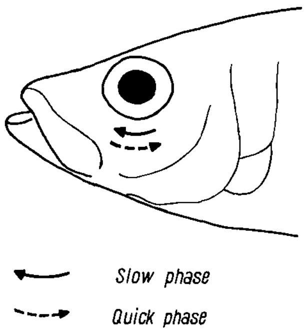
A Peculiar Nystagmus and a Corresponding Foveal Structure in the Eye of the Herring *(Clupea harengus* L.)

In herring swimming in aquaria (the techniques developed for the capture, transport, and maintenance of these particularly delicate fishes were described in previous papers[1]) we observed a peculiar type of eye movement. While a fish is swimming forward, the eyeball rotates around an axis through the pupil and about at right angles to the plane of the pupil. When a fish passes the observer from the right to the left, the left eye shows alternately a slow clockwise rotation and a rapid jerk-like anti-clockwise rotation (Figure).



A peculiar nystagmus in the eye of the herring (*Clupea harengus* L.).

These movements are highly reminescent of nystagmic movements. Sometimes the slow phase of an eye nystagmus is a compensatory or adjusting movement by which the image of an object is kept on an area of the photosensitive surface with a highly developed resolving power.

The nystagmic movements described above are thus suggestive of such an area at the ventral side of the retina of the herring's eye. This would be in accordance with the feeding behaviour of this fish. The prey is usually captured with a visually steered switching movement from below[2]. Moreover, the position of the lens in the eye of the herring seems to be indicative of a wide field of vision above the head of the fish[3].

Histological study of the herring's eye revealed a foveal structure at the ventral side, situated immediately below the spot where the optic nerve penetrates the retina. Here the cones have a smaller cross-sectional size and they are about ten times more densely packed as compared with the rest of the retina. Rods are almost absent in this foveal region, whereas in the other parts of the retina there are some hundreds of rods to every cone. Moreover, some layers of nerve cells – especially the bipolars – are more highly developed in the foveal region. Similar retinal structures have been described in the eye of the sardine (*Clupea pilchardus* W.)[4].

The origin and the function of 'optokinetic' movements have been elaborately discussed[5]. The question at issue seems to be whether the nystagmic movements observed in an actively moving animal are optokinetically released by the movements of images along the photosensitive surface of the eye, or whether they are of central origin. Since nystagmic movements are found in lower animals like arthropods as well as in vertebrates, generalizations are difficult and dangerous. Keeping this in mind it still seems useful to realize in which ways nystagmic movements can be evoked.

Von Buddenbrock[6] restricted the concept of 'optomotor reactions' to responses to retinal movements of the complete image pattern of the entire visual field. He discriminated 'optomotor reactions' from the visual perception of some moving object which may release following movements of the eyes or of the whole animal. The first example of 'optomotor reactions' he gives, the human 'railway-nystagmus', reveals however the weakness of his concept, for the slow phase of the railway-nystagmus is a following movement by which the image of a definite object is kept on the fovea for some time. The movements of the peripheral retinal images of all other objects in the visual field – each image moving with its own speed in accordance with the distance between the eye and the relative object – are without effect.

The twofold character of the optokinetic nystagmus was recognized by ter Braak[7], who described a 'look nystagmus' and a 'stare nystagmus'. The 'look nystagmus' was elicited by a moving object across a stationary background, while the 'stare nystagmus' was observed when the entire visual field rotated around the experimental animal. Obviously the 'stare nystagmus' is related to extra-foveal photic orientation while the 'look nystagmus' is related to detailed foveal vision[8]. In animals with some type of foveal vision, we must always reckon with the possibility that the eyes are coupled to some object in the visual field by retinal feedback, whether the movements of the retinal image of the object are the result of active movements of the animal or not. This coupling serving the visual function does not necessarily interfere with the animal's capacity to discriminate via photic information between these two types of movement. For non-foveal vision this exact coupling is not necessary because the movement of an image across a non-foveal retinal region does not impair the perception of the object so long as the speed of this movement is not too high.

It is conceivable that in organisms with poorly developed foveal structures the eye movements as a result of a kinetic component of central origin need almost no correction via retinal feedback. As far as observation and registration permits to decide, the eye nystagmus in the

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actively turning lobster *Palinurus vulgaris* and in the crab *Carcinus maenas* is identical, whether the animal is blinded or not. It has been concluded that this nystagmus is not a photokinetic response but a spontaneous action of central origin with possibly a steering component originating from the perception of movements of the limbs relative to the body[9].

It is hoped that further studies will reveal whether the function of the slow phase of the eye nystagmus described in the herring is restricted to the keeping of images on the ventral foveal region or whether it has an additional and more general function in photo orientation, and whether it is released exclusively by image movements or whether it has an active central component. In this way some contribution might be made towards a further understanding of the various aspects of 'optokinetic' movements in general. The described eye nystagmus of the herring has the advantage that the labyrinth and other receptors which might registrate rotations are precluded as sources of extra-retinal information since rotations are not involved in the genesis of this nystagmus. The delicacy of the animals, however, makes surgical interference rather precarious.

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Zusammenfassung

An Heringen, die in Aquarien schwimmen, kann ein Nystagmus beobachtet werden. Hierbei rotiert das Auge um eine Achse, die ungefähr senkrecht zur Pupillenebene steht. Der Nystagmus steht wahrscheinlich in Beziehung zu einer fovealen Struktur auf der ventralen Hälfte der Retina. Die Auslösung und Bedeutung «optokinetischer» oder «optomotorischer» Reaktionen wird diskutiert.

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High-fat Diet and the Development of Obesity in Albino Rats

The relationship between the ratio of the main nutrients in the diet and the development of obesity in man is still the subject of extensive research[1]. Among experimental work concerned with this problem, the findings of Mickelsen *et al.*[2] and of Barboriak *et al.*[3] who described the development of obesity in rats fed for a prolonged time on a high-fat diet, deserve special attention. However, it must be recalled that the hight-fat diet used in these authors' experiments had a higher energy value than the high-carbohydrate control diet and a lower percentage of energy derived from protein. It was therefore of interest to elucidate whether a high ratio of dietary fat *per se* leads to the development of obesity.

Young adult male rats (Wistar strain) were fed *ad libitum* for 44 weeks diets with different proportions of fat, carbohydrate, and protein. The diets contained the same ratio of a basal mixture; the nutrient administered in excess was provided in the form of an isocaloric amount of margarine, starch, or casein. The diets were supplemented by a 2·5% solution of agar to make them not only isocaloric (1 g = 2·3 cal), but also roughly isovoluminous. Except for the nutrient given in excess, the ratio of energy derived from the remaining two nutrients was practically equal (Table). These diets are a slight modification of the diets described in a previous work[4]. The rats were weighed once a week and the food intake of the different groups was measured. After 44 weeks on the experimental diets the animals were killed and the fat content of the whole eviscerated carcass was estimated by the method used by Cohn *et al.*[5].

The results of the experiment are summarized in the table. We can see that the animals fed the high-fat and high-carbohydrate diet do not differ significantly in the weight increments nor in the amount of body fat. The growth of both groups was harmonious and the animals did not develop any signs of deficiency. In agreement with data in the literature[6], the weight increment and body fat were reduced in the group that were fed an excess of casein. The food intake per animal in all three experimental groups was practically equal. The caloric efficiency of the high-fat and the high-carbohydrate diet was thus the same while that of the high-protein diet was considerably lower. It must be mentioned that identical results

Table

Influence of Different Diets on Weight Gains and Body-Fat of Albino Rats after 44 Weeks of the Experiment

Group	Composition of diet			No. of animals	Initial weight (g)	Final weight (g)*	Weight gain (g)*	Fat content of eviscerated carcass (%)*
	Cal.% protein	Cal.% fat	Cal.% carbohydrate					
High-fat	14·9	70·0	15.1	14	191 ± 6·5	447 ± 18·2	256 ± 16·0	20·45 ± 1·23
High-carbohydrate	15·2	10·5	74·3	13	189 ± 4·4	421 ± 18·3	232 ± 13·6	19·88 ± 1·58
High-protein	73·1	11·5	15·4	14	191 ± 6·9	314 ± 12·1	123 ± 10·1	10·69 ± 0·99

The values are given in the averages of the groups (weights as the nearest whole number) ± S.E.

* The values of the high-fat and high-carbohydrate group do not differ significantly. The difference between the high-protein group and the remaining two groups is statistically significant for $P < 0{\cdot}01$.

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