The Fovea. By J. R. Stonaker.

In a brief discussion of a subject like this one can but touch upon a few of the many interesting and important points which present themselves in a careful study. The following is mainly an abstract of a paper that will appear soon in a number of the "Journal of Morphology" under the heading of "A Comparative Study of the Area of Acute Vision in the Vertebrates," to which any one is referred who may desire a more thorough and systematic treatise on this subject.

The term *Fovea* comes from the Latin, and means a pit or depression. It is in this sense that I have used it, and not as the point of acute vision in any eye. The significance of this statement will be readily seen when you consider the fact that many animals do not possess such a pit or fovea, but do have an area of most acute vision. However, when a fovea is present it *is* the point of most acute vision.

Before giving a minute description of the fovea a few words concerning its embryological development may be desirable.

J. H. Chievitz, a German investigator, has done a great deal on this subject. He finds that there is first developed, in the place where the fovea afterwards appears, a thickening of the retina. This thickening he terms the "Area centralis." It is present in the human fœtus about the sixth month, after which time the fovea begins to appear. This increase in thickness is due largely to an accumulation of cells in three layers, viz.: the nerve cell layer and the inner and outer nuclear layers. Then follows a gradual pitting in of the vitreal surface, due to a thinning out or pushing toward the periphery of the elements of all the layers of the retina excepting the rod and cone and the pigment layers. This development has proceeded in some animals only to the formation of an area, in others to a very shallow fovea; while many have a very deep and well-defined depression. In a very shallow fovea all the layers may be present in the center, though somewhat thinner; but in the center of a deep fovea some of the layers will be entirely absent, and those which remain very much reduced, excepting, of course, the rod and cone and the pigment layers. The layer which disappears first is the nerve fibre layer. Then follow the nerve cell layer, inner molecular layer, inner nuclear layer, and, in a very deep fovea, the outer molecular and nuclear layers may also be wanting. This is readily seen in the foveæ of the turkey, pigeon, robin, hawk or human. We thus have a fovea developed which is always surrounded by an area, or, in the terms of human physiology, a macula lutea.

As one approaches the fovea the rods and cones have less diameter, and are more numerous per given area. This necessitates an increase in the number of cells which form the connection with the nerve fibres (ganglion or nerve cells and cells of the inner and outer nuclear layers). But this is not the only cause for an increase in number of these cells. Raymon y Cajal has carefully worked out the manner in which these cells form the connection between the rods and the cones and the nerve fibres. In general, processes pass outward (dendrites) from the ganglion cells and branch profusely among the ingoing processes (neurites) from the cells of the inner nuclear layer. A similar relation obtains in the outer molecular layer between the dendrites and the neurites of the cells of the inner and outer nuclear layers. Each ganglion cell, and consequently each nerve fibre, comes in contact with from ten to thirty rods or cones. But in the region of the area the dendrites and neurites of these cells branch less and finally reach that condition in the center of the fovea where each ganglion cell is in contact with but a single cone.

In the peripheral part of the retina the rods generally exceed the cones in number, but as one approaches the area or fovea the cones become more numerous, and finally in the center of the fovea the rods are entirely wanting.

The fovea varies greatly in form, number and position in different animals. It varies from a very questionable depression found in the domestic guinea hen to a very sharp and deep funnel-like pit found in most birds, especially birds of prey, and in many lizards. The depression may be very broad, as seen in man and some fishes; or, according to Chievitz, we may have a trough-like fovea of various depths, extending horizontally across the retina. In my researches I have not been able to find such a fovea. It is true that in many birds I have seen what appears, to the unaided eye, to be a trough-like depression, but when sections were made across such a region and examined microscopically such a fovea was not discerned. I have been able to examine but one of the species which he has mentioned as having this peculiar fovea, so have included them in my tabulation as he has described them.

As a rule but one fovea is present, but twelve birds have been examined in which two distinct foveæ have been found. Chievitz has described some as having also a trough-like fovea. A double fovea has been discovered only in birds. Among those which I have found to possess double foveæ are three species of hawks, the white-bellied swallow, the common tern and the kingfisher.

The position of the fovea may be either on the nasal side of the entrance of the optic nerve (fovea nasalis), as in most birds, or it may be situated on the temporal side (fovea temporalis) as in man and the owls. The fovea nasalis occupies about the central point of the retina and functions only in monocular vision. The temporal fovea functions in binocular vision. In man it is located about the center of the retina, but in the owl it is some distance to the temporal side of the center. In the case of two foveæ, the one at the center of the retina (fovea nasalis) functions in monocular vision; the other (fovea temporalis) corresponds in position to that of the owl, and functions, likewise, in binocular vision. If a trough-like fovea is present it would function in acts of sight anywhere between monocular and binocular vision.

The area centralis also has a variety of forms, number and positions corresponding to those of the fovea and similarly named. A simple fovea is always surrounded by a round area which is frequently on or in a band-like area extending horizontally across the retina. If a trough-like fovea should be present it would lie along a band-like area. Frequently when two foveæ are present the areas surrounding each are connected by a band-like area.

We may thus have various combinations of area and fovea. The most common is a simple fovea surrounded by a round area. Further, this round area may be continuous with a band-like one. Or two foveæ may each be surrounded by a round area, one of which may be continuous with a band-like area, or each may be so connected.

When one considers the prevalence of a fovea in the different vertebrates he finds that, though each class has representatives which possess a fovea, by far the greater number have only an area centralis. Many have been examined in which not even an area has been observed.

The following tabulation represents in a condensed form the results, so far as I have been able to collect them, of all investigations up to the present time:.

	No. of Species.		No. Area Found.	Area Found.		Fovea Found.		
				Round.	Band-like.	Simple.	Trough-like.	Double.
	51	Mammals	10	33	8	18	......	......
	104	Birds	......	104	36	91	22	12
	28	Reptiles	3	23	3	8	2	......
	14	Amphibians	3	3	8	1	1	......
	30	Fishes	10	20	......	5	......	......
Total	227		26	183	55	123	25	12

Of all the animals which I have been able to tabulate (227 species) no area was found in 26, a round area was perceived in 183, and a band-like area in 55. Of this number, 120 possessed a simple fovea, 12 a double fovea, and according to Chievitz 25 had a through-like fovea.

Mammals do not as a rule possess a fovea, but generally have an area. Of the 51 species tabulated 10 were found in which no area was demonstrated; 33 had a round area and eight a band-like area. Only 18 species (all primates) possessed a well-defined fovea.

In the 104 birds all had a clear fovea excepting one, the common chicken. Why the chicken does not have a fovea when it is present in all the nearest allied forms remains a query. A round area was found in every case, and in 36 a band-like area was also observed. Ninety-one had a simple fovea, twelve double fovea, and twenty-two the questionable trough-like fovea.

Among reptiles a well-defined fovea has generally been found in the lizards and crocodiles, but it has not been observed in the snakes and turtles. Of the twenty-eight species examined only three were found which did not possess an area, while twenty-three had a round area and three band-like ones. A round fovea was seen in the lizards tabulated and a trough-like fovea in the crocodiles.

A fovea has been observed in only two of the fourteen amphibians tabulated. Chievitz reports a trough-like fovea in *Bufo calamita* and Hulke a simple fovea in *Bufo vulgaris*. I have not found a fovea in any of the amphibians which I have examined. In the tabulation, three of the number had no area, three had a round area, and eight possessed a band-like one. I have found the band-like area common to frogs and toads.

In fishes the absence of a fovea is the rule. In the thirty species given a fovea was observed in but five, and no area in ten. In these ten, however, the material at hand was not sufficient to warrant a definite statement. Of the twenty-six fishes I have examined only one was found with a fovea. This was the pipe fish (*Siphostoma fuscum*).

When one compares the retinas in the different vertebrates he finds a marked diversity. A great difference is noticed in the relative thickness of the different layers. But the most marked change is noticed in the rod and cone layer. Comparing the diameter, length, shape and relative number of the rods and cones we find that fishes, frogs and mammals possess the longest rods. In mammals the rods have the smallest diameter, and in frogs the greatest of any of the vertebrates. In birds they are comparatively short and thick. The cones are the longest in some of the reptiles (chameleon) and of greatest diameter in amphibians and mammals. They have about the same length in birds and amphibians, while in fishes they are the shortest. In birds the diameter of the cones approaches very closely to that of the reptiles.

When one is comparing the sensitiveness of the retina of different animals the diameter of the rods and cones is of vast importance. For since these sensitive elements are arranged close together, where the diameter is small there would be more per given area and a more sensitive retina.

The relative number of rods and cones is also of importance. In mammals and amphibians the rods far surpass the cones in number. In birds, with few exceptions, the reverse is true, while in reptiles few or no rods are present. In fishes they are more equally divided.

Investigations by experiment and histological examination prove that the rods are more sensitive to faint impressions than the cones, but that the cones have the greatest power of discrimination both of color and shade. Most nocturnal animals that have been examined have few or no cones.

Experiments on the human retina show that the fovea has the power of most acute vision, and that the power of distinct vision grows rapidly less toward the periphery. We may thus assume that in other animals the fovea, which has the same general arrangement of retinal elements as in man, when present bears the same relation to the more peripheral parts. The human macula, though inferior to the fovea, sees objects more distinctly than the peripheral parts, and we may reasonably say that in general the area centralis bears this relation to the other parts of the retina.

The peripheral part serves as a sentinel. for it perceives objects in motion more easily than objects at rest. Moving objects attract all animals more quickly than stationary ones, and this is especially true in those animals whose retinal development has not proceeded beyond the differentiation of an area. Only those animals which possess a fovea seem to have the power of quiet and close discrimination of an object at rest.

In speaking of the powers of sight in the different classes of vertebrates, I can do no better than quote from the original article of which the foregoing is a summary.

Fishes as a rule depend upon sight for their food, excepting such as the shark, which depends almost wholly on its smell. This class of vertebrates does not, however, usually possess a fovea.

How distinctly they see we can not say, but we know that the trout quickly takes the fly when thrown on the water, or the pickerel the whirling spoon as it is drawn before it. They see the objects while in motion and are apparently unable to distinguish them from the real article of food. An experience in fishing confirms the fact that a pickerel will not bite at a motionless spoon-hook. The retina of these fish has simply a thickening or area at the axis of vision.

A somewhat similar experiment can be tried with the frog or toad. If one attaches a bit of red flannel, a green leaf or any other small object to a thread and dangles it before a frog he will quickly jump for it. A toad may be fed on meat in a similar way, but in no case will the meat be taken unless it is in motion. Neither do these animals show any marked power of discrimination by sight. They will jump at any small moving object and are apparently not able to distinguish, till they have it in their mouths, whether it is an article of food or a pebble. Investigations again show the presence of an area and absence of a fovea.

In some of the reptiles, however, a marked difference in power of discrimination by sight is noticed. Experiments were made wholly on a small lizard (horned toad). If a dead fly were put before him when he was hungry he would eye it closely for a brief time then quickly take it. His aim was also certain, never missing his mark, while that of the ordinary toad was more at random, throwing out her tongue indiscriminately at moving objects. It is true the lizard was attracted more by a live and moving fly than by a dead, motionless one, but he also had the power of perceiving things at rest. This little creature possessed a sharp and well defined fovea.

In general, bird's eyes are almost as perfect as man's, and, likewise, the optic lobes are even greater in proportion to the size of the body than that of man. It is true that the bird often catches flies as they buzz about, but it also inspects each leaf carefully above and below for a worm or bug which may be there in hiding and which it seldom fails to recognize. The hawk as it soars high in the heavens sees the snake, rat or mouse in the grass and is frequently seen to dart and secure its prey. Very acute sight is present in all birds and especially in birds of prey.

A great difference exists in the power of sight in mammals. The primates possess the power of most acute vision. Many of the mammals depend on smell and hearing more than on sight. The dog picks his master out of the crowd by smell, so does the sheep her lamb. Sight in this case being only partial recognition and they are not sure until they have confirmed their sight by the sense of smell. The same is true of the cow, for she must smell of the strange cow when introduced into the herd. The horse is cured of his fright by smelling of the object which caused it. In all these cases we find a motion of the ears showing that the animal is not only using sight and smell but also hearing. Mammals in general do not recognize a man by sight if he remains quiet, but the crow easily sees him and does not fail to distinguish his stick from a gun. The dog looks into your face, but you can not tell whether he is looking into your eyes or at your mouth. He has an indefinite gaze, and, like most mammals, is not satisfied with the sense of sight alone, but must confirm and improve with the sense of smell and hearing.

In conclusion, we may say, that though all animals may have the power of accurate observation, yet the power to perceive the delicate lines and shades of an object distinctly seems to reside only in those forms whose retinal development has reached the highest stage, that is, a fovea centralis.