STUDIES IN ADAPTATION

I THE SENSE OF SIGHT IN SPIDERS

BY

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WITH SIX PLATES

Whether the organization of an animal is the result of continuous adaptation to the conditions of life, or whether the animal adapts itself as best it may to the use of organs in the possession of which it has been put by nature, an impartial observer sees everywhere the remarkable balance between structure and function. The few apparent incongruities which we meet with in all groups of the animal and vegetal kingdoms, only serve to confirm the rule, since they are due largely to our lack of knowledge of the conditions under which such organs exist to their best advantage or of the rôle which they played in the phylogenetic development of the species. But however this may be, we should expect to find, and there surely must be a marked difference between the origin of organs by means of which the animal communicates actively with the surrounding world and that of such organs or structures as lie entirely outside of the personal activity or control of the animal. It is very probable that many, perhaps the majority of arthropods are entirely unaware of the presence on their bodies of so-called decorative structures, designs or colors and whether a male possessing a slight variation in such a structure, design or color, will or will not be preferred by a female, is to my mind entirely a matter of chance. In this connection I can only confirm the observation of earlier naturalists that females often choose defective males in the presence of other in every respect perfect ones. I have caught in Europe a pair of large beetles (*Prionus coriarius*), in coitu in the presence of two other perfect males, when the male in question had

one eliter and one leg malformed and showed other minor defects. Upon investigation the male proved to have normal spermatozoa and the female laid an extraordinarily large number of eggs. Similar cases are common among all insects as well as other animals. I have made the same observation in the beetle, *Lucanus cervus*, the males of which have the beautiful horns on their heads. Of the beautiful moth, *Samia cecropia*, over a hundred of which I allowed to develop in a cage for other experiments, many couples with entirely defective and malformed wings were found in coitu. Among orb-weaving spiders are several species in which during the mating period the female allows several males to remain in her net, of course at a good distance from her, and it is a common occurrence for defective males to be accepted by the female while perfect ones will be chased away for their dear life or will even fall victims to the voracity of the much stronger female. Protective structure or coloration belongs to the same group of phenomena and here a great number of cases might be recorded where an animal remains entirely unaware of the protection afforded by its form and color if in the proper surroundings and of the danger of disregarding this. I have seen butterflies that would be protected by the leaf-like coloration of their wings if they should sit motionless, instantly caught on the wing by large dragonflies, and in the West Indies I could observe regularly a hemipteron of the group *Emesidæ*, which would resemble a dead twig if in an appropriate position, swinging to and fro on the four hind legs in the center of a large leaf. All this I bring here by no means with the object of denying the existence of adaptation or of the principle of selection itself, which only one who has never observed nature outside of the laboratory can do. But I want to show that in all those instances where the animal itself cannot make use of a new variation or mutation, in the possession of which it has been placed by nature, its advantageous character will be a mere matter of chance, and selection, if it take place, must be greatly retarded in its progress.

Quite different must it be with those structures which the animal is able to put to active use, however unconscious it may be of the advantage it enjoys over other individuals of the same species.

A caterpillar that is able to construct a better protected cocoon than its fellows, an animal that can run faster from danger, a bird of prey that distinguishes its victim at a greater distance, all these will evince their superiority over other individuals of the same species upon the first occasion. Here, then, opportunity is given for a more rapid accumulation of characters and an accelerated selection. Several years ago I studied, together with Dr. von Guaita, although with a different object in view, the stridulating organs of Orthoptera. These organs are undoubtedly not of a protective character as the insects in question are safer when silent. This is sufficiently shown by the fact that they stop their cry instantly upon the approach of danger. The origin of the stridulating organs has therefore to be sought in some advantage which they may afford the sexes during the mating period. That they are a rather late acquisition is evidenced by their late appearance, only with the last moulting, while the rapidity of selection which in this case must still have been retarded by the danger arising from their possession, is apparent from the complete absence of any traces of similar organs previous to the last moulting. The great variability in the number of teeth on the chord or bow of the stridulating apparatus, which permits of difference of pitch in the tones produced by friction, the fact, with other words, that the stridulating organs are in respect to their details, not absolutely fixed structures, seems to be due to this antagonism between the advantage afforded by the organs in the relation of the sexes toward each other and their disadvantage in respect to diminished safety from the aggression of enemies. But how is it with organs in which the advantage arising from their perfecting will be immediately exploited to its fullest extent by the animal possessing them? With this question before me I commenced my research on the sense of sight in spiders. The results of this research which now extends over more than a year, I bring in this paper.

Two factors in the life of spiders have left a deep impression on their organization, the first, that they subsist exclusively by means of prey and the second, that the external sexual organs,

the organs of copulation in the male, are entirely separate from the internal sexual organs. If we may judge of the amount of food required by the quantity of insects captured in the orb-net of a single spider, a quantity that is sometimes appalling, it was necessary for the spiders, in order to satisfy this want, to develop as they indeed have done, either the instinct and the engineering capacity for constructing nets or else the instinct for hunting their prey freely on the ground or on plants. Two different directions are thus given to the development of the whole spider group and we should naturally expect to find differences in the structure of the corresponding organs of sense and of the spinning apparatus. But while in higher animals, as for example, birds of prey, all organs of sense are developed to a remarkable degree of perfection, we cannot say the same for the hunting spiders. It is a matter of common observation that vultures discern their prey from a distance amounting at times to several thousand feet and they are undoubtedly able to scent a carcass hidden among bushes at a considerable if not so great a distance as this. Their ears are sensitive to high and low sounds of a very small amplitude and only the sense of touch which could scarcely be of use to them, is little developed. It is otherwise with the hunting spiders. They possess doubtless, a very fine sense of touch, the whole body being covered with hairs and bristles sensitive to the slightest stimulus. In regard, however, to the organs of hearing and smell we are as yet without definite results of any kind. At any rate these two senses are very little developed. Even the question as to the existence of such organs is to my mind far from being settled. Whether the organs discovered by Dahl and the lyriform organs have anything to do with these senses must be determined by new investigation. I myself have made some experiments on the sense of hearing, thus far without any definite results. I also repeated the experiments of Pritchett on the sense of smell in large lycosids but even to such irritants as formaldehyde, osmic acid and acetic acid, they did not respond so readily or so quickly as to the slightest touch with the end of a silk thread. As the sense of touch is solely protective, there remains only the sense of sight to guide the spiders on their hunting trips. The

splendid experiments of Mr. and Mrs. Peckham on the jumping spiders (*Attidæ*), during the mating period, have clearly demonstrated that the sexes recognize each other by the use of their eyes alone, the male remaining unaware of the presence of a female, nor will he perform the peculiar, characteristic love dance, if his eyes are covered with paint. But is the sense of sight in spiders as sharp as we should be led to expect by comparison with that of birds of prey? This question has not yet been answered with sufficient certainty owing to the difficulty of experimenting. Plateau came to an entirely negative conclusion, asserting that spiders possess an indistinct and very poor vision, being unable to discern objects beyond a distance of from 8 to 10 cm. Forel was of the same opinion, while the more ingenious experiments of the Peckhams leave no doubt that the males of the *Attids* recognize their females at a distance of about 30 cm. and moreover that they distinguish colors. But whether spiders can see beyond this distance and how sharp their vision is, the experiments of the Peckhams also, leave unanswered. In fact it would be impossible to answer this question merely by observing the behavior of spiders during an experiment or in nature. A close anatomico-physiological study is required and only by combining the experiment on the living specimen with its after examination may one reach a satisfactory answer. This answer I hope to have given in the present research.

Keeping in mind all that has been said in the preceding pages, we may conclude that the study of the eyes of spiders and of their sense of sight, as examples of adaptation of the first kind, possesses several advantages as well as certain disadvantages and these we have next to consider. The advantages are:

- 1 That the sense of sight is beyond any doubt the only sense that guides hunting spiders on their hunting excursions and in finding the females during the mating period.

- 2 That the eyes of spiders are organs which are for each species definite in number and position on the cephalothorax.

- 3 That the sense of sight is a sense common to the great majority of lower and higher animals and that some analogizing is therefore not only admissible but may be of great value.

The disadvantages are:

1 That beyond some experiments of Plateau and the Peckhams, nothing definite is known in regard to the acuity of vision in spiders and no method has been brought forward for its study.

2 That the eyes are complicated organs, consisting of a refraction and a perception apparatus, each of which and the separate parts of which may possibly be capable of adaptation and which have therefore to be considered separately.

Let us now begin with a closer study of the ocular group on the cephalothorax of various adult spiders.

THE POSITION OF THE EYES ON THE CEPHALOTHORAX

The number of eyes in the great majority of spiders is eight and the group which they form on the cephalothorax is so characteristic for the different families that it was for a long time used as a systematic character of great value. The group consists usually of two or three rows, more rarely of two or three smaller groups containing three or two eyes each. Of importance for systematics are the length of each row, the distances between the eyes taken in relation to their diameters, the form of the row, whether straight or bent in the middle forward or backward, as well as the shape and to some extent the color of the eyes. Even a superficial observer will notice in addition, that both in the jumping and the ground spiders (*Attidæ* and *Lycosidæ*), two of the eyes on the forehead are larger than the others, especially in the former. But the reason for such a configuration in the eye-group was never sought for and the apparent similarity in the eye-groups of spiders belonging undoubtedly to different families, led to the conclusion that the value of the eye-group as a systematic character had been overestimated.

The position of the eyes on the cephalothorax becomes more comprehensible when we begin to study the directions of their respective axes and the angles that these axes form with the three chief planes of the body. Unluckily we at once meet with great difficulties even though we choose species having perfectly round eyes. The first of these is to ascertain with exactitude the posi-

tion of the two planes intersecting the plane of symmetry of the body. After experimenting for a long time I decided upon the following method. The spider is killed in alcohol and then kept in it for several days. When the muscles have become entirely rigid, so as to allow of no change in the shape of the cephalothorax while drying, the abdomen is severed from the cephalothorax through the petiolus with a sharp pair of scissors. Next the pars labialis, together with the laminæ, the palpi and the chelæ, is carefully removed with forceps. At the same time care must be taken not to tear the chitinous bridge connecting the opposite sides of the cephalothorax immediately behind the chelæ since this would lead to a flattening of the cephalic part and consequent distortion of the true angles. The legs are now carefully removed leaving the coxæ alone in their normal position attached to the sternum. Next a thin line is drawn with chinese ink on a very thin layer of Canada balsam that has been spread with the finger over a small cover-glass. It is best to use rather a thick cover-glass and to draw the line quite across it parallel to two edges. A drop of fish glue is now put in the center of the glass and on this the cephalothorax is placed with the sternum toward the glue and gently pressed until all the coxæ and the sternum are in contact with the glass. The glass now represents one of the two planes intersecting the plane of symmetry at right angles. I shall call it *the horizontal or foundation plane*. It is only approximately parallel to the surface of the earth or to that of any object upon which the spider may be, since the spider is able to raise itself up on either front or hind legs, in this way changing the angle between the foundation plane and the horizon. At the same time it is essential that the plane of symmetry should coincide with the black line on the cover-glass. This is accomplished by using a needle under the microscope at a magnifying power of about twenty diameters. It is now easy to determine the *plane of symmetry* by taking the point midway between the front middle eyes, the central, longitudinal groove of the cephalothorax when it is a species possessing this groove, and the point at an even distance between the two chitinous plates of that part of the petiolus which remains with the cephalothorax after the abdomen has been

severed. The third plane which I call the *vertical or transverse plane* and which intersects the two other planes at right angles, is geometrically determined by these. After the cephalothorax has been prepared in this manner and thoroughly dried in a warm place, the cover-glass upon which it is fixed is laid upon the center of a square glass plate, which is at the same time the center of a circle drawn upon the surface of the plate with radii forming angles each of which measures ten degrees. If we now use an eye-piece having two lines intersecting in the center at 90° , we can readily measure the angles that the eye-axes form with the plane of symmetry. To know how this is done we must remember that the eyes of spiders have each a lens, the outer surface of which forms part of the surface of a sphere. When we look at a lens in the direction of the eye-axis, it appears to us as a circle while if we look at it under an angle of less than 90° , its outer surface appears to us as two curves intersecting each other at two points. If we place the eye in the center of the microscopic field and move the eye-piece until one of its lines falls upon these two points of intersection of the curves of the lens and the other passes through a point midway between them, then the latter line represents the projection of the eye-axis on the horizontal or foundation plane and the angle that it forms with the plane of symmetry can be read directly from the scale. More exact results would of course be obtained by using a goniometer ocular such as is made by Zeiss, but even the arrangement I have described here, the ocular with intersecting lines, gives an error of not more than a few (3 to 4) degrees. When the angles have in this way been measured a drawing is made with the aid of an Abbe drawing apparatus of the entire eye-group and the eye-axes are then drawn in, in accordance with the data given by the measurements. We obtain in this way a correct figure of the projection of the eye-group on the horizontal or foundation plane. In order to gain a clear picture of the position of the eyes it is necessary to make two other projections, one on the plane of symmetry and the other on the vertical plane. To accomplish this I put a small drop of beeswax in the center of the circle on the glass plate into which the edge of the cover-glass holding the cephalothorax is pressed. This

cover-glass is held in a vertical position with the aid of two straight angles which are removed as soon as the wax is hard enough to keep the glass in position. Another method, much simpler and perhaps just as good, consists in adjusting the cover-glass until its upright edge forms a straight line with its own reflection in the slide. The angles are now measured in the same way as before. The drawing is of course made under the same magnification and the upper edge of the glass holding the cephalothorax is likewise drawn. It represents a cross-section through the horizontal or foundation plane.

To make a drawing of the projection on the vertical plane one proceeds in the same manner with that difference that the cover-glass carrying the cephalothorax is placed on its other edge.

Two facts become immediately apparent upon comparing the drawings made in this way, of eyes of spiders belonging to different families. First, that there is not a single pair of eyes which are focused upon a single point like, for instance, the eyes of man. On the contrary, *the axes of all eight eyes are so directed as to form divergent angles with each other*. Second, that not only do the positions of the eyes on the cephalothorax of spiders belonging to different families differ from each other, but *the axes of the same eyes in different spiders do not lie in the same direction but form with the three planes of the body, the planes of projection, angles differing considerably from each other but fixed for each species*. To make this clear let us look at the drawings (Figs. 1-9) representing the eyes of three hunting spiders, *Lycosa nidicola*—a common large ground spider of northern America, *Phidippus tripunctatus*—a large jumping spider belonging to the same region and *Heteropoda venatoria*—a cosmopolitan tropical and subtropical spider of very large size, belonging to the family *Heteropodidæ* and resembling in habitus the crab spiders (*Thomisidæ*) among which it was wrongly placed by earlier systematists.

Translating the results of these measurements into common language, we may thus describe the positions of the eyes in the three spiders. The anterior middle eyes in the jumping spider, *Phidippus tripunctatus*, are directed forward and a little outward and downward. In *Lycosa nidicola* more outward and consider-

ably upward. In this respect *Heteropoda venatoria* resembles *Lycosa* more than it does *Phidippus*, since its anterior middle eyes are also directed frontward but still more outward and considerably upward although not so much so as in *Lycosa*.

TABLE I

Projection on the horizontal or foundation plane. See Figs. 1, 2 and 3

The angles which the axes of the eyes form with the plane of symmetry. The right side with a plus, the left with a minus sign

		AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	±	8	21	67	95
<i>Lycosa nidicola</i>	±	12	24	24	94
<i>Heteropoda venatoria</i>	±	32	27	0	109

TABLE II

Projection on the transverse or vertical plane. See Figs. 6, 8 and 9

The angles which the axes form with the plane of symmetry. Signs as before

		AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	±		?	57	63
<i>Lycosa nidicola</i>	±	?	155	?	56
<i>Heteropoda venatoria</i>	±	?		8	71

TABLE III

Projection on the plane of symmetry. See Figs. 4, 5 and 7

The angles which the axes of the eyes form with the horizontal or foundation plane. Zero in front of the head, 180° at the back. Positive quantities for eyes looking upward, negative for those looking downward.

	AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	- 2	0	+ < 90	+ > 90
<i>Lycosa nidicola</i>	+ 14	- 18	+ 10	+ > 90
<i>Heteropoda venatoria</i>	+ 8	+ 8	+ 92	

The anterior side eyes in *Phidippus* are so directed that their axes are parallel to the horizontal or foundation plane and turned a little sidewise. In *Lycosa* they are directed a little more outward and at the same time downward. In *Heteropoda* they are directed still more outward but at the same time upward.

The posterior middle eyes in *Phidippus* are directed considerably toward the side and upward. In *Lycosa* they are directed much more frontward and also upward, while in *Heteropoda* they look straight upward. Their axes are in this case almost perpendicular to the horizontal plane.

The posterior side eyes in *Phidippus* are directed sidewise, considerably upward and a little backward. In *Lycosa* they are directed in the same way sidewise and backward but considerably more upward, while in *Heteropoda* they are directed considerably less upward and much more backward.

I studied the positions of the eyes as I have described them here, originally in perfectly ripe females. Six individuals of each species were measured and showed only slight differences in the angles. Since the method employed is not an absolutely exact one, it is difficult to say whether these differences depend upon variation in the position of the eyes or upon defects in the method itself. However, the following facts speak rather for defective measurements than for natural variation. I expected to find that during the post-embryonic development the position of the eyes on the cephalothorax would change with each moulting, approaching more and more nearly to that of the adult female, which should be considered an adaptation to the particular life of the spider. An observation that made this seem still more probable has been made by various scientists at different times, that the eye-group in young spiderlings occupies a relatively larger part of the cephalothorax than it does in the adult spiders. Nevertheless there seemed to me to be occasion for a more thorough study of the eye-group and the eye-axes in spiders of different ages. I had in my possession perfectly ripe females of the three species I have mentioned, several specimens of *Heteropoda* just before the final moulting, others that had to moult twice and three specimens of very small spiders that had still to moult at least three times before attaining maturity and also a cocoon filled with very young spiderlings. I kept several females of *Lycosa nidicola* for a time in large glass jars and preserved both mother and the spiderlings which were in part taken from the cocoon, in part killed while on the back of the mother just as they were about to

leave her. I had, besides, several unripe specimens of unknown age. I had also *Phidippus* in the same stages as *Lycosa*. It is not difficult to obtain these since the female of this species make a tent of web in which she lays the eggs, afterward guarding the young ones for a considerable time. I caught in addition several females of *Pardosa nigropalpis* with young ones on the back.

The method employed is as follows: Instead of measuring each eye and the distances between the eight eyes in each spider, I make with the aid of the Abbe apparatus a drawing of the entire eye-group of an adult female. Leaving the drawing in the same position on the drawing table, I remove the adult female and substitute a younger one. I then try different objectives and oculars until the image on the paper of the eye-group of the younger spider is of the same size as the drawing of the adult. A sheet of clean paper is now put in place of the one with the drawing and the new drawing is made. In this way drawings are obtained of all stages. The angles of the eye-axes are next measured and the axes drawn in on the corresponding figures. In all cases, beginning with the young spider at the time when it is ready to leave the mother in order to commence its own, independent existence and ending with the mother herself, the configuration of the eye-group and the angles of the axes proved to be the same and the drawings made of them on paper, when superposed and examined against the light, coincide absolutely. But this does not apply to the youngest spiderlings, those taken directly out of the cocoon. Although in such spiderlings the eye-group is in general very nearly the same as in the adults, careful measurements show differences which, while not appreciable to the unaided human eye, are nevertheless of great importance. I give these measurements here (Table IV) but shall discuss them farther on when examination of the fields of vision will reveal more clearly their significance. It is unfortunately still more difficult to measure the angles in such spiders than it is in older ones so I give only figures of which I am certain.

If we compare these tables with those for the adult females we shall at once notice the following differences. In the youngest spiderlings of *Phidippus* and *Lycosa* the anterior middle eyes

are directed a little more outward and in *Phidippus* a little more downward also, than the same eyes in the adult. In *Heteropoda*, on the contrary, the anterior middle eyes of the spiderling are directed much more frontward than in the adult.

The anterior side eyes in *Phidippus* and *Lycosa* are directed much more toward the side than in the adult, in *Heteropoda* much more toward the front. The angles of projection on the two

TABLE IV

SHOWING THE ANGLES THAT THE AXES OF THE EYES FORM WITH THE THREE PLANES OF THE BODY IN VERY YOUNG SPIDERLINGS

a Projection on the horizontal or foundation plane. Compare Figs. 4, 5 and 7

		AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	±	10	30	?	88
<i>Lycosa nidicola</i>	±	?	30	25	85
<i>Heteropoda venatoria</i>	±	11	22	18	60

b Projection on the transverse or vertical plane. Compare Fig. 9

		AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	±	?	?	?	?
<i>Lycosa nidicola</i>	±	?	?	?	68
<i>Heteropoda venatoria</i>	±	?	?	?	?

c Projection on the plane of symmetry. Compare Figs. 4, 5 and 7

	AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	-5	0	?	?
<i>Lycosa nidicola</i>	?	?	+ 30	?
<i>Heteropoda venatoria</i>	?	?	+ 87	?

other planes could not be ascertained for these eyes. It is impossible to study the posterior middle eyes in the young spiderlings of *Phidippus* at all, on account of their extreme minuteness. In *Lycosa* the projections of the axes of these eyes on the horizontal plane is approximately the same as in the adult but their projection on the plane of symmetry shows that they are directed upward at an angle about three times as great as in the adult

In Heteropoda spiderlings they are directed somewhat sidewise and nearly upward but more toward the front, while in the adult they are directed straight upward and a little backward.

The posterior side eyes in the spiderlings of all three species, especially in Heteropoda, are directed a little frontward instead of backward and in *Lycosa* less upward, also, than in the adult.

The relative sizes of the eyes and of the distances between them are also different for spiderling and adult. Tables V, VI, VII and VIII may serve to illustrate this.

TABLE V
Lycosa nidicola. Diameter of eyes in millimeters

	AME	ASE	PME	PSE
Mother.....	0.361	0.279	0.689	0.541
Spiderling, ready to leave mother.....	0.074	0.057	0.148	0.115
Spiderling, taken out of a cocoon.....	0.049	0.038	0.115	0.115

Or in proportion to the anterior middle eyes which we take as unit of comparison

	AME	ASE	PME	PSE
Mother.....	1	0.77	1.90	1.50
Spiderling, ready to leave mother.....	1	0.77	2.00	1.55
Spiderling, taken out of a cocoon.....	1	0.77	2.30	2.30

TABLE VI
Heteropoda venatoria. Diameter of eyes in millimeters

	Length of cephalo-thorax	AME	ASE	PME	PSE
Adult female.....	10.6	0.45	0.75	0.55	0.70
Immature female before last moulting....	6.8	0.28	0.55	0.40	0.50
Two moultings before maturity.....	5.4	0.22	0.43	0.34	0.45

Or in proportion to the anterior middle eyes

	AME	ASE	PME	PSE
Adult female.....	1	1.66	1.22	1.55
Immature female before last moulting.....	1	1.93	1.43	1.78
Two moultings before maturity.....	1	1.95	1.54	2.04

TABLE VII

Pardosa nigropalpis. Diameter of eyes in millimeters

	Length of cephalo-thorax	AME	ASE	PME	PSE
Mother.....	2.8	0.115	0.115	0.328	0.246
Spiderling, ready to leave mother.....	0.85	0.049	0.049	0.115	0.820

Or in proportion to the anterior middle eyes

	AME	ASE	PME	PSE
Mother.....	1	1	2.85	2.13
Spiderling, ready to leave mother.....	1	1	2.34	1.67

TABLE VIII

SHOWING THE DISTANCES BETWEEN THE EYES AND BETWEEN THE EYES AND THE EDGES OF THE CEPHALOTHORAX

Lycosa nidicola. Measurements in millimeters

	Length of cephalo-thorax	Breadth of cephalo-thorax	Distance between outside edges of the PSE	Length of quad-range	Distance between the edge of the cephalothorax and the PSE
Adult female.....	8.1	6.0	2.2	1.1	2.2
Spiderling taken out of a cocoon.....	0.984	0.771	0.459	0.197	0.180

Or in proportion to the length of the cephalothorax as a unit

	1	0.74	0.27	0.13	0.27
Adult female.....	1	0.78	0.46	0.20	0.18
Spiderling taken out of a cocoon.....	1				

Heteropoda venatoria. Measurements in millimeters

	8.0	8.0	3.2	1.4	1.6
Adult female.....	1.017	0.902	0.525	0.180	0.131
Spiderling taken out of a cocoon.....					

Or in proportion to the length of the cephalothorax

	1.	1.	0.4	0.17	0.20
Adult female.....	1.	0.88	0.51	0.17	0.12
Spiderling taken out of a cocoon.....					

By a comparison of all these tables we may now gain considerable light on the question as to what happens to cephalothorax and eye-group during the post-embryonic development. When the spiderling sheds its first skin in the cocoon, the eye-group occupies almost the whole breadth of the cephalothorax which is comparatively very low. The first change, of which I shall speak farther on, is in the directions of the eye-axes. *When the spiderling leaves the cocoon, that is, before the next moulting takes place, the eye-axes have become fixed in the positions which they will occupy during the whole life of the growing and mature spider.* Whatever change takes place from the time the spiderling leaves the cocoon, is only in the relative size of the space on the cephalothorax occupied by the eye-group and to a certain extent, in the relative sizes of the eyes themselves. *The cephalothorax grows more rapidly than the eye-group, so that the latter occupies with each moulting a relatively smaller part of the cephalothorax.* We shall presently see that this also is of advantage to the spider.

THE MAXIMUM ANGLE AND THE FIELDS OF VISION

While handling under the microscope a dried out cephalothorax from which all organs and muscles had been removed to permit of the study of the endoskeleton, I chanced to notice that the faint images, visible in the eyes, of the trees which grow before my laboratory window, were not of the same size. I very soon found that boiling or even keeping in a cold solution of potassium hydrate so changes the optical property of the eye-lens that it becomes entirely intransparent so that it is necessary to use some other method. I have finally adopted the following one. The spider is killed in strong alcohol from which it is at once removed. The abdomen, all appendices and the sternum are then removed and the organs and muscles filling the cephalothorax are carefully taken out with a forceps. Next the inside of the cephalothorax must be cleaned under water with a soft brush. I use a small camel's hair brush of the kind used for water colors but cut the hairs quite short. With this brush it is possible to remove all the remaining muscles as well as the vitreous bodies of the

eyes. Care must be taken, however, not to remove the black pigment ring surrounding each lens on the inside surface of the cephalothorax and forming a sort of iris, as this would make a difference in the measurements. Even in spiders that have been kept for a long time in alcohol the lenses are often still so transparent that one may see the images formed by them, but such lenses are yellow and the images rather poor. If on the contrary the eyes are prepared in the manner just described, it is scarcely possible to give an idea of the beauty of the little images. The lenses are then entirely colorless and transparent and the images render correctly color and line.

For the study of the fields of vision, each eye together with a little of the surrounding chitin must now be cut out of the cephalothorax. The lens is then placed with its inner surface on a small drop of liquid on a slide and in a hanging position examined under the microscope through the slide. By this means three advantages are gained. First, the object examined sends its rays through the lens in the normal direction so that the eye of the examiner is substituted for the retina of the spider; second, the observer looks in the direction of the eye-axis or at least very nearly in that direction; and third, the outside surface of the lens remains dry, limited by the air alone, as is the case with the living spider. More difficulty is presented by the fact that the refraction-coefficient of the vitreous body is not known. However it is sometimes possible to prepare an eye fresh with the vitreous body in its natural position and the retina cut off with the aid of a razor. We are then able to measure the image of a scale at a given distance. But since the vitreous body coagulates too rapidly to be used in the study of the maximal and minimal angles of vision, we have to use in its stead a drop of water and also of some liquid possessing a *higher* refraction-coefficient than the vitreous body. With the latter we obtain a somewhat larger image than in reality and may *overestimate* the acuity of vision. Such a liquid I found in a mixture of equal parts of pure glycerine and egg albumen. The results obtained by the use of water we may then employ for control, to guard us against the opposite extreme of an *underestimation* of the acuity of vision.

The proportion between the two media is according to my measurements as 4 : 5, *i. e.*, that an image will occupy four divisions of a scale if water is used as the medium of suspension as against five divisions when glycerin-albumen is used.

The microscope also must be arranged in a special manner. The diaphragms with the mirror and the Abbe lens must be removed. The instrument is then placed on a high box open to the window, with a long slit occupying the whole space between the legs of the stand. Next a scale in the form of a cross with right angles is drawn on bristol board. Each arm of the cross is two centimeters wide and consists of alternating black squares like those on a checker-board. For the sake of convenience as well as to avoid error, the numbers are written in each white square in roman numerals in one direction and arabic in the other. This cardboard is now placed under the microscope so that the distance between it and the spider's eye is exactly 10 cm. Excessive light around the eye is excluded by means of a small diaphragm or a black paper with a small round hole arranged so that the spider's eye hangs directly in the middle of the hole. Of course any objective with small magnifying power may be used. As for myself I either use the a* or the A achromatic system of Zeiss and the compensation ocular 6 with the ocular micrometer. This micrometer is adapted to apochromats but may just as well be used with achromats if one ascertains the size of each division. In my instrument each division of the micrometer with the A objective corresponds to 0.0164 mm., while the correction of the a* lens makes possible a magnification where each division will correspond to 0.1 mm. The light reflected from the white bristol board on which the scale is made, is sufficient to give a perfect image of the scale in the microscope.

The scale is so placed that the center of the cross falls exactly on the axis of the spider's eye. I found that the eyes of the hunting spiders are quite round and that the maximum angle of vision is therefore the same in each direction, *i. e.*, the limit of the field of vision in such eyes is a circle representing the circumference of the base of a cone. In order to find the maximum angle in each case, there remains only to read on the image of the scale

in the eye, how many centimeters are visible. Since the distance between the spider's eye and the scale equals 10 cm. a simple calculation will give the value of the angle in question, or it is still simpler and entirely sufficient for our purpose, to draw on paper an isosceles triangle, the base of which must be as many centimeters long as are visible on the image of the scale in the eye and its height 10 cm. The angle can now be directly measured. When the angles have been measured for all the eyes, they are represented on the drawings in each projection, showing the field covered by each eye. Optically the angle depends upon the curvature of the lens and the refractive coefficient of the substance of which it consists. But what is of interest for us here is the general fact that the larger the spider's eye, the smaller, as a rule, is its field of vision.

If we compare the drawings of corresponding projections in different spiders after the maximum angles of vision have been introduced, we cannot fail to recognize the remarkable relation between the particular life of the spider and the position of its eyes. In order to make this clear I must state here that which I shall prove farther on, that the larger the spider's eye, the sharper its vision or power of distinction. Let us begin with an examination of the projection on the horizontal or foundation plane (Fig. 1). We see that the largest eyes in *Phidippus* are the anterior middle ones covering a field of 40° each or both together about 55° , owing to the fact that their axes are a little divergent. Each of the anterior side eyes also covers a field of 40° or both together 83° , *i. e.*, more than the entire field covered by the AME.¹ But the ASE are considerably smaller than the AME. The minute eyes of the second row, the posterior middle eyes, cover a field of 62° and the PSE one of 48° or the whole eye-group covers about 240° of the horizon. The projections on the other two planes (Figs. 4 and 6) show in addition that the PME and the PSE guard chiefly the sides of the spiders, leaving about 52° in the vertical plane and more than 80° at the back on the dorsum, entirely unguarded. This is the only direction from which the

¹ These are abbreviations commonly used by arachnologists. AME stands for anterior middle eyes; ASE for anterior side eyes; PME for posterior middle eyes, and PSE for posterior side eyes.

jumping spider can be taken unawares by an attacking enemy. We know besides from the behavior of the spider that whenever an insect or anything else approaches it from the side, it immediately turns toward the intruder as though with the desire to see it better by using its front eyes.

Lycosa nidicola is a spider that lives on the ground under stones, making excursions in the grass. Its manner of walking like that of all ground spiders, is distinctly straight forward and we find that the largest eyes, the posterior middle eyes, are so situated as to guard the front of the animal. In the projection on the horizontal (Fig. 2) plane they together cover a field of 48° , *i. e.*, considerably less than the four eyes of the front row, which cover all together a field of 77° . Between the eyes of the second and those of the third row there is an unprotected area of about 7° , or remembering that the drawing is considerably enlarged, we may say that an object 1 cm. sq. will be invisible within the space of these 7° as soon as it is farther than 8 cm. from the spider. The presence within this area of a spider of the same species could be already noticed at a distance of about 25 cm., quite sufficient to protect against sudden onslaught. The posterior side eyes which are second in size, guard the spider at the sides and back. Thus the entire eye-group covers about 253° of the horizon and leaves unprotected a space on top and at the back.

In *Heteropoda* (Fig. 3) the largest eyes are the posterior side eyes. The four front eyes cover a field of 145° . Between them and the posterior side eyes there is an unprotected area similar to that in *Lycosa*, of about 10° . Or since an adult of *Heteropoda* covers with extended legs about 8 to 10 cm. in each direction, a spider of the same species approaching it within this unprotected area, would become visible at a distance of about 40 cm. The sides are therefore very well guarded especially when we consider that the largest eyes are used in their protection. The eyes of the front row together with the posterior side eyes cover with the interruption mentioned, fully 267° . The dorsal surface of this spider is extraordinarily well protected as compared with the two preceding spiders. There remains an unprotected field of about

10° in front of the posterior middle eyes and about 55° of unprotected field at the back behind these same eyes. In the projection on the plane of symmetry (Fig. 7) the eyes cover 152° or in the normal position of the spider, on a wall, 125°, as may be readily understood from the drawing. In the vertical plane (Fig. 8) the eyes of *Heteropoda* cover a field of 193°. This spider lives in buildings where it runs along the walls and ceilings hunting insects and other spiders and it is distinctly crablike in motion. The comparatively large fields of vision in this species are possibly to be accounted for in connection with the habit of the spider to remain quiet during the day and to begin its activity at dusk. But this does not obscure the fact that the sides of this spider are better protected than the front.

It was next necessary to ascertain whether or not the fields of vision vary in spiders of the same species at different ages. With this object in view many spiders were examined, always with the same result, *i. e.*, from the time when the eyes assume their permanent position on the head of the spiderling, the maximal angles of vision and the fields covered by these eyes are the same as in the mature female. As to spiderlings taken directly from the cocoon, I am sorry to say that I was unable to make any observations upon them. They are so small and their chitin so soft that it is impossible to prepare them in the manner described and I have not as yet devised another method. But assuming that their maximal angles of vision are the same, which is indeed very probable, we may readily see the advantage in the changes of direction in the eye-axes as I have described them. A glance at the accompanying drawings will make this clear. To attain their permanent position the axes of the AME in *Phidippus* move upward and inward. This slight upward change makes it possible for an image to be formed of an object on the central part of the retina of an adult on the same plane, a good deal farther away than is possible in the eye of the spiderling. We shall see farther on that the central part of the retina is much more sensitive than the periphery. The change inward tends to the same end as the change upward and the final position of the anterior middle eyes in *Phidippus* allows therefore of a more perfect distinction of

objects in front of the spider. In the same eyes in *Heteropoda* the direction of the axes changes in the opposite sense, *i. e.*, outward and this change serves to bring about a better discernment of objects considerably at the side of the median line, while the same eyes still guard the front sufficiently. In the posterior middle eyes of *Lycosa*, the most sensitive ones in this spider, the direction of the axes changes to one more downward and inward thus serving to protect better the front. The direction of the axes in the posterior side eyes of the same spider changes in such a way that the adult eyes look farther backward. In both PME and PSE this change takes place at the expense of the field protected in the young spiderling, which now becomes relatively exposed. And here the advantage of a slower growth of the eye-area as compared with the growth of the rest of the cephalothorax, becomes evident. Indeed if the eye-group should occupy in the adult spider relatively the same portion of the cephalothorax as it does in the youngest spiderling, the unprotected field would become in consequence of the change in the direction of the axes, so large that the presence within it of an object even larger than a spider of the same species, would remain entirely unnoticed. In *Heteropoda* the change in the direction of the axes of the PME is in exactly the opposite sense to that in the same eyes in *Lycosa* and affords more protection to the dorsal surface. At the same time in the axes of the PSE in *Heteropoda*, the change of direction is in the same sense as in *Lycosa* and *Phidippus*. But this change is considerably more marked in *Heteropoda* with the result that in the adult spider the eyes cover fully 267 degrees instead of the (probable) 166° in the spiderling. This advantage cannot be gained however, without the formation of an unprotected field. Again, as in *Lycosa*, this field would have been much larger but for the difference in growth between the eye-group and the cephalothorax.

THE LIMIT OF VISION

If we examine under small magnifying power at once all eight eyes of a cephalothorax, freshly prepared and suspended on a drop of glycerin-albumen as I have described, we shall remark

that the four pairs of eyes form four pairs of images differing from each other in size. As a rule we shall find that the largest eyes form the largest images. The question at once occurs, are all eyes equally sensitive notwithstanding that they form images differing in size, or are the larger eyes more sensitive than the smaller ones? The surest way to find the answer to this question is to determine the minimum angle of vision for each eye. But how are we to do this when we do not even know with sufficient exactitude the distance at which under normal conditions a spider recognizes another of the same species. The experiments of the Peckhams, in spite of their ingenuity, still admit of too great range for error, to be utilized in a study of the normal angle of vision. Of what advantage, then, would be a similar experiment but with some of the eyes blackened with paint? It could serve merely to control another method, a method of comparative morphology. We have to start from the proposition that the physiology of the nervous system is analogous in the other animals and man, a proposition which few are disposed to admit, but here the experience gathered in many fields and from observations made on different animals, comes to our aid, an experience that leaves scarcely any room for doubt that the stimulation of a single nerve-ending transmits to the central nervous system a single sensation only, whether or not the stimulus itself is a simple one or in reality composed of many contemporaneous stimuli. Thus, as is well known, in order to perceive two pin-pricks as two distinct sensations, it is necessary that they should be applied to two separate nerve-endings as otherwise the sensation is that of a single prick and again, when the image of two stars falls on only one cone of the retina of the unaided human eye, the eye perceives but a single star. These are well known facts which justify us in saying that in the spider's eye two rods must be stimulated by light rays in order that the image of two points should be produced. But here the analogy ends. How strong the effect produced and whether the corresponding image in the brain is of the same kind as in man, we cannot know. We cannot know whether a spider sees colors as we do, whether green appears to it in the same way as it does to us, although we do know from the experiments of

the Peckhams that spiders are able to discriminate between colors. Neither can we know whether gradations of light and shade are the same for the spider as for us nor how great the amplitude of the light wave, which would be required to produce the same effects as in us.

Nevertheless we do know that an image is formed in each spider eye; we do know that the four pairs of images differ from each other in size; we do know that the more rods covered by the image the more detail can be perceived by the eye. We may thus work on a fairly safe basis.

Let us first examine the images as they appear under the microscope. When a black square is placed under the microscope so that the axis of the eye is perpendicular to the center of the square, it is not possible to detect any spherical aberration by common means. But if we place the eye so that the black square lies considerably to one side of the eye-axis, the aberration at once becomes appreciable. For the accompanying drawing (Fig. 11) an eye of *Lycosa* was put so that it was a little outside the center of the microscopic field and the axis of the eye formed a more or less sharp angle with the slide, while the black square, each side of which was 5 cm. long but having one side prolonged into a straight black line, the whole made with chinese ink on a plate of milk-white glass, was absolutely parallel to the slide. The Zeiss drawing table was carefully arranged beforehand so that a small square placed under the microscope and drawn with the aid of the Abbe apparatus, gave on paper a perfect square. Then drawings of the image in the spider's eye of the black square were made from different positions of the eye, obtained by revolving the table of the microscope on its axis. It is clear from the drawing that in this case the base and one side of the square are especially distorted. Is the spider's vision then distorted of all things that lie out of the axis of the eye? It is impossible to know but I believe that the spider forms a true idea of objects, first because the distortion in each eye of a pair is in the opposite sense to that in the other eye of the same pair, thus offsetting it, and second, because the retina is not a plane but is of very complicated form differing in different eyes and for different species. Generally speaking we may compare

the retina to a boat or canoe in some eyes and to a deep bag in others. This may be ascertained not only from sections. It is sometimes possible to remove the entire retina intact from the vitreous body whose proximal end fills it out and to examine it in toto under the microscope. The vitreous body also varies in shape in different eyes and is usually considerably elongated in the direction of the eye-axis in those eyes which form the largest images. The vitreous body is especially long in the anterior middle eyes of jumping spiders, *Phidippus tripunctatus*, for example, and is shaped something like a long cone with its base which is concave, toward the lens, its axis being at the same time the axis of a conical hole which extends through its entire length. This hole also is largest at the lens and much smaller at the retina and may be seen in sagittal and cross-sections. It is also sometimes visible in young spiderlings of the jumpers, where it presents a likeness to a pupilla. In life it is probably filled out with a liquid.

Roughly speaking the size of the image is in direct proportion to the size of the eye but measurements show discrepancies which must be due to differences in the curvatures of the lenses. The following table illustrates this.

TABLE IX

Ratios of diameters of eyes and of images to the diameter of the AME and its image. Compare with Fig. 10

		AME	ASE	PME	PSE
<i>Phidippus tripunctatus</i>	eye	1	0.595	0.166	0.524
	image	1	0.4285	0.0800	0.3143
<i>Heteropoda venatoria</i>	eye	1	1.66	1.22	1.55
	image	1	1.75	1.50	2.00
<i>Lycosa nidicola</i>	eye	1	0.77	1.90	1.50
	image	1	0.8	2.266	1.8666

This table shows that while there is a dependence of the size of the image upon the size of the eye, this dependence is not of such a kind as to allow of definite conclusions in regard to the smallest angle of vision from measurements of the eyes and

images in one individual and of the elements of the retina in another. I have therefore applied two other methods. The one consists of choosing two individuals of the same species, having eyes of the same diameter and preparing one for the study of the image, the other for sections through the retina. This is possible and yields good results when one has a large quantity of living spiders. By far the better method, the one which I now use exclusively and upon which the conclusions I have reached in this research are based, consists in preparing the spider in such a way as to obtain from the same individual at the same time the lenses intact for the study of the size of the image and the retina for sectioning. This is perfectly feasible even in young spiderlings although it requires not a little patience and experience. I proceed in the following manner: a spider is killed by a cut across the middle of the cephalothorax so as to allow the fixing liquid to penetrate as rapidly as possible. Thus far I have obtained the best results for the purpose with the picro-formalin mixture of Bouin and my sublimate modification of the Gilson liquid. The cephalothorax is allowed to remain for six hours in the fixing liquid and is then transferred in the usual manner to 70 per cent alcohol. The sternum and the mouth parts are now carefully removed with a fine pair of scissors. Then the cephalothorax is placed in a low dish containing alcohol and held by the side with forceps while a thin and flexible spatula is carefully introduced between hypoderm and chitin. Pushing the spatula slowly forward it is possible to separate the entire chitinous part of the cephalothorax from the underlying hypoderm with all its muscles and organs. The vitreous bodies of the eyes remain with the retinas attached by the optic nerves. These are now separated from the remaining organs, carefully noted to exclude error and placed in separate dishes in paraffin in the usual manner. They are then sectioned with a microtome, either parallel to the eye-axis or perpendicular to it. The sections are depigmented in chlorine gas dissolved in 70 per cent alcohol and after washing stained in Heidenhein's hæmatoxylin. The eye-lenses of the same individual, which have been removed together with the tergum, in the manner described, are now placed in water and carefully cleaned

with the brush on both sides. They are then cut separately out of the cephalothorax and suspended, each first on a drop of water and then on one of glycerin-albumen and the image which each forms of a 10 cm. square at a distance of 10 cm. is measured with the aid of the ocular micrometer. These measurements may then be directly compared with those obtained from the sections through the retina. In measuring the distance between the rods I use the highest power only and count how many microns are occupied by ten rods. This is essential since the distances between the rods are apt to vary a little. Besides, the

TABLE X

An adult Lycosa nidicola, small individual. Average distance between the centers of the two rods in micromillimeters

	In the center	Toward the periphery	At the periphery
AME.....	8	12	15
ASE.....	6	10	12
PME.....	8	12	15
PSE.....	9	16	21

rods are larger and farther apart at the periphery, gradually becoming smaller and lying closer together toward the center. I do not give a drawing of this but Table X affords sufficient demonstration.

It seems to me, in view of the strange shape of the retina, that we may form an idea of the acuity of vision in the spider's eye only from images that cover the central part of the retina alone. In order to diminish the possible error, I measured the image of 10 cm. as mentioned, but divided the result by ten so as to find the size of the image of 1 cm. from 10 cm. distance.

In this way we obtain the following table:

TABLE XI

Phidippus tripunctatus

		AME	ASE	PME	PSE
Size of the image of 1 cm. at 10 cm. distance. Eye suspended on glycerin-albumen.....	μ	115	49	10	36
Distances between the centers of rods in the center of the retina.....	μ	3	6	4	5

On dividing the size of the image by the distance between the rods, we find that the image of a line 1 cm. long (measured in an eye suspended on a glycerin-albumen drop) occupies respectively 38 rods in AME, 8 rods in ASE, 2 rods in the PME and 7 rods in the PSE. One square centimeter at a distance of 10 cm. gives an image that occupies $38^2 = 1444$ rods in the AME, $8^2 = 64$ rods in the ASE, $2^2 = 4$ rods in the PME and $7^2 = 49$ rods in PSE. With other words the front middle eyes in *Phidippus* are by far the most sensitive, then come the front side eyes, then the eyes of the third row and last, the posterior middle eyes.

In *Lycosa nidicola* the difference in the sizes of the eyes is less than in *Phidippus* and consequently the difference in sensitiveness or power of distinction is less. I examined several specimens. Since in the one used for the measurements which I give here the image of 10 cm. at 10 cm. distance did not coincide with the divisions on the scale on my ocular micrometer, it was necessary, in order to avoid error, to arrange the experiment somewhat differently. The bristol board containing the centimeter scale was brought nearer to or farther from the eye until a number of centimeters not fewer than five, came to occupy a certain number of divisions on the scale. Thus I found that at a distance of 37 cm. the image in the PME of 6 cm. occupies exactly 5 divisions of the micrometer scale. Each division being equal to 0.0164 mm., it follows that the image of 1 cm. would occupy $0.0164 \times \frac{5}{6} = 0.0136$ mm. Since the distance between the centers of the rods in the center of the retina in this specimen equals 13μ , it follows that 1 sq. cm. placed at a distance of 37 cm. from the PME will form an image occupying 4 rods (2×2). The image of 7 cm. placed at a distance of 36 cm. from the posterior side eye, occupies 5 divisions of the scale or the image of 1 sq. cm. equals 0.0117^2 mm. and occupies 4 rods, the distance between the centers of these being 12μ ; but this image does not occupy the rods completely. The image of 9 cm. placed at a distance of 30 cm. from the AME, occupies five divisions of the scale or the image of 1 sq. cm. at 30 cm. distance equals 0.009^2 mm. The distance between the centers of the rods in this eye is 9μ , *i. e.*, the image occupies 4 rods (2×2).

The image of 14 cm. placed at a distance of 27.5 cm. from the ASE corresponds to five divisions of the scale or the image of 1 sq. cm. = 0.006^2 mm. The distance between the centers of the rods in this eye being equal to 6μ , the image will occupy 4 rods (2×2). We have then in *Lycosa* also, four pairs of eyes of different sensitiveness in the following sequence from more to less sensitiveness: PME, PSE, AME, ASE.

Unfortunately I have no material of *Heteropoda venatoria* fixed in the manner described, but from comparison with *Lycosa* and *Phidippus* we should expect to find that in this spider the most sensitive eyes are the posterior side eyes followed by the ASE, PME and AME.

In order to form a clear conception of the acuity of vision of the spider's eye, we shall compare the anterior middle eye of *Phidippus* and the posterior middle eye of *Lycosa*, the two most sensitive eyes, with the average human eye. The distance between the centers of the cones in the yellow spot of a human retina is, according to measurements made by various scientists, somewhere between 4 and 5μ . One square centimeter placed at a distance of 30 cm. occupies somewhere in the neighborhood of $114^2 = 12996$ cones in the human eye, $13^2 = 169$ rods in the AME of *Phidippus* and only $2^2 = 4$ rods in the PME of *Lycosa* (Fig. 12). The difference becomes still more tangible if we find the distance at which 1 sq. cm. will fall on one rod in the spider's eye, with other words, if we ascertain the smallest angle or limit of vision. This may be done either by direct calculation from the data obtained or by measuring the image of a centimeter scale that is gradually moved away from the eye until the image becomes smaller than the distance between the rods. In this way I found that the minimal angle of vision, using glycerin-ablumen for suspension of the eye, equals $8'$ for the AME of *Phidippus* and about $60'$ for the PME of *Lycosa*, while from observation of the double stars it is known that the smallest angle of vision in man equals $1'$. Thus a creeping insect about 1 sq. cm. in size would be perfectly visible to the human eye, even perhaps to the extent of recognizing the species, at a distance of about 3 m., while it would appear merely as an indefinite, tiny moving speck to *Phidippus* and would be entirely beyond the range of vision of *Lycosa*.

These figures certainly show the great superiority of the human eye over even the best eye of spiders. This is especially manifest from the fact that even if we use a drop of Canada balsam with its 1.535 refraction-coefficient, for the suspension of the eye we still find the limit of vision for the AME of *Phidippus* to be 6' and for the PME of *Lycosa* to be 45'. At the same time we must not forget that the minimal angle of vision in the spiders is in inverse proportion to the maximal angle and that with the use of the Canada balsam the measurements would show a reduction in the fields of vision from 40° in the AME of *Phidippus* to about only 30°. On the other hand the measurements made with the use of glycerin-albumen show that a female jumping spider placed at a distance of 30 cm. from its mate, would still give a sharp image covering a sufficient number of rods in the eye of the male to be recognized by him—a result which stands in conformity to the experiments of the Peckhams. Perhaps this relation between field of vision and acuity of vision was responsible for the fact that the eyes of spiders did not attain the acuity of vision of the human eye.

We have already seen that the smaller the diameter of a spider's eye, the smaller the image it forms. We have also seen that this does not apply with exactness to different eyes of the same eye-group but measurements show that for the same eyes in spiders at different ages the ratio holds good as far as it is possible to ascertain with the methods used. The younger the spider the smaller the images in its eyes and the question arises: are the eyes of spiderlings as sensitive as those of adults or does the power of distinction grow with increasing age? Spiderlings that are ready to leave the mother can be prepared as I prepared the adult spiders and image and retina may be studied in the very same eye. But this cannot be done with spiderlings taken out of the cocoon so we may base our conclusions on the admission only, that the ratio between diameter of eye and image holds good for these spiderlings also. This is indeed probable since I have proved that such a ratio exists in all ages beginning with the oldest spiderlings. In every case I examined for comparison purposely the mother spider with her young ones, to avoid errors

arising from possible variations hereditarily fixed through several generations. I scarcely need to add that several mothers and many young ones of the same species were examined.

The distance between the centers of the rods in all eyes of the spiderling is smaller than the corresponding distance in the eyes of the adult. Thus in the PME of an adult *Lycosa nidicola* the distance between the rods in the center of the retina was found to be 8μ while the corresponding distance in the PME of the young is only 2.5μ . The diameters of these eyes are respectively 689μ and 148μ . Or the proportion between the diameters is $\frac{689}{148} = 4.65$, while the proportion between the rods is only $= 3.2$. With other words, the image of the same object will cover a smaller number of rods in the eye of the spiderling than in that of the adult, say $6 \times 6 = 36$ rods in the former and $9 \times 9 = 81$ rods in the latter. The same proportion holds for all eyes of *Lycosa* but when I compared the images in the eyes of this adult female with those of her young ones that had been allowed to remain on her back for several days longer and were beginning to leave her, I found that this ratio already falls to $4 : 3.5$ and becomes $1 : 1$ after the next moulting. *Pardosa nigropalpis* showed the same conditions and we should expect the same to be true of other spiders, too.

CONCLUSIONS

In drawing conclusions from the facts described, I am well aware that the methods employed in this research are far from perfect. It is possible that the angles of the eye-axes will with time be measured more exactly, that the figures given for the maximal angles of vision will be a little altered in the one or the other sense, that the minimal angle or limit of vision will be found to be one minute larger or smaller, but in one respect the method employed gives facts that cannot be disputed; I mean that the error, whether large or small, is the same for the entire series of the same kind, so that the relation or ratio will remain unchanged. We cannot be sure that the maximum angle of vision in the AME of *Phidippus* is exactly 40° or that its smallest angle of vision is precisely $8'$, but we may be sure that the larger eyes of an individual

are more sensitive than the smaller ones of the same individual; we may be sure that the eyes of the young spiderling are less sensitive than the same eyes in the adult; we may be sure of the proportional sensitiveness of the eyes; we may be sure that changes take place in the directions of the eye-axes and of the direction of these changes as well as of the time when they take place; and all this goes to show unmistakably the existence of a perfect balance between function and structure in the eyes as well as a remarkable degree and an extraordinary rapidity of adaptation. Thus when the spiderling first begins to lead an independent life, it finds in its eyes an organ already sufficiently perfect to be relied upon in the struggle for existence.

The changes in the angles of the eye-axes may well be looked upon as an adaptation. I have also tried to show that the slower growth of the eye-group as compared with that of the cephalothorax, is to be considered advantageous. The way in which these changes came about is also well understandable but when we ask ourselves in what way in the phylogeny was the increasing acuity of vision accomplished, we have to depend for the answer upon theoretical considerations. We know that in the individual this increasing acuity of vision is brought about as a consequence of the slower growth of the retina elements compared with that of the lens. Is it then a retarding influence of which nature took advantage in order to accomplish its own end, that was responsible or was it a possible capacity on the part of the lens to grow more rapidly than the retina? Or were perhaps both factors at work? And at what time in the phylogenetic development did the eyes differentiate into smaller and larger and why did they not all reach the same degree of perfection? What was it that arrested the progress toward perfection or is further perfection possible and still in process of attainment? All these are questions before which we stand without answer as before a door behind which treasures lie concealed. To find the key to that door would mean to understand adaptation. For a long time science remained satisfied with the explanation afforded by the principle of selection and the attempt was made to apply this principle to all the phenomena of organized life. But the very ease with which it answers

the most intricate questions proves to be its weak point and it no longer suffices. How indeed, for example, can we accept the explanation given for the existence of the black shield at the base of the bill of the white swan, as a protection against the blinding light reflected from the surface of the water, when another water bird of the same fauna—*Fulica atra*—has black plumage and a snow white shield? The difficulty is gotten round by explaining the latter case from the point of view of sexual selection or in some other way. The number of similar cases could be multiplied indefinitely. It is clear that if we desire to hold to the principle it will be necessary to show step by step the progress of adaptation in indisputable cases. Of this nature are variations of which the animal itself can immediately make use to its own advantage over its rivals. While the origin of the variations themselves is a field for other research I hope to have shown in the present study of the sense of sight in spiders, the probable course of adaptation in the survival of the fittest.

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EXPLANATION OF THE DIAGRAMS

In the Figs. 1, 2, 3, 6 and 8 the axes of the eyes are represented by dotted lines, the maximal angles of vision and the plane of symmetry by common black lines. In the Figs. 4, 5 and 7 the heavy black line represents the horizontal plane for the upper part of the figures and the plane of symmetry for the lower part of the same figures. The axes of the eyes and the maximal angles of vision in these figures are represented by common black lines for the mature spider and by heavy dotted lines for the young spiderling.

PLATE I

Fig. 1. *Phidippus tripunctatus*, adult female. Projection of the eye-group on the horizontal plane showing the axes of the eyes and the maximal angle of vision for each eye.

Fig. 2. *Lycosa nidicola*, adult female. Same projection as in the preceding figure.

Fig. 1

Fig. 2

PLATE II

Fig. 3. *Heteropoda venatoria*, adult female. Same projection as in the two preceding figures.

Fig. 4. *Phidippus tripunctatus*, same adult female as in Fig. 1. The upper part of the figure shows the projection of the eye-group on the plane of symmetry while the lower part represents the projection of the left half of the eye-group on the horizontal plane. In the same figure the axes and the maximal angles of vision of the spiderling are indicated by heavy dotted lines and the direction in which the change from the spiderling to the adult takes place is shown by the arrows.

Fig. 3

Fig. 4

PLATE III

Fig. 5. *Lycosa nidicola*, same individual as in Fig. 2. Same projections as in Fig. 4.

Fig. 6. *Phidippus tripunctatus*, same individual as in Figs. 1 and 4. Projection of the eye-group on the transverse or vertical plane. The heavy line HH' represents the horizontal plane.

PLATE IV

- Fig. 7. *Heteropoda venatoria*, same individual as in Fig. 3. Same projections as in Fig. 4.
Fig. 8. *Heteropoda venatoria*, same individual. Same projection as in Fig. 6.

Fig. 7

Fig. 8

PLATE V

Fig. 9. *Lycosa nidicola*, same individual as in Figs. 2 and 5. Projection on the transverse plane. The arrow indicates the direction in which the change in the position of the axis of the posterior side eyes took place. The axes of the eyes in the mature spider are represented by light interrupted lines, the maximal angles of vision by common straight lines, while the axes and the maximal angles of vision for the spiderling are represented by heavy dotted lines.

Fig. 10. This figure shows the respective size of the image on the retina formed by a black square placed at the same distance from each eye in the three species of hunting spiders. If compared with Figs. 1, 2 and 3 this figure shows also that the larger eyes form the larger images.

Fig. 9

Fig. 10.	AME	ASE	PME	PSE
<i>Phidippus</i> <i>triguttatus</i> (AME = 1.) AME - 1 ASE - 0.985 PME - 0.8 PSE - 0.343				
<i>Lycosa</i> <i>nidicola</i> (AME = 0.771) AME - 1 ASE - 0.8 PME - 8.247 PSE - 1.847				
<i>Heteropoda</i> <i>venatoria</i> (AME = 0.84) AME - 1 ASE - 1.75 PME - 1.50 PSE - 2.00				

PLATE VI

Fig. 11. Aberration in the spider's eye. The figure represents the images formed by an eye from a perfect square which was placed in eight different places near the periphery of the field of vision. When a square is placed in the eye-axis its image is free from aberration.

Fig. 12. This figure represents the comparative acuity of vision in man, and in two hunting spiders. The posterior middle eyes possess the greatest acuity of vision in *Lycosa nidicola*, and the anterior middle eyes possess the greatest acuity of vision in *Phidippus tripunctatus*. The black discs represent a row of rods in the retina of *Phidippus* and *Lycosa*, and of cones in the yellow spot of man, all equally magnified. The heavy black lines represent the length of the images formed by the same object placed at the same distance from each of the three eyes. In the human eye this image will occupy 57 cones, in the anterior middle eye of *Phidippus* nearly seven rods, while in the posterior middle eye of *Lycosa* the image is only a little longer than the diameter of a rod.