RHYTHMIC SUSCEPTIBILITY CHANGES IN THE CLEAVING *ARBACIA* EGG

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(*Received 3rd September* 1928.)

(With Seven Text-figures.)

THE fertilisation reaction initiates a remarkable series of events in the egg. Lyon (1) first showed that *Arbacia* eggs were especially sensitive to heat just before cleavage and most resistant 10–20 minutes after fertilisation. However, the susceptible period for cold seemed to be quite different from that for heat, being almost exactly the same as the resistant period for heat. He (2) further found that eggs were especially susceptible to *M*/100–*M*/200 KCN about 10–15 minutes after fertilisation and that the resistance gradually rose as the time for the first cleavage approached.

Spaulding (3) found that great susceptibility to ether occurred immediately prior to segmentation.

Mathews (4) re-examined Lyon's work on the action of KCN and found that the period of greatest susceptibility coincides with the development of the asters; and the period of greatest immunity coincides with the retrogression of the asters and the development of the nucleus.

In 1909 Lyon (5) demonstrated that following fertilisation there is an increase in the ability of the *Arbacia* egg to catalyse H_2O_2. This he interpreted as an expression of the greater permeability of the eggs to the peroxide after fertilisation. In the next year Harvey (6) showed that neutral red stains fertilised eggs more rapidly than unfertilised, and also that 2–5 minutes after fertilisation there seemed to be an increase in permeability to NaOH. Lyon and Shackell (7) found that artificial activation increased dye intake, and they noted that loss of pigment occurred after fertilisation.

Moore (8) states that resistance to hypertonic sea-water is least immediately before and during cleavage; that maximal resistance is shown 35–45 minutes after fertilisation and just after each division.

Baldwin (9) found that with certain aliphatic alcohols the resistance of the *Arbacia* egg is least after fertilisation, rises to a peak of resistance shortly before cleavage, followed by a rather sharp increase in susceptibility during division.

McClendon (10) demonstrated an increase in conductivity of the eggs after fertilisation, but Gray (11) made more accurate measurements, finding that the

entrance of the sperm into the egg causes an increase in conductivity which attains a maximum within 10 minutes of adding the sperm.

Warburg (12) investigated the respiratory exchange in *Strongylocentrotus* eggs and found that 10 minutes after fertilisation there is a sixfold increase in O_2 consumption over that of the unfertilised egg. Shearer (13) discusses the evidence which seems to point fairly conclusively to the cortical layer of the egg and egg membrane as being the controlling factor in the oxidation processes of the egg. He further suggests that upon fertilisation there is an immediate increase in the glutathione content of the egg. He has shown that within a minute after the addition of sperm to the eggs the O_2 consumption greatly increases and the CO_2 output parallels this increase. The fusion of the male and female pronuclei in the latter phases of fertilisation is correlated with no additional increase in O_2 consumption. Rogers and Cole (14) measured the rate of heat production after fertilisation and found that at the instant of fertilisation the heat produced is ten to twelve times that of the unfertilised egg. It then decreases constantly for 20 minutes when it reaches about 65 per cent. of the value at fertilisation and then remains nearly constant until the first cleavage.

R. S. Lillie, in an important series of papers (15, 16, 17), has shown that following fertilisation the rate of entrance of water into fertilised *Arbacia* eggs in hypotonic sea-water is approximately four times that into unfertilised eggs. The artificial formation of fertilisation membranes (by butyric acid) is followed by a similar marked increase of permeability to water. He further found that the osmotic properties of unfertilised and normally fertilised eggs remain approximately constant during the first eight or more minutes of immersion in dilute sea-water. The essential constancy in the rate of entrance of water (relative to the existing gradient of osmotic pressure) into fertilised and unfertilised eggs, during a period in which the water content of the egg is almost doubled, shows that the difference between the two kinds of eggs is not due to a difference in the condition of the internal protoplasm, but simply to a difference in the resistance of the membrane to the passage of water. Fertilised eggs shrink rapidly, whereas unfertilised shrink slowly in the same hypertonic sea-water or van 't Hoff solution. During the first few minutes after insemination the eggs, when placed in hypertonic sea-water, shrink slowly like the unfertilised eggs. No noticeable increase in permeability was found until 5–6 minutes had elapsed, and the change reached its final equilibrium in about 20 minutes (20–22° C.).

In 1916 Lillie (16) demonstrated that in moderately hypotonic sea-water about the time of formation of the cleavage furrow a marked decline takes place in the resistance of the egg to hypotony, and cytolysis is then rapid and complete.

Just (19) has shown the same type of phenomenon to occur in the *Echinarachinus* egg, and has emphasized the fact that during the period of susceptibility before cleavage the egg in dilute sea-water bursts over the spindle pole indicating a drop in the tensile strength of the hyaline plasma layer. At this time the hyaline plasma layer is moving away from the polar area to the equator. As Just says, the egg is being denuded of hyaline plasma layer in the polar areas. He concluded that