Haemolymph protein concentration varied cyclically during ovarian development, being high during yolk deposition. Electrophoresis suggested that a particular protein fraction was involved. Ovariectomy resulted in a dramatic increase in haemolymph protein concentration, and after electrocautery of the cerebral neurosecretory cells, it remained low. (The SCI® indicates that this paper has been cited in over 140 publications since 1962.)

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This research formed a part of my PhD work in the Department of Zoology at the University of Sheffield. My supervisor, Ken Highnam, had spent the two years before I started work looking at the activity of cerebral neurosecretory cells in relation to egg development in the desert locust, mainly from a histological viewpoint.1 In 1960, I started a PhD with the intention of extending this work into a more physiological area. The earlier work of Ellen Thomsen had suggested that protein metabolism might be central to egg development,2 and so I decided to examine the concentrations of amino acids and proteins in the haemolymph. In doing this, I was very much on my own since there was little expertise on measuring haemolymph metabolites and mammalian techniques had to be adapted for insect work. Fortunately, it proved possible to measure total protein and amino acid concentrations in 5μl haemolymph samples, and so individual insects could be sampled rather than using pooled samples. I also used a simple paper electrophoresis technique to separate haemolymph proteins. This was a technique I learned as an undergraduate student during a vacation project on sheep and cattle haemoglobins at the Animal Breeding and Research Organisation in Edinburgh. Perhaps the difficulties of taking blood samples from the jugular veins of bulls edged me toward the safer confines of insect physiology.

The measurements revealed cyclical changes in normal development, with a high haemolymph protein concentration during ovarian development. When the cerebral neurosecretory cells were removed by electrocautery, resulting in a failure of ovarian development, the haemolymph protein concentration remained low. After ovariectomy, the haemolymph protein concentration increased enormously. These results suggested that there was a hormone-directed synthesis of yolk protein occurring outside the ovaries and that yolk protein was transported to the ovaries in the haemolymph. The electrophoretic results suggested that a single protein fraction was involved.

I believe this paper has been frequently cited as one of the first pieces of research to suggest a hormone-directed synthesis of a female-specific protein in insects. Subsequent research by a variety of workers showed that the hormone involved was not a neurosecretory hormone but the juvenile hormone secreted by the corpora allata. The neurosecretory cells control the activity of the corpora allata. This initial work was followed by rapid advances in the area, particularly by Franz Engelmann in Los Angeles, to whom we now owe much of our understanding of the control of yolk protein synthesis,3 and in whose laboratory I spent a happy and productive year in 1969.

I received my PhD in 1963 and my thesis was awarded a certificate of commendation by the Zoological Society of London for original contributions to zoology.