Electrical activity of the oviduct of the laying hen during egg transport

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Summary. Electrical activity in the oviduct wall of the laying hen was studied. The frequency of spike discharges increased in the magnum and isthmus when the egg approached close to the recording sites. The frequency of discharge remained high in the magnum until the egg had passed, but it decreased in the isthmus during the stay of the egg. In the uterus, a relatively high activity was found immediately after oviposition and this was followed by low activity for about 5 h. Electrical activity began to increase again and reached maximum 1–2 h after the egg entered the uterus. The direction of propagation of electrical activity in the magnum was determined by using two electrodes and was towards the ovary or towards the uterus for periods of several minutes.

Introduction

The major functions of the avian oviduct are egg formation and egg transport. However, as Gilbert (1971) has stated, little is known of the mechanisms which move the developing egg along the oviduct although the amount of albumen, the formation of the shell membrane and the deposition of egg shell may depend on this movement. Many previous studies on oviductal motility are mainly related to the motility of isolated segments *in vitro* (Sykes, 1955; Prasad, Davis & Dale, 1964; Chen & Hawes, 1970; Verma, Prasad & Slaughter, 1976; Verma, Prasad & Yancey, 1977). Rzasz & Ewy (1971), Crossley, Ayuy & Ferrando (1975) and Verma *et al.* (1976, 1977) have measured the intraluminal pressure in the oviduct *in vivo* to investigate oviductal responses to chemical agents. The hens in some of these studies were anaesthetized and it is known that anaesthetic drugs such as sodium pentobarbitone and ethyl-carbamate prematurely expel the egg present in the uterus (Verma *et al.*, 1976). These drugs may, therefore, also alter uterine activity when there is no egg in the oviduct. In addition, the recording balloon technique used in the previous studies may have interfered with the spontaneous activity of the oviduct.

The present study was designed to record spontaneous electrical activity of the oviduct of the laying hen by using chronically implanted electrodes as the first step toward more precise understanding of the changes in motility of the magnum, isthmus and uterus (shell gland) during egg transport.

Materials and Methods

Eighteen cross-bred laying hens (Goto 360), 8–12 months old and weighing 2.2–2.6 kg, were maintained in individual cages. The lighting regimen was 14 h light/24 h and food and water were always available. The oviposition time was recorded daily by a mercury switch–digital clock assembly. The birds were anaesthetized with an i.v. injection of sodium pentobarbitone (25 mg/kg) for exposure of the magnum and isthmus by a left laparotomy and of the uterus by an incision in the dorsal caudal area of the back between the ischiadic bones. The tips of electrodes were inserted into the oviductal or uterine wall and secured to the surface of each segment by sutures. Lead wires passed subcutaneously to the back of the bird and exteriorized there through a puncture of the skin. The small incisions were closed by sutures. All the birds resumed egg-laying with relatively regular clutches of more than 3 eggs

about 1 week after surgery. Recordings of the electrical activity of the oviduct were made after the oviposition of an egg in the middle of a clutch sequence. The legs of the bird were tied and the bird was placed laterally in a dark room to reduce body movements which cause artefacts in the recordings. The electrical activity was recorded by using a 2-channel polygraph with low frequency filtering and 2–4 recordings were made from each segment of 4–6 birds.

The bipolar electrodes were made of insulated platinum–iridium except at the tip. The inter-tip distance was 1.5 mm and the diameter of each electrode tip was about 0.1 mm. The exact locations of the electrodes in each segment of the oviduct were confirmed after the experiment. Three areas were studied: the middle region of the magnum, the middle region of the isthmus, and the dorsal caudal uterus.

In the second part of the study, the direction of propagation of electrical activity was studied in the middle region of the magnum by using two electrodes with a short inter-electrode distance (12 mm). Two birds were used and 3 recordings of 5 h each were made for each bird.

Ovulation was confirmed by the oviposition which occurred on the day following the recording. Ovulation normally occurs about 30–60 min after the oviposition of the preceding egg in the clutch and the ovulated egg moves at a relatively constant rate in the various segments of the oviduct in the chicken which lays 3 or more eggs successively (Warren & Scott, 1935; Meleik, Morris & Jennings, 1973). Therefore, the location of the egg in the oviduct was estimated by the time of oviposition and the interval from one oviposition to the next.

Results

Activity in relation to passage of the egg

Although hens either laid no egg or laid soft-shelled eggs within 1 week after electrode implantation, they later laid 3 or more hard-shelled eggs successively in a clutch, as they had done before operation. In each segment of the oviduct, definite action potentials were recorded as shown in Text-fig. 1. The amplitude and frequency of the potentials varied considerably during the course of egg transport: the largest amplitude and frequency of spike discharge were approximately 500 μ V and 26/min, respectively. The number of spike discharges with more than 30 μ V of amplitude was counted for 10-min periods at 30-min intervals. The frequency was then expressed as a percentage of the highest frequency found during the recording period for each segment of each bird.

Text-fig. 1. Action potentials of (a) the magnum, (b) the isthmus and (c) the uterus of the hen's oviduct 11 h after oviposition. The electrical activity of the magnum and isthmus was simultaneously recorded from one bird but that of the uterus was from another bird.

Magnum. Text-figure 2 shows one of the patterns of electrical activity recorded from the magnum during the period between 20 min and 5 h after oviposition. Changes in the frequency of electrical activity are shown in Table 1. Potentials with relatively regular intervals were seen 1½ h after oviposition but when the egg approached the electrode, about 2 h after oviposition, the frequency of spike discharges markedly increased. The egg was located at the recording site 2 h 20 min after oviposition

Table 1. Frequency (mean $\pm$ s.e.m., no. of birds in parentheses) of electrical activity of the hen magnum and isthmus after oviposition

Segment	Period	Time after oviposition (h)					
		0	1	2	3	4	5
Magnum	First		43.6 ± 7.4 (4)	$74.5 \pm 13.4^*$ (4)	$79.8 \pm 10.1^*$ (4)	30.5 ± 2.4 (4)	25.6 ± 6.1 (4)
	Second	34.6 ± 5.5 (4)	$56.3 \pm 13.6^\dagger$ (4)	$82.4 \pm 6.7^*$ (4)	42.8 ± 7.8 (4)	30.7 ± 5.3 (4)	29.9 ± 8.1 (4)
Isthmus	First			39.2 ± 4.2 (6)	44.7 ± 3.9 (6)	$74.1 \pm 8.3^\dagger$ (6)	$91.4 \pm 3.6^\dagger$ (6)
	Second			44.3 ± 4.5 (6)	44.4 ± 2.7 (6)	36.2 ± 4.9 (6)	$90.3 \pm 5.1^\dagger$ (6)

Frequency is expressed as a % of the highest frequency found during the recording period (10 min out of the first and second 30 min of each hour) in each bird.

* These values significantly different from the other values recorded in the magnum ($P < 0.01$, Student's t test) except that marked † .

† These values significantly different from the other values recorded in the isthmus ($P < 0.01$, Student's t test).

Text-fig. 2. Electrical activity of the magnum after oviposition. The interval from one oviposition to the next was 25 h and 54 min.

and the amplitude of the potentials was decreased. At 2½–3 h after oviposition, the frequency of spike discharges reached maximum. These potentials were grouped but the number of spikes in each group had decreased. Then, the frequency rapidly decreased 3½ h after oviposition and remained at low levels thereafter. Four of the 6 birds examined displayed a pattern of electrical activity identical to that described above but the pattern in the other 2 birds was one in which spike discharge frequency varied irregularly throughout the recording periods and was perhaps attributable, at least in part, to the position of the recording electrodes in the long magnum.

Isthmus. It was assumed that the egg was located at the recording site about 4½ h after oviposition, and recordings were made between 2 and 6 h after oviposition. The changes in the electrical activity of the isthmus are shown in Text-fig. 3 and Table 1. There were usually 3–5 spikes/min until 3½ h after oviposition: the spike discharges then increased and were high between 4 and 4½ h. During the next 30 min electrical activity was low and this relatively quiescent period was in accordance with the presence of the egg at the recording site. Subsequently, the activity increased progressively and the high-amplitude and high-frequency potentials continued for about 1 h.

Text-fig. 3. Electrical activity of the isthmus after oviposition. The interval between ovipositions was 25 h 39 min.

Uterus (shell gland). Recordings were made continuously for 9 h after oviposition in 4 of the 6 birds (Text-fig. 4) and the frequency changes are shown in Table 2. It was estimated that the ovulated egg entered the uterus between 6 and 7 h after oviposition. High-frequency activity was observable immediately after oviposition and lasted for about 30 min. This was followed by quiescent activity for approximately 5 h. There was a marked change to discharges with high amplitude and high frequency between 7 and 9 h after oviposition. In 3 of the 6 birds, other recordings were made about 13 and 24 h after oviposition. The high electrical activity was continuously observed at both times. The next oviposition occurred between 25 h 49 min and 27 h 24 min after the preceding oviposition.

Text-fig. 4. Electrical activity of the uterus after oviposition. The interval between ovipositions was 25 h 49 min. The recordings marked 'x' are immediate continuations from those above.

Table 2. Frequency (mean $\pm$ s.e.m., no. of birds in parentheses) of electrical activity of the hen uterus after oviposition

Period	Time after oviposition (h)							
	0	1	2	5	6	7	8	9
First	47.9 $\pm$ 13.1 (6)	9.8 $\pm$ 4.4* (6)	9.7 $\pm$ 3.7* (6)	12.8 $\pm$ 4.6† (6)	19.8 $\pm$ 4.8† (6)	44.1 $\pm$ 4.3 (6)	74.4 $\pm$ 5.5 (6)	88.9 $\pm$ 2.1 (5)
Second	20.1 $\pm$ 6.6* (6)	7.5 $\pm$ 2.4* (6)	6.1 $\pm$ 3.0* (6)	13.8 $\pm$ 4.6† (5)	32.1 $\pm$ 5.0 (6)	67.3 $\pm$ 6.6 (6)	89.1 $\pm$ 4.4 (5)	93.5 $\pm$ 3.8 (5)

Frequency is expressed as a % of the highest frequency found during the recording period (10 min out of the first and second 30 min of each hour) in each bird. It is estimated that the egg enters the uterus 6½ h after oviposition.

* These values significantly different from that in the first period at 0 h ($P < 0.01$, Student's t test).

† These values significantly different from all other values except those marked by * ($P < 0.01$, Student's t test).

Text-fig. 5. An original recording of electrical activity by electrode pairs on the cranial part (a) and the caudal part (b) of the magnum. The times before (–) and after (+) oviposition are indicated. Arrows in the recordings of A and B at the faster paper speed indicate the direction of propagation spreading cranially or caudally, respectively. Note that there is a change of direction in the middle of recording C and predominantly cranial propagations are present in D.

Table 3. Directions of propagation of electrical activity in the magnum of 2 hens during 10-min recording periods at the times shown

Hen	Time after oviposition (h)			
	0	1	3	4
1	A A A P P P	P P P — — —	A A A P A P	— — —
1	— — P P	P P P P P P	A A A A A A	A A A A A A
2	A A A	A A P P P P	— — A A A A	A A A A — —
1	— —	— A P P P P	A A A A A A	A A A A A A
2	A A	A P A P P P	P P — — — P	— — P P P P
2	— —	A A A A P P	P — A P P A	A P P P P P

The occurrence of more than 70 % of the spike discharges propagating in the cranial direction is denoted by A and in the caudal direction by P. — indicates a period when these conditions were not met. Each recording was made on a different day.

Propagation of electrical activity

The criterion for the propagation of electrical activity was the synchronous appearance of spike discharges recorded from both the cranial and caudal parts of the middle region of the magnum (Text-fig. 5). The direction of propagation occasionally changed randomly and simultaneous discharges were recorded from both regions, especially 2 h after oviposition. Generally, however, most spike discharges spread in the same direction at the rate of 6 mm/sec for long periods before the direction changed. The results are presented in Table 3. Electrical activity of the magnum was propagated predominantly towards the ovary until 30–90 min after oviposition when ovulation was probably occurring, but later the direction changed towards the uterus when the egg approached the electrodes. After the egg had moved to the caudal end of the magnum, or the isthmus, the electrical activity was mainly propagated towards the ovary again. These results may indicate that the excitation of electrical activity of the regions near the egg originates from the region of the magnum distended by the egg.

Discussion

Talo & Kekäläinen (1976) showed double-peaked frequency histograms of electrical activity in the magnum and isthmus of the quail oviduct *in vitro* when the egg moved through each segment examined and a low frequency of electrical activity during residence of the egg. In the present study, however, low-frequency activity was found in the magnum only for a short time and high frequency was mainly observed. This discrepancy may be due to species difference and the different experimental conditions: it seems reasonable to consider that the low-frequency activity found in the isthmus when the egg is there could be due to distension by the egg which is then surrounded with albumen and shell membrane. The lumen of the magnum is larger than that of the isthmus and mainly deformable albumin is secreted, so the musculature of the magnum may be able to contract, as shown by the persistently high electrical activity in this study.

One new and clear finding of the present study was the drastic change in the electrical activity of the uterus when compared with that of the magnum and isthmus during the ovulatory cycle. In the uterus, the activity was low even though the egg had nearly arrived, perhaps indicating that there is less propagation of excitation either between the isthmus and the uterus or among the various regions within the uterus. Secondly, it takes about 1–2 h for maximum activity to be reached after the entry of the egg into the uterus. It seems unlikely that a high electrical activity is related to the changes in hardness of the egg because only a small amount of the shell components of the complete egg has been deposited by this time (Burmester, 1940). The delay of appearance of high electrical activity is partly associated with the recording site, the caudal region of the uterus. The delay may also be related to

the time of onset of deposition of egg shell. In the magnum and isthmus, secretion of albumen and formation of shell membrane are initiated soon after the egg enters an initially inactive segment, but the uterus does not begin shell formation immediately after the entry of the egg. Progressive electrical activity in the uterus continued for about 20 h and may be involved with persistence of the egg in the uterus while the shell is deposited uniformly (Clavert, 1960).

Tanaka & Nakajo (1962, 1963) have shown that the posterior pituitary hormones are depleted shortly before oviposition. These hormones probably act on the musculature of the uterus (Rzasa & Ewy, 1970), although it has been suggested that substance(s) from the postovulatory follicle may be involved in controlling the time of oviposition (Rothchild & Fraps, 1944; Tanaka & Nakada, 1974; Day & Nalbandov, 1977) and the high electrical activity of the uterus found immediately after oviposition could be related to either or both of these substances. An abrupt decrease in the frequency between 0 and 1 h after oviposition and the quiescent activity for the subsequent 5 h are probably due to depletion of the pituitary hormones and other substances as well as absence of the egg in the uterus. It seems likely that the presence of the egg exerts its effect as a mechanical stimulus to develop muscular contraction of the oviduct.

Crossley *et al.* (1975) reported peristaltic and antiperistaltic contraction waves in the magnum during the period of egg formation but found that 80% of the waves were peristaltic. In the present study, we observed propagation of electrical activity towards the uterus and towards the ovary for considerable periods depending on the location of the egg. It would seem valuable to investigate changes in the direction of electrical activity in the infundibulum because this segment, which engulfs the shed oocyte, is known to become extremely active about the time of ovulation (Gilbert, 1971).

Although we have demonstrated changes in oviductal motility during egg transport in the conscious hen, the restraint effect on oviductal motility was uncertain. Radiotelemetric determinations of heart rate and EEG have previously been performed on free-moving chickens (Shimada & Oshima, 1973; Oshima, Shimada & Tonoue, 1974) and I am hoping to apply this technique for recording uterine activity with special reference to the time of oviposition.

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