Egg Transport in the Rabbit Oviduct: The Roles of Cilia and Muscle

Abstract. *Ciliary ovum transport through the oviductal ampulla was investigated, in vivo, by blocking smooth muscle activity. Isoproterenol eliminated rapid muscle-induced egg movements, yet the egg and its surrounding cells reached the site of fertilization within normal time limits. The role of cilia in ovum transport thus seems more important than that of the smooth muscle.*

The mammalian oviduct is morphologically and functionally complex. Successful reproduction requires that the egg be transported through the oviduct according to a highly regulated and programmed time schedule. Since this transport process is vulnerable to interference—its acceleration or delay alters fertility in many species—the details are of interest in terms of fertility control and contraception. In many mammals the egg requires only minutes to move through the ampulla to the site of fertilization, whereas the remainder of the journey to the uterus takes several days (*1*). Precise information regarding the forces responsible for propelling the egg in this controlled fashion, however, is not available. Such knowledge is desirable since the two structures hitherto recognized as potential effectors, tubal musculature and ciliary apparatus, appear to respond differently to various stimuli and controlling agents.

In vivo techniques for direct observation of ovum transport through the rabbit oviductal ampulla have been developed by Harper (*2*) and Blandau (*3*, *4*). These investigators noted that the movement of the egg with its surrounding mass of cells (cumulus cells) was slow and steady along the first few millimeters beyond the abdominal ostium of the oviduct. Thereafter, ovular motion changed to a complex pattern of rapid forward and backward movements associated with segmental contractions of the oviduct wall. Net forward progress ceased at the end of the ampulla, approximately midway in the oviduct, a point at which ovum transport is delayed for 12 to 18 hours. However, periodic rapid to-and-fro movements persisted in the terminal segment of the ampulla. They concluded from these observations that transport through the first several millimeters may be effected by the cilia of the cells lining the tubal lumen but that the remainder of the journey to the ampullo-isthmic junction can probably be ascribed to the smooth muscle of the oviduct wall. An analysis of the relative contributions of cilia and muscle to ampullary transport was not possible, however, since the direct observational techniques did not permit them to separate the possible effects of ciliary activity underlying the rapid and complex muscle-induced movements.

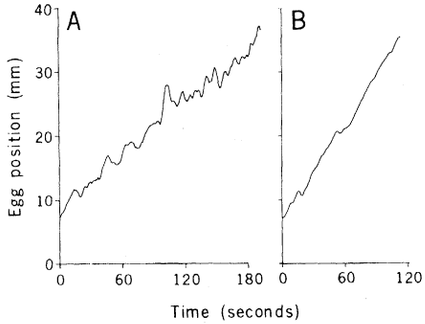

Fig. 1 Ampullary ovum transport. Egg position along the longitudinal axis of the ampullar lumen was plotted by computer as a function of time. The experimental animal was an estrogen-primed castrate rabbit to which CI628, an estrogen antagonist, had also been given for 24 hours. (A) Control. (B) Muscle activity was inhibited with isoproterenol infused through the ear vein at a rate of 0.1 μg/kg per minute.

The present studies were designed to elucidate the relative contributions of the propelling forces by inhibiting muscular activity. The experimental protocol, essentially as described earlier (*5*), utilized the anesthetized, laparotomized rabbit preparation developed by Blandau (*4*) for studying ovum transport. To obtain reversible inhibition of the oviductal musculature we intravenously administered isoproterenol (Isuprel hydrochloride, Winthrop), a β-receptor agonist, either with an infusion pump or by intravenous drip. The infusion rates ranged up to 0.5 microgram per kilogram of body weight per minute; a rate sufficient to maintain a quiescent ampulla was selected in each instance. Electrocardiogram monitoring indicated a 10 to 20 percent increase in heart rate accompanying these doses. Muscular activity of the ampulla was assessed by direct viewing and by recording from miniature extraluminal strain gages (*6*). The ampulla was partitioned with markers applied extraluminally, and the length of each section was measured at the end of the experiment. The progress of supravitally stained cumulus egg masses was followed visually throughout the ampulla, and times of transit through the predetermined regions were recorded with a stopwatch. The midampullar region was preferred for analysis over both the initial segment, where transport is not significantly influenced by muscle activity, and the terminal segment, where the end point of ampullary transport is frequently difficult to establish with precision. A determination of the transport velocity of each ovum over the midampulla segment was obtained by dividing the segment length by the transit time.

During isoproterenol infusion, cumulus egg masses continued to travel through the ampulla despite the complete absence of muscular activity in the oviduct wall. When inhibition of the musculature was maintained, the ova progressed to the ampullo-isthmic junction in a slow, deliberate fashion. Here the cumulus masses stopped and remained relatively motionless. The total transit times through the ampulla under these conditions were approximately the same as those observed prior to isoproterenol administration. After stopping the drug infusion, the muscular activity recovered within 1 minute, and the ova resumed their normal to-and-fro motion whether they were in midampulla or at the ampullo-isthmic junction. We repeated this experiment in four estrous rabbits and four rabbits induced to ovulate with gonadotropins. Gonadotropin-induced ovulation increases vigor and orderly programming of ampullary muscle contraction and accelerates transport (*7*). In each case the effect of blocking muscular activity was essentially identical.

Measurements were obtained from a total of 45 cumulus egg masses including 16 made during isoproterenol infusion (Table 1). In both estrous and ovulatory rabbits, the rates of transport through a region in the midampulla when muscle-induced movements were absent were statistically indistinguishable from those when muscle-induced movements were present.

The slow steady forward movement of

Table 1. Summary of in vivo ampullary ovum transport data. Observations of ovum transport were made in the exposed rabbit oviduct preparation of Blandau (*5*). Ovulatory rabbits were examined 12 hours after being given an intravenous injection of luteinizing hormone (NIH-LH, 100 μg). Transit times were measured over predetermined distances in the midampullar region.

Experimental condition	Midampullar transport velocity (mm/sec)	
	Mean ± standard error	Range
Estrous (N = 4)		
Control (12 ova)	0.11 ± 0.02	0.04 - 0.18
Isoproterenol (8 ova)	0.12 ± 0.02	0.06 - 0.20
Ovulatory (N = 4)		
Control (17 ova)	0.12 ± 0.02	0.03 - 0.27
Isoproterenol (8 ova)	0.11 ± 0.02	0.05 - 0.19

the egg mass during isoproterenol infusion indicates that the cilia provide the sole propellant force under these experimental conditions. Indeed, the cilia by themselves appear to be capable of transporting the ovum to the site of fertilization within normal time limits. Obviously the rapid muscle-induced movements are not necessary for transport.

There are at least three ways of interpreting the observations as to the mechanisms underlying ampullary egg transport. (i) The ciliary and muscular influences could be independent and their propellant forces additive. The rapid muscle-induced movements would therefore be randomly superimposed on slower ciliary transport and ineffective for net transport. (ii) At the opposite extreme, the forces exerted by the cilia might act on the egg mass only when muscle forces are negligible, that is, the cilia-induced and muscle-induced movements are mutually exclusive. In such case, the cilia may completely compensate for the absence of muscular activity if they are as effective as the muscle in transporting ova. (iii) There may be some intermediate degree of interaction between muscular activity and the ciliary apparatus. The roles of both muscle and cilia might be variable and dependent on various properties of the oviductal wall, luminal surface, and intraluminal fluid and, thus, be controlled or regulated by the sex hormones.

To explore further the third interpretation, we studied the interaction of the muscle and cilia under experimental hormonal control. We chose a hormonal state associated with remarkably enhanced muscular activity, dramatic rapid movements of the cumulus egg masses, and rapid ampullary transport (*8*). Castrate rabbits were treated with estrogen for 4 days; for the 24 hours before the experiment, these estrogen-primed subjects were also treated with CI628, a nonsteroidal estrogen antagonist. If the exceptionally rapid rate of transport induced by hormonal treatment were due to alteration of the muscle activity, dramatic slowing of transport would follow pharmacological inhibition of the muscle.

In order to characterize transport through the ampulla as precisely as possible, we analyzed 16-mm motion pictures of the CI628 experiment and, with the help of a computer, plotted a graph of the movement of the egg through the ampulla (Fig. 1). Transport under the influence of isoproterenol was, as expected, relatively free of high velocity movements. Totally against expectations, the transport was of shorter total duration. The average velocity is about 0.25 mm/sec, substantially greater than the velocities measured under the influence of isoproterenol in the experiments on estrous and ovulatory rabbits.

Although these data also support the hypothesis that muscle contractions per se do not contribute to net ampullar transport, they do not preclude a functional role for the muscle; the motion imparted by the muscle to the egg may play some other important role in fertility. The alteration of ciliary transport by hormonal manipulation, however, is clearly apparent. These studies emphasize the importance and relative autonomy of the ciliary apparatus in effecting ovum progress within the mammalian oviduct. Further studies aimed at selective control appear desirable.

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Segmentation in Cinema Perception

Abstract. *Viewers perceptually segment moving picture sequences into their cinematically defined units: excerpts that follow short film sequences are recognized faster when the excerpt originally came after a structural cinematic break (a cut or change in the action) than when it originally came before the break.*

A central theme in the study of the cinema interprets the structure of film as a metaphorical "language" (*1*). Such a conceptualization has apparent validity. A motion picture sequence attempts to portray an event by imposing a structure of cuts, zooms, tracks, pans, framings, and the like on that event. Analogously, a sentence represents an idea by imposing a syntactic and phonological structure on a set of lexical items. The task of the viewer of a film sequence is to apprehend the event represented in the sequence. The analogous task of the listener is to recover the idea encoded in the sentence.

Up to now, the metaphor of film as language has been restricted to purely theoretical accounts of cinema. We show that the methodologies used in the psychological investigations of sentence perception can give experimental support to this characterization. Our report demonstrates that just as the syntactic structure of sentences plays an organizing role in their segmentation into major processing units (*2*), the structural organization of a film sequence plays an analogous part in segmentation of films.

We examined two aspects of organization in motion picture sequences, events and scenes. Events are sequences of constituent actions (*3*). Scenes are sequences of cinematic shots (*4*).

We showed viewers short film sequences, each of which was divided into two segments by a change in the action (type E), by a cut (type C), or by both (type EC). After the film sequence we presented the viewers with brief excerpts (probes) from either the first or second segment of the sequence. Viewers recognized probes from the second segments faster than those from the first, indicating that the material in the first segment is organized separately and more abstractly than the material in the second segment (*5*). This demonstrates that cinematic structure organizes viewers' perceptual processing. Furthermore, it demonstrates the validity of applying psycholinguistic techniques to the study of an art form.

Table 1. Mean affirmative decision times.

Type of stimulus sequence	Source of probe	
	First segment (msec)	Second segment (msec)
EC	951	816
C	906	895
E	1055	917
Total	971	876

The film sequences depicted ordinary daily experiences, such as conversation, scenes of people walking around in rooms or outdoors, traffic scenes, or meals. The cuts in the type EC and the type C sequences involved changes in camera distance (medium shot to close shot or medium shot to long shot) or a change in camera angle (a lateral change of 45° or 90°)