



## Review

# Mechanism for greater frequency of contralateral than ipsilateral relationships between corpus luteum and ovulatory follicle for wave 3 in heifers



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## ABSTRACT

During the last wave of the interovulatory interval (IOI), the permutations of the relationship between the ovulatory follicle and the CL (ipsilateral vs. contralateral) and the number of follicular waves (two vs. three) per IOI differ in frequency of occurrence as follows: ipsilateral relationship and two waves (34%), contralateral relationship and two waves (34%), ipsilateral relationship and three waves (8%), and contralateral relationship and three waves (24%). Deviation or the continuation in growth rate of the future ovulatory follicle and a decrease in growth rate of the future subordinate follicles begin well before luteolysis in two-wave IOIs and during luteolysis in three-wave IOIs. The largest follicle decreases in diameter and loses its dominant status before completion of deviation when it is ipsilateral and adjacent to the regressing CL during wave 3. Dominant status switches from the largest follicle in the ipsilateral ovary to the next-largest follicle which may be in either ovary. Switching accounts for the greater frequency of a contralateral follicle–CL relationship than for ipsilateral follicle–CL relationship during the ovulatory wave in three-wave IOIs. It is proposed that the phenomenon results from commonality in angioarchitecture so that the decrease in blood flow to the regressing CL is associated with a decrease in blood flow to adjacent follicles.

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## 1. Introduction

In cattle, two or three follicular waves [1] and associated FSH surges [2] develop during the interovulatory interval (IOI). Each wave emerges as a cohort of small antral follicles (review [3,4]). The follicles increase in diameter during a common-growth phase. When the largest follicle reaches about 8.5 mm, growth rate of the future dominant follicle continues and the growth of the subordinates begins to wane in a process termed deviation. The differences in follicle dynamics among sequential waves of an IOI go well beyond the difference in the number of waves per IOI [5]. During the past 2 years, a phenomenon was characterized

in which the frequency of a contralateral relationship between the future ovulatory follicle and the CL is greater than the frequency of an ipsilateral relationship during the ovulatory wave of three-wave IOIs (wave 3) but not during the ovulatory wave of two-wave IOIs (wave 2). This report reviews a series of studies beginning with the discovery of the phenomenon and culminating in the unraveling of a credible underlying mechanism.

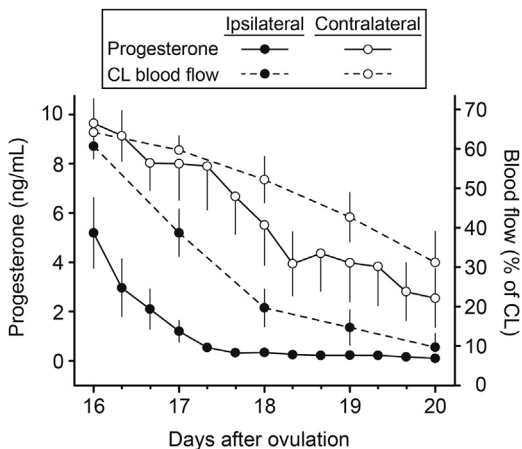
## 2. The puzzle

An unexpected observation was made during a study of the effect of an induced increase in prolactin on the luteal phase [6]. Concentration of progesterone on Day 16 (Day 0 = ovulation) was greater when the CL and future ovulatory follicle were contralateral than when ipsilateral. This

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observation was tested beginning on Day 16 in a subsequent study [7]. Concentration of progesterone, area of CL (cm<sup>2</sup>), and percentage of CL with color-Doppler signals of blood flow during the ovulatory wave were greater for the contralateral relationship than for the ipsilateral relationship until the end of the study on Day 20 (Fig. 1). The interval from ovulation to the end of luteolysis (20 vs. 17 days) and the length of the IOI (23 vs. 20 days) were longer in the contralateral relationship. Design of the study reflected the focus on encompassing the luteolytic period, and no thought was given to earlier reports of a 3-day longer luteal phase and IOI in three-wave IOIs than in two-wave IOIs (review [1]). It was not determined whether the prolonged luteal phase was a cause or consequence of the contralateral relationship between the future ovulatory follicle and the CL, a third follicular wave, or both.

To consider the main effects of the two factors (follicle–CL relationship and number of waves per IOI) and their interaction, a large number of IOIs was needed to accommodate the four permutations of ipsilateral relationship and two waves, contralateral relationship and two waves, ipsilateral relationship and three waves, and contralateral relationship and three waves. Therefore, two surveys were performed from records of the controls for previously reported experiments [8]. Interpretation of the results was as follows: (1) in two-wave IOIs, the frequency of the follicle–CL relationship during the ovulatory wave was equivalent between the ipsilateral relationship (34%) and the contralateral relationship (34%) and (2) in three-wave IOIs, the frequency of an ipsilateral relationship during the ovulatory wave was 8% less than that for equivalency, and the frequency of a contralateral relationship was 8% greater than that for equivalency (Fig. 2). That is, during the ovulatory wave in three-wave IOIs but not in two-wave IOIs, an unknown mechanism decreased the number of ipsilateral relationships and increased the number of contralateral relationships.



**Fig. 1.** Mean ± standard error of the mean for concentration of progesterone and percentage of CL with color-Doppler signals of blood flow for ipsilateral (n = 5) and contralateral (n = 10) relationships between the ovulatory follicle and the CL. Both end points were greater in the ipsilateral relationship. Adapted from the study by Ginther et al. [7].

Waves/IOI: Follicle–CL:	Two		Three	
	Ipsilateral	Contralateral	Ipsilateral	Contralateral
Survey 1 (n=196)	61 (31%)	63 (32%)	24 (12%)	48 (25%)
Survey 2 (n=96)	33 (34%)	34 (35%)	8 (8%)	22 (23%)
Interpretation	34%	34%	8%	24%

**Fig. 2.** Mathematical illustration of the frequency of interovulatory intervals (IOIs) with contralateral and ipsilateral relationships between the ovulatory follicle (large white dot) and the CL (black dot) during the last follicular wave of an IOI for two or three follicular waves per IOI. The interpretation was that the frequencies between the two follicle–CL relationships are similar in the IOIs with two waves. In IOIs with three waves, the frequency of an ipsilateral relationship decreased by 8% in association with an increase of 8% in the contralateral relationship. Adapted from the study by Ginther et al. [8].

### 3. Endocrinologic aspects

Adequate rationale was not available for developing a hypothesis on the mechanism involved in the increased frequency of the contralateral relationship between the ovulatory follicle and the CL during wave 3 of three-wave IOIs. Several characterization studies were performed to determine if differences in hormone concentrations between two-wave and three-wave IOIs would provide rationale for critical study of the increased frequency of the contralateral relationship. A minor follicular wave (no dominant follicle) and a temporally associated minor FSH surge were discovered about 4 days before ovulation and occurred more in two-wave IOIs (59%) than in three-wave IOIs (22%) [9]. The minor surge apparently played a role in boosting the growth rate of the preovulatory follicle in two-wave IOIs; a decrease in growth rate began 7 days before ovulation and resurged between 4 and 3 days before ovulation (Fig. 3). A lower frequency of a minor FSH surge in wave 3 of three-wave IOIs did not appear to be an enabling factor in the increased frequency of the contralateral relationship. Apparently, the shorter interval between the peak of FSH surge 3 and ovulation in three-wave IOIs than between the peak of FSH surge 2 and ovulation in two-wave IOIs did not accommodate the development of a minor surge.

A comparison of FSH concentrations throughout an IOI supported the hypothesis that the development of three-wave IOIs occurs in individuals that have a propensity for greater overall FSH concentration [10]. Support was from the following FSH results in three-wave IOIs compared with two-wave IOIs: (1) greater overall concentration for Days 0 to 18 and for the 3 days before ovulation and (2) greater concentration on the day of ovulation combined for the beginning and end of the IOI (Fig. 4). These results were consistent with repeatability or a propensity for greater FSH concentration in some individuals and may account for the reported 70% repeatability in individuals in the number of waves per IOI [11]. However, the greater FSH output in individuals did not seem to account for the greater frequency of the contralateral follicle–CL relationship in three-wave IOIs.

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