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Behavioral Responses to Intramuscular Injections of Prostaglandin $F_{2\alpha}$ in Female Pigs

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BURNE, T. H. J., P. J. E. MURFITT AND C. L. GILBERT. *Behavioral responses to intramuscular injections of prostaglandin $F_{2\alpha}$ in female pigs*. PHARMACOL BIOCHEM BEHAV **66**(4) 789–796, 2000.—This study investigated the effect of different doses (0–1.25 mg/kg IM) of prostaglandin (PG) $F_{2\alpha}$ on the behavior of female pigs (*Sus scrofa*). Six-month-old cyclic nulliparous sows (gilts) were housed and tested individually in strawed pens (2.8 × 1.7 m). All doses of $PGF_{2\alpha}$ induced rooting, pawing at the ground, and gathering straw. In the hour following treatment the frequency of pawing increased with increasing dose to reach a maximum level with the highest dose given. The frequency to gather straw was highest in pigs treated with the lowest dose (0.008 mg/kg). The frequency of oronasal contact with the floor and pen walls was unaffected by dose. Scratching, locomotion, and changes in body posture were highest following treatment with the three highest doses of $PGF_{2\alpha}$. Many of the behaviors observed following $PGF_{2\alpha}$ treatment are characteristic of prepartum nesting behavior in pregnant sows. We conclude that two key components of maternal nest-building behavior, pawing, and gathering straw, are affected differentially by different doses of $PGF_{2\alpha}$. The implications of these results on the mechanisms underlying maternal nest building in pigs are discussed. © 2000 Elsevier Science Inc.

Prostaglandin Behavior Nest building Dose–response Pigs

PROSTAGLANDIN (PG) $F_{2\alpha}$ has been isolated from and measured in a wide range of tissues, and is involved with a diverse range of physiological activities. Among these are its involvement in the initiation of regression of the corpus luteum (luteolysis), and thus, in the induction of parturition in the pig. Administration of exogenous $PGF_{2\alpha}$ to nonpregnant nulliparous sows (gilts) induces luteolysis when given after days 12–13 of the estrous cycle, as well as being luteolytic when given to early pregnant and pseudopregnant gilts (11,12). In late pregnant animals the luteolytic actions of $PGF_{2\alpha}$ have been used to control the timing of parturition (13). In addition, $PGF_{2\alpha}$ elicits a number of behavioral responses. Intramuscular administration of $PGF_{2\alpha}$ to nonpregnant and pregnant sows rapidly induces nesting behavior (4,5,8,9,36,37). By contrast, male pigs treated with $PGF_{2\alpha}$ display sexual behavior (14) and $PGF_{2\alpha}$-treated juvenile pigs (6 weeks old) only show changes in activity and discomfort (36).

Under seminatural conditions the preparturient behavior of sows involves distinct periods of wandering, nest-site selection, and nest building, culminating in the creation of a protected nest in which she gives birth to her piglets (21,22). The preparturient behavior of sows housed under intensive conditions also involves nest-building activities (2,20), although some of these behaviors are constrained or altered by the sows' surroundings. There are some differences between parturition and $PGF_{2\alpha}$-induced nest building, such as the duration of nesting activities, but many of the behaviors are common to both (8,36). These include pawing, rooting, and gathering nest material, as well as increases in locomotion, the latter possibly an attempt to isolate themselves and/or select a suitable nest site. Other workers have reported that the prepartum behavior of free-ranging sows could be separated into four factors (explaining 78% of the variation in the data) consisting of carrying, depositing, and arranging straw (material factor), walking and nosing (walking factor), pawing and rooting in the nest (pawing factor), and rooting at the earth

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[rooting factor; (23)]. These authors found that there was a high variability in the total amount of nesting behavior between sows, but that the temporal patterning of different nesting activities was similar. Moreover, the phases of maternal nest building after wandering, which includes rooting at the earth, is thought to be mainly under endogenous control, whereas the second phase of nest building, which involves gathering and arranging of nest material, depends on feedback from external stimuli (23). Concentrations of 15 keto-13,14-dihydro prostaglandin $F_{2\alpha}$ (PGFM; the major metabolite of $PGF_{2\alpha}$) begin to rise to ca. 2 ng/ml in plasma on the day preceding parturition, and then show a further increase to peak levels of ca. 25 ng/ml at birth (18,35). It is, therefore, possible that endogenous $PGF_{2\alpha}$ initiates changes in prepartum behavior.

There are some similarities between $PGF_{2\alpha}$-induced behavior in pigs and other species including both peripherally and centrally mediated affects such as erythema, slight incoordination, itching, urination, abdominal muscle spasms, hyperpnoea, dyspnoea, and salivation (3,24). However, there have been no reports of $PGF_{2\alpha}$-induced nesting behavior in most other species studied, for example, rabbit (1), rat (7), horse (24), and cattle (3). Two notable exceptions are the tammar wallaby, *Macropus eugenii*, in which males and females treated with $PGF_{2\alpha}$ assume a characteristic birth posture and display typical prepartum behavior (25), and in teleost fish, in which $PGF_{2\alpha}$ stimulates male spawning behavior and digging in females (33). Because, among eutherian mammals, $PGF_{2\alpha}$-induced nesting behavior has only been recorded in female pigs, it represents a unique model with which to explore the endocrine mechanisms controlling nesting behavior. However, no study so far has systematically investigated $PGF_{2\alpha}$-induced nesting behavior in pigs. Therefore, the present study examined in detail the effects of different doses of $PGF_{2\alpha}$ on the behavior of gilts and includes detailed summaries of the latency, frequency, and duration of behaviors.

METHOD

Animals and Housing

Thirty nulliparous female Large White pigs (gilts) from the Babraham herd were used. At testing (see below), the gilts were ca. 6 months of age, and weighed on average 120 kg (range 110–130 kg). They were kept in groups of eight in large strawed pens prior to selection for experimentation, and had no previous experience of individual housing. Two weeks before testing they were transferred to individual pens in a large enclosed fan-ventilated barn. Each pen (2.8×1.7 m) was constructed with solid walls and a concrete floor subdivided by a step into a raised lying area with under floor insulation (1.8×1.7 m) draining onto a dunging area at the rear of the pen (1.0×1.7 m). Gilts were floor fed 1.5-kg pelleted ration and given 2-kg fresh straw in the lying area once a day after their pen was cleaned (0800–0830 h), except on the testing day when straw was provided at 1020–1025 h. Water was available ad lib from a bite drinker on the wall above the dunging area. Animals were kept under artificial light from fluorescent strip lights (0800–1800 h) in addition to natural daylight and the temperature varied between 10–25°C. The gilts were handled for at least 10 min a day while they were housed individually to permit familiarization with the experimenters.

Experimental Procedure

The procedures used in this study were in compliance with the UK Animals Scientific Procedures Act 1986. At 1030 h on the test day the gilts received a single IM neck injection of 1

TABLE 1
BEHAVIORAL ETHOGRAM

Posture
Kneel: standing on rear legs with two front legs folded
Lie belly: lying with belly concealed
Lie side: lying with belly exposed
Sit: sitting upright with two front legs on the ground
Stand: standing on all four legs
Nesting behaviors
Carry straw: grasping straw in the mouth and taking at least two steps (as defined below)
Lift straw: grasping straw in the mouth and raising the head and taking no more than one step (as defined below)
Paw straw: raking movement of either foreleg at an area of floor covered in straw
Paw floor: raking movement of either foreleg at an area of floor devoid of straw
Paw wall: raking movement of either foreleg at the walls of the pen
Root straw: oro–nasal contact with straw and head movement
Root floor: oro–nasal contact with floor and head movement
Root wall: oro–nasal contact with wall and head movement
Step: number of steps made by the rear left leg
Other behaviors
Inactive: no part of the pig is moving
Defecate
Urinate
Drink: oro–nasal contact with drinker
Chew fixture: chewing at any of the fixtures within the pen (apart from the drinker)
Object scratch: scratch or rub any part of the body against another object
Rear leg scratch: scratch, or attempt to scratch, any part of the body with the rear leg
Shake head: vigorous sideways movement of the head

ml 0.9% saline, or 1, 5, 10, or 15 mg of $PGF_{2\alpha}$ (5 mg/ml dinoprost in water; Lutalyse, Upjohn, Crawley, UK; $n = 6$ gilts per dose). These doses were approximately equivalent to 0, 0.008, 0.04, 0.08, and 0.125 mg/kg, respectively. Each treatment was split across four separate batches of pigs ($n = 8$ for three batches and $n = 6$ for one batch).

Behavior

Each gilt's behavior was recorded for 1 h following treatment by a centrally placed camera, positioned 3 m above the floor of the pen and connected to a video recorder. The gilts' behavior was scored from video recordings by an experimenter blind to treatment using a computerized event recorder (28). The activities of the pigs during the hour period were recorded continuously. Data were obtained for 22 defined behaviors (see Table 1). Behaviors defined as states, with a relatively long duration, were scored for latency, frequency, and duration, and behaviors defined as events, with a relatively short duration, were scored for latency and frequency. The behaviors were divided into (a) postures, (b) nesting behaviors, as defined previously (23), and (c) other behaviors. In addition, a note was made following the occurrence of other activities, such as salivation and changes in respiration rate.

Statistical Analysis

The behavioral data were quantified using the elementary statistics option of the Observer computer package (28). A Kruskal–Wallis test (H $df = 4$, $n = 6$ per treatment group) was used to analyze the effect of treatment at various doses on each behavior (32). If this test indicated significance ($p < 0.05$), then post hoc multiple comparisons were made between treatments with a Dunn's test for multiple comparisons. Behaviors in which the Kruskal–Wallis value indicated that, overall, there was only a tendency for differences between treatments ($0.10 > p > 0.05$) were followed up with a single post hoc Mann–Whitney test (U) between the groups with the highest and lowest mean values. Relationships between frequencies of behavior affected by treatment were subjected to factor analysis using the SPSS statistical package. Both the within-treatment analysis ($n = 6$ per group) and the pooled analysis for groups receiving $PGF_{2\alpha}$ (1, 5, 10, and 15 mg $PGF_{2\alpha}$) were performed as a principal component analysis, with orthogonal varimax rotation (15).

RESULTS

$PGF_{2\alpha}$ treatment induced behaviors that were clearly distinguishable from those of saline-treated animals. A typical sequence of behaviors included an increase in locomotion and postural change, scratching, and rubbing against objects, salivation, increase in respiration rate, which was followed by distinct bouts of rooting and pawing at straw and, particularly at lower doses, gathering (the summation of lift and carry straw) and arranging of straw.

TABLE 2

MEAN (±SEM) LATENCY (s) TO (i) CHANGE POSTURE, AND (ii) PERFORM DIFFERENT BEHAVIORS, DURING THE HOUR AFTER TREATMENT WITH DIFFERENT DOSES OF $PGF_{2\alpha}$

	Dose of $PGF_{2\alpha}$ (mg)					
	0	1	5	10	15	H
Posture						
Kneel	2466 ± 557	2125 ± 488	672 ± 158	1216 ± 534	698 ± 293	9.3*
Lie belly	2360 ± 516	1701 ± 558	1006 ± 527	1195 ± 542	881 ± 303	5.0
Lie side	2778 ± 562	3236 ± 182	1539 ± 552	1718 ± 602	749 ± 282	10.6*
Sit	2434 ± 738	1517 ± 478	1428 ± 576	551 ± 119	453 ± 104	4.3
Stand	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.0
Nesting behaviors						
Carry straw	3600 ± 0	1911 ± 551	3122 ± 3467	2793 ± 520	3475 ± 125	11.0*
Lift straw	3089 ± 333	1184 ± 502	2471 ± 426	2095 ± 500	2699 ± 470	9.4*
Paw straw	2618 ± 567	394 ± 70	1238 ± 410	1267 ± 219	1015 ± 265	12.7*
Paw floor	3600 ± 0	3600 ± 0	3076 ± 524	3143 ± 457	3600 ± 0	3.1
Paw wall	3600 ± 0	3600 ± 0	3600 ± 0	3600 ± 0	2450 ± 728	1.6
Root straw	70 ± 41	147 ± 35	144 ± 123	65 ± 49	66 ± 41	2.2
Root floor	1654 ± 651	803 ± 565	401 ± 147	737 ± 309	168 ± 42	0.1
Root wall	1132 ± 510	931 ± 228	1098 ± 512	1504 ± 667	1517 ± 667	3.7
Step	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.0
Other behaviors						
Defecate	2999 ± 569	2029 ± 708	3431 ± 169	2953 ± 410	2499 ± 604	2.8
Urinate	3600 ± 0	2516 ± 686	3600 ± 0	3009 ± 591	3017 ± 583	3.6
Drink	628 ± 245	1297 ± 729	2735 ± 549	2551 ± 672	1875 ± 772	6.5
Chew fixture	3600 ± 0	3009 ± 591	2623 ± 543	3600 ± 0	3013 ± 587	6.0
Object scratch	2295 ± 714	687 ± 95	619 ± 107	538 ± 77	261 ± 75	7.4
Rear leg scratch	3072 ± 528	705 ± 166	432 ± 126	357 ± 85	269 ± 79	14.2*
Shake head	906 ± 534	854 ± 551	1566 ± 647	1248 ± 571	3508 ± 92	11.5*

The test statistic (H) from separate Kruskal–Wallis tests ($df = 4$, $n = 6$ per treatment) are shown (*$p < 0.05$). Means on the same row with different letters are significantly different, $p < 0.05$, Dunn's multiple comparison test.

Latency Data

There were significant effects of treatment on the latency to carry and lift straw (Table 2) and the latency to paw straw. Gilts administered with 1 mg of $PGF_{2\alpha}$ had a significantly reduced latencies to carry and lift straw compared to saline-treated controls. There were no significant differences in the latency to carry or lift straw between saline-treated controls and gilts treated with the three highest doses of $PGF_{2\alpha}$. By contrast, treatment with each dose of $PGF_{2\alpha}$ resulted in significantly reduced latency to paw straw when the data were compared to saline-treated controls; the shortest latency was found after treatment with 1 mg.

There were significant effects of treatment on the latency for gilts to lie on their side and on the latency for them to shake their heads; there was a significantly shorter latency to perform these behaviors at the highest dose when compared to saline-treated controls (see Table 2). Gilts treated with all doses of $PGF_{2\alpha}$ had significantly reduced latencies to scratch with the rear leg than saline-treated controls. There were no significant effects of treatment on the latency to initiate bouts of any of the remaining behaviors measured.

Frequency Data

Overall analysis of the frequency data (see Table 3) for carry and lift straw indicated a tendency for differences between groups ($0.10 > p > 0.05$); the frequency to carry or lift straw was highest in gilts treated with the 1-mg dose of $PGF_{2\alpha}$, and this differed significantly from that of saline-treated controls ($U = 4$, $p = 0.01$). There were significant effects of $PGF_{2\alpha}$ dose on the frequency data for paw straw. Gilts showed elevated levels of pawing after treatment with the 1, 5, and 10-mg doses of $PGF_{2\alpha}$, compared to saline-treated controls, and pawing frequency was highest at the 15-mg dose.

There were significant effects of $PGF_{2\alpha}$ on the frequencies of scratching, on all of the postures measured, as well as on drinking and on the number of steps taken (Table 3). Gilts showed elevated levels of scratching with a rear leg after treatment with all doses of $PGF_{2\alpha}$ compared to saline-treated controls. The frequency of scratching against an object increased to maximal levels at the three highest doses of $PGF_{2\alpha}$ given. The frequencies to adopt postural categories for sit, kneel, lie on belly, and stand were all significantly affected by treatment ($H > 9.32$, $p < 0.05$, for each behavior analyzed). Frequencies to stand and kneel were elevated at the three highest doses, whereas the frequencies to sit and lie on belly were only elevated in gilts treated with 10 and 15 mg. The frequency data for lie on side was only elevated following treatment with 15 mg. The frequency of steps in the hour after treatment was significantly higher in gilts treated with the three highest doses of $PGF_{2\alpha}$. The frequency of drinking showed a tendency to be altered by treatment and the levels were lowest after treatment with the 10-mg dose. No other behaviors were significantly affected by dose.

In addition to the above, the number of animals in each treatment group (0, 1, 5, 10, and 15 mg) showing key components of nest building were quantified; carry straw (total number of pigs showing behavior, $n = 6$ per group; 0:5:3:2:1), lift

TABLE 3

MEAN (±SEM) FREQUENCIES PER HOUR OF (i) POSTURAL CHANGE, AND (ii) BEHAVIORS, DURING THE HOUR AFTER TREATMENT WITH DIFFERENT DOSES OF $PGF_{2\alpha}$

	Dose of $PGF_{2\alpha}$ (mg)					
	0	1	5	10	15	*H*
Posture						
Kneel	0.8 ± 0.5	1.2 ± 0.3	3.7 ± 1.1	5.0 ± 1.3	3.3 ± 1.3	11.1*
Lie belly	1.3 ± 0.8	1.2 ± 0.3	6.2 ± 3.0	7.3 ± 2.4	6.2 ± 2.5	9.3*
Lie side	0.8 ± 0.7	0.5 ± 0.2	3.7 ± 1.7	3.3 ± 1.5	4.3 ± 2.0	8.6†
Sit	1.2 ± 0.8	1.0 ± 0.3	4.8 ± 2.4	6.7 ± 1.8	4.8 ± 2.0	12.8*
Stand	2.3 ± 0.8	2.2 ± 0.3	7.0 ± 2.0	9.5 ± 2.0	7.2 ± 1.9	18.2*
Nesting behaviors						
Carry straw	0.0 ± 0.0	5.3 ± 3.0	6.2 ± 4.5	8.7 ± 7.4	0.8 ± 0.8	8.6†
Lift straw	1.2 ± 0.8	40.0 ± 15.8	19.5 ± 9.0	16.0 ± 9.0	5.8 ± 3.8	7.9†
Paw straw	11.2 ± 5.6	62.3 ± 18.5	139.0 ± 77.1	101.3 ± 47.2	246.3 ± 53.4	15.1*
Paw floor	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.3 ± 0.3	0.0 ± 0.0	3.1
Paw wall	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.7	1.6
Root straw	48.2 ± 7.9	69.8 ± 17.2	74.2 ± 17.5	63.5 ± 17.6	69.3 ± 13.9	1.1
Root floor	6.7 ± 3.4	4.0 ± 1.1	7.2 ± 4.0	6.5 ± 3.5	3.7 ± 1.3	0.2
Root wall	6.0 ± 2.9	4.7 ± 2.2	9.3 ± 1.3	6.2 ± 1.7	10.0 ± 5.1	4.0
Step	202.8 ± 23.5	263.2 ± 26.0	440.5 ± 97.3	406.0 ± 54.4	412.2 ± 69.5	9.8*
Other behaviors						
Defecate	0.5 ± 0.2	0.5 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.8 ± 0.5	2.4
Urinate	0.0 ± 0.0	0.3 ± 0.2	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	3.9
Drink	4.7 ± 1.4	3.0 ± 1.1	2.2 ± 1.4	0.5 ± 0.3	0.8 ± 0.4	9.1†
Chew fixture	0.0 ± 0.0	0.2 ± 0.2	0.5 ± 0.2	0.0 ± 0.0	0.2 ± 0.2	7.0
Object scratch	2.2 ± 1.1	4.5 ± 2.5	11.7 ± 2.3	7.3 ± 1.3	9.8 ± 2.3	13.9*
Rear leg scratch	0.3 ± 0.3	16.0 ± 4.7	46.0 ± 14.5	51.5 ± 12.3	45.0 ± 12.9	18.1*
Shake head	2.2 ± 0.6	1.7 ± 0.3	1.5 ± 0.6	2.0 ± 0.6	0.3 ± 0.3	7.8

The test statistic (*H*) from separate Kruskal–Wallis tests ($df = 4$, $n = 6$ per treatment) are shown (*$p < 0.05$; †$0.10 > p > 0.05$).

Means on the same row with different letters are significantly different, $p < 0.05$, Dunn's multiple comparison test; paired comparison, Mann–Whitney *U*-test, see the Methods section for further details.

straw (2:5:5:4:3) and paw straw (3:6:6:6:6). As these are only nominal data, no statistical analysis was carried out; however, some trends are apparent. In the case of carrying straw, saline-treated pigs were not observed to perform this behavior. The number of pigs carrying straw was greatest at the lowest dose (1 mg) and then decreased in a dose-dependent manner with increasing dose. A similar pattern was evident for lifting straw. Pawing straw was induced in all pigs at all doses of $PGF_{2\alpha}$ given.

Duration Data

Overall analysis of the duration to carry straw indicated a tendency for differences between groups ($H = 8.49$, $p = 0.08$). Gilts treated with the lowest dose (1 mg) lifted straw for the longest duration, and this response differed significantly to that of saline-treated controls. The duration of time carrying straw was highest in gilts treated with 1 mg of $PGF_{2\alpha}$. There was a significant effect of $PGF_{2\alpha}$ on the time spent scratching (see Table 4). Saline-treated gilts had a significantly shorter duration of scratching with the rear leg compared to gilts treated with each dose of $PGF_{2\alpha}$. Gilts treated with all but the lowest dose of $PGF_{2\alpha}$ scratched against an object for a longer duration than saline-treated controls in the hour after treatment. The mean duration of time spent drinking was significantly altered by dose. Gilts spent the least amount of time at the drinker following treatment with the three highest doses of $PGF_{2\alpha}$. The duration of the remaining behaviors measured did not depend on the dose of $PGF_{2\alpha}$ administered.

Factor Analysis Between Treatments

There appeared to be eight main behavioral categories altered by $PGF_{2\alpha}$ based on the frequency data, namely the categories for stand (as a measure of postural change), carry straw, lift straw, paw straw, step, drink, object scratch, and rear leg scratch. The relationships between these behaviors were further examined with principal component analysis. The results of this analysis are shown in Table 5. In gilts treated with 1, 10, and 15 mg the frequencies to lift and carry straw loaded on one and the same factor. In saline-treated controls pawing straw and the frequency of steps were loaded on the same factor with opposite signs. Pawing straw was loaded on the same factor as the frequency of steps at 1 and 5 mg doses, whereas it was loaded with the frequency to scratch against an object at 10 mg and the frequency to stand at 15 mg. Scratching with the rear leg and drinking were loaded on the same factor with the same sign in saline-treated controls, but were loaded with opposite signs at the two highest doses. Object scratch was not consistent in its factor loading across treatments.

Factor Analysis of Data after $PGF_{2\alpha}$ Treatment

The results of the factor analysis of the pooled data from gilts treated with the different doses of $PGF_{2\alpha}$ are shown in Table 6. Three factors were extracted, explaining 69% of the variation in the correlation matrix. The typical behavioral components associated with the factors appeared to be related to gathering, scratching and pawing. Each factor did not correlate with any of the other factors.

DISCUSSION

The present study shows that different doses of $PGF_{2\alpha}$ have differential effects on certain aspects of nesting behavior in nonpregnant pigs. Gilts given the highest dose of $PGF_{2\alpha}$ (15 mg) displayed maximal levels of pawing at straw, whereas maximal levels of gathering straw occurred in gilts given the lowest dose of $PGF_{2\alpha}$ (1 mg). It appears that $PGF_{2\alpha}$ had a specific effect on straw-directed behavior, rather than causing a

TABLE 4

MEAN (±SEM) PROPORTION OF TIME (%) SPENT (i) IN DIFFERENT POSTURES, AND (ii) PERFORMING DIFFERENT BEHAVIORS, DURING THE HOUR AFTER TREATMENT WITH DIFFERENT DOSES OF $PGF_{2\alpha}$

	Dose of $PGF_{2\alpha}$ (mg)					
	0	1	5	10	15	*H*
Posture						
Kneel	0.1 ± 0.1	0.1 ± 0.0	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	8.4†
Lie belly	11.1 ± 4.8	20.2 ± 8.2	12.6 ± 7.9	17.4 ± 6.5	13.8 ± 4.6	1.7
Lie side	15.4 ± 9.7	10.1 ± 5.1	15.5 ± 8.3	14.6 ± 7.7	14.1 ± 5.1	1.9
Sit	1.3 ± 0.9	0.3 ± 0.2	2.0 ± 1.5	1.1 ± 0.5	1.7 ± 0.4	5.3
Stand	72.0 ± 12.6	69.3 ± 9.2	69.6 ± 12.3	66.5 ± 10.1	70.1 ± 9.5	0.3
Nesting behaviors						
Carry straw	0.0 ± 0.0	0.4 ± 0.2	0.7 ± 0.5	1.2 ± 1.1	0.1 ± 0.1	8.5†
Lift straw	0.1 ± 0.1	3.4 ± 1.3	1.1 ± 0.4	1.3 ± 1.0	0.5 ± 0.4	7.8†
Root straw	37.4 ± 9.5	29.7 ± 4.6	28.9 ± 7.2	26.5 ± 7.1	24.5 ± 4.2	1.4
Root floor	0.8 ± 0.4	0.8 ± 0.5	1.7 ± 0.9	0.5 ± 0.1	0.9 ± 0.5	4.3
Root wall	4.8 ± 3.3	10.0 ± 5.4	1.8 ± 1.0	1.8 ± 1.3	0.5 ± 0.2	3.4
Other behaviors						
Defecate	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	3.1
Urinate	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	4.3
Drink	3.8 ± 0.7	2.2 ± 0.8	1.0 ± 0.8	0.2 ± 0.1	0.5 ± 0.3	12.9*
Chew fixture	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	7.2
Object scratch	0.3 ± 0.2	0.6 ± 0.3	2.0 ± 0.7	0.8 ± 0.1	1.2 ± 0.4	12.0*
Rear leg scratch	0.0 ± 0.0	0.9 ± 0.3	3.4 ± 1.0	3.6 ± 0.9	3.7 ± 0.7	19.4*

The test statistic (*H*) from separate Kruskal–Wallis tests ($df = 4$, $n = 6$ per treatment) are shown (*$p < 0.05$; †$0.10 > p > 0.05$).

Means on the same row with different letters are significantly different, $p < 0.05$, Dunn's multiple comparison test; paired comparison, Mann–Whitney *U*-test, see the Methods section for further details.

TABLE 5

RESULTS OF PRINCIPLE COMPONENT ANALYSIS ON FREQUENCIES OF BEHAVIOR AFFECTED BY $PGF_{2\alpha}$

Dose (mg)	Variance Explained by the Factors (%)	Number of Factors Extracted	Factor* A	Factor* B	Factor* C
0	95.0	3	Pws, −Stp, Obj, Std	Lts	Drk, Rls
1	86.7	3	Pws, Stp, Drk, −Rls	Lts, Cys, Obj	Std
5	85.9	3	Pws, Stp, Drk	Lts, Rls	Cys, Obj, −Std
10	81.2	2	Pws, Obj	Lts, Cys, Stp, −Drk, Rls, −Std	
15	80.6	3	Pws, Std	Lts, Cys, Obj	Stp, −Drk, Rls

*Only behavior patterns loading more than 0.50 on the same factors are shown (− indicates negative loading).
Factors are arranged from A–C for convenience and do not necessarily indicate the first factor for all treatments.
Abbreviations are the same as those used in Table 6.

general increase in activity, as there were significant effects of $PGF_{2\alpha}$ on paw and gather straw but no effect on behaviors directed at the fixtures, bare floor, or pen walls. Other significant changes that occurred following $PGF_{2\alpha}$ treatment included increases in locomotion (steps), scratching, and changes in body posture.

Effects of $PGF_{2\alpha}$ on Nesting Behaviors

The hypothesis that $PGF_{2\alpha}$ acts as the internal component of prepartum activity (wandering and nest building) is credible because the present results indicate that $PGF_{2\alpha}$ can alter both nesting behaviors and patterns of locomotion. The increases in the number of steps taken may be comparable to the wandering phase, and the increases in pawing and gathering straw are comparable to the nest-building phase typical of prepartum behavior (22). Although we did not measure peripheral hormone levels in this study, we have previously shown that intramuscular administration of 15 mg $PGF_{2\alpha}$ results in an increase in circulating levels of PGFM to maximal levels of ca. 50 ng/ml within 30 min after IM administration to pseudopregnant gilts (9). However, it is difficult to reconcile the present results with the known sequence of nest building and $PGF_{2\alpha}$ changes during the prepartum period. As mentioned earlier, $PGF_{2\alpha}$ levels rise gradually during the 36–24 h prepartum and the prepartum phases of behavior move from wandering, nest-site selection to gathering, and arranging of nest material. By contrast, the present results suggest that the opposite occurs; at low doses of $PGF_{2\alpha}$ gathering straw is elicited, whereas locomotion and pawing straw are evoked by the highest concentrations of $PGF_{2\alpha}$. Clearly $PGF_{2\alpha}$ is able to modulate aspects of nesting behavior. It may be that pulsatile secretion of $PGF_{2\alpha}$ from the uterus and its interaction with other hormones, such as prolactin and relaxin, together with external cues, such as availability of suitable substrate and temperature, alters the sequence and extent of nesting behaviors in prepartum animals. One further complication with relating exogenous $PGF_{2\alpha}$ treatment to endogenous levels is that $PGF_{2\alpha}$ is metabolized very rapidly (26).

TABLE 6

ORTHOGONAL (VARIMAX) ROTATION OF THE POOLED DATA FOR ALL DOSES OF $PGF_{2\alpha}$

Behavior (Frequencies per Hour)	Factor Loadings* 1	2	3	
Lift straw (Lts)	0.85			
Carry straw (Cys)	0.74			
Stand (Std)	−0.76			
Object scratch (Obj)		0.59		
Rear leg scratch (Rls)		0.76		
Drink (Drk)		−0.87		
Paw straw (Pws)			0.88	
Step (Stp)			0.77	
Variance (%)	29.4	21.2	18.4	Total: 69.0

*Only loadings more than 0.50 are shown.

The present result confirms other work from this laboratory, in which gilts housed in an extensive environment also showed an increase in locomotion after treatment with 15 mg of $PGF_{2\alpha}$ (16). It is possible that overall behavior even more closely resembling that of a prepartum sow could be achieved by using a delivery system for $PGF_{2\alpha}$ that more closely resembles prepartum endogenous secretion patterns. This is currently being investigated.

Despite the commercial significance of the pig relatively little is known about the mechanisms underlying their maternal behavior. The initiation and maintenance of prepartum nesting behavior appears to be under different hormonal control to that found in other mammals. For example, inhibition of prolactin secretion with the dopamine receptor agonist bromocriptine blocks nest building in rabbits (17) but is without effect in the pig (6). In rabbits, high progesterone and estradiol levels result in burrow digging, whereas progesterone withdrawal and increased prolactin levels are associated with an increase in straw-carrying behavior (17). Nesting behavior in pigs occurs in the presence of both increasing and decreasing progesterone concentrations, and while some studies indicate that progesterone is correlated with gathering (10) others do not (37). Estradiol supplementation to already pseudopregnant gilts has no effect on $PGF_{2\alpha}$-induced nesting behavior (8) and, moreover, the behavior of pseudopregnant gilts induced to nest build is also similar to that found for cyclic gilts (8,9). This suggests that a period of prolonged progesterone dominance and elevated estrogen levels, such as in pregnancy, is an unnecessary precursor to nesting behavior in pigs. It seems unlikely that $PGF_{2\alpha}$ is the only endocrine component underlying nesting behavior in pigs, although clearly it has an important role in the initiation of nesting behaviors as shown here, and elsewhere (4,5,8,36,37). It would seem more likely that $PGF_{2\alpha}$, or one of its metabolites, is part of a biochemical cascade in which other, currently unknown, endocrine and

environmental components are required for adequate expression of nesting behavior.

There were no effects of $PGF_{2\alpha}$ dose on oronasal contact with straw (here defined as rooting) even though we have previously shown that rooting, as distinct from foraging, is increased in $PGF_{2\alpha}$-treated gilts when compared to saline-treated controls (9). The difference between the findings of these two studies is most likely because gilts in the present study received straw 5–10 min before the injection, whereas in the previous study straw was provided 1–2 h before giving an injection. That is, the provision of fresh straw at the same time as the injection appears to have stimulated rooting behavior in all gilts, irrespective of treatment and thus the effect of $PGF_{2\alpha}$ was most likely masked in this study. However, previous studies have been unable to show a relationship between rooting and hormone levels once nest-building behavior has been initiated in late pregnant sows (10).

Nesting behavior does not seem to be brought about by $PGF_{2\alpha}$-induced luteolysis, as there have been no reports of dose-dependent effects of $PGF_{2\alpha}$ on luteolysis in the pig (30), when doses similar to those used in the present study were used intramuscularly. In addition, the time course for the behavioral and ovarian effects of $PGF_{2\alpha}$ on progesterone secretion are very different with behavioral effects being more rapid. Thus, either $PGF_{2\alpha}$ or an intermediary may be acting directly via central mechanisms to bring about the observed behavioral changes. In rats, a small amount (0.01%) of peripherally administrated $PGF_{2\alpha}$ crosses the blood–brain barrier to reach the brain (19), and direct application of PGE_2 and $PGF_{2\alpha}$ to rat hypothalamus results in increases in neuronal firing rate (34). However, it remains to be tested whether the same is true for the pig.

Effects of $PGF_{2\alpha}$ on other Behaviors

$PGF_{2\alpha}$ has a wide range of effects, which appear unrelated to nesting behavior, on a number of different tissues, such as blood vessels, cardiac and smooth muscle, gut, eye, and brain (31). Some of the observed behavioral responses, such as scratching, may have resulted from physiological changes mediated by $PGF_{2\alpha}$ on these or other systems. Based on the negative loadings found between drinking and scratching with the rear leg, there does not appear to be a direct effect of $PGF_{2\alpha}$ on drinking behavior. In other words, it appears that the gilts were unable to drink because they were more strongly motivated to perform other behaviors, such as scratching. It is clear that scratching, particularly at these high levels, is not part of "normal" prepartum behavior, and may be as a result of the bolus intramuscular injection of $PGF_{2\alpha}$. It is, however, interesting to note that sows treated with 10 mg of $PGF_{2\alpha}$ (to induce parturition) on day 112 of pregnancy display nesting behavior, but are not reported to show elevated levels of scratching. The reason for the discrepancy between pregnant and nonpregnant pigs is not known. The increase in postural change seen with increasing dose did not appear to be related to the nesting behavior per se. Previous reports have shown that $PGF_{2\alpha}$ induces an increase in rectal temperature (27), and intravenous injection of PGE_2 induces fever (29). It appeared to us that the pigs were lying down in the dunging area to cool themselves by attempting to wallow in the wettest area of the pen. Given that mares treated with $PGF_{2\alpha}$ begin sweating rapidly (24), and pigs are unable to sweat, this increased rate of postural change could be interpreted as a "cooling" response.

In summary, this study demonstrates that $PGF_{2\alpha}$ is able to modulate at least two aspects of nesting behavior. Wandering, pawing, and gathering are components of nesting that would usually occur during distinct phases of maternal nest building. It is possible that on the few days before parturition differences in behavior are elicited by different concentrations of circulating $PGF_{2\alpha}$. The mechanism whereby $PGF_{2\alpha}$ induces nesting behavior is not known, but it is possible that $PGF_{2\alpha}$ crosses the blood–brain barrier and acts centrally to modulate nesting behavior in the pig. Whatever the mechanism, nonpregnant and inexperienced female pigs already have established the neural pathways necessary for nesting behavior to occur in response to exogenous $PGF_{2\alpha}$ treatment.

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