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Intramammary pressure in the lactating sow in response to oxytocin and during natural milk ejections throughout lactation

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We developed a simple, non-invasive method to measure the intramammary pressure (IMP) response in sows during natural milk ejection and after i.v. injections of oxytocin. The teats of sows were cannulated and the amplitude and duration of IMP changes were measured via a pressure transducer linked to a computer. During natural milk ejections, the amplitude of the response was 5·5±1·8 kPa (mean±SD) and the duration of response at half the peak amplitude was 6·8±1·6 s. In response to oxytocin a threshold response occurred at 60 mIU oxytocin with no further change up to 200 mIU. The amplitude of the response to an i.v. dose of 60–200 mIU oxytocin (5·5±2·2 kPa) and duration (6·4±1·7 s) were similar to that during a natural milk ejection. The responses of two galactophorous ducts of a teat measured simultaneously were similar in peak amplitude and duration. When the responses of four glands of a sow were measured simultaneously, there was a lag time in the onset of the IMP peak from the anterior to the posterior glands, and an increase in the peak amplitude from anterior to posterior. Both during natural milk ejections and in response to oxytocin injections, there were significant differences in peak amplitude between sows. We also aimed to determine whether the pressure or duration of milk flow during natural milk ejections was limiting piglet growth rates. IMP of nine sows and the growth rates of their piglets were measured. Both the peak amplitude of IMP response and the growth rate of piglets increased over the course of lactation, but the relationship was not causal. We found that the growth rate of piglets did not depend on IMP amplitude or duration, but we suggest that it may depend on the frequency of suckling and/or the ability of piglets to withdraw milk while it is available.

Keywords: Piglet, growth rate, peak amplitude, duration.

A contradiction exists between lactation physiology of the sow and piglet growth in that piglets fed *ad libitum* grow almost twice as fast as suckling piglets (Williams, 1995). However, the sow has the ability to produce a greater volume of milk than is removed by the piglets (Auldist & King, 1995; Spinka et al. 1997). The growth rate of piglets is related to milk consumption (King et al. 1989). Thus, if we are to optimize the growth rates of piglets we need to understand better the control of lactation in the sow during established lactation. Compared with other domesticated mammals, the most distinctive feature of lactation in the sow is the strict control on the duration of milk flow (10–15 s) during each suckling (Whittemore & Fraser, 1974). It is probable that the amount of milk taken in by the piglet is determined by its ability to remove milk over this period, rather than by the sow's capacity to produce milk. It follows that for a given litter size, milk production in the sow would increase if the frequency of successful sucklings increased, if stronger piglets withdrew more milk at each suckling, or if the pressure or duration of milk flow at each suckling increased.

Milk flow in the sow, as in most mammals, occurs in response to stimulation of the teats resulting in the release of oxytocin from the posterior pituitary gland, which in turn causes contraction of the myoepithelial cells surrounding the alveoli. This process is termed the milk ejection reflex (Tindal, 1974). Since the contraction of the myoepithelial cells results in an increase in intramammary pressure (IMP), this can be utilized as a method for studying the milk ejection reflex. Early studies in the lactating sow

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recorded IMP in response to an i.v. injection of oxytocin or whole pituitary extract (pituitrin) (Whittlestone, 1954a, b). Although these studies provided relevant information on the IMP response in sows, the number of animals was limited and the equipment used was relatively insensitive. Furthermore, Ellendorff et al. (1982) reported studies on the IMP responses to both a natural milk ejection and milk ejection induced by i.v. oxytocin. However, these measurements were made on sows that had been cannulated over 12 h before measurement, without subsequent milk removal from the cannulated glands. Kim et al. (2001) have shown that significant involution of unsuckled glands occurs within 48 h. Therefore it is possible that involutional changes were occurring when measurements were made. Measurements were made on some of these sows during a 3-h period of anaesthesia.

Therefore, we aimed to characterize the IMP response of lactating sows under physiological conditions using a sensitive and non-invasive method on a larger number of animals, both during natural milk ejections and in response to i.v. oxytocin. In addition, we aimed to obtain quantitative measurements of the milk ejection reflex during the first 3 weeks of lactation and study their relation to piglet growth.

Materials and Methods

Animals

Sows (*Sus scrofa*) of breeds Landrace, Large White, Landrace × Large White, and their litters were housed in farrowing crates at an intensive commercial piggery (Wandalup Farms Piggery, Mandurah, WA 6210, Australia). The sows were studied in their farrowing crates and no anaesthesia or restraint were used for cannulation of the ear vein or the galactophorous ducts, or for measurement of IMP. For characterization of the IMP response, the sows had a mean parity of 3 ± 1 (SD), and included two first-parity gilts. There were nine or ten piglets in each litter. For all these studies the IMP measurements were made on sows on either day 5 or 6 of lactation, when lactation was established. The investigation of the relationship between milk ejection and piglet growth used a total of nine sows of parities 1–4, including two first-parity gilts. There were 5–11 (average 8·3) piglets in each litter. Sows were selected during farrowing and the IMP measurements were made on days 1, 7, 14 and 21 of lactation. All piglets in the litter were numbered and weighed (Mettler PM16 integrating electronic balance, Mettler Toledo Ltd, Port Melbourne, VIC 3207, Australia) on the day of farrowing and on days 1, 7, 14 and 21 of lactation. The procedures described were approved by the Animal Ethics Committee at The University of Western Australia.

Measurement of IMP

IMP was measured by recording the change in pressure through a disposable pressure transducer (Cobe Laboratories, Frenchs Forest, NSW 2086, Australia) attached to an amp bridge (ADInstruments, Castle Hill, NSW 2154, Australia) and recorded using the computer hardware, MacLab (ADInstruments) and software package Chart v3.5.7 (ADInstruments) on a portable computer (Macintosh). A Venflon cannula (diameter 0·8, length 25 mm) (Viggo AB, SE-252027 Helsingborg, Sweden), with needle removed, was attached by Luer lock connection to the disposable pressure transducer and filled with sterile saline (Baxter Healthcare Pty Ltd., North Ryde, NSW 2113, Australia). The transducer was then connected via an interconnect cable (Cobe Laboratories) to the amp bridge and the output was recorded. The system was calibrated by attaching the cannula to a column of water. The voltage at a height of zero cm was measured and recorded as zero kPa. The column of water was increased to a height of approximately 100 cm and the voltage measured. The height of the column of water in cm was multiplied by 0·0981 to give the pressure in kPa. To measure the IMP response within the gland, the cannula was inserted 2·5 cm into the opening of the galactophorous duct in the teat of the sow and the fluid within the cannula was made contiguous with the fluid in the gland by injecting 0·5 ml of sterile saline via the filling cap on the cannula. Therefore, the measurement of IMP was actually a measure of the pressure within the galactophorous duct. A stable baseline pressure was established before an IMP response was measured.

IMP measured during a natural milk ejection

The IMP response was measured during natural milk ejections by cannulating one or two teats of nine sows just before the milk ejection occurred for one to three sucklings. The Venflon cannula was inserted into one of the two galactophorous ducts in the teat. Piglets sucking the cannulated teats and one or two adjacent piglets were removed, leaving sufficient piglets to stimulate a natural milk ejection. The IMP response was recorded continuously from at least 10 s before milk ejection until approximately 1 min after the commencement of the rise in IMP until the pressure was once again stable. The IMP response was recorded and the peak amplitude (kPa) was measured. Since the pressure did not always return to the original baseline, the width of the peak (in seconds) at half the peak amplitude was used as a measure of the duration of the IMP response (Fig. 1a).

IMP measured after i.v. injections of oxytocin

The ear of each of five of the above sows was shaved and an ear vein cannulated with a Venflon cannula (diameter 0·8, length 25 mm) attached to an extension tube (12·5 mm) and three-way tap (Perth Surgical Supply Company Pty Ltd., Balcatta, WA 6021, Australia). The cannula was taped in place and flushed with 5 ml heparinized saline (20 U ml^{-1}) (Commonwealth Serum Laboratories,

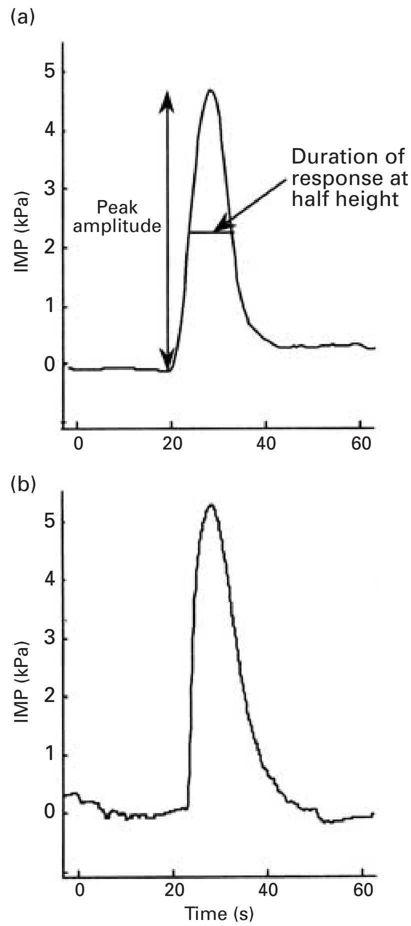

Fig. 1. Intramammary pressure (IMP) response in a gland of a sow (a) during a natural milk ejection, and (b) after an i.v. dose of 100 mIU oxytocin.

Melbourne, Vic 3000, Australia). Before each dose of oxytocin, the cannula was flushed with heparinized saline (2 ml). Three of the sows were given five i.v. injections of oxytocin at 5-min intervals. In random order, a range of oxytocin doses (20, 30, 40, 50, 60, 100 and 200 mIU in 0·1 ml saline; Heriot Agvet Pty Ltd., Rowville, Vic 3178, Australia) was injected into the cannula and flushed through with a further 2·5 ml of heparinized saline. A minimum interval of 5 min was allowed between injections. The IMP response of two individual glands to oxytocin was recorded and the peak amplitude and duration of the response were measured.

IMP measured from two galactophorous ducts

Each teat normally has two galactophorous ducts draining separate, interdigitated mammary glands. Both ducts of one or two glands of three sows were cannulated and the IMP responses were measured simultaneously after an injection of oxytocin (100 mIU) into an ear vein cannula. Measurements of each pair of ducts were made on two to four occasions on the same day.

IMP measured simultaneously

The IMP response of five sows was measured in four glands on the same side simultaneously. Piglets were removed from the sow and cannulae inserted into the most anterior teat (gland 1) and glands 2, 3, 4 or glands 3, 4 and 6 also were cannulated. The IMP response and the latency (time from injection of 100 mIU oxytocin to the onset of increase in pressure) of all four glands was recorded simultaneously. The responses to two or three injections were recorded for each sow, with an interval of at least 5 min between injections. Preliminary studies on three sows showed that the CV of the peak amplitude in response to five consecutive doses of 100 mIU every 5 min was $<6\%$, and there was no trend to increasing or decreasing amplitudes.

IMP relationship to piglet growth

The IMP response during one natural milk ejection on each of days 1, 7, 14 and 21 was measured by cannulating one or two teats of sows as above. Teats were cannulated when it was observed that piglets were nuzzling the udder and the sow was grunting. To avoid potential differences in the IMP response between the anterior and posterior glands of a sow, we chose to study the IMP response of the third and fourth glands from the anterior. Occasionally the teat of gland 1, 2 or 5 was cannulated if gland 3 or 4 was inaccessible. Piglets sucking these teats were removed prior to cannulation and it was sometimes necessary to remove several adjacent piglets. A baseline pressure was established and the IMP response measured during the natural milk ejection. A successful milk ejection was monitored by the rapid suckling of piglets and the visible removal of milk. The peak amplitude of the IMP response was measured and the duration of the response was determined as above.

Statistical analysis

Results are presented as mean ± SEM unless otherwise stated, *n* is the number of observations. Comparisons of the IMP responses were performed with peak amplitude and the duration at half peak amplitude as dependent variables. During natural milk ejections one-way analysis of variance was used (SuperANOVA, Abacus Concepts Inc. Berkeley, CA 94704, USA, 1989) with sow as the main effect. Since the responses to different doses of oxytocin were measured in the same gland two-way repeated measures analysis of variance was used (SuperANOVA) with dose of oxytocin and sow as the main effects. Comparisons between two galactophorous ducts of one gland were made using paired *t* test. When multiple glands of each sow were compared, two-way repeated measures analysis of variance was used (SuperANOVA) with peak amplitude, the duration at half peak amplitude and latency as the dependent variables, and gland and sow as the main effects.

Comparisons of IMP responses on days 1, 7, 14 and 21, and comparisons of growth rates as the dependent variable during days 1–7, 7–14 and 14–21 were made using two-way repeated measures analysis of variance (SuperANOVA) with time and sow as the main effects. Correlations of the rate of growth of piglets, the peak amplitude and duration of the IMP response with the number of piglets being fed by each sow were made using Statview SE+graphics (Abacus Concepts). Pearson partial correlation coefficients relating piglet growth rates to amplitude and duration of the IMP response were calculated using the SAS System for Windows v. 6.12 (1998), The SAS Institute Inc., Cary NC, USA. *P* values >0·05 were considered not significant.

Results

IMP during a natural milk ejection

A typical IMP response during a natural milk ejection is shown in Fig. 1a. Peak amplitude and duration of the IMP response for all sows are shown in Table 1. The peak amplitude ranged from 2·97–9·12 kPa and the duration from 4·8–11·8 s. There was a significant difference between sows in peak amplitude (*P*=0·008) but not in the duration of the response.

IMP response to oxytocin

Peak amplitude and duration of the IMP response over a range of oxytocin doses are shown (Table 2). There were differences between sows in the peak amplitude (*P*=0·0004) and duration (*P*=0·0001). The differences between sows in peak amplitude occurred in response to all doses of oxytocin except 30 and 60 mIU, and the differences in duration between sows occurred in response to all doses of oxytocin except 50 and 60 mIU. There was an increase in peak amplitude between 20 and 50 mIU oxytocin (*P*=0·045) but no difference between 30, 40 and 50 mIU. There was a significant increase in peak amplitude between 50 and 60 mIU oxytocin (*P*=0·037) at which a threshold response to oxytocin was reached, and beyond which there was no significant difference in the peak amplitude of the IMP response with doses up to 200 mIU of oxytocin. There was no difference between doses in duration of the response.

It is noteworthy that the peak amplitudes of the IMP response after i.v. injections of 60–200 mIU oxytocin did not differ significantly from that during a natural milk ejection. Nor did the duration of the IMP response to 60–200 mIU oxytocin differ significantly from that during a natural milk ejection. Therefore to ensure that a physiological IMP response was elicited in later studies a dose of 100 mIU oxytocin was used (Fig. 1b). This dose was chosen to allow for the possibility that an occasional sow may have a threshold higher than 60 mIU oxytocin.

Table 1. The intramammary pressure response of the glands of nine sows during natural milk ejection

			Coefficient of variation (%)	
	Mean ± SD	*n*	Within-sow	Between-sow
Peak amplitude (kPa)	5·46 ± 1·80	22	16·79	17·34
Duration (s)	6·82 ± 1·63	20	10·09	10·16

Variability of IMP between ducts within a teat

Eleven comparisons were made between the IMP responses of anterior and posterior galactophorous ducts. The responses occurred simultaneously. There was no significant difference in the peak amplitudes of the IMP response in anterior and posterior ducts (5·51 ± 0·44 kPa and 5·15 ± 0·35 kPa, respectively). Nor was there any significant difference in the duration of the response in anterior and posterior ducts (6·4 ± 0·4 and 6·7 ± 0·4 s, respectively).

Variability of IMP response between glands of a sow

The IMP responses in four glands of one sow after an i.v. injection of oxytocin are shown in Fig. 2 and the results are presented in Table 3. Although there was no significant difference between sows in the peak amplitude, there was a difference between glands within sows (*P*=0·0004), with the response of gland 4 being higher than that of gland 1 (*P*=0·03). The peak amplitude measured in the most posterior gland (gland 6) of two sows was quite different, with one sow showing a much higher response in that gland compared with the more anterior glands, and the other showing a much lower response. The latter may have been undergoing involution. There was a significant difference in the duration of the response between glands (*P*=0·005), but not between sows.

There was a delay in IMP response to exogenous oxytocin between the anterior and the posterior glands (Fig. 2, Table 3). Latency for gland 1 after the injection of oxytocin was different from that of gland 2 (*P*=0·003) and there was a further delay between gland 3 and gland 4 (*P*=0·001). There was no difference in latency between glands 4 and 6. The lag time between glands 1 and 4 was 3·18 ± 0·58 s (*n*=11) and between glands 1 and 6 was 2·78 ± 0·12 s (*n*=7). One of the sows showed a different pattern of response, with the increase in IMP of gland 2 being delayed and coinciding with that of gland 4.

Effect of stage of lactation on IMP

Since the IMP peak amplitude during a natural milk ejection was variable between glands of a sow, we used the responses of two glands in the mid-section of the sow to be representative of the IMP response of the whole sow for the comparison of the growth rates of all the piglets within

Table 2. The intramammary pressure response of the glands of five sows to i.v. injections of oxytocin

	Peak amplitude (kPa)			Duration (s)		
Oxytocin dose (mIU)	Mean ± SD	n	CV (%)	Mean ± SD	n	CV (%)
20	1·47 ± 2·65[a]	13	181	4·53 ± 1·60[a]	4	35
30	2·75 ± 1·61[a,b]	16	64	7·56 ± 1·90[a]	9	25
40	2·97 ± 1·52[a,b]	19	52	7·19 ± 2·15[a]	19	30
50	2·76 ± 2·32[b]	24	74	6·92 ± 2·56[a]	21	38
60	5·09 ± 2·29[c]	10	58	6·11 ± 2·51[a]	10	38
100	5·79 ± 2·01[c]	26	39	6·50 ± 1·64[a]	26	25
200	5·67 ± 2·03[c]	12	36	6·64 ± 1·27[a]	11	19
60–200	5·51 ± 2·15[c]	48	39	6·39 ± 1·69[a]	47	26

Within a column, values without common superscripts differ significantly ($P<0·05$)

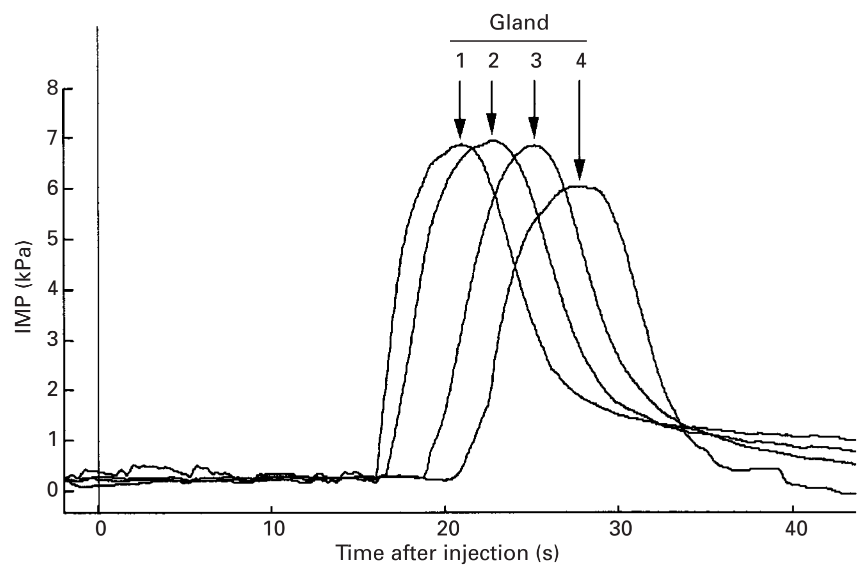

Fig. 2. Intramammary pressure (IMP) response of four glands from one sow measured simultaneously after an i.v. dose of 100 mIU oxytocin.

a litter. The sows were identified with letters A to D and F to J and the characteristics of the sows and their piglets are presented in Table 4. Peak amplitude and duration of the IMP response throughout lactation are presented in Table 5. Peak amplitude of the IMP response on day 1 of lactation was significantly lower than at any other stage of lactation ($P=0·0015$). The peak amplitude of the IMP response was lower on day 7 than on days 14 or 21 of lactation ($P<0·005$). However, there was no significant difference in the peak amplitude between days 14 and 21 of lactation. The duration of the IMP response was greater on day 1 than on days 7, 14, and 21 of lactation ($P<0·0001$). However, there was no significant difference between the duration of IMP response on days 7, 14 and 21 of lactation.

Effect of IMP on piglet growth

Piglet weight at birth was 1·29±0·04 kg ($n=75$) and increased to 6·34±0·18 kg ($n=75$) by day 21 of lactation. The growth rate increased from days 1–7 to days 7–14 ($P=0·0001$), and increased further from days 7–14 to days 14–21 ($P=0·016$) (Table 5). There were differences between sows in both the birth weights of piglets ($P<0·02$) and the growth rates of litters ($P<0·013$) (Table 4). There were significant relationships between the birth weight and the growth rate of the piglets during days 1–7, 7–14, and 14–21 ($r^2=0·126$, 0·191, 0·098; $P=0·002$, 0·0001, 0·007, respectively; $n=75$). There was no significant relationship between the number of piglets being suckled by each sow and the rate of growth of its piglets, or the peak amplitude or duration of the IMP response. Though both the growth rate and the peak amplitude of the IMP response increased over the lactation period, when the effect of duration of lactation was eliminated there was no relationship between the peak amplitude and the growth rate (Pearson partial correlation coefficient=0·06, $P=0·79$). In addition, there was no relationship between the duration of the IMP response and the growth rate (Pearson partial correlation coefficient=−0·17, $P=0·43$).

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Table 3. The intramammary pressure response of four glands (1, most anterior–6, most posterior) from five sows to i.v. injections of 100 mIU oxytocin

Values are means ± SEM

Gland	Peak amplitude (kPa)	Duration (s)	Latency† (s)	n
1	4.93 ± 0.28^{a}	7.28 ± 0.22^{a}	15.6 ± 0.7^{a}	15
2	$5.66 \pm 0.26^{a,b}$	7.52 ± 0.30^{a}	18.4 ± 0.8^{b}	8
3	$5.46 \pm 0.31^{a,b}$	6.72 ± 0.22^{b}	17.2 ± 0.7^{b}	15
4	5.94 ± 0.35^{b}	$6.62 \pm 0.35^{b,c}$	18.6 ± 0.9^{c}	11
6	7.29 ± 0.68^{c} ($n=4$) 1.14 ± 1.06^{d} ($n=3$)	$7.60 \pm 0.41^{a,b}$	17.1 ± 1.0^{c}	7

† Latency is the time from injection of oxytocin to rise in pressure
Values within a column without common superscripts differ significantly ($P<0.05$)

Table 4. The birth weights and growth rates of the piglets of nine sows in the first 21 d of lactation

Values are means ± SEM

Sow	Parity	Number of piglets	Birth weight (g)	Piglet growth rate (g/d) (over 21 d)
A	3	8	1322 ± 67^{a}	285.1 ± 7.4^{a}
B	3	11	1346 ± 57^{a}	274.1 ± 16.2^{a}
C	1	8	1317 ± 75^{a}	181.8 ± 15.0^{b}
D	4	9	901 ± 53^{b}	182.8 ± 14.0^{b}
F	1	9	1465 ± 41^{a}	256.4 ± 16.3^{a}
G	1	5	1865 ± 93^{d}	271.0 ± 21.1^{a}
H	4	9	1260 ± 81^{c}	244.2 ± 14.7^{a}
I	3	8	$1073 \pm 59^{b,c}$	248.2 ± 17.9^{a}
J	2	8	1413 ± 87^{a}	284.4 ± 18.1^{a}

Within a column, values without common superscripts differ significantly ($P<0.05$)

Discussion

Most of these studies were performed on days 5–6 of lactation to ensure that lactation was established. They were carried out before we had found evidence that IMP responses changed up to day 14. However, this does not invalidate within-sow comparisons. Moreover, comparisons with the results of other investigators can only be made in general terms because the stage of lactation of the sows in their studies was not defined. The peak amplitude of the IMP response measured during a natural milk ejection in the sow was almost double that measured by Whittlestone (1954a) after an i.v. injection of oxytocin (500 mIU). Our results, however, are in agreement with measurements made by Bruhn et al. (1981) who found pressure amplitudes of 4·0–6·7 kPa during a natural milk ejection in the sow. The amplitudes measured by Ellendorff et al. (1982) (2·7–5·3 kPa) are similar to ours between days 1 and 7, yet they measured responses 12–24 h after the catheters were inserted into the ducts, that is, 12–24 h after the last suckling from that teat. Although Atwood & Hartmann (1995) found no changes in the composition of milk during the first 5 h following partial weaning, the mammary glands of sows may be influenced by autocrine mechanisms (Atwood et al. 1995) which may, in turn, influence the IMP response to oxytocin after longer intervals.

Whittemore & Fraser (1974) found the duration of milk flow during natural milk ejection by hand-milking to be 10–15 s. In response to doses of 50–500 mIU of oxytocin or pituitrin, the duration of milk flow determined by hand-milking was 14·1–45·1 s (Whittlestone, 1954a). In that study, milk flow coincided with the increase in IMP in an adjacent gland and usually ceased when the IMP returned to baseline levels, but it sometimes ceased when the IMP was still significantly above baseline. Ellendorff et al. (1982) used IMP to assess the duration of natural milk ejection as the interval between the onset of the rise in IMP and the return to baseline. They found that duration of milk ejection was not easy to determine owing to large variations, but they estimated it to be 8–41 s. Considering both this variability and the difficulty in determining accurately the time at which the IMP returns to baseline (Fig. 1a), we decided to use the duration of the IMP response at half the peak amplitude as a measure of the duration of milk ejection. We found that the ranges of duration of the IMP response at half peak amplitude were 4·8–11·8 s and 3·1–11·5 s for milk ejections in natural nursings and those in response to 100 mIU of oxytocin, respectively. When the pressure did return to the original baseline, the time for which the IMP was above baseline was twice the duration at half the peak amplitude. If milk was able to flow for all this time, this would give a range of duration of milk ejection of 6·2–23·6 s, which is consistent with the milk flow data of Whittemore & Fraser (1974) and less variable than the data of either Whittlestone (1954a) or Ellendorff et al. (1982).

We established a dose-response curve and a threshold response to oxytocin in the lactating sow. Doses of oxytocin >60 mIU did not elicit higher IMP amplitudes. Furthermore, the peak amplitude of the IMP response to a dose of 60 mIU or more was similar to that observed during a natural milk ejection. The suggestion of 60 mIU as a threshold is also supported by the high variability of peak amplitude in response to doses up to 50 mIU (CV 52–181%) and the lower variability of responses to doses of 60–200 mIU (CV: 36–58%) (Table 2). Previous studies provide no evidence for a dose-response curve of IMP response to oxytocin. Whittlestone (1954b) reported that, in two sows, doses of oxytocin equivalent to or greater than 50 mIU consistently resulted in a milk ejection. We found that the IMP response was not consistent at 50 mIU of oxytocin. Our method of IMP measurement was more sensitive than that used in Whittlestone's study, thus a lower IMP response could be more accurately recorded. Yet, our results are in agreement with a very low response at 25 mIU oxytocin in most sows, as was observed by Whittlestone (1954b). Ellendorff et al. (1982) measured IMP responses to increasing doses of oxytocin but did not indicate whether a statistical relationship existed between

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Table 5. The intramammary pressure (IMP) response of nine sows during natural milk ejections and the growth rates of their piglets in the first 21 d of lactation

Values are means ± SEM of two glands per sow

Days of lactation	IMP peak amplitude (kPa)	CV (%)	IMP duration (s)	CV (%)	Piglet growth rate (g/d) (over previous 7 d)	CV (%)
1	2·93 ± 0·31[a]	38	14·1 ± 1·3[a]	35	N/A	
7	5·33 ± 0·53[b]	30	6·5 ± 0·4[b]	20	196·4 ± 17·7[a]	22
14	7·79 ± 0·40[c]	21	6·6 ± 0·5[b]	29	256·6 ± 12·7[b]	15
21	7·52 ± 0·84[c]	34	6·1 ± 0·3[b]	17	289·7 ± 14·3[c]	15

Within a column, values without common superscripts differ significantly ($P<0·05$)

amplitude and dose. Furthermore, the measurements were made in teats that had been cannulated at least 12 h prior to the measurement of IMP and therefore the possibility of early involutionary changes cannot be dismissed. Kim et al. (2001) show that significant involution of unsuckled glands occurs within 48 h.

Although there was no significant difference between the IMP responses measured in two galactophorous ducts of one mammary gland, the variability of responses in both peak height and duration was at least as much as the variability between glands. This emphasizes the fact that the two galactophorous ducts of one teat drain two separate mammary glands.

The latency from injection of oxytocin to the rise in IMP was previously determined by measuring the time between injection of oxytocin and the occurrence of milk ejection determined by hand milking (Whittlestone, 1954a). For a 'front' gland of two sows the latency was found to be 17·4–28·9 s and 14·1–17·2 s, respectively. It was Ellendorff et al. (1982) who demonstrated that the onset of quiet suckling by the piglets, i.e. the availability of milk, coincided with the onset of the rise in IMP. These authors determined the latency by measuring the time from injection of oxytocin to increase in IMP and found values to be 15·5 ± 1·0 s for the anterior three glands of anaesthetized sows, which is similar to our value of 15·5 ± 0·8 s for the most anterior gland in conscious sows. Thus, while nonremoval of milk from a gland for more than 12 h (Ellendorff et al. 1982) has the potential to result in involutionary changes (Kim et al. 2001) neither this nor the anaesthesia affected the latency of response to exogenous oxytocin.

We found that the IMP response to oxytocin showed a lag time along the udder, from anterior to posterior glands. Ellendorff et al. (1982) measured a lag time of 3·8 s between IMP responses of an anterior and a posterior gland separated by 80 cm. The measurement of a lag time of 3·2 s from gland 1 to gland 4 with our technique was not dissimilar. Since oxytocin is secreted from the pituitary gland and travels in the blood to the mammary glands, blood flow may influence the timing of milk ejection between teats. In the sow, the anterior mammary glands are supplied by branches of the internal thoracic and by the caudal superficial epigastric arteries, while the posterior mammary glands are supplied by branches of the pudendal artery (Trottier et al. 1995). The increase in latency from gland 1 to gland 4 was therefore consistent with the pattern of blood supply from anterior to posterior. Anastomosis of the anterior and posterior arteries has been suggested (Trottier et al. 1995), but the location of the anastomosis is unknown. Some mammary glands in the abdominal region may therefore receive blood from both the anterior and posterior arteries. Each sow in the current study was suckling nine or ten piglets and since piglets prefer anterior teats (Dyck et al. 1987) it was not possible to study glands 4, 5, 6 and 7 simultaneously on day 6 owing to the regression of some of the glands. Indeed, the low response in gland 6 of one of the sows (Table 3) may be due to the commencement of regression of the gland (Kim et al. 2001). When glands 4 and 6 were measured simultaneously there was no significant difference in the latency. Therefore it was not possible to illustrate the posterior to anterior blood flow in the inguinal region. The lag time between the anterior gland 1 and the posterior gland 6 may be due to the delay in blood entry from the anterior artery, or to blood in the posterior artery taking longer to reach the gland. While the duration of the IMP response was similar between glands within a sow, the posterior glands 4 and 6 usually showed a higher amplitude of response. This was unexpected because the evidence of Dyck et al. (1987) suggested that anterior suckled glands produced heavier piglets. Nielsen et al. (2001) also found that piglets suckling anterior glands had higher growth rates, but only in multiparous sows; they found no difference in growth rates of piglets suckling anterior or posterior glands of primiparous sows.

Colostrum is freely available from the mammary glands prior to parturition until about day 2 in the sow, when the flow of mammary secretions is closely regulated. This was reflected by the observed changes in IMP. Indeed, while the IMP peak amplitude on day 1 was significantly lower than on days 7, 14 and 21 of lactation, the duration of the milk ejection on day 1 was much longer than that during established lactation.

The growth rate of piglets in this study was lowest in the first week after birth and increased thereafter, similar to the growth rates of 183, 219 and 236 g/d during days 4–7, 7–12 and 12–22, respectively, calculated from the data of King et al. (1989) from a study of six sows suckling 6–10

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piglets. In addition, Auldist et al. (2000) in a study of six sows each suckling six piglets found a higher piglet growth rate during days 14–28 (283 g/d) than during days 0–14 (222 g/d). The growth of the piglets in the present study was related to the birth weight, consistent with the findings of Dwyer et al. (1993). This provides a possible explanation for the low growth rate of the piglets of sow D in our study, but does not explain the low growth rate of the piglets of sow C. The variation in peak amplitude and duration of IMP during natural milk ejections between sows and the variation in the growth rates of their piglets provided an opportunity to undertake a preliminary investigation of the possibility of a causal relationship between the characteristics of milk ejection and milk intake.

If the duration of the IMP response controlled milk intake, a longer duration of milk flow would be expected as the milk intake of the piglets increased throughout lactation. The duration of the IMP response decreased after day 1, however, and Pearson partial correlation analysis showed no relationship between duration of the IMP response and the growth rate of the piglets. Therefore, the duration of the IMP response cannot be a controlling factor. Since IMP peak amplitude increased from days 1–14 and both this study and others (King et al. 1989; Auldist et al. 2000) showed increasing growth rates of piglets as lactation proceeds, it is tempting to hypothesize that milk yield was dependent on IMP peak amplitude. Despite the variability of peak IMP response between sows, and the comparatively low growth rates of two litters of piglets, however, if we allow for effects of stage of lactation, there was no relationship between IMP peak amplitude and piglet growth rate. The present study suggests that we should consider other factors in the control of growth rate.

In summary, we have developed a non-invasive, simple and sensitive method to measure IMP in the domestic sow. The technique is suitable for the measurement of IMP both during a natural milk ejection and following i.v. injections of oxytocin. We found that, during established lactation, there was a threshold response to oxytocin, equivalent to 60 mIU. We confirmed previous observations that the latency after an oxytocin injection into the ear vein of sows is about 15 s and that there is a lag time in the IMP response along the udder, from anterior to posterior. Our results indicate, however, that piglets suckling posterior teats are not disadvantaged with respect to exposure to milk ejection. Rather than anterior suckled teats producing heavier piglets (Dyck et al. 1987), it may be that stronger piglets prefer anterior teats, as suggested by Nielsen et al. (2001) for multiparous sows. There was no evidence that the growth rate of piglets was dependent on either the pressure or duration of milk flow during natural milk ejection. We suggest that growth rate is more likely to be influenced by the frequency of suckling and/or the ability of piglets to withdraw milk while it is available.

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