

From the State Veterinary Serum Laboratory, Copenhagen, Denmark.

STUDIES ON IMMUNOGLOBULINS AND TRYPSIN INHIBITOR IN COLOSTRUM AND MILK FROM SOWS AND IN SERUM OF THEIR PIGLETS*

By

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THODE JENSEN, P. and K. B. PEDERSEN: *Studies on immunoglobulins and trypsin inhibitor in colostrum and milk from sows and in serum of their piglets*. Acta vet. scand. 1979, 20, 60—72. — The concentrations of IgG, IgM, IgA and the specific sow colostrum trypsin inhibitor (SCTI) were measured by radial immunodiffusion in colostrum and milk samples from sows and in serum samples from their offspring during the suckling period. A clear time dependence was found for all the measured variates in both whey and serum. Statistically significant positive correlations were found between, on the one hand, concentrations of IgG and IgA, but not IgM, in sera from 39 suckling piglets 1 and 3 days old, and, on the other hand, concentrations of the same immunoglobulins and of the trypsin inhibitor in maternal colostrum ($n = 7$). Multiple regression analyses showed that at day 1 and day 3 the levels of both IgG and IgA in serum samples from the suckling piglets were positively influenced by both the SCTI and the IgG or IgA contents in maternal colostrum.

pig immunoglobulins; sow colostrum trypsin inhibitor; immunoglobulin absorption.

The antibody dependent immunity in newborn and young pigs rests almost entirely upon antibodies from the maternal colostrum, absorbed from the gut during the first and second day of life or exerting a local function in the gastrointestinal canal (for rev. see *Bourne* 1976). The immunoglobulins known to be related to immunity in pigs are IgG, IgM and IgA (*Porter & Allen* 1972). These are all relatively resistant to acid denaturation in the stomach, and the secretory IgA is resistant also to

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enzymic proteolysis in the gut (Tomasi & Bienenstock 1968). For protection of the other immunoglobulins in the gut the presence of the specific sow colostrum trypsin inhibitor (SCTI) is assumed to be essential (Baintner 1973).

An immunochemical method to measure the concentration of SCTI in biological fluids has previously been described (Jensen 1977).

The object of the present study was, through simultaneous measurements of the levels of IgG, IgM, IgA and SCTI in colostrum and milk from sows and of the levels of immunoglobulins in serum from their offspring, to relate the serum immunoglobulin uptake in the piglets to the SCTI levels in the ingested maternal colostrum.

MATERIAL AND METHODS

Animals

The investigation included 9 SPF Danish Landrace sows and the suckling piglets of some of these sows. In all parts of the study the animals used were randomly selected.

Colostrum, milk and serum

Colostrum and milk samples were collected at parturition and at varying intervals during lactation, each sample consisting of a pool of secretions from a number of teats. Fat was removed by centrifugation at $18,000 \times g$ for 1 hr. at 4°C . The fat layer at the top and the pellet at the bottom were discarded. Whey was produced from de-fatted colostrum and milk by the method of Aalund (1968). Blood samples were drawn from the anterior vena cava of the piglets at fixed intervals after they had started colostrum ingestion. The blood samples were allowed to clot, whereafter the serum was separated by centrifugation. All serum samples were frozen as soon as possible and stored at -20°C until analysed. A serum pool for preparation of IgG and IgM and for use as reference in quantitations was made from 100 blood samples collected from normal bacon pigs at slaughter. A whey pool for IgA preparation was made from milk samples taken from each of 20 sows on the 10th day of lactation. Serum and milk whey were prepared as described above and stored at -20°C until used. The reference serum pool was divided in 1-ml volumes and stored at -70°C .

Chromatographic methods

Ion exchange chromatography was performed at 4° C on a 5 × 30 cm DEAE-Sephadex A-50 column (Pharmacia, Sweden). A 0.1 M tris-HCl 0.05 M-NaCl 15 mM-NaN₃ buffer, pH 8.3, was used for swelling the gel and for the elution. The protein content in the effluent from the chromatography columns was monitored continuously at 280 nm on an LKB 8300 Uvicord (LKB-product AB, Sweden).

Gel filtration chromatography was performed at 4° C on a 2.5 × 90 cm Sephadex G-200 column (Pharmacia, Sweden) equilibrated with a 0.01 M tris-acetate 1.0 M-NaCl 3 mM EDTA 15 mM-NaN₃ buffer, pH 7.4, and on a 2.5 × 90 cm Sepharose 6B column (Pharmacia, Sweden) with the same buffer. A constant upward flow was maintained, and the protein concentration in the effluent was recorded as described above. Concentration of the chromatographic fractions was made by vacuum dialysis.

Preparation of porcine immunoglobulins

IgM was purified from the serum pool by the method of *Gambier & Butler* (1974) with modification, i.e. the euglobins were precipitated from serum by dialysis against a 0.01 M potassium phosphate buffer, pH 5.4, for 24 hrs. at 4° C. After repeated washing with cold dialysis buffer, the precipitate was redissolved at 37° C in a 0.01 M acetate 0.15 M-NaCl buffer, pH 5.4, and a 0.1 M-ZnSO₄ solution was slowly added at 22° C, under stirring, to a final concentration of 50 mM-ZnSO₄. After centrifugation, the zinc ions in the supernatant were chelated with tetrasodium EDTA to a concentration of 1 % (w/v) and after a second centrifugation the supernatant was dialysed against gel-filtration buffer and filtered on a Sephadex G-200 column. The top of the first peak was concentrated and rechromatography performed on Sepharose 6 B. While a small first peak was discarded, the top of the adjacent peak, judged by immunoelectrophoresis to contain "pure" IgM, was concentrated and dialysed against a tris-buffered salt solution with 0.02 % (w/v) NaN₃, pH 7.9 (TBS) and stored at 4° C.

IgG was isolated from the same serum pool as IgM. After euglobulin precipitation, the immunoglobulins were precipitated from the supernatant by addition of 22 g ammonium sulphate

per 100 ml supernatant at 4° C. After centrifugation, the precipitate was redissolved at 22° C in the swelling buffer for ion exchange chromatography, dialysed against the same buffer, and after centrifugation passed through a DEAE-Sephadex A-50 column. The ascending part of the break-through peak was concentrated, dialysed against gel-filtration buffer, and filtered on Sephadex G-200. The fractions from the first peak, judged by immunoelectrophoresis to contain almost "pure" IgG, was re-filtered on Sephadex G-200, concentrated, dialysed against TBS and stored at 4° C.

IgA was isolated from the pool of milk whey after precipitation of lipoproteins by the method of *Burstein* (1960). The immunoglobulins were precipitated by adding ammonium sulphate to the whey at 22° C (235 g/l). After centrifugation the precipitate was redissolved in gel-filtration buffer and dialysed against the same buffer. The solution was centrifuged at $30,000 \times g$ for 45 min. at 4° C and filtered through an 8 μ Millipore filter before being passed through a Sephadex G-200 column. The fractions from the top of the first peak were concentrated and gel-filtered on Sepharose 6 B. As evaluated by immunoelectrophoresis, IgA was purest and most concentrated in a second, broad elution peak. The fractions from this peak were concentrated and rechromatographed on Sepharose 6 B until a symmetric peak with "pure" IgA was obtained. The preparation assumed to be 10S—11S IgA was concentrated and dialysed against TBS and stored at 4° C. The immunoglobulin preparations were all found to be free from contaminating antigens as evaluated by immunoelectrophoresis and crossed immunoelectrophoresis against anti-porcine serum.

Preparation of antisera

Antisera were prepared by immunization of rabbits by the method of *Harboe & Ingild* (1973). Anti-porcine serum was prepared by immunization with the serum pool. Monospecific sera for IgG, IgM and IgA were obtained by absorption of antisera produced against the respective "pure" immunoglobulin preparations, as follows: Anti-IgG serum was absorbed with IgM preparation, anti-IgA serum with a pool of IgG and IgM, and anti-IgM serum with IgG and pre-nursing pig serum. The exhaustiveness of the absorptions was checked by crossed immuno-

electrophoresis against porcine serum and milk whey. The specificity of the absorbed antisera was verified by identity reactions with known specific antisera in immunoelectrophoresis (Axelsen *et al.* 1973).

Immunochemical procedures

Immunoelectrophoresis was performed by the micromethod of Scheidegger (1955). Crossed immunoelectrophoresis was performed as described by Weeke (1973b). The electrophoresis medium was a gel consisting of 1 % agarose (w/v) ("Indubiose" A 37, L'industrie Biologique Française S.A.), in a 0.016 M barbital-Na 0.003 M barbital 0.003 M sodium azide buffer, pH 8.6. The same buffer 4 times concentrated was used in the electrophoresis vessels. The electrophoresis was performed in a 0.1 cm thick gel layer on 10 × 10 cm glass slides with the equipment described by Weeke (1973a). After completion of the electrophoresis process the plates were pressed, washed, dried and finally stained with Coomassie Brilliant Blue R. Single radial immunodiffusion (SRI) for immunoquantitation (Mancini *et al.* 1965) was made in the same agarose gel plates as described above, supplemented with polyethylene glycol 6000 to a concentration of 2.5 %. The purified immunoglobulin preparations and a pool of pig serum were used as reference antigens.

Sow colostrum trypsin inhibitor was determined as described previously (Jensen 1977) using a known whey standard.

Total protein determinations

The protein concentrations in the immunoglobulin preparations were determined by the method of Lowry *et al.* (1951) using bovine γ -globulin as standard.

Statistical methods

Arithmetic mean, standard deviation and coefficient of correlation were calculated by standard procedures. Analysis of multiple regression was made by the general linear model procedure of Barr, Goodnight, Sall and Helwig, SAS Institute Inc., Raleigh, N.C., USA.

RESULTS

The concentrations of immunoglobulins and SCTI in colostrum and milk whey from 9 sows at different intervals from parturition are shown in Table 1. The content of SCTI in the whey is almost nil after a few days of lactation, and during the same

Table 1. Immunoglobulins and SCTI in colostrum and milk whey from 9 sows. The samples were collected at different intervals from farrowing.

Day	IgG g/l \pm s	IgM g/l \pm s	IgA g/l \pm s	SCTI mg/l \pm s
0	57.77 \pm 19.04	10.68 \pm 6.89	23.99 \pm 9.33	1305 \pm 232
1	14.20 \pm 5.54	3.18 \pm 2.33	7.53 \pm 2.99	445 \pm 277
2	4.54 \pm 2.80	1.84 \pm 0.69	4.04 \pm 1.85	89 \pm 74
3	1.95 \pm 1.06	1.63 \pm 0.65	3.62 \pm 1.62	36 \pm 39
7	0.69 \pm 0.28	1.21 \pm 0.33	3.19 \pm 0.94	3 \pm 5
15	0.28 \pm 0.12	1.16 \pm 0.81	2.82 \pm 0.74	0.2 \pm 0.3
22	0.18 \pm 0.07	1.26 \pm 0.64	3.38 \pm 0.78	0
30	0.21 \pm 0.07	1.47 \pm 0.84	3.91 \pm 1.41	0
45	0.20 \pm 0.06	1.66 \pm 0.46	4.64 \pm 2.03	0

period there is a rapid fall in the immunoglobulin content. While IgG and IgM continue to be present in milk whey at a low level, the IgA level begins to rise after 2 to 3 weeks of lactation. IgA is the major immunoglobulin in milk whey after 2 to 3 days of lactation. Table 2 gives the concentrations of immunoglobulins in sera from 23 piglets (offspring of 4 sows) measured at dif-

Table 2. Immunoglobulins in serum from 23 piglets — offspring of 4 sows — in relation to age.

Age (days)	IgG g/l \pm s	IgM g/l \pm s	IgA g/l \pm s
1	24.35 \pm 8.80	3.54 \pm 1.75	16.95 \pm 5.06
3	21.52 \pm 8.53	1.54 \pm 0.68	8.65 \pm 3.10
6	18.45 \pm 7.36	0.68 \pm 0.30	2.69 \pm 1.35
15	11.69 \pm 4.77	0.41 \pm 0.15	0.40 \pm 0.14
22	7.73 \pm 2.70	0.68 \pm 1.13	0.43 \pm 0.22
30	11.09 \pm 7.27	0.94 \pm 0.69	0.78 \pm 0.41
45	7.61 \pm 6.33	0.73 \pm 0.41	0.44 \pm 0.17
60	7.94 \pm 4.95	0.79 \pm 0.29	0.41 \pm 0.15

ferent ages between day 1 and day 60. Both the mean values and the standard deviations fall until the pigs are about 1 month of age; then there is a sudden rise, especially for IgG, followed by another fall. On scrutiny of the values for each litter, the rise is seen to be ascribable to pigs from 1 particular litter.

The relation between, on the one hand, the content of SCTI and immunoglobulins in colostrum collected from 7 sows at parturition, and, on the other hand, the immunoglobulin concentrations in sera collected from their suckling piglets ($n = 39$) on day 1 and day 3, is calculated as coefficients of correlation and as the regression of serum values of the piglets on colostrum values of their mothers. The correlation coefficients are given in Table 3. The equations of multiple regression are as follows:

- (1) serum-IgG-day 1_{estimate} =
 $-644.30 + 2.79 \text{ colostrum TI} + 0.12 \text{ colostrum IgG}$
 $P_{\text{TI}} = 0.04^* \quad P_{\text{IgG}} = 0.10$
- (2) serum-IgG-day 3_{estimate} =
 $-2013.01 + 2.72 \text{ colostrum TI} + 0.17 \text{ colostrum IgG}$
 $P_{\text{TI}} = 0.02^* \quad P_{\text{IgG}} = 0.01^*$
- (3) serum-IgA-day 1_{estimate} =
 $-1345.35 + 2.07 \text{ colostrum TI} + 0.28 \text{ colostrum IgA}$
 $P_{\text{TI}} = 0.03^* \quad P_{\text{IgA}} = 0.001^{**}$
- (4) serum-IgA-day 3_{estimate} =
 $-625.91 + 1.00 \text{ colostrum TI} + 0.15 \text{ colostrum IgA}$
 $P_{\text{TI}} = 0.04^* \quad P_{\text{IgA}} = 0.001^{**}$
- (5) serum-IgM-day 1_{estimate} =
 $589.62 - 0.23 \text{ colostrum TI} + 0.04 \text{ colostrum IgM}$
 $P_{\text{TI}} = 0.15 \quad P_{\text{IgM}} = 0.17$
- (6) serum-IgM-day 3_{estimate} =
 $256.37 - 0.05 \text{ colostrum TI} - 0.02 \text{ colostrum IgM}$
 $P_{\text{TI}} = 0.49 \quad P_{\text{IgM}} = 0.32$

where P_{TI} and P_{Ig} express the probabilities of the regression of piglet-serum Ig's on colostrum TI and Ig's being due to chance. The partial regression coefficients and their P values for TI and Ig's are calculated after correction for influence of Ig on TI and TI on Ig, respectively.

The concentration of trypsin inhibitor in colostrum is almost statistically significantly correlated with the serum levels of IgG

Table 3. Coefficients of correlation between concentrations of IgG, IgM and IgA in serum from 39 suckling piglets 1 and 3 days old (s-Ig-d1 and s-Ig-d3) and concentrations of the immunoglobulins and the TI in colostrum of their mothers (n = 7). Figures in brackets give the probabilities of the coefficients being due to chance.

	s-IgG-d1	s-IgM-d1	s-IgA-d1	s-IgG-d3	s-IgM-d3	s-IgA-d3	Colostrum TI
Colostrum TI	0.31 (0.06)	-0.22 (0.19)	0.33 (0.04)*	0.32 (0.049)*	-0.13 (0.44)	0.31 (0.06)	
Colostrum IgG	0.24 (0.14)	-0.21 (0.21)	0.05 (0.76)	0.38 (0.02)*	-0.15 (0.37)	0.22 (0.17)	-0.05 (0.77)
Colostrum IgM	-0.09 (0.56)	0.20 (0.22)	0.46 (0.003)**	0.19 (0.26)	-0.17 (0.29)	0.48 (0.002)**	0.08 (0.64)
Colostrum IgA	-0.09 (0.57)	0.09 (0.57)	0.50 (0.001)**	0.27 (0.10)	-0.33 (0.04)*	0.52 (0.007)**	0.05 (0.74)

* $P < 0.05$ ** $P < 0.01$.

and IgM in the piglets on days 1 and 3 after birth. The serum IgG level is significantly correlated with the colostrum IgG level only on day 3 after birth, whereas for the IgA levels the correlation is significant on both day 1 and day 3. The correlation between colostrum IgM and piglet-serum IgA on day 1 and day 3, and between colostrum IgA and piglet-serum IgM on day 3, could be explained by the fact that there is a high correlation between IgA and IgM in colostrum ($r = 0.92$).

The positive partial regression coefficients and the significant P_{TI} and P_{Ig} values (* $P < 0.05$; ** $P < 0.01$) in the regression equations 1—4 indicate that the IgG and the IgA levels in serum from suckling piglets on day 1 and day 3 are positively influenced by the trypsin inhibitor and IgG and IgA contents in the colostrum of their mothers.

DISCUSSION

The rapid fall in the concentrations of both the specific SCTI and the immunoglobulins in whey samples collected at different intervals from parturition (Table 1) is a result of the shift from colostrum to normal milk. The results correspond to those of other investigators (Porter 1969, Porter *et al.* 1970, Curtis & Bourne 1971, Svendsen & Brown 1974, Chidlow & Porter 1977) and confirm that IgA is the major immunoglobulin in milk. The

high level of IgA in milk and the resistance of secretory IgA to enzymic proteolysis in the gut (Tomasi & Bienenstock 1968) endow the milk IgA with a protective effect against intestinal infections in the suckling piglets (Porter *et al.* 1970, Hill & Porter 1974).

The concentrations of IgG, IgA and IgM in serum from piglets at different ages (Table 2) are also consistent with the findings of others (Porter 1969, Porter & Hill 1970, Curtis & Bourne, Svendsen & Brown, Yabiki *et al.* 1974, Senft *et al.* 1975, Chidlow & Porter) except in the cases of IgA on days 1 and 3 and IgM on day 1, where 2 or 3 times higher values were found by the present authors. The differences may be due to the use of different standards, but also to the high degree of heterogeneity of IgA in sow colostrum (Tomasi & Bienenstock, Bourne & Curtis 1973, Porter 1973). The rise in the mean serum immunoglobulin concentration of the piglets 3—4 weeks old was ascribable to 1 particular litter, and could possibly be explained by some sub-clinical infections.

While the immunoglobulins are regular components of milk whey (*cf.* Table 1) the SCTI is specific for colostrum and will have almost disappeared after a few days of lactation, as shown earlier by Laskowski *et al.* (1957), Carlsson *et al.* (1974) and Jensen (1977). The disappearance of the trypsin inhibitor has been shown by Baintner (1973) to be synchronous with the start and rise of the tryptic activity in the intestinal fluid of the suckling piglets, and with the closing of the intestinal mucosa for protein absorption.

In 1951, before the first isolation of SCTI, Laskowski & Laskowski postulated that the physiological role of the colostrum inhibitors was to protect colostrum antibodies against tryptic digestion in the gut of the newborns. This assumption was later substantiated by other investigators, who measured the influence of cow colostrum on the absorption of immunoglobulins by newborn piglets (Nordbring & Olsson 1958a,b, Hardy 1969). On the other hand, in 3 days old piglets Chamberlain *et al.* (1965) found no effect of purified SCTI on the absorption of isotope-labelled γ -globulin, presumably because the phase of protein absorption had finished at that age (Brambell 1970). Since after its absorption SCTI is eliminated very quickly through the kidneys (Baintner 1970, Carlsson & Karlsson 1973, Carlsson *et al.*, Jensen) it is assumed to be operative in the intestinal tract to

protect the maternal immunoglobulins during the phase of non-selective protein absorption (*Baintner* 1973).

The results of the present investigation, showing an influence of the trypsin inhibitor content in the first colostrum on the serum levels of IgG and IgA in piglets 1 and 3 days old, support the above assumptions regarding the physiological role of the SCTI. The higher levels of statistical significance on day 3 than on day 1 for both correlation coefficients and partial regression coefficients concerning IgG and SCTI may reflect differences in the occurrence of equilibrium between the intravascular and the extravascular pools of IgG (*Waldmann & Strober* 1969). It may be concluded that IgG and IgA levels in newborn suckled piglets are influenced not only by immunoglobulin concentrations in maternal colostrum but also by the concentration of colostrum trypsin inhibitor.

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SAMMENDRAG

Undersøgelser over immunoglobuliner og trypsin-inhibitor i kolostrum og mælk fra søer og i serum fra deres grise.

Koncentrationen af IgG, IgM, IgA samt den specifikke so-kolostrum trypsin-inhibitor (SCTI) blev målt ved radial immunodiffusion i kolostrum- og mælkeprøver fra søer og i serumprøver fra deres afkom udtaget under hele diegivningsperioden. Alle målte variabler i både valle og serum viste en klar afhængighed af tidspunktet i laktationen. Der blev fundet statistisk signifikante positive korrelationer mellem, på den ene side, serumkoncentrationer af IgG og IgA, men ikke IgM, hos 39 diende grise, en og tre dage gamle, og, på den anden side, koncentrationer af de samme immunoglobuliner samt SCTI i deres mødres kolostrum ($n = 7$). Multiple regressionsanalyser viste, at niveauet af både IgG og IgA i serum fra de diende grise, en og tre dage gamle, var positivt afhængig af koncentrationen af både SCTI og IgG eller IgA i deres mødres kolostrum.

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