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Cross-fostering of the tammar wallaby (*Macropus eugenii*) pouch young accelerates fore-stomach maturation

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ABSTRACT

There are two phases of fore-stomach development during the first 200 days of pouch life in tammar wallaby. For the first 170 days, the mucosa displays an immature gastric glandular phenotype that changes to a cardia glandular phenotype, which remains for the rest of the animal's life. During this 200-day period after birth, the pouch young (PY) is dependent on maternal milk, which progressively changes in composition. We showed previously that PY cross-fostered to host mothers at a later stage of lactation accelerated development. In this study, we investigated whether cross-fostering and exposure to late lactation stage milk affected the transition to cardia glandular phenotype. In fostered PY fore-stomach, there was increased apoptosis, but no change in cell proliferation. The parietal cell population was significantly reduced, and expression of gastric glandular phenotype marker genes (*ATP4A*, *GKN2*, *GHRL* and *NDRG2*) was down-regulated, suggesting down-regulation of gastric phenotype in fostered PY fore-stomach. The expression of cardia glandular phenotype genes (*MUC4*, *KRT20*, *CSTB*, *ITLN2* and *LPLUNC1*) was not changed in fostered PY. These data suggest that fore-stomach maturation proceeds via two temporally distinct processes: down-regulation of gastric glandular phenotype and initiation of cardia glandular phenotype. In fostered PY, these two processes appear uncoupled, as gastric glandular phenotype was down-regulated but cardia glandular phenotype was not initiated. We propose that milk from later stages of lactation and/or herbage consumed by the PY may play independent roles in regulating these two processes.

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1. Introduction

Eutherians and marsupials are placental mammals, but they differ in their lactation strategies. Eutherians undergo a long gestation relative to their lactation period and the milk composition does not alter significantly during this period. In contrast, marsupials, such as the tammar wallaby (*Macropus eugenii*) undergo a relatively short gestation, give birth to an altricial young and have a long lactation (Tyndale-Biscoe and Renfree, 1988). The major milk constituents change progressively during this period (Green and Merchant, 1988; Green et al., 1980; Green and Renfree, 1982; Nicholas, 1988; Renfree et al., 1981) to accommodate the changing nutritional needs required for the considerable growth and development of the altricial neonate.

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Lactation in the tammar wallaby has been well characterised and has three main phases (Nicholas et al., 1997; 1995). Phase I is the 26–27 days gestation followed by birth of the altricial neonate, also termed the pouch young (Tyndale-Biscoe and Renfree, 1988). The subsequent 200 days (Phase II) is characterised by lactogenesis and the secretion of dilute milk enriched in complex carbohydrates and low concentrations of proteins and lipids (Green et al., 1983, 1980; Green and Renfree, 1982; Messer and Green, 1979). At the onset of Phase III of lactation, the young begins to exit the pouch and commences consumption of herbage while still consuming milk. This phase is characterised by a large increase in volume of milk secretion, but a sharp decrease in carbohydrate levels that are mostly monosaccharides (Messer and Green, 1979), while protein and lipid levels increase to become the major components in the milk (Green and Merchant, 1988; Green et al., 1980; Nicholas, 1988). Protein composition changes considerably with secretion of different proteins at specific phases of lactation (Green and Renfree, 1982; Sharp et al., 2009). Using a cross-fostering strategy in which younger pouch young are fostered onto mothers secreting later stage milk, it has been convincingly demonstrated that late Phase II milk contains factors that accelerate development of the fostered neonate (Menzies et al., 2007; Trott et al., 2003; Waite et al., 2005). Therefore, the tammar wallaby provides an excellent opportunity to identify potential factors that play a critical role in regulating neonatal development.

In particular, this model provides an excellent opportunity to investigate the effects of milk on development of particular organs and tissues, such as the stomach. The adult tammar wallaby has a digastric stomach composed of fore-stomach and hind-stomach with a distinct separation of function within these two regions (Gemmell and Engelhardt, 1977; Langer et al., 1980). The fore-stomach region functions as a microbial fermentation chamber, which is crucial for the digestion of complex carbohydrates derived from the animal's plant-based diet (Hume, 1999). The hind-stomach region is involved in gastric acid secretion, which is necessary for further digestion of food. However, during the first 170 days of pouch life, the developing stomach has a uniform mucosal morphology and has functions associated with gastric glands in both regions; this includes acid secretion as indicated by the low pH in the stomach contents in both regions (Janssens and Ternouth, 1987), and peptic activities as shown by expression of gastric protease (prochymosin and pepsinogen) genes (Kwek et al., 2008). In addition, during this period the stomach appears to play an absorptive role (Waite et al., 2005).

Dramatic changes in morphology take place around day 170 post-partum (Waite et al., 2005). In what will become the adult hind-stomach region, parietal cells increase in number, gastric glands enlarge and adopt the adult-like phenotype of very long, thin glands (Waite et al., 2005) and peptic activity becomes elevated (Davis, 1981). In contrast, the fore-stomach region undergoes a transition from an immature gastric glandular phenotype in which there is a progressive loss of parietal cells and the cardia glandular phenotype becomes apparent in the region that will become the adult fore-stomach. By day 230 post-partum, parietal cells are undetectable in the fore-stomach mucosa (Kwek et al., 2008; Waite et al., 2005). This phenotypic change in the fore-stomach is accompanied by functional changes, such as an increase in pH to neutrality (Janssens and Ternouth, 1987), a decline in peptic activity (Davis, 1981) and the gastric glandular cell type gene markers, prochymosin and pepsinogen are down-regulated (Kwek et al., 2008). As these changes in fore-stomach morphology during tammar development are correlated with significant changes in milk composition, it raises the possibility that these processes may be regulated by specific components in milk.

A recent study (Waite et al., 2005) attempted to address this hypothesis with respect to stomach development by transferring pouch young at 67 days of age to host mothers that were at day 100 of lactation. After the 30-day cross-fostering period, there was significantly increased growth of the fostered pouch young, but there were no obvious morphological changes in either stomach regions of non-fostered control or fostered pouch young. These data suggest that while factors in later stage milk accelerated gross development as shown previously (Trott et al., 2003), there was no effect on stomach maturation. However, in the study by Waite and colleagues (Waite et al., 2005), the period selected for cross-fostering across pouch young development was between day 60 and 100 post-partum, a stage during which stomach mucosal morphology normally remains uniform for at least another 70 days. To examine whether milk from later stages of lactation can regulate changes in morphology in different regions of the stomach, we targeted a later period of pouch young development when there are dramatic changes in stomach morphology. In this study, pouch young at day 120 of age were cross-fostered to host mothers at day 170 of lactation. Examination of the fore-stomach after the 60-day cross-fostering period, showed that while the gross morphology was not altered, there was increased apoptosis, decreased parietal cell numbers but no changes in cell proliferation. Co-localisation studies suggest that parietal cells are lost by apoptosis. Analysis of the expression of gastric and cardia glandular phenotype marker genes by quantitative RT-PCR revealed down-regulation of gastric, but no change in cardia, phenotype genes. These data indicate that the pouch environment, particularly the milk produced at later stages of lactation, triggers the molecular events involved in the loss of the gastric glandular phenotype.

2. Results

2.1. *Fostering promotes growth of pouch young*

Three of nine fostered pouch young survived the 60-day cross-fostering period. Two of the host mothers died of natural causes, four of the young were lost from the host mothers' pouches during the first 4 weeks after transfer.

Prior to transfer, the pouch young in both control (Fig. 2A) and fostered (Fig. 2B) groups had similar physical features at day 120 of age. The eyes with visible rings of darkened pigments remained closed. Pigmentation in the nails in all extremities, ears, rhinarium and tails appeared the same in both groups and they had very short, fine fur. Before transfer, the average head length was 47 ± 0.60 mm (Table 2). After the 60-day cross-fostering period, pouch young in the control group (control PY 180; Fig. 2C) were markedly smaller in size

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