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Implications of Marsupial Births for an Understanding of Behavioural Development

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A review of birthing in marsupials shows that there are at least three distinct methods. In the opossums (Didelphidae), possums, and kangaroos (Phalangeroidea), the expelled newborns crawl from the urogenital sinus to the pouch. In the bandicoots (Peramelidae), the expelled newborn remain attached to the placenta via the umbilical cord while they swim from the urogenital sinus to the pouch. In the carnivorous Dasyuridae, the newborn are expelled in a column of viscous fluid in which they "swim up" to the tunnel between the urogenital sinus and the pouch and then move to the pouch. Some of the recent anatomical studies, on the relative development of the neural system in newborn marsupials and on the behaviours of the newborns within the three birthing methods, have reawakened interest in the mechanisms that might be used to find the pouch. The motor patterns occurring in the newborn marsupials have many similarities to the motor patterns that appear in eutherian embryos at these same developmental stages. Studies that correlate the motor behaviours with the sensory and neural development of newborn marsupials could have important benefits for the understanding of the early organization of behaviour in mammals in general.

Although it is well known that marsupial newborn move unaided from the uterus to the pouch, the mechanisms that they use to locate the pouch are still unknown. As a consequence of the marsupial method of birth, the newborn is faced with the problem of having to move from the urogenital sinus to the pouch and then to locate and attach to a nipple at a time when it is essentially an embryo. This is a complicated task that not only varies across species, in the manner in which it is done, but also varies in the neural mechanisms that are used for its accomplishment. In marsupials, as in most groups of mammals, there have been few species in which correlations have been made between the neural development of the newborn and its behaviour. Hence, conclusions about such correlations in these groups must remain tentative until further study is undertaken.

In marsupials, data are available for newborns of only one or two species in five marsupial families; in one American family, (*Didelphidae*, opossums) and four Australian families (*Dasyuridae*, carnivorous marsupials; *Peramelidae*, bandicoots; *Phalangeridae*, possums; and *Macropodidae*, wallabies and kangaroos). The didelphids have between two to twelve young; the dasyurids six to ten; the bandicoots four to five; the possums usually one, but the smaller species of pygmy possums can have up to four; and in all bar one of the approximately sixty species of kangaroos, there is only one young born (Tyndale-Biscoe & Renfree, 1987). The gestation periods of the didelphids are about 13 days, the dasyurids from 10.5 to about 21 days; the bandicoots 12.5 days; the possums about 18 days, and the kangaroos about 30 days (Table 1).

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Table 1
The Developmental Stage and Weight at Birth of those Species of Marsupials for which Data are Available.

Species	Stage at Birth	Weight at birth (mg)	Gestation period (days)	Litter size	Source
Sminthopsis macroura	15	14	10.5-11	8	(1)
Dasyurus hallucatus	15	18	21	8	(2)
Dasyurus viverrinus	15	18	21	6	(3)
Antechinus stuartii	17	16	27	6-10	(4)
Monodelphis domestica	17?	100	14	8	(5)
Didelphis virginiana	17	130	13	3-13	(6)
Isoodon macrourus	17	180	12.5	4	(4)
Perameles nasuta	17	237	12.5	4	(4)
Trichosurus vulpecula	19	200	18	1	(4)
Macropus eugenii	19	370	29	1	(4)
Macropus giganteus	19	740	32	1	(4)

Note. (1) Gemmell and Selwood (1993); (2) Nelson (1992); (3) Hill and Hill (1955), interpreted from their data by Nelson (1992); (4) Unpublished data of Nelson; (5) Pflieger and Cabana (1996, p. 84), where they equate PI with the rat at E13-14; Knott et al., (1999, p. 431) equate birth with the rat at E16-17 (stage 17); (6) McCrady (1938), interpreted from his data by Nelson (1992).

We shall see that the studied species within the opossums, possums, and kangaroos have a similar method of birth; the bandicoots have a different method; and the dasyurids have a third method. The Didelphidae (and other South American families) have been separated from the Australian marsupials for about 50 million years and both are more derived than their North American ancestor (Long et al., 2002). Within the Australian marsupials, the Dasyuridae and Peramelidae are their closest relatives, yet the didelphids share the same birth method as the more derived groups, the possums and kangaroos. The bandicoots and the dasyurids are closely related and are considered to be the closest groups to the ancestral marsupial but they differ markedly from each other with regards to birth methods. It is not possible to say which birth method is the more derived until more species in more families have been examined. Marsupials and eutherians have been separated for about 100 million years (Long et al., 2002). While it was considered that marsupials were inferior to eutherians, it is now considered that they are two groups that have their own way of adapting to a changing world and that they have different ways of doing this, with neither having the better way. In marsupials like the red kangaroo (Tyndale-Biscoe & Renfree, 1987), the production of a very small young, that moves into the pouch and feeds on milk to complete its embryological and later development, costs little energy. If the environment becomes dryer and less productive, then the young on the teat will die when it reaches the size where the milk production is insufficient. A new young will then move into the pouch as gestation does not inhibit the oestrus cycle and they have a post partum oestrus and mating. As the drought continues, smaller and smaller young will die and eventually the oestrus cycles, and the production of young, may cease. So the early birth of marsupials could be seen as an adaptation to the dry and unpredictable Austra-

lian environment. Since the South American marsupials have the same early movements of young to the pouch, then their North American ancestor must also have had this. In both North and South America there was an eastwards expansion of highlands from the middle to the late Cretaceous (Ruddiman et al., 1997). This uprising, that displaced the inland seaway covering today's Colorado, Wyoming, Utah and Montana, would have produced a dryer climate on one side of North America that may have favoured the marsupial method of reproduction over the eutherian method.

The result of the strong selection for smaller and less energetically costly young to be produced also meant that either the mother had to then put them in a pouch or else the newborn had to have behaviours to get them to the pouch. These behaviours may have evolved independently or they may have evolved by utilising some existing motor patterns that occur during the development of all vertebrates and which are presumably in the basic group from which both marsupials and eutherians arose. If they arose independently, then they would be of a pattern that does not appear in eutherian embryos. If they have been derived from some basic pattern then they should have some homologue in eutherian ontogeny. An examination of the behaviours used in the different methods of marsupial births can help to answer these questions.

Birth Methods

The births of *opossums, possums and kangaroos* are similar and are the births that most people associate with marsupials [in the opossums - *Didelphis virginiana* Hartmann, 1920; McCrady, 1938; Reynolds, 1952; and *Marmosa robinsoni (= mitis)* Barnes & Barthold 1969; in possums, - *Trichosurus vulpecula* Lyne et al., 1959; Veitch et al., 2000; in the kangaroos (Flynn, 1928 summarised early observations on unnamed species) - *Macropus rufus* Sharman & Calaby, 1964; *Macropus giganteus* Poole, 1975; *Setonix brachyurus* Cannon et al., 1976; and *Macropus eugenii*, Renfree et al., 1989].

These marsupials have a forward-facing pouch except for *Monodelphis* which has an open pouch. In the hour or so before birth, the mother licks the urogenital sinus and the pouch and sits on her rump, usually with the tail stretched out in front of her (except in the Grey Kangaroo where the tail extends backwards) and with her hips raised so that the urogenital sinus is directed upwards but is below the pouch. A few drops of fluid may fall from the sinus just before the young is expelled from the urogenital sinus still within its amniotic sac. This sac is ruptured by the movements of the newborn. At emergence from the urogenital sinus the orientation of the head is random. The newborn quickly orientates itself so that the head faces upwards, towards the pouch. The forelimbs of the newborn are relatively well developed with obvious fingers and claws but the hindlimbs are almost undifferentiated. The newborn moves, unaided by the mother, by raising an arm from the mother's body and swinging this bent arm forward, while bending the head and the forepart of the body to the opposite side, and then, when the bent arm is ahead and in an approximate line with the axis of the body, the fur is grasped by the hand of that arm. The hand of the other arm then releases its grip and that arm repeats the above movement. This cycle is repeated until the newborn reaches the pouch (Figure 1), into which it moves and then attaches to a nipple.
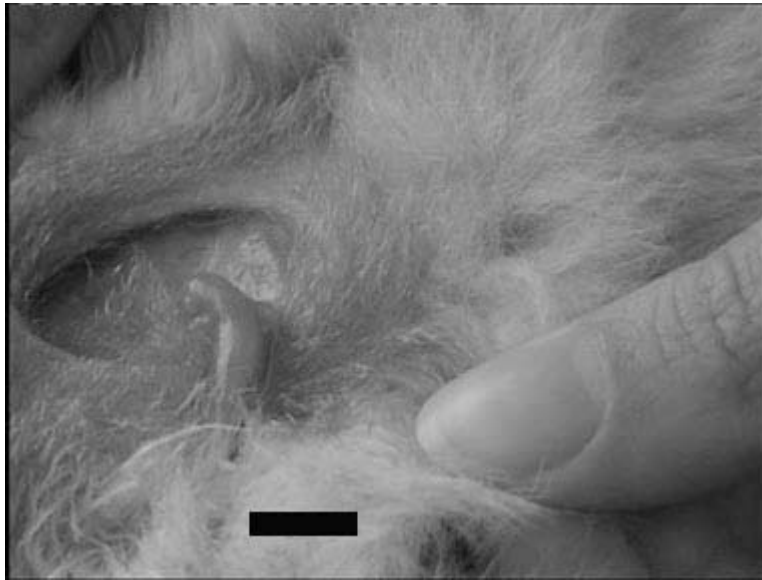
Figure 1. Newborn Brush-tailed Possum, *Trichosurus vulpecula* (200 mg) moving into the pouch. In all figures the bar is one centimetre.

The *bandicoots* have a backward-facing pouch, an allantoic placenta and their gestation period is twelve and a half days. In the period preceding birth, the mother licks the inside of the hindlegs, the urogenital sinus, the pouch and the area in between. She lies on her side with one hindleg raised and with the body bent around so that the head is near the pouch. The urogenital sinus is higher than the pouch but horizontally displaced. When the newborn are expelled from the urogenital sinus the mother licks away the amniotic membranes. The three to five newborn move with lateral sinusoidal movements through the fur but remain attached to their umbilical cords (Figure 2) until they are attached to the nipples. The mother changes sides and may stand upright during the period when the young are born (about three minutes) and moving to the pouch (about five minutes). This sometimes results in the newborn being swung by the umbilical cords into the pouch but usually they slither along the moist pathway (some of the fluid from the urogenital sinus and possibly from being licked by the mother) from the urogenital sinus to the pouch (*I. macrourus* Lyne, 1974; Gemmell et al., 1999).

In the third group (*dasyrids*) the pouch develops during pregnancy and is often open with folds around the sides. For several hours before birth, the female Northern Quoll (*D. hallucatus*) licks her feet, the inside of the legs, the urogenital sinus, the pouch and the "tunnel." The "tunnel" is the area between the urogenital sinus and the pouch. It has relatively short hairs but is covered by the longer hairs laterally (Figure 3). At birth, the mother stands with the hindlegs extended, the tail held away from the urogenital sinus and curling down to the ground and the head is held low or on the ground. Just before birth a few drops fall from the urogenital sinus. A column of viscous fluid flows from the urogenital sinus to the ground and the young appear almost at the same time within the column. The female has stretched the rump area forwards just before birth so the column flows close to the "tunnel". Some newborn are in their amnions but all are soon "swimming" with lateral sinusoidal movements within the column. Those that are carried down past

the tunnel are seen swimming upwards and then leaving the column and disappearing into the tunnel and then move over the posterior lip and into the pouch (Nelson & Gemmell, 2003)
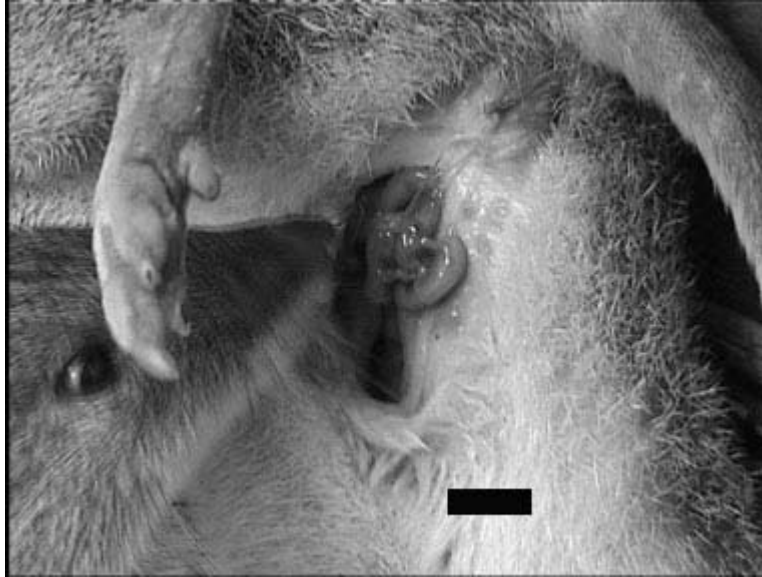

Figure 2. Newborn Brown Bandicoots, *Isoodon macrourus* (each 180 mg) hanging from their umbilical cords above the pouch.

In this species, about sixteen young are born but there are only eight nipples. The gestation period is about 20 days. Births were observed in some other dasyurids, *Dasyuroides byrnei* (Hutson, 1976; Frazer, in Life on Earth, BBC film) and *Antechinus swainsonii* (Williams & Williams, 1982), and although the details of the births could not be observed because the technology at the time could not focus on the very small newborn, they appear to have a similar mode of birth. In this species and in *I. macrourus*, there is often enough fluid in the pouch for the newborn to "swim" or wriggle sinusoidally. This could be from the birth fluid (or saliva) in the bandicoot as the urogenital sinus is above the pouch and so it may fall into the pouch as the mother turns over from side to side. In *D. hallucatus*, it is from the column that made contact with the pouch, in some births, as the female stretches forwards on her hindlegs.

After close examination of the exit of all the filmed newborn marsupials from the urogenital sinus, it is apparent that the young have a passive role in their transport from the uterus to the urogenital sinus. The expulsion of the young is accompanied by fluid and the young are still within their amniotic membranes. These membranes are removed by the mother in the bandicoot or by the young themselves in the quoll. The marsupial newborn does not pass down through the vagina, as does the eutherian newborn, but passes from the uterus to the urogenital sinus via the birth canal. For a summary of the anatomical formation of the birth canal in a variety of marsupials see Tyndale-Biscoe & Renfree (1987).

In all three groups, the young in the pouch display a similar alternating swing of the arms to grasp hairs although the rate can vary. The newborn bandicoot moves its head from side to side every 2 secs (Gemmell et al., 1999), as does the

newborn possum (Veitch et al., 2000), while the newborn quoll takes 0.8 sec for a cycle (Nelson & Gemmell, 2003). However the bandicoot and the quoll show "swimming" movements that are not seen in the opossum, possum and kangaroo. Newborn marsupials also appear to have different energy reserves. The young of the kangaroos and the possum can be removed immediately after they have reached the teat, and when placed at the urogenital sinus, have the energy to reach the pouch and attach to the teat again (Cannon et al., 1976; Veitch et al., 2000). This procedure cannot be carried out with newborn bandicoots or quolls that appear to have enough energy to reach the teat only once.
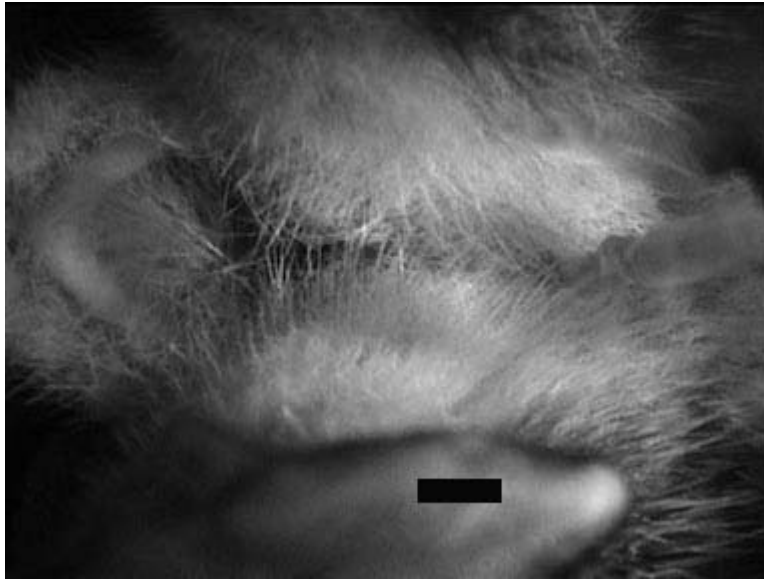
Figure 3. Newborn Northern Quolls, *Dasyurus hallucatus* (each 18 mg) moving from the gelatinous column (on right) to the hairs above the tunnel, that runs from the column to the pouch on the left. One young can be seen in the column and another has just reached the hairs of the tunnel.

Although the kangaroo, *M. giganteus* has a newborn that at 740 g is about 40 times the weight of one *D. hallucatus* newborn (Table 1), both are about the same proportion of the mother's weight (2.7^{-05}, 3.6^{-05}). The quoll newborn has a smaller distance to travel from the urogenital sinus to the pouch than the kangaroo newborn but the small size of the quoll makes this task equally as challenging as that for the larger newborn. Each species is adapted to the task, a large dasyurid newborn might not be able to swim up in the column against gravity and a small kangaroo newborn would have an impossible task to climb the distance from the urogenital sinus to the pouch. The odd species are *M. domestica* and *D. virginiana* that have a large number of newborns but have the birth mode of the kangaroos and possums with only one newborn. Hartman (1952) states that the young of *D. virginiana* were expelled both singly and in groups of up to six at a time and that the members of a group got in one another's way and that only 60 percent of 57 young born to four females reached the pouch.

Development of Newborn Marsupials

Just as there are differences in the mode of birth, there are also differences in both the size (14 to 740 mg) and the stage of development (15 to 19) of newborn marsupials (Table 1). The stage 15 newborn (all dasyurids with weights from 14 to 18 mg) have mothers that range in weight from 20 to 500 g; the stage 17 newborn [one dasyurid, (16 mg) opossums (100 to 130 mg) and bandicoots (180 to 237 mg)] have mothers from 30 to 3000 g; and stage 19 newborn [possums (200 mg) and kangaroos (370 to 740)] from 2500 to 27000g. Thus while the mother's size does influence the size of the newborn, the overlap in ranges suggest that there are also other influencing factors. Following the Carnegie system, embryonic development has been divided into 23 successive stages (see Gribrau & Geijsberts, 1981) where the rhesus monkey stages are related to stages in seven mammalian species). Each stage has been defined on the basis of internal and external morphological characters. Stages 1 to 8 involve the prosomite phase, 9 to 12 the somite phase and 13 to 23 the organogenetic phase.

The range from 15 to 19 may not appear to be a wide variation in birth stage, but at this period of development, there are many changes occurring within the nervous system and this has been best documented in a series of papers on the human by Müller & O'Rahilly (Müller & O'Rahilly, 1988, 1989a, 1989b, 1990a, 1990b, O'Rahilly et al., 1987, 1988). At stage 15 (birth in *D. hallucatus*), the cranial nerves V to XII have reached their innervations, but the olfactory field of the telencephalon only has an intermediate layer (Müller & O'Rahilly, 1988: in *D. hallucatus* Nelson, 1992). In *D. hallucatus* the cells for the olfactory bulbs do not begin to generate until day 2 (stage 17) in the pouch (unpublished radioactive thymidine data). By stage 17, the olfactory bulb is forming, fibres are appearing in the internal capsule, and the tegmentum (motor area) of the mesencephalon has differentiated but not the sensory area of the tectum (Müller & O'Rahilly, 1989b; Nelson, 1992, for *D. hallucatus).* By stage 19, the olfactory bulbs have fibres entering from the olfactory epithelium, as does the accessory olfactory bulb from the vomeronasal organ and the olfactory tubercle from the nervus terminalis. There are also fibres from the olfactory bulb to the olfactory tubercle (Müller & O'Rahilly, 1990a; Nelson, 1992, for *D. hallucatus*). So it may be possible that possums and kangaroos have olfactory receptors that are passing information to parts of the olfactory system, but it would appear that this information could not access any motor system to produce a response.

Even at the latest stage of birth in marsupials (stage 19), there are not yet any fibres from the future neocortex to the internal capsule (lateral forebrain bundle continues to dorsal thalamus) so a definitive internal capsule is not formed although it does contain the fibres from the amygdala to the thalamus (Nelson, unpublished data on *M. giganteus*). There is a possible connection from the olfactory bulb to the olfactory tubercle to the amygdala to the stria terminalis to the habenula nuclei (both in the thalamus) to the interpeduncular nucleus of the tegmentum of the mesencephalon (documented in the human at this stage by Müller & O'Rahilly, 1990a). This would appear to be the only possible route for olfactory information to reach a motor area at this stage. This would then need to connect to a motor area in the medulla to the pattern generator. It would involve many synapses and, if such a route were functional at this stage, it would probably be too slow to allow

the behaviours seen by the newborn. There is not as yet any studies that show a clear connection between the forebrain and the hindbrain at this stage so any sensory information received in the forebrain at this stage has no clear connection to any motor area.

Knowledge of sensory input and neural connections within the brain and spinal cord at these early embryonic stages is based on neuroanatomy and not on neurophysiology, neurotracing or other techniques that might test the sensory abilities of these newborn. Originally, textbooks considered that smell must be used to locate the pouch because the newborn had large nostrils. This "anatomical insight" did not take into account that the nostrils were also used for breathing and especially so when the mouth was completely blocked by a nipple. Anatomical data are only useful when they are related to function. This may require several experimental manipulations before the function is determined, especially in the neural system where there are so many potential functions that might be achieved by a similar neuroanatomy. Although Martin and his associates began seminal studies on the neural development of newborn marsupials in 1978, it is only recently that such anatomical studies have been carried out on a range of species over several families. The observed differences in the newborns and in the methods of birth have reawakened investigations on the birth processes in marsupials. The use of modern tools, such as the confocal microscope and the synchrotron, in conjunction with vital dyes, could allow the inner structures to be seen not only in the live newborn but also in the same individual at different times, and so provide the means to greatly expand knowledge of the neural development at the various stages.

The small size of the newborn makes behavioural, neurotracing, and neurophysiological studies difficult because all of the technology needs to be on a scale that is at the margins of present technology. The small dimensions of the limbs, as well as the differing proportions of their components compared to the adult, make the movements difficult to analyse because they are so different in form from those seen in the adult. Another difficulty is that the connections in the brain and spinal cord are based on adult structures and, as has been shown in many studies, developing animals have exuberant connections to many parts of the brain and these connections are pruned during development (O'Leary, 1992). Even if the connections persist in the adult, they may be so small compared to others in the pathway, that they are ignored. Many reflexes seen in young animals (rooting reflex) still have the pathways for such behaviour in the adult but these are under constant inhibition in the adult from higher brain centres and so are only apparent when those centres are destroyed (Teitelbaum, 1967). Thus there may be functional connections in the newborn marsupial that are not seen in the adult. In *Monodelphis*, there is such a connection between the utricle and the vestibular nucleus, and from then to the cervical cord, so the utricle could give information to guide the position of the head and the rhythmic movements of the forelimbs (Pflieger & Cabana, 1996).

In all newborn marsupials examined by us in Table 1 (4), the upper spinal cord and hindbrain (and possibly the mid-brain in those born at stage 19) are the only regions of the newborn brain that are developed to a level where sensory input could be forwarded to motor areas that could direct movements.

Motor Controls

The following is a brief overview of the motor parts of the spinal cord and hindbrain that are most likely functional in the newborn marsupial and hence move the newborn to the pouch. The details are in Nieuwenhuys et al. (1998). The trigeminal (V) motor nucleus has outputs to the muscles of the jaws, to the reticular formation, to the tongue (via hypoglossal motor nucleus) and to cervical segments C1 and C2. The facial (VII) nerve has motor output to the posterior belly of the digastric muscle, and with the trigeminal, which innervates the anterior belly, controls swallowing. The glossopharyngeal (IX) nerve has motor output to the sylopharyngeus muscle that lifts the epiglottis during swallowing. The vagus (X) nerve sends somatic motor output to the pharynx and larynx and visceral motor to heart, lungs and anterior digestive system. The accessory (XI) nerve has somatic motor output to the muscles of the larynx and to the sternocleidomastoid and trapezius muscles and so is involved in the turning of the head and the raising and lowering of the upper arm (motor neurons in cervical segments C1 to C5). The hypoglossal (XII) nerve has purely motor output to control all of the movements of the muscles of the tongue (except the palatoglossus that lowers the soft palate onto the tongue). The pontine reticulospinal tract arises from the nucleus reticularis pontis caudalis and facilitates extensor, and inhibits flexor, motor neurons. The olivospinal tract connects to motor cells (via interneurons) in the spinal cord and is involved in co-ordinating upper arm and head movements.

The motor control of the neck arises from the spinal cord in segments C1 to C4 and that of the arms from C4 to T1. The motor neurons that control the shoulder and upper arm are in the ventrolatral nucleus that extends from cervical segments C4 to C8. Those that control the muscles of the forearm and hand are in the dorsolateral nucleus in segments C4 to T1 and those that control the small muscles of the hand are in the retrodorsolateral nucleus in segments C8 to T1. Thus the motor controls of the movements to the pouch are in the nuclei of the spinal cord, of cranial nerves V, IX and XI, and of the inferior olive and pons.

The red nucleus is in the tegmentum of the mesencephalon and is present in stages after stage 15. The rubrospinal tract innervates discrete groups of motor neurons and controls independent movements of the limbs, especially the distant parts. When it establishes connections to centres in the medulla, it contributes to the more refined movements seen in older young.

This brief overview of the motor systems in the medulla shows that the newborn has the circuitry for producing the movements seen in the newborn and that some of these movements may be controlled by a central pattern generator in the brainstem or spinal cord (Hughes & Hall, 1988; Hughes et al., 1989; Pflieger & Cabana, 1996). In *D. hallucatus*, the hand has no sensory feedback to control the reach and grasp until day 12 in the pouch (Nelson et al., 2003) and in *M. domestica* after post natal day 15 (Cassidy et al., 1994*)*, Such a pattern generator must control any grasping of hairs by the newborn, as it alternatively advances one arm and grasps hairs. Many systems within the brain first develop the motor components and only later develop the sensory input to this system. The advantage of such a sequence is that the motor components can be perfected into a functional sequence without interference from sensory input (Fentress, 1983). Grooming studies on the rat (Fentress, 1983) showed that motor sequences at first were relatively constant in

form but became more variable in form and sequence when sensory information was first connected to them and later became more constant in form (possibly different from the original) as appropriate stimulus and response movements were selected with time. The early movements of the arm of *D. hallucatus* show little variation in timing or form but after day 12 become more variable (Kingham, 1994, and unpublished data).

Senses Used to Locate the Pouch

The utricle is developed in all newborn marsupials examined (*D. hallucatus* Gemmell & Nelson, 1989; *T. vulpecula* Gemmell & Rose, 1989; *Potorous tridactylus* and *Bettongia gaimardi* Gemmell & Rose, 1989; *D. virginiana* Krause, 1991, 1998; and *Sminthopsis macroura* Gemmell & Selwood, 1993; *Monodelphis domestica* Pflieger & Cabana, 1996). The otoliths in the utricles are suspended in fluid. Their size is such, that in this fluid, the effects of gravity may not produce as much distortion on the stereocilia, upon which they are resting, as would their movement across the stereocilia when the head is moved. Thus it is possible that this is one sense that is used to guide the movement to the pouch. It may be that the utricle, by providing information on the change in position of the head, is able to maintain the lateral movements of the head within limits so that the newborn does not continue the head movement laterally until it falls on its side. The finding that static vestibular head righting, which depends on the otoliths, is not present until well after birth (Pellis, Pellis, & Nelson, 1992), supports the inference that gravity is insufficient to stimulate the otoliths at birth.

That part of the vestibular nucleus (lateral) that receives projections from the utricle is well developed in the newborn *M. domestica* and it sends projections to the motor neurons that are involved in movements of the neck and limbs (Pflieger & Cabana, 1996a). This is the only species in which these connections have been traced by modern techniques (DiI). This dye can be used in preserved material and should be used to trace connections in newborn marsupials to give us some idea of what connections are established at that time. The vestibular nuclei receive afferents from the spinal cord and nucleus prepositus hypoglossi (Nieuwenhuys et al., 1998).

There is variation across species in the development of the saccule and semicircular canals at birth. In *D. hallucatus* they are still forming; in *M. domestica*, they have formed but the macula and ampullae have not; and in *T. vulpecula* and *P. tridactylus*, all are formed (Gemmell & Rose, 1989). So it is possible that newborn possums and kangaroos are able to sense angular head acceleration in some if not all planes as the three semicircular canals develop in the order of the anterior, then posterior and finally the lateral one (Larsell et al., 1935, in opossum; Lannou et al., 1988).

Since the urogenital sinus was below the pouch, it was first thought that gravity must be the most important cue in locating the pouch–the newborn needs to move upwards from the urogenital sinus, and in doing so, it will reach the pouch which is directly above (Hartmann, 1920, in the opossum; Cannon et al., 1976, in the small kangaroo, *S. brachyurus*). That gravity was not the sole cue was indicated by some opossums that turned 90 degrees to reach the pouch (Reynolds, 1952). This was later seen in kangaroos where some newborn moved to the pouch at near

horizontal routes (Sharman & Calaby, 1964; Poole, 1975). It was also seen when newborn possums, that were placed to the side of the pouch or even above it, still moved to the pouch, as long as the displaced distance was about the same distance as that between the urogenital sinus and the pouch (Veitch et al., 2000; Gemmell et al., 2002). However, if the young possum was placed more than 3 cm above the pouch the young continued to crawl upwards away from the pouch.

The trigeminal ganglion is very large in newborn marsupials. In *D. hallucatus*, for a considerable part of the length of the trigeminal ganglion, it is as large in cross section as the adjacent hindbrain. Both sensory and motor parts are developed at birth (Nelson et al., 2003). The sensory trigeminal nucleus receives most of the tactile, pain, temperature and chemical information from the skin of the head, nasal mucosa, anterior tongue and temporomandibular joint and is a relay for gustatory stimuli from the facial, glossopharyngeal and vagus cranial nerves.

The three modes of births require very different abilities to allow the newborn to reach the pouch and attach to a teat. With the marsupials with a forward-facing pouch, such as the kangaroos and possums, gravity cannot be the sole cue in locating the pouch as displaced newborn turned and moved to the pouch, as long as they had not been displaced too far from the pouch. In the possum, a newborn that had passed some centimetres past a closed pouch, turned 180° and moved back to, and into the pouch, when it was opened by the experimenters (Veitch et al., 2000). This would suggest that there was a chemical cue from the pouch. The pouch undergoes large changes in anatomy in the day or so before birth and produces chemical secretions at this time. Surprisingly, there has been no study that has examined what chemicals are produced by the pouch during pregnancy or at birth.

If chemical cues are being used, how are they detected? Although there are sensory cells in the olfactory epithelium of the newborn (*T. vulpecula* Hughes & Hall, 1984; Kratzing, 1986; Gemmell & Nelson, 1988; *D. hallucatus* and *I. macrourus* Gemmell & Nelson, 1988; *P. tridactylus* and *B. gaimardi* Gemmell & Rose, 1989; *D. virginiana* Krause 1992) there is no evidence for the development of olfactory pathways in the forebrain to any motor area. The few anatomical descriptions of the forebrain at birth suggest that olfaction is not likely to guide the newborn (*I. macrourus* Kratzing, 1986; *D. hallucatus* Nelson, 1992; *M. domestica* Brunjes et al., 1992). However as discussed elsewhere (Nelson et al., 2003) the trigeminal nerve could provide information on chemicals that enter the nasal cavity.

In the marsupials with a backwards facing pouch, such as the bandicoots, gravity is unlikely to provide a significant cue as to the direction of the pouch, as the young initially move horizontally and then are flipped over as the mother changes the side on which she is lying. Unlike in birth in the other marsupial species, the mother licks the young when they are expelled and while they are moving to the pouch. Some mothers also oriented some of the young in the direction of the pouch. In many births, the turning movements of the mother and the associated opening of the entrance to the pouch, resulted in some newborn litters being almost dropped into the pouch. There are normally enough teats for the number of young born. Again it is more likely that these newborn are guided to the pouch along a chemical gradient.

Within the third group, mainly the dasyurid species, more young are born than there are nipples so there is a need for the young to get to the pouch and on to a nipple before all are occupied. The birth is quick. The first newborn is in the

pouch four seconds after the appearance of the column and all are in the pouch within thirty seconds. Although it would seem that the newborn are using a sense of gravity to move up the column (and they do have some development of the utricle) it may be that they are guided by a chemical sense. If it was just the sense of gravity alone, why do they stop near the tunnel rather than moving on to the urogenital sinus? To do this they would need some other cue and how would this cue override the ongoing response to gravity? There could be a chemical gradient that is the result of an interaction between the saliva (left by the mother when she licks the urogenital sinus, tunnel and pouch) and the fluid of the column. It needs to be some chemical that contacts the column so it cannot be a chemical from the pouch. In some births, there were live young that passed down the column and ended on the floor. These were relatively inactive compared to those that left the column and we had thought that these may have been less fit individuals, but it could also mean that they had passed too far from the chemical cue that may stimulate motor activity as well as providing a gradient.

While it can be postulated that the rhythmic swinging movement of the arms and the grasp and release of the hairs is controlled by a pattern generator, there must be some signal that initiates these movements, and also stops (or modifies) them when the appropriate task (entry into pouch or attachment to a nipple) is achieved. It may be that taste, touch or temperature could be involved in either of these.

In mammals, taste (as well as tactile and thermal) information comes into the hindbrain via the facial (anterior tongue and palate), the glossopharyngeal (posterior tongue and soft palate) and vagus (epiglottis) nerves (Nieuwenhuys et al., 1998). The gustatory information terminates in the nucleus of the solitary tract and overlaps with general viscerosensory components of glossopharyngeal and vagus (from heart, lungs, air passages and anterior gut). The nucleus of the solitary tract also receives somatosensory fibres from the trigeminal and has efferents to the reticular formation and to motor nuclei in the medulla with projections to the spinal cord (Nieuwenhuys et al., 1998).

During its progression to the pouch, the newborn releases the grasp on the fur, swings this arm forward and at the same time moves the head laterally to the other side and raises it above the mother's fur. As the hand of the swinging arm grasps the fur, the head is also brought back to the fur. The cycle is then repeated to the other side. The tongue is not protruded during the move to the pouch so taste is unlikely to be used in that journey. It is no doubt an important sense during attachment to the nipple. It is possible that the newborn is getting information from contact with the fur. This could be from the lie of the fur, from the chemicals in the saliva trail licked by the mother or from the temperature of the saliva trail compared to neighbouring areas. Evidence against such a mechanism is that some displaced newborn possums were able to move to the pouch at right angles to the path that would normally be taken to locate the pouch. This does not mean that these cues might not have been used in the normal path. In all species, in the period immediately before birth, the mother vigorously licks for long periods, inside the pouch, around the urogenital sinus and in between these two areas. The mother does not usually lick the young and may lick ahead of the newborn as well as behind it.

The head of the newborn has Merkel cells around the lips that could allow sensitive touch reception (in *M. domestica* Jones & Munger, 1985; in *T. vulpecula, D. hallucatus* and *I. macrourus,* Gemmell et al., 1988; and in the rat-kangaroos, *P. tridactylus* and *B. giamardi* Gemmell & Rose, 1989). Tactile information from the lips might initiate closure of the hand on the arm that is carried forward, the release of the fur by the other hand, and the initiation of the swing forward of the other arm. The application of a local anaesthetic on the skin of the lips could show whether there is such feedback in the rhythmic alternation of the swinging of the arms. The same test could be used to see if the application changes the direction of the movement to the pouch or the ability to attach to a nipple. Even though such tests are possible, there have been no such experiments to explore the importance of touch even though there is anatomical evidence that it is developed in the newborn marsupial.

In *D. hallucatus*, when the newborn are in the pouch and attached to a nipple, the pouch is closed over the young and the young (observed via an endoscope) become relatively inactive (Kingham, 1994). When the pouch is opened experimentally, the young begin to move (while remaining attached to the nipple). It is possible that the change in temperature, that the newborn experiences as it moves from the warm amniotic or uterine fluids to the outside world, could stimulate motor activity in some species like the bandicoots, possums and kangaroos. However this could not explain the movements of newborn *D. hallucatus* that can be seen moving in the warm fluid column as soon as they appear out of the urogenital sinus. Again no measurements have been made to see if the temperatures of the area from the urogenital sinus to the pouch or of the pouch are different from surrounding areas.

From the above review, it is obvious that there are few data on the sensory input controlling the movements of newborn marsupials from the urogenital sinus to the pouch. There are even less data on the sensory information that might be used by the newborn to locate and attach to a nipple. The development of reflexes and their neural correlates in post-natal young have been examined only in *Monodelphis* (Cassidy et al., 1994; Pflieger et al., 1996). There is an obvious need for detailed studies correlating behavioural and neural development as knowledge of the mechanisms used by newborn marsupials out of the uterus have implications for understanding development of eutherian embryos in the uterus at equivalent stages.

Implications for Eutherians

Cranial nerves develop during stages 12 and 13 in the order XII, V, VII, VIII, IX/X and XI and during stage 16 there is a marked development of the hindbrain (O'Rahilly et al., 1987; 1988). The first reflexes occur within the uterus at about stage 16 in the human (Hooker, 1958; Humphrey, 1964; de Vries et al., 1982) in the rat (Angulo y Gonzâlez, 1932; Narayanan et al., 1971) and in the cat (Windle & Griffin, 1931). In all of these studies the results were similar in that the first movements were a small turning movement of the neck away from the applied stimulus, but over time, the movements became larger and involved the trunk. The arm, on the side that was stimulated, moved forwards. This early movement has some of the features seen at birth in marsupials. It could be that tactile information,

received by contact of the head of the newborn marsupial with the mother's fur at the end of the forward movement of a limb, is a trigger for the head to turn away to the other side, and for the limb on that side to move forwards.

In vertebrates, the first movements are head flexures that have no predictable sequence and that are not initiated by external stimuli. The next movements are C-coils, that also occur spontaneously and which put the body into a lateral C shape, and these are replaced by S-waves that are undulatory axial movements (see Bekoff, 1985, for review). In anamniotes, the next movement is a coordinated swimming pattern while in amniotes, the next is a disorganised movement called Type I. The movements of the newborn quoll and bandicoot could be of the S-wave or "swimming" type. It may be that amniotes have the 'swimming" pattern but that it is not shown unless the embryo is "free to swim" in a viscous fluid. The study of the movements of newborn marsupials is not then divorced from studies of the first movements made by eutherians in the womb. Birth in marsupials is occurring at about the same stage of development as when the first reflex movements can be elicited in eutherians in the womb. The advantage of the staging system is that, by examining serial histological sections that have been cut through the head of a series of embryos, it is possible to place each embryo at a stage of development that is based on the relative development of the brain and its component parts, and not on the chronological age. Comparisons can then be made across species so that it is possible to see what components might be advanced or retarded at each stage relative to the general plan.

The behaviours used by the newborn marsupial to move to and to enter the pouch are not only similar to movements seen by eutherians in the uterus, but they are also occurring at about the same stage of development that they appear in eutherians. So marsupials and eutherians have the same basic developmental program and the marsupials have utilised the "spontaneous" movements in an early reflexogenic stage to navigate to the pouch. Since the eutherians in the uterus and the marsupials in the pouch follow the same developmental sequence it is most likely that the ancestral group of both also followed the same plan. Since the environment of the pouch is very different from the environment of the eutherian uterus yet both follow the same developmental sequence, then the sequence of neural and motor development must be very important for normal functional development.

The stage of development when movements are first appearing in the embryo is a very critical stage in the development of all vertebrates, as the lack of motility results in abnormalities in many parts of the body. It is then a very important period to study in depth. One difficulty has been the need to anaesthetise the mother to look in the pouch or to surgically enter the uterus and so there has been a problem in fully accepting the results of such studies, as the young may have also been anaesthetised or had a depleting supply of oxygen, and hence their movements may not have been normal for that stage. As mentioned, the new tools available makes it possible to record the movements of small embryos within the pouch or uterus of restrained (but undrugged) mothers, and to examine the developing nervous pathways in the same embryo over time. Such tools should now be used to begin a new wave of interest in the first movements of embryos and the results of studies on pouch-young and embryos in the uterus can be of mutual benefit.

Their behavioural movements can be easily videotaped, as can their responses to various stimuli that can be easily applied to the exposed young. Correlations that could then be made between the form of the movements and the stages of development of the nervous system would provide data that would be of great significance in helping to answer many questions in developmental biology. Such questions as: - Is the form of the first "spontaneous" movements correlated with neural connectivity at that time? Can these unorganised spontaneous movements be traced to the organised movement of a pattern generator? When the various sensory inputs connect to the various movements that are organised by the pattern generator what changes are produced in the movements (are they more variable in form) and what is the functional significance? What is the first sensory input to influence a "spontaneous" motor pattern and is there a sequence in the type of sensory inputs to types of motor pattern?

There are obviously some features in marsupials that are functional earlier than in eutherians. The closure of the secondary palate marks the transition from embryo to foetus and occurs in stage 23 in most amniote vertebrates that have been studied. This has obviously occurred by birth (stages 15-19) in marsupials but even in some eutherians it occurs earlier than stage 23, as in the Chinese Hamster in which, for some unknown reason, it occurs at stage 19 (Donkelaar et al., 1979). Closure of the palate is necessary to ensure that the newborn marsupial can drink from a nipple and still breathe, even though some respiration occurs through the skin (Frappell & Mortola, 2000). It would be would be of immense aid in defining the mechanisms involved, as well as in determining how abnormalities in this development could be corrected, if the method of closure in the marsupials and the Chinese Hamster at these very early stages of development were known, and especially so if it was different from that occurring in most eutherians at stage 23.

Some of the movements seen at birth stages in marsupials (swallowing, limb, and head movements) are seen at those same stages in eutherians. Swallowing and drinking amniotic fluid are important in ensuring normal development of the gut and the lungs, and the associated movements of the tongue are necessary for the development of the palate (Alberts & Cramer, 1988). Limb movements are also important to ensure their normal development and a reduced embryonic activity leads to joint contractures, small lungs, short umbilical cords, small stomachs, and growth retardation (see Gandelman, 1992, for review). These behaviours occur in similar stages in eutherians and marsupials and so it is not surprising that some anatomical and behavioural features of the newborn marsupial are similar to those of eutherians at the same stages.

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