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The early development of motor control in neonate rat

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Abstract

Neonates of altricial species show reduced motor performances with reference to precocial species. Supposedly, their unachieved motor output mirrors the poorly matured underlying structures. Reviewing the developmental timetable of neural, motor and postural structures involved in rats' walking shows that fundamental elements for a basic locomotion are present early after birth, whereas late developing structures are implied in complex behaviours. Whereas rat pups spontaneously show limited motor properties, they can reveal better motor capacities in particular behavioural situations. It is proposed that motor output spontaneously performed by pups does not mirror the actual properties of the motor structures, but results also from a selected behavioural mechanism whose function is to maintain the pups to the nest. ***To cite this article: M. Jamon, C. R. Palevol 5 (2006)***.
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Résumé

Le développement précoce du contrôle moteur chez le rat nouveau-né. Les nouveau-nés des espèces nidicoles ont des performances motrices retardées par rapport aux espèces nidifuges. Ces performances réduites sont supposées refléter le caractère inachevé des structures impliquées dans la motricité. L'analyse du développement des structures neuronales, motrices et posturales montre que les éléments fondamentaux pour une motricité rudimentaire sont présents tôt après la naissance. Le développement plus tardif concerne des structures impliquées dans des comportements plus complexes. Les ratons montrent spontanément des comportements moteurs limités, mais révèlent des capacités motrices plus performantes dans des situations expérimentales particulières. On propose ici que les habilités motrices exprimées spontanément ne représentent pas les propriétés réelles des structures motrices, mais répondent plutôt à des comportements sélectionnés pour maintenir le raton dans le nid. ***Pour citer cet article : M. Jamon, C. R. Palevol 5 (2006).***
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Mots clés : Espèces nidicoles ; Développement moteur ; Posture ; Locomotion ; Retour au gîte ; Rat

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1. Introduction

The offspring of placental mammals differ in their maturation level at birth. Depending on their degree of neonatal development, mammals are divided into *altricial* and *precocial* species, referring to the terms *aves altrices* and *aves precoces* first introduced in ornithology [59]. Typically altricial species have poorly developed offspring, with eyes and ears closed at birth, virtually no hairs on the body, and are typically born in multiple litters, whereas precocial species have well developed offspring with eyes and ears open at (or soon after) birth, hair coat well developed, and are typically

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born as singletons. Derrickson [18] completed this description by ranking mammal species in four categories based on increasing neonate independence: hair covers the body (thermoregulation), eyes open (sensory), move independent of parents (locomotion), eat solid food (nutrition). Precocial species have relatively heavier neonates, smaller litter sizes and longer gestation period with reference to body weight [42,62,69] (about four times longer than an altricial species of the same size). The longer gestation period in precocial species results in increased development of the central nervous system [53]. The shift in gestation timing may also affect changes in other related phenomena such as size and life history traits [6].

Although the majority of extant mammal species produce altricial neonates, precocial forms occur in many orders. As a general trend, smaller mammals (insectivorous, rodentia, carnivorous) have altricial offspring, and larger species (ungulates, cetaceans, primates) have precocial offspring. This is far from being a common rule, however, and many exceptions and intermediate situations occur. For instance, small mammals, like elephant shrew (*Elephantulus rufescens)*, guinea pig (*Cavia cobaya)*, or spiny mice (*Acomys cahirinus)*, produce well developed neonates, and large mammals like black bears *Ursus americanus*, or giant anteaters *Myrmecophaga tridactyla* produce young with closed eyes and sparse fur. The scattered distribution of precocial species among taxa indicates that the timing of birth in relation to stage of development changed often during mammalian evolution. The trend to altriciality versus precociality seems to respond to ecological adaptations rather than to a general evolutionary trend. The early delivery of altricial species allows the female to produce large litter size while maintaining a supportable weight level during gestation. Conversely, neonates suffer from a reduced autonomy and increased mortality risks, and the mother invests tremendously in nesting (nesting facilities, sedentariness, food management). Precocial species produce smaller litter size, but neonates are more developed, and have better survival rate, allowing greater autonomy of the mother to forage over larger areas.

A tacit assumption has been that development proceeds similarly in altricial and precocial species, with the only difference being the arbitrary point of birth [10]. Altricial and precocial mammals exhibit no difference in the rate of growth to 50% of adult mass [12], and show similar trend course of neural development [16]. The duration of gestation is therefore the main factor of maturity at birth. The comparative development of guinea pig (Caviidae) and rat (Muridae) shows a typical example of the dichotomy in the level of maturity at birth in rodents. After 66 days of gestation the newborn guinea pig resembles the adults, while rats, with a gestation period of 21 days, are very immature at birth: they are nude, deaf, blind, and show behavioural retardation that can be seen on their sensory motor functions, postural control and locomotor performance. Even amongst Muridae, however, strong differences exist in the level of maturity at birth. For instance, the spiny mice (*Acomys cahirinus*) after a gestation period of 38 days, have their eyes open and can walk at birth, they correspond to a 15 days old rat. *Acomys* and rats show a quite different overall pattern of brain maturation [10]. For example, *Acomys* exhibits considerably more rapid postnatal olfactory bulb and hippocampal formation growth than expected from curves derived from same post-conception aged rats, while maturation in the visual neocortex seems very similar across the species. In addition, prenatal telencephalic development varies between these species.

It is always astonishing to notice that some mammals, like ungulates, can run a few minutes after birth, while altricial species, like mice and rats, need three weeks to perform an adult-like quadruped walking. Researchers interested in the early development of motor control in neonate rats pondered about the cause of the delay in the acquisition of motor control [25,44,64]. To be effective, locomotion needs several levels of motor integration: a musculoskeletal system sufficiently developed to support the body on the legs, an efficient neural control of movement, and a postural control to maintain equilibrium. These various levels of motor control are not fully operational at birth, but none of these maturational aspects can explain alone the postponed development. Possibly, they interact to degrade the motor performance, but other causes can explain the delayed motricity in altricial species.

The present paper reviews the progressive stages of maturation of the main structures underlying rat locomotion, then describes the last updates in the timetable of early motor development. The discrepancy between the development of structures and functions is discussed in the context of the ecological significance of altriciality.

2. Developing structures

The locomotion involves a set of structures hierarchically distributed. Skeletal muscles are needed to counteract gravity constraints and allow movements. The coordinated firing of the motoneurons controlling these muscles is organised at the level of the spinal cord by neural networks, called *central pattern generators* (CPG) [68]. A rostral CPG, located between C7-T1, controls the fore limbs [3], and a lumbar CPG, located between L1–L5 controls the hind limbs [13,14,36]. CPGs are made of two lateral hemi-neural networks, that rhythmically stimulate a pool of motoneurons through glutamatergic synapses and inhibit the motoneurons of the ipsilateral antagonist muscles and the contralateral agonist muscles through glycinergic commissural interneurons (see [26] for a recent review). This peripheral organisation is capable of producing autonomously rhythmic patterns of movement, but a central command, involving various parts of the brain, initiates and controls the type of movement (speed, gait, etc.) by modulating CPG activities through four main descending pathways. The *reticulospinal pathway* mediates locomotor signals issued from the *mesencephalic locomotor region* (MLR), that receive axons of neurons coming from the basal ganglia; the *vestibulospinal pathway* mediates signals coming from the vestibular nucleus; the *rubrospinal pathway* mediates signals from the *red nucleus*; the *corticospinal pathway* originates form the motor cortical areas. The development of all these pathways is required to perform the whole adult behavioural repertoire, but they are not equally required to perform locomotion. The reticulospinal pathway adjusts postural muscles and produces basic motor activities, the vestibulospinal pathway is involved in the control of equilibrium, the rubrospinal pathway is in charge of precise and automated movements, the corticospinal pathway is in charge of the fine and precise adjustment of voluntary movement. The two former pathways are required for basic expression of movement; the two latter are involved in movements that are more complex and are not mandatory for basic motor outputs [45]. For instance, decerebrated animals with only the MLR activating the reticulospinal pathway are capable of automatic locomotion.

In addition to the motor command, the development of control sensory pathways needs to be achieved to allow the body stabilisation during movement [25].

This chain of motor output, motor control and postural control must be fully operational to allow the adult locomotion, and missing elements at any level can seriously alter the motor output. These various levels are not equally mature at birth, and in successive days, but they are at least partly functional, and the interactions of these differently matured structures on the motor abilities are not straightforward. The timetable of these various elements of the organization of locomotion is summarised below (Fig. 1).

2.1. Motor output

The locomotion uses two main types of muscles, depending on their majority proportion of slow (type-I) or fast (type-II) fibres: *posture* requires weak muscles producing moderate force of near isometric nature with long contraction properties, whereas *movement* requires muscles with rapid and brief contraction and possible high forces. During postnatal development, the muscular fibres progressively differentiate in slow and fast fibres [35], when the motor units mature and become progressively homogeneous in relation with the change in motoneuron activity. During this time, several changes occur in the morphological, immunohistochemical and contractile characteristics of skeletal muscles [49]. In the *soleus*, for instance, a slow postural extensor, type II fibres gradually convert into type I. This transformation can be correlated with a decrease in both calcium sensitivity and affinity of the contractile system and by transitions in the contractile proteins, especially the *myosin heavy chain* (MHC) isoforms that seems to be under neural influence. The early environmental influence is an important inductor of muscular plasticity. Rats born and reared in hypergravity environment showed changes in the morphological and contractile properties (decrease in absolute muscle weight, increase in fibre cross-sectional area, increase in relative maximal tension) [7,51]. The *soleus* changed into a slower type, while the *plantaris* muscle, its fast agonist, presented a faster contractile behaviour. These changes were related to modifications in MHC and regulatory troponin contents in *soleus*. Moreover, the diversity of hybrid fibre types expressing multiple MHC isoforms was increased in *plantaris* muscle. Conversely, unloading conditions atrophied skeletal muscles to different degrees, according to the muscle type and muscle function [19,23,50]. The *soleus*, changed into a faster type and showed modified properties [19] (muscular atrophy; decrease in absolute and relative strength; decrease in twitch contraction time confirmed by changes in histochemical and electrophoretic properties [58]). Less drastic effects have been reported in the *plantaris* muscle (slight muscular atrophy [8,21,61], no change in the relative tetanic tension [8,23] and no change [23] or an increase in time to peak [8]). The effects induced in the skeletal muscles by the alteration of gravity are in part *irreversible*, and support the existence of *critical periods* in the neuromuscular development [66]. Clearly, the early motor experience and postural needs are required to adjust the adult profile of skeletal muscles.

The *stretch reflex*, in charge to adjust the muscle stiffness, appears at E19 and the magnitude of mono-

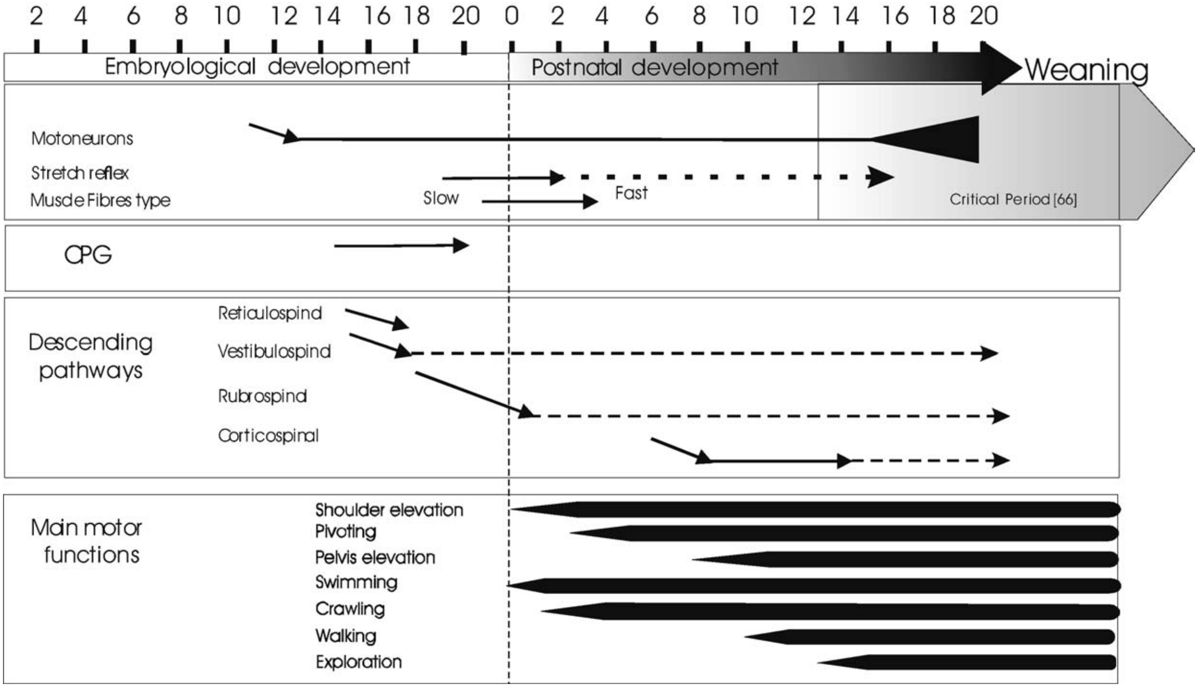

Fig. 1. Timetable of motor maturation in rat. The time of apparition and maturation of the main structures involved in the locomotion are symbolized here by arrows. Embryological development refers to processes occurring in utero (in the text they are referred to as E. followed by the corresponding day; postnatal development is referred as PND in the text). Inclined arrows show the time of migration from the anterior to posterior level. Dotted arrows indicate a continuing maturation. The diagram below shows the commonly described maturation time of some motor functions. Bevel edges show the acquisition window.

Fig. 1. Programme de maturation motrice chez le rat. Le moment d'apparition et de maturation des principales structures impliquées dans la locomotion est symbolisé par des flèches. Le développement embryonnaire correspond aux processus apparaissant in utero (dans le texte il est représenté par un E suivi du jour d'apparition ; la date de développement postnatal est indiquée par PND dans le texte). Les flèches inclinées indiquent le temps de migration du niveau antérieur vers le niveau postérieur. Les tirets indiquent la période de maturation. Le diagramme du bas montre le calendrier de maturation communément décrit pour quelques fonctions motrices. Les bords biseautés indiquent la période d'acquisition de la fonction.

synaptic response is stable from postnatal day 2 (PND2). This reflex is therefore functional early after birth, but continues to develop until PND12, when spindles are fully developed [37,38] and needs a few weeks to eliminate inappropriate contacts.

Innervation plays a major role in the maturation of muscles fibres. The motoneurons themselves differentiate early, between embryological days 11 and 13 (E11–E13) for the anterior then posterior limbs [1]. They continue to develop, with increasing size and dendritic complexity during the two weeks after birth [60]. At birth, muscles fibres have polyneuronal innervation and the motor units are heterogeneous. This polyneuronal innervation persists until about postnatal day 14, then fibres become progressively mono-innervated [9], and their dendrite bundles develop progressively. A strong bundles development was noted in the *soleus*, from PND15 [39], i.e. when the pups begin to stay on their legs, suggesting that motononeuron development and the regression of polyneuronal innervation is critically dependant on motoneuronal activity. The late progressive development of muscles and motoneurons probably results from the refining of the motor command in response to motor expression.

2.2. Motor control

The organization of rhythmic limb movement is organised at the spinal cord level by the CPGs. These neuronal networks connect very early, rhythmic CPG activities can be detected from E14 [46]. The inhibitory glycinergic relations to the lower segments can be found at E18.5, and the commissural interneurons are active at E20.5 [29,47]. CPGs are therefore ready to work before birth, and the rostral and caudal CPGs are probably already linked at birth to produce coordinated forelimb–hindlimb movements [3,22].

The various descending pathways that mediate the supraspinal control to CPGs progressively develop along the spinal cord with different timetables [40]. The reticulospinal pathway, responsible for initiating the locomotion and automatic patterns reaches the anterior CPG on E15 and the posterior CPG on E18. The vestibulospinal pathway, issued from vestibular nuclei, reaches the CPG at the same time. The rubrospinal pathway develops later, between E18 and PND1 [41], and probably becomes functional around PND14 [25]. The corticospinal pathway, responsible of the fine control of movement and the learning of new motor patterns, appears much later; it reaches the anterior and posterior CPG from PND6 and PND8 respectively, and continues to develop until PND15 [33,54]. This latter pathway does not seem mandatory, however, to the expression of locomotion [45].

The timetable of anatomical development shows that most of the basic structures in charge of initiating and controlling the movement are acquired early after birth. The existence of the anatomical link does not mean, however, that the connections are functional [64]. Projections are not yet mature, e.g. adult pattern of vestibular pathway establishes during the third postnatal week. In addition, the speed and amplitude of neural connection increases progressively in relation to the change from polysynaptic to monosynaptic connections and myelin formation.

2.3. Postural control

When the rat is capable of performing adapted rhythmic activities, it needs to maintain a postural control in order to walk efficiently. Several authors assumed that unachieved postural control could be the limiting factor for the appearance of locomotion in the rat [17,25,44]. The postural control needs a set of functions to mature. Amongst them, a sufficient muscular force and operational tuning of stiffness in the antigravity muscles is a prerequisite to support the body. As was shown above, the unachieved maturation of postural muscles (polyneuronal innervation, undefined slow/fast properties) is a possible source of body instability during locomotion, even though it is partly compensated by a plantigrade locomotion and the exo-rotated position of feet [25]. The muscular force is another important aspect to consider, but is not well documented. The diameter of fibres increases during the first postnatal weeks, but the ratio between cross-sectional area and body weight changes only little, suggesting that muscle force is not a limiting factor [24]. The role of long back muscles received more attention. Their synchronous contraction with limb movement is a main element of the trunk stabilisation, and is considered as important for the adult locomotion. This stage of postural control is only reached at PND21 [25], i.e. after the rats adopt an adult-like walking, the maturity of long back muscles is therefore not a limiting factor for the acquisition of preliminary forms of walking, suggesting a relatively independent development of postural control mechanisms and neural mechanisms of locomotion. These constraints cannot therefore be the main limiting factor for the inactivation of locomotion of pups.

3. Developing functions

The timetable of the development of the motor function in neonate rats refers to a set of studies that recorded the spontaneous activities of pups placed in a neutral enclosure (open field or corridor) for a few minutes [2,5,24,67]. These studies agreed on a progressive development based on the acquisition of motor capacities following an antero-posterior and proximo-distal gradient. Geisler et al. [24] distinguished three phases: an early postnatal period until PND4–5, when only head lifting and rooting movement occurred; from PND6 to PND12–13 rats were able to rise their ventral body from the floor while walking a few steps; in a third period, from PND16, complex motor patterns as locomotion, rearing and grooming acquired adult and fluent characteristics.

Whereas these studies clearly showed a progressive acquisition of locomotion in rats, the conditions for observations did not allow detecting what pups are potentially capable of performing. Recent observations of pups in relation to their mother showed that maternally directed behaviours involve, early after birth, righting and pivoting movements [20] as well as motor activities, including crawling, much earlier than previously assumed [52]. Altman & Sudarshan [2] themselves admitted that brief periods of patterned motor responses could appear earlier under high level of activation. They mentioned, for instance, that placing the pups on a refrigerated surface elicited a walking-type of locomotion with elevated trunk as early as PND4. These observations support the idea that spontaneous activities of pups do not reflect their potential capacities.

Electrophysiology studies of rats' spinal cords isolated early after birth showed the existence of rhythmic neuron firing in the CPGs. The recording focused on the lumbar CPG [14,36] and showed stable alternating bursts between agonist contralateral motoneurons and antagonist ipsilateral motoneurons. More recently, stable rhythms were also recorded in the forelimb CPG of mice, and links between rostral and caudal CPG were showed to be functional at birth [3]. The

CPG activities recorded in vitro are defined as fictive rhythmic locomotion because they are produced without muscle activity [55], but they are commonly considered as an expression of potential locomotion even though the frequency is very low.

Early coordinated forelimb-hindlimb motor activities were also recorded in vivo early after birth (PND0–4) during swimming [4,15]. The swimming paradigm allows producing early alternate limb beating, by relaxing the postural constraints, but the meaning of these gaits suffers from a strong limitation, because swimming does not require the same fore- hind limbs coordination than walking. This could explain the higher variability and the progressive reduction in forelimb coupling in swimming neonate rats [15]. The ambiguity on the nature of the movement of pups after water immersion strongly reduces the pertinence of the swimming paradigm for studying the evolution of limb coordinations. An alternative protocol consists in placing the rat in a harness and stimulating the locomotion by a subcutaneous injection of L-Dopa [43,56,63]. L-dopa induces regular rhythmic movements in both fore and hind limbs for about half an hour, revealing therefore the ability of the neuromotor control system to produce regular locomotion bouts. This protocol was widely used to investigate motor activities in rats aged from PND3 [32] to adultness [43]. The pharmacological L-Dopa injection probably stimulates dopaminergic locomotor pathways at the level of the brainstem [30] and is equivalent to a chemical decerebration [57].

A modified air-stepping protocol consisted in placing a tube containing material of the nest in front of the nose of the rat to stimulate an olfactory mediated homing behaviour (Fig. 2). The olfactory stimulation was used in rats as young as PND0 [22] and was efficient in premature rats whose birth date was experimentally anticipated by one day (E20). The kinematic study of the olfactory induced air stepping revealed that rostral and lumbar CPGs were able to modulate their respective frequencies as soon as PND0. The olfactory stimulation produced slower movements compared to L-dopa injection, and was capable of slowing down L-Dopa induced movements in PND3 rats [32]. As the olfactory stimulation involves most probably the cortical areas, this demonstrated that higher centres are capable of modulating the dopaminergic pathways.

The experiments on early air stepping showed that CPGs were capable of maintaining stable rhythmic movements over a long period of time; the contralateral and even the ispsilateral CPG reacted reciprocally, showing therefore that some connection existed between anterior and posterior CPGs, and cortical control was capable of modulating the motor activities. Altogether, these results argue for a capacity or the neuromotor system to control efficiently locomotor movements early after birth.

Air stepping releases the postural demand, however, and leaves open the possibility that postural control and musculoskeletal properties are not enough developed to support the body. Stimulating ground walking in pups by

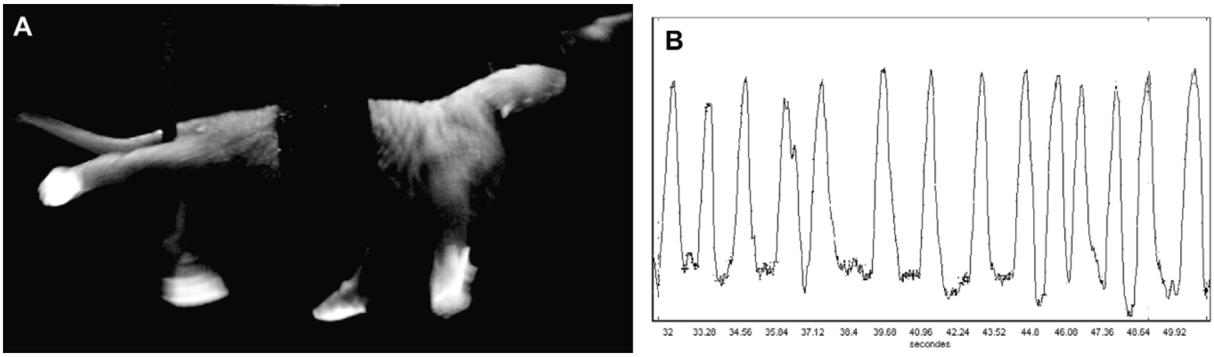

Fig. 2. Air-stepping protocol with olfactory stimulation. (**A**) Newborn rat installed in the set-up. A Harness supports the rat's belly. The muzzle is introduced in a tube containing sawdust from the rat cage. The tips of the legs are coloured with fluorescent markers and appear in white on the picture. The moving right forelimb and left hindlimb, appear fuzzy (diagonal gait). (**B**) Example of a moving leg record during an air-stepping session. Abscissa shows the time (s), ordinate shows the forward (up) and backward (down) movement of the leg. The slowing down phase in the backward position is characteristic of the olfactory-induced air stepping.

Fig. 2. Protocole de *air stepping* olfactif. (**A**) Raton placé dans le dispositif. Un harnais maintient le raton en l'air. Le museau est introduit dans un tube contenant de la sciure de la cage. Les extrémités des pattes sont colorées avec des marqueurs fluorescents, qui apparaissent ici en blanc. Les pattes avant droite et arrière gauche, ici en mouvement, apparaissent floues (allure diagonale). (**B**) Exemple d'enregistrement du mouvement d'une patte durant une session de *air stepping*. L'abscisse représente le temps ; l'ordonnée, le mouvement avant (vers le haut) et arrière (vers le bas) de la patte. La phase de ralentissement du mouvement, quand la patte est en position arrière, est caractéristique du *air stepping* olfactif.

means of the olfactory stimulation answered this latter question [31]. The neonate rats show a strong tendency to move towards the nest odour presented in front of them. This reaction induced a walking-like movement characterized by an attempt to raise the belly off the ground and strong coordinated legs pushes, as early as PND3. This experiment demonstrated that neonate rats could show walking-like bouts very much earlier than previously suspected. When the nest odour was presented in a tube, the rat entered the nose into the tube, and pushed it. The range of speed and step amplitude measured between PND 4–9 corresponded to the performance previously recorded in PND 11–17 spontaneously walking rats [67], and showed that rats are potentially capable of performing much better than that they actually do. Placing the head in the tube allowed to get longer stepping sequences, by preventing the pup's lateral head oscillations to loose contact with the odour, but also improved equilibrium. At this age, the head amounts for more than 20% of the body weight and can unbalance the pups. This latter point can be a strong limiting factor for the pup to move spontaneously, especially as the trunk stabilisation is not achieved (see above), nevertheless, pups motor capabilities appear as much more developed as was previously assumed.

4. Discussion

As was shown in this short review, the development of motor functions does not parallel the neuroanatomical changes. The development of the structures underlying locomotion is not fully achieved at birth, and will continue even after pups perform adult-like walking. On the other hand, the basic elements underlying locomotion are ready in a few days after birth, well before spontaneous walking is observed. Undoubtedly, the reorganization and refinement of initially established neural connections [44,65], and the inefficiency to cope with postural requirements [25,44] are limiting factors that contribute to the delayed motor output in neonate rats, but they cannot satisfactorily explain it, because pups are potentially capable of performing better than they spontaneously do. On the other hand, neural connections quickly develop around PND15–16 when a fluent walking pattern emerges and adult-like type of postural control starts to develop [25]. This coincident emergence of fluent walking and sudden change in the rate of neural connections was supposed to have various causes: either locomotion appears because the neural connections have reached a level of maturation, or connections correspond to a final tuning related to a new stage of the progressive maturation of locomotion. On the other hand, both structures and functions could also have their operational stage switched on by a trigger somewhere in the developmental process.

Behavioural observations support this latter interpretation. Olfactory stimulation with nest odour can activate air stepping and even ground walking in pups [22, 31]. The olfactory stimulation is assumed to trigger a homing reaction. This behaviour allows bringing the pups back to the nest and has a high survival value. Besides, homing capacity was used to test various capacities in pups aged from 2 to 14 days (e.g., [34]). In these studies, pups were placed in the opposite corner of the cage and the percent of return was measured, however locomotion was not the main concern of these studies, and movement was not particularly studied.

Resolving the discrepancy between the development of structures and functions needs to refer to the ecological significance of altriciality. It would be ecologically irrelevant for neonate to move far from the nest: they take the risk of being lost and they would have difficulties to return in case of danger, while the mother would expend a lot of energy recovering dispersed pups. A more adaptive strategy consists in developing a control system to inhibit the pups' locomotor activities, while preserving an efficient homing behaviour. We can therefore hypothesize that the development of structure and their motor output are disconnected by a silencing mechanisms, of unknown nature, that inhibit motor activities, except for situation of survival emergency (e.g., homing). The sudden and almost concomitant apparition of exploratory behaviour, eye opening, and a burst in neural connections could result from this mechanisms' switch off at the end of the second postnatal week.

The idea that the delay in the motor output is not directly linked to the immaturity of motor properties, but is under a central control is reminiscent of a hypothesis presented earlier by Oakley and Plotkin [48]. On the assumption that maturation of mesencephalic arousal system results in a direct increase in general motor arousal, and is transiently reflected by a sharp increase in locomotor activity [11], these authors supposed that motor activity happens at different ages among species, depending on their degree of brain maturation at birth. To test their hypothesis they compared the timing of occurrence of the peak of spontaneous locomotor activity in three small mammal species with varying levels of maturity at birth, namely the rat, the rabbit and the guinea pig (Fig. 3). The peak did not appear in guinea pig for which mesencephalic maturation was supposed to happen in utero, and occurred at PND5 and PND18, in rabbit and rat, respectively. It is interesting to notice the comment by the authors that rabbits showed a

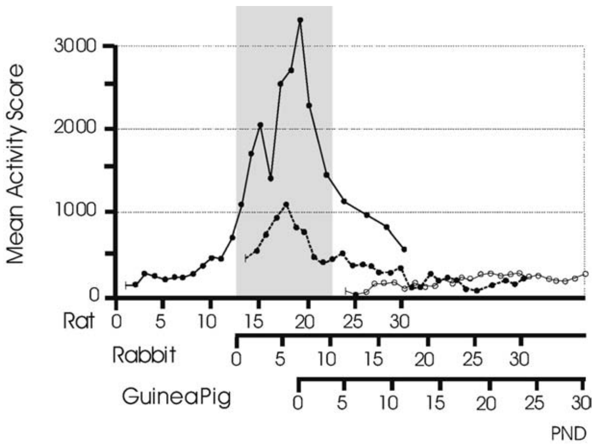

Fig. 3. Mean locomotor activity score as a function of age in rats, rabbit, and guinea pig (redrawn after [48]). The locomotor scoring and test duration differ between species, vertical scale is only shown for qualitative purpose. Abscissa shows the postnatal age for the various species. Continuous line: rats; dashed line: rabbit; white circles: guinea pig. Grey area shows the supposed period of maturation of mesencephalon.

Fig. 3. Score moyen d'activité locomotrice en fonction de l'age chez le rat, le lapin et le cobaye (redessiné d'après [48]). L'abscisse montre l'âge postnatal pour les diverses espèces. La mesure du score locomoteur et la durée de test diffèrent pour les différentes espèces, l'échelle de l'axe vertical donne donc uniquement une indication qualitative. Ligne continue : rat ; tirets : lapin ; cercles blancs : cobaye. La zone grise montre la période supposée de maturation du mésencéphale.

poorly coordinated and clumsy movement during their peak phase of activity and therefore did not mirror the maturity of the motor system. Some prerequisites, like caudo-rostral development of the brain and comparable interspecies developmental timetable, were probably not met in their study. Their hypothesis, however, has an heuristic value, assuming that important changes in the motor output are not the image of the level of maturation of the motor system itself but correspond to a switch in the central command of movement that released the inhibition of motor output.

Another point was pertinently disputed by Henderson [27,28], who suggested that a high rate of locomotor activities would be maladaptive for altricial species. On the contrary, a quite strong selective pressure would have produced animals having a low activity level during their first weeks because of the high mortality risks early in life. Low activity and reliance on highly efficient parental retrieval response would be genetically selected. Henderson compared the early motor activity in wild mice, trapped outside and maintained in the laboratory for three generations, with the performance of inbred mice, with the underlying hypothesis that the selective fitness of low

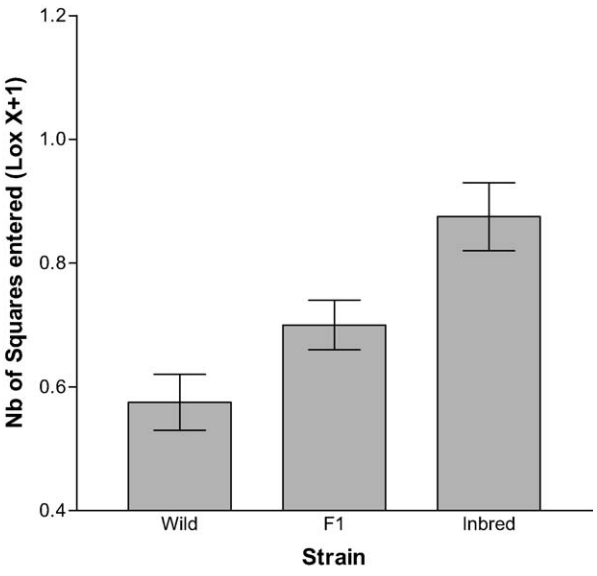

Fig. 4. Mean locomotor activity score in mice. Wild, inbred and their F1 hybrids are tested for motor activity at P14. The motor score is computed as the number of 2.5-cm squares entered in an open field in a 1-min period. Data are log transformed to eliminate correlation between means and standard deviation. Bars show mean score ± S.E. M. (after [27]).

Fig. 4. Score locomoteur moyen chez la souris. L'activité motrice de souris sauvages, consanguines, et de leurs hybrides F1 est testée à P14. Le score moteur est calculé comme le nombre de carrés de 2,5 cm de côté entré dans un *open field* pendant 1 min. Les données sont log transformées pour réduire la corrélation entre moyenne et écart-type. Les histogrammes indiquent le score moyen (± erreur moyenne standard) (d'après [27]).

activity is relaxed in laboratory condition (Fig. 4). A significant difference in the early motility of wild and inbred mice suggested that low activity level was indeed selected under environmental pressure. It is also noticeable that mobility varies between pups of various inbred mice [27]. Likewise, the various laboratory rats' strains show different timetables of motor development [24]. These remarks are consistent with the hypothesis that protective conditions of laboratory relaxed the selective pressure on delayed motricity.

These two examples support the assumption that low motor performance in the altricial murid species does not reflect the immaturity of the motor system, but instead results from an adapted silencing of the motor output in view of maintaining the pups in the nest area. This does not mean that pups are early capable of walking, obviously they are not, and even the characteristics of walking-like behaviour induced by olfactory stimulation evolved with age [31]. It would be misleading, however, to speculate about a straight link between the occurrence of a motor function and the development of the underlying structures. The functions are not expressed when the underlying structures are ready, they are expressed when the context for use is appropriate. The development of locomotion is the result of a dialogue between structures and functions, in the context of adaptability. The neuromuscular activities are involved in the tuning of underlying structures. In the same way, the behavioural output is dependent both on the maturation of structures and the adaptive context for expression of a given behaviour.

From an evolutionary point of view, there is no qualitative difference between altrical and precocial strategy, both being successful in the context of different ecological strategies, where the trade-off among various life history traits parameters varies. Though the first mammals were supposed to be altricial, this probably corresponded to an adaptive solution for small species with a large reproduction rate, rather than a phylogenetic stage. On the other hand, it is noteworthy that the most evolved species (men and apes) mix both precocial and altricial characteristics giving them a small reproduction rate, but great autonomy, and high plasticity and 'learning' process in the young.

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