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Development of posture in the rat

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Abstract. Postural development has not attracted much attention in investigations of neuro-ontogeny. In the rat, motor behaviours have been studied repeatedly but the development of postural control has been largely neglected. In the present study we have taken inventory of behavioural aspects of postural development. Postures and postural skills of 10 pups were 3-dimensionally recorded on video tape from the 2nd to the 20th day. The development of posture may be subdivided into three periods. During the first period, lasting until the 4th or 5th day, neonates were unable to lift their trunk from the floor, and the only indication for postural activity being head lifting. From then until the 12th - 13th day, pups were able to walk, though staggering, and in addition they groomed and reared with forelimb support. From then, in a rapid development lasting until day 16, the adult type of fluent locomotion developed as well as grooming and rearing without support. In addition, complex motor acts developed. These results are discussed in the perspective of the structural and functional development of postural systems.

Key words: posture, motor patterns, rat, development, neuro-ontogeny

INTRODUCTION

The position of the head, trunk and limbs relative to each other as well as the orientation of the body in space are the main aspects of posture. Optimal postural control is a prerequisite for effective movement. At adult age, postural adjustments are fluently integrated in ongoing movement patterns. Many aspects of the mechanisms involved in postural control are still unknown. Because of the relatively low degree of complexity of brain mechanisms and behaviour at early stages, developmental research may help to provide insight into the causal network of postural mechanisms. It is with this background that we became interested in the ontogeny of the development of posture in the rat. In precocious animals such as the guinea pig, neural development occurs for the greater part before birth and postural mechanisms might be inhibited due to a low oxygen pressure in the fetal circulation (Schwartze 1968). The development of postural control in the rat, which is an insessorial species, occurs largely after birth. This enables to study this development postnatally.

In the rat, the lack of adequate control of postural muscles and the immaturity of postural mechanisms during the first 2 weeks of life are probably limiting factors for the development of locomotion and other motor patterns. The first movements in rats may be observed from the 15th day of gestation (G15; Angulo y Gonzalez 1932) and even alternating leg movements occur before birth (Bekoff and Lau 1980). However, in the first days after birth these movements are ineffective in locomotion unless rats are immersed in water (Bekoff and Trainer 1979, Cazalets et al. 1990). Apparently, the upward pressure on the body by water displacement supports the trunk, which is essential for this movement pattern to occur. Overground locomotion with the ventral body surface free from the floor develops only from the middle of the 2nd week of life (e.g. Bolles and Woods 1964).

The development of posture in the rat has been relatively neglected. While motor development in general was described by such investigators as Small (1899), Tilney (1934), Bolles and Woods (1964), Altman and Sudarshan (1975), Blanck et al. (1967), Westerga and Gramsbergen (1990, 1993), the main focus of these investigations was on the development of locomotion, behavioural patterns such as grooming, or reflexes such as hopping and grasping.

Specific questions addressed in the present study include what is the developmental profile of postural maturation in the first 20 days and how does posture develop in relation to such motor behaviours as locomotion, rearing and grooming. At a later stage we plan to relate the results to neuroanatomical and neurophysiological maturation of postural mechanisms.

METHODS

Hooded rats of the Lister strain were housed in an animal room which was lighted from 8AM until 6.30PM. One female rat with 2 males was housed in a cage and inspection for new litters occurred at least twice daily. The day of birth is referred to as P1. Rats of both sexes from 3 litters were observed daily from P2 - P20. Litter size was 7 pups in 2 of the litters and 10 pups in the other litter. The rats were weighed daily. Their weights were within the range of normative data collected over the years in our institute. The pups were marked individually by a non-toxic ink in the first days. Thereafter, the black and white pattern of their skin enabled identification.

The rat pups, one at a time, were taken from the litter and observed while in a perspex runway (100x15x50cm high). Lighting conditions were similar to those in the animal room. Pups were placed in prone position at the middle of the cage and their stationary and locomotor movements were recorded for 10 min on video tape (VHS camera Panasonic F11 with a stroboscopic shutter operating at 25 frames per second; Panasonic video recorder AG 6200). Observations occurred between 8 and 10AM.

The behaviour of the rats was assessed during several play back runs of the video tape at real time and slow speed. In particular, attention was paid to the occurrence of head lifting, horizontal and vertical head movements, trunk control during standing and locomotion, supported and unsupported rearing, grooming, and the occurrence of complex behaviours such as head movements while walking.

RESULTS

At P2 the trunks of all rats remained in contact with the floor of the cage during resting, pivoting and during crawling. The pups generally remained in a prone position during the observations. After an accidental turn on the back, which could be caused by vigorous paw movements or a startle, none of the rats was able to right themselves. Head lifting for a few seconds was observed in only 50% of the rats.

At P4 head movements in the horizontal plane were observed in 9 of 10 pups. These movements included not only single movements but also bouts of rhythmic movements from left to right and back (so-called rooting movements; Prechtl and Schleidt 1950). Vertical head movements occurred as well but in only 2 of the rats. During crawling, pivoting and also during head movements, the belly remained in contact with the floor in all rats. Three animals fell on their side during vigorous movements and these subjects were able to right themselves.

At P5 all rats were able to lift their head while lying in prone position. Four of the rats succeeded in making a few steps with the belly free from the floor. During these brief bouts, the belly was raised. The head pointed downward and touched the floor. This pattern of locomotion still strongly resembled crawling with markedly extended hindpaws. Two rats repeatedly attempted to stand on their hindlegs against the wall of the cage (rearing with forelimb support). Successful righting was observed in 4 out of the 6 rats that accidentally turned on their back.

At P6 and P7 no important developmental changes in behaviour were observed.

From P8 vertical head movements frequently occurred in all rats while they were lying flat on the floor. Walking and standing with the ventral body surface free from the floor was observed in 9 rats. Locomotion was slow and staggered, lasting only a few steps, after which the rats sagged down again. The nose still pointed downward and touched the floor. The shoulders were elevated in relation to the rest of the body. In only one rat free walking was not observed at this age.

At P10 locomotion on four paws with the belly free occurred in all rats. Walking was still remarkably jerky and tremulous with walking episodes consisting of only 2 - 4 steps. The spine was concave in most of the rats but 2 pups kept their back straight. The shoulders were still elevated relatively to the hip during the stance phase. During locomotion, the hindpaws were abducted and exorotated. During the swing phase, the toes of the hindpaws remained in contact with the floor. Successful and stable rearing with forelimb support could be observed in all subjects at this age.

At P12 and P13 walking was still slow and tremulous. The spine swayed from side to side, apparently due to poor control of the trunk and the limbs, but the head did not touch the floor anymore. Even horizontal head movements occurred and it seemed as if the rats were able to orient themselves during locomotion from this age onwards. Vertical head movements, by contrast, were observed only when the trunk rested on the floor.

At P14 rats were also able to perform vertical head movements while standing. During locomotion, the back and head were kept straight. The hindpaws were still abducted during locomotion. From this age, grooming occurred without support against the wall of the cage. Also rearing without forelimb support was observed from this age.

At P15 and P16 the style of locomotion changed drastically. From this age, hindpaws remained adducted during the stance phase and exorotation was absent. Movements of the trunk and the limbs were smooth and skilful. Locomotor speed increased and varied even during bouts of locomotion. Shoulder and hip were at the same level, such that the back remained in a horizontal position during locomotion. Grooming and rearing were performed fluently and efficiently and resembled the adult pattern.

No important qualitative changes in posture and style of locomotion were observed from this age until P20, the last day of observation.

It is worth stressing the general observation that the developmental course of motor behavior in individual rats was not consistently advanced or retarded. A particular rat may be late in walking with the belly free around P8 - P10 but early in the smooth and adult type of locomotion at P14. This means also that no particular relation with gender or weight gain could be detected in our material.

Figure 1 summarizes the pattern of postural development, which may be distinguished by 3 phases. In the early postnatal period until P4 - P5, only head lifting and rooting movements occurred. The trunk remained constantly into contact with the floor. In the second phase, lasting from P6 until P12 - P13, rats were able to raise their ventral body surface from the floor while walking a few steps. Rearing with forelimb support occurred in this period. In the third period from P12 - P16, complex motor patterns as locomotion, rearing and grooming acquired adult and fluent characteristics. More complex motor acts develop in this period, e.g. rats become able to perform head movements during walking and rearing.

DISCUSSION

The ecological biotope of the developing rat is tailored to its insessorial development. In the neonatal period the pup is dependent on its mother for several physiological needs. Only several days after birth, the development of metabolism and that of motor functions enable increasing independence. The emergence of postural functions parallels this late development. Our observations of motor development correspond to those of other authors (Bolles and Woods 1964, Altman and Sudarshan 1975, Almli and Fisher 1977). However, the present re-

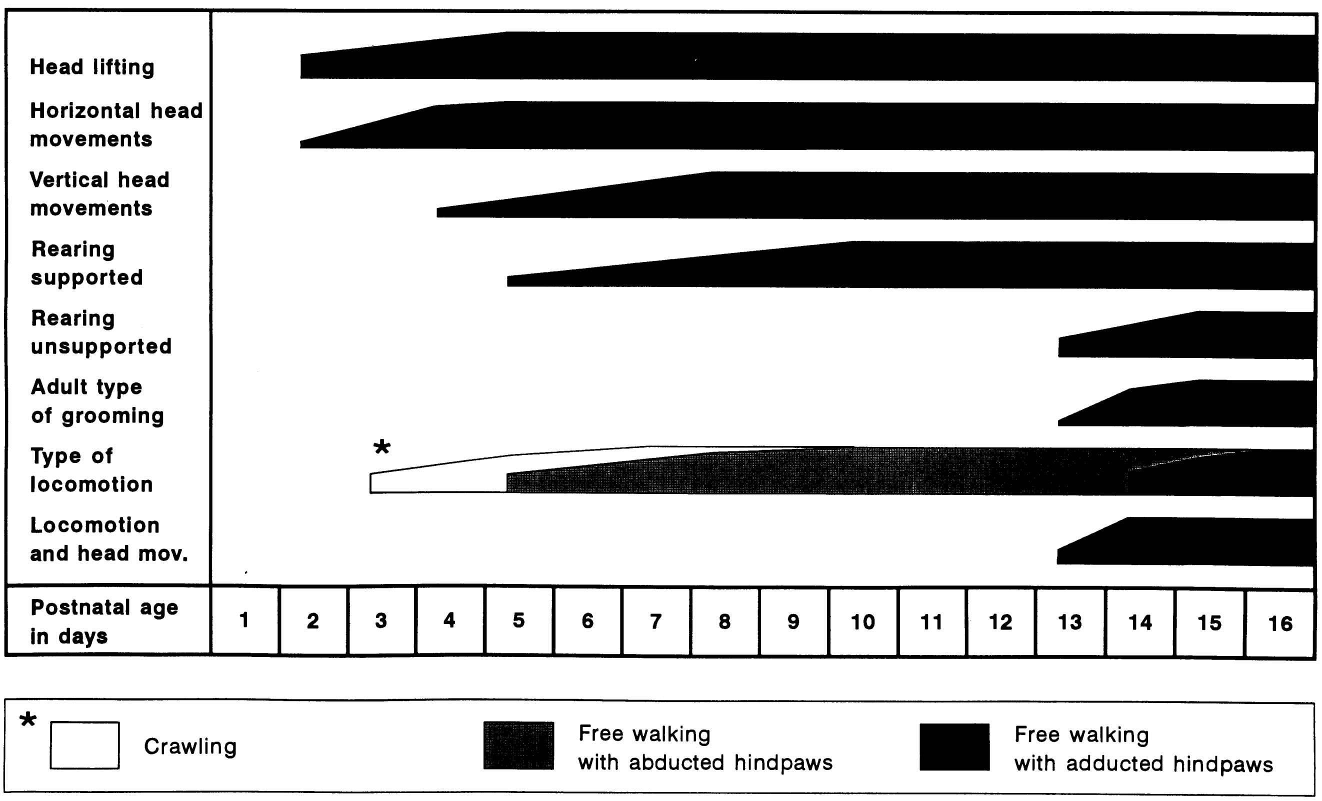

Fig. 1. Diagram presenting the development of the different movement patterns as a function of age. Vertical dimensions of the horizontal bars represent percentages of rats with positive responses.

sults indicate that the early development of motor behaviour in hooded rats is advanced by about 1 or 2 days. Such behaviours as head lifting, trunk elevation, and rearing consistently occurred earlier compared to data obtained from rats of Sprague-Dawley, Purdue-Wistar, Holtzman and Charles River CD strains. This may be attributed to strain differences, differences in behavioural categorisation and perhaps also to differences in balances of nutrients in their feeding (Smart, pers comm., 1988). This indicates that correlative studies on motor development should be performed on animals of the same strain.

Postural development obviously depends on muscular development as well as on neural control. Muscles which are important for maintaining a stable posture involve trunk muscles as well as so-called postural muscles in the extremities. Most is known of the development of the soleus muscle in the hindlimb. The soleus muscle is activated phasically until P12, and from that age until P21 the adult tonic activation pattern develops (Navarrete and Vrbová 1983). In this same period the fibre type differentiation of this muscle shows a remarkable shift. Until P11 a minority of about 26% of the fibres is of the slow twitch type I. This percentage increases to 56% at P16 and further increases, at a slower rate, to 80 - 90% at P140 (Ho et al. 1983). In concordance with this, the activity of enzymes involved in oxidative metabolism increases substantially during the first postnatal month, which presumably permits longer periods of sustained activity (Villa-Moruzzi et al. 1979, Zuurveld et al. 1985). These data corroborate our observations on the development of hindlimb posture.

An important aspect is the development of muscle force, which depends both on muscle properties such as cross sectional area and neural innervation. The cross sectional areas of the soleus and plantaris muscles increase markedly in the first weeks after birth (Chiakulas and Pauly 1965). However, the relation between body weight and the cross sectional area of the tibialis anterior muscle changes only little in the first weeks after birth (Ontell and Dunn 1978). This suggests that immature neural activation is the limiting factor for force development in this period. To our knowledge, nothing is known of the development of postural trunk muscles in quadrupeds, but there is no reason to suspect that the situation is essentially different for axial muscles.

The innervation of muscles changes drastically in the first weeks of life. In the first postnatal days extrafusal muscle fibres in the soleus muscle, the diaphragm and other muscles are polyneuronally innervated (Redfern 1970, Brown et al. 1976, Korneliussen and Jansen 1976, Betz et al. 1979). After the first week supernumerary axon terminals are retracted - around P9 in the intercostal muscles (Dennis et al. 1981) and around P14 in the diaphragm and in the soleus muscles (Redfern 1970, Brown et al. 1976). The effects of this regressive development on muscle force and on the characteristics of contraction are not known, but it is likely that a graded control of tension can only be achieved after regression of polyneuronal innervation.

Afferent feed back is a crucial factor with respect to maintenance of posture. Proprioceptive fibres from the hindlimb muscles have reached the spinal motor nucleus already before birth in the rat and from that stage reflexes can be elicited (Saito et al. 1986, Kudo and Yamada 1987). However, the spindles of the lower hind limb muscles are morphologically mature only from P12 (Milburn 1973) and firing patterns reach adult characteristics between P14 and P18 (Bursian 1973, Vejsada et al. 1985). This development parallels the maturation of walking and standing in our rats during the third period.

None of the suprasegmental systems which are involved in postural control is fully developed in young animals. An exception may be the reticular formation as descending reticulospinal fibres onto lower spinal levels have been demonstrated before birth (Das and Hine 1972). However, nothing is known as to their functional status. Some vestibular reactions can be elicited already shortly after birth, such as the vestibulo-ocular reflex from P1 (Lannou et al. 1983). The righting reflex is present before the end of the first week (Smart and Dobbing 1971, Almli and Fisher 1977), but further maturation of the vestibular system is protracted and is not complete before 4 weeks of age (Karhunen 1973, Curthoys 1983, Lannou et al. 1983). This developmental course precludes an assessment of the role of the vestibular system in postural development by observation alone. Therefore, we have initiated an EMG study on the effects of early vestibular deprivation on motor development and the response to postural perturbations.

Cerebello-rubral connections have been demonstrated already at G16 (Cholley et al. 1989) and rubro-spinal projections from G17 (Lakke and Marani 1991). However, the maturation of the cerebellar cortex is not finished by then. Purkinje cells are spontaneously active from P1 but only after 1 week they can be driven by electrical stimulation of their afferents (Puro and Woodward 1977a,b). Effects of cerebellar lesions at early ages suggest that the cerebello-rubro-spinal system only plays a significant role in motor behaviour from about P15 (Gramsbergen 1982, Gramsbergen and IJkema-Paassen 1984). The corticospinal system develops even later. The first corticospinal axons reach lumbar levels between P6 and P11 (Gribnau et al. 1986, Joosten et al. 1987, 1989), but the myelination of these fibers is only complete around P28 (Hicks and d'Amato 1975, Schreyer and Jones 1988). These data indicate that these systems are not involved in postural mechanisms in the first and second period. It is conceivable that they are at least partly responsible for the skilful integration of posture and movement at the end of the third period.

When interpreting our results in the light of data in the literature, the following conclusions may be drawn. Firstly, our data clearly indicate that the maturation of postural muscles and their neural control proceeds in a rostrocaudal direction. In the first period only the head is lifted from the surface and moved in a to-and-fro fashion. In the second period, postural control also involves the trunk and the extremities. Poor postural control in this period may be due to inadequate muscular force. This seems to be related to inadequate neural drive rather than muscular weakness *per se*.

Secondly, it is striking that the development of postural control until P12 only permits simple motor acts, such as standing, overground walking, and rearing with forelimb support. Thereafter, various motor patterns can be performed simultaneously. For instance, the animal is able to perform head movements during walking. The interpretation that seems reasonable suggests that these complex behavioural patterns are possible by virtue of the integration of supraspinal postural control mechanisms with segmental circuits. Our further research aims at substantiating the neuroanatomical and neurophysiological substrate of this development.

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