

THE DEVELOPMENT OF INTERLIMB CO-ORDINATION DURING SWIMMING IN POSTNATAL RATS

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SUMMARY

The postnatal ontogeny of interlimb co-ordination was studied in rats from day 1 after birth to day 22. Swimming rather than walking was studied in order to minimize any effect of weak limb muscles in very young rats. Videotape records of swimming were analysed on a frame-by-frame basis to determine stroke cycle duration for individual limbs and interlimb latency and phase relationships.

Interlimb co-ordination typical of swimming (or trotting) in adult quadrupedal vertebrates was already present on postnatal day 1, and so apparently the neural pattern generating circuitry for this behaviour is already established by this stage. In young rats it was possible to see 1 limb, or almost any combination of 2, 3 or 4 limbs, moving during swimming, and usually with proper phase relationships. This suggests that each limb has its own separate neural pattern generator and that there are effective interlimb co-ordinating mechanisms controlling moving limbs during swimming, even at very early stages.

There was a gradual decrease in stroke cycle duration (increase in frequency) during the first two postnatal weeks. This may be due to maturing sensory input.

INTRODUCTION

The patterns of interlimb co-ordination during adult locomotion have been quantitatively described for numerous vertebrate and invertebrate species (e.g. von Holst, 1939; Gray, 1968; Delcomyn, 1971; Graham, 1972; Burns, 1973; Stuart *et al.* 1973; Cohen & Gans, 1975). Since the pioneering work by von Holst (1939), several more recent studies have been aimed at elucidating the underlying neural mechanisms (e.g. Pearson & Iles, 1973; Stein, 1971, 1974, 1976; Miller, van der Burg & van der Meché, 1975*a, b*; Halbertsma, Miller & van der Meché, 1976).

The development of interlimb co-ordination has been studied less extensively. Studies of several insects have shown that interlimb (forewing-hindwing) co-ordination develops gradually, after intralimb co-ordination has been established, near the

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time of the imaginal moult (Bentley & Hoy, 1970; Kutsch, 1971; Altman, 1975). Among the vertebrates which have been studied, interlimb co-ordination has been reported first to occur at varying times during ontogeny. There is no information available on the ontogeny of interlimb co-ordination in fishes, and little for amphibians and reptiles. However, it has been reported that in *Eleutherodactylus*, a species of amphibian which develops legs as an embryo, interlimb co-ordination develops gradually prior to hatching (Hughes, 1966) while in *Xenopus* (Hughes & Prestige, 1967) and *Ambystoma* (Coghill, 1929), species in which the legs develop after hatching, stepping movements of the limbs were first observed to appear during larval life. In the two reptile species which have been examined, no interlimb co-ordination was observed during embryonic stages (Decker, 1967; Hughes, Bryant & Bellairs, 1967). However, limb movements during hatching were not observed in these studies.

In birds, it is clearly established that interlimb co-ordination develops in the last few days of embryonic life as part of pre-hatching and hatching behaviour (Hamburger & Oppenheim, 1967; Kovach, 1970; Oppenheim, 1973; Provine, 1977).

Walking movements have been described in some mammalian foetuses (cat: Brown, 1915; Windle & Griffin, 1931; Coronios, 1933; Windle, 1940; human: Humphrey, 1970), but only after the blood supply to the placenta had been compromised. The ontogeny of motor behaviour, both prenatal and postnatal, has been studied more extensively in rats than in any other species except chickens. A recent study of rat foetuses, in which care was taken not to interrupt the placental circulation, found no evidence of organized interlimb co-ordination prior to birth (Narayanan, Fox & Hamburger, 1971). Moreover, qualitative studies of postnatal behaviour in rats have suggested that the diagonal pattern of limb movements seen during walking develops only gradually from birth. In rats the diagonal pattern is usually first reported during locomotion at 6–8 days (Tilney, 1933; Stelzner, 1971; Altman & Sudarshan, 1975), although Bolles & Woods (1964) noted that some of their rats showed a four-legged crawl at 3 days or earlier. Schapiro, Salas & Vukovich (1970) found that interlimb co-ordination was absent when rats less than 6 days old were placed in water. In that study, co-ordinated swimming using all four limbs was not observed until the second postnatal week.

Thus the available qualitative evidence suggested that in the rat, a mammal which is born in a relatively immature state, interlimb co-ordination of the four legs develops gradually during postnatal life and is therefore amenable to study (prenatal studies of mammalian foetuses pose formidable technical problems: Windle, 1940; Hamburger, 1963; Carmichael, 1970; Bradley & Mistretta, 1975). In the present study we examined the postnatal ontogeny of interlimb co-ordination in rats by quantitatively analysing: (1) the time course of changes in the rate at which swimming strokes occurred by measuring stroke cycle duration and (2) the first appearance and time course of changes in co-ordination in (a) the two homologous limb pairs (forelimb and hindlimb pairs) and (b) a homolateral pair (forelimb and hindlimb on the same side). We analysed the pattern of limb movements during swimming rather than walking in order to minimize the resistance encountered by the relatively weak limb muscles of the early postnatal rat pups (Tilney, 1933; Fentress, 1972, 1978).

MATERIALS AND METHODS

Animals

A total of 35 male and female Long-Evans hooded rat pups from four litters were used in this study. Except during observation sessions, pups were housed with their mothers and littermates in standard $44 \times 23 \times 20$ cm cages.

Observations of swimming

Each litter was observed daily from day 1 (day of birth is called day 0) to day 22. During the first postnatal week litters were often observed twice, once in the morning and once in the afternoon, in order to obtain sufficient data. For each observation session, rat pups were chosen in random order from each litter. Each pup was then observed individually after it was placed gently into the centre of a 90 cm long \times 90 cm wide \times 30 cm deep Plexiglass tank filled to a depth of 15–20 cm with warm (approximately 36 °C) water. Each older rat pup was allowed to swim until it encountered a side of the tank. Young rat pups (1–14 days) often swim in circles and therefore did not bump into the sides. They were removed after approximately 30 seconds if the nose was not being held above water (1–9 days), immediately if they began to sink (1–10 days), or when they appeared to tire.

While one observer watched the rats from above, a second observer filmed the swimming sequences with a Sony AVC-3400 videotape camera (60 frames per second) from below, through the transparent bottom of the swimming tank. A ventral view was chosen because it gave the clearest view of all four limbs at all ages studied.

Data analysis

Videotapes were analysed on a frame-by-frame basis. Swimming sequences in which 6–27 (usually 8–12) consecutive complete swim stroke cycles were present were chosen for analysis. Only sequences in which all four limbs (left fore, LF; right fore, RF; left hind, LH; right hind, RH) participated were used except on day 1 when, in addition to the usual 4-limb sequences, some 1-, 2- and 3-limb sequences were analysed. For each limb two points in each stroke cycle were determined: the onset of power-stroke and the onset of return-stroke. Only power-stroke will be considered here since return-stroke data were not used in the analyses. The onset of the power-stroke was defined as the beginning of the stroke cycle. It was identified as the frame in which the limb had reached its maximum anterior extension and one frame before the limb actually began to move posteriorly. The first frame of a sequence was numbered frame 0 and the frame number of the onset of each power-stroke for each limb was recorded.

For each age analysed in detail (1, 2, 4, 5, 6, 8, 14, 20, 22 days), data obtained from 4 to 8 sequences, each from a different rat pup, were pooled. From these data the following information was computed using a computer program written by W.T.

(1) Stroke cycle duration (D): the time from the onset of one power-stroke in a limb to the onset of the subsequent power-stroke in that same limb. Stroke cycle duration was calculated for each stroke cycle in LF and LH. Stroke cycle duration of LF is expressed as D_{LF} .

(2) Latency (L): the time from the onset of a power-stroke in one limb to the onset of the subsequent power-stroke in a second limb. Latency of RF with respect to LF is expressed as $L_{RF, LF}$. Latencies were calculated for both homologous pairs ($L_{RF, LF}$; $L_{RH, LH}$) and one homolateral pair ($L_{LH, LF}$).

(3) Phase (ϕ): the fraction of the total stroke cycle of one limb which has elapsed when a second limb begins its stroke cycle. Phase of RF with respect to LF is expressed as $\phi_{RF, LF}$ and can be calculated from: $\frac{L_{RF, LF}}{D_{LF}}$. Phase relationships were calculated for both homologous pairs ($\phi_{RF, LF}$, $\phi_{RH, LH}$) and one homolateral pair ($\phi_{LH, LF}$).

Mean, standard error of the mean and variance were calculated for each age for each of the three variables (D , L , ϕ). These means became the data for further analyses. We used a repeated-measures analysis-of-variance approach to test the hypothesis that these variables changed over time. Since there were missing values for some litters on some days, we used an SPSS (Statistical Package for the Social Sciences) stepwise multiple regression program to calculate the sums of the squares for the ANOVA.

RESULTS

Qualitative behavioural observations

On day 1 rat pups were able to use all four limbs during swimming. However, they were not able to keep their noses consistently above water until day 8 or 9. Moreover they tended to swim in circles until approximately day 14. After this time pups often swam in a straight line. The change occurred at about the time that eye opening took place.

While all four limbs could be used during swimming at all ages studied, there were age-related differences in the proportion of swimming cycles during which 4, 3 or 2 limbs were used. Between day 1 and day 9 it became increasingly common for all four limbs to participate in swimming. However, sequences or parts of sequences in which only the forelimb pair, or a homolateral pair, or three limbs (always the two forelimbs and a hindlimb) were used were also common. Quite often a swimming sequence would begin with activity of a pair of limbs, then after several stroke cycles a third and finally the fourth would join in. Between day 9 and day 16 all four limbs were almost always used, but after days 16 to 18 it became more and more common for the forelimbs to drop out as the hindlimbs appeared to provide the main propulsive force. In these older pups the forelimbs were often used during the first few strokes, but were held motionless against the chest thereafter or were used sporadically.

Stroke cycle duration

The duration of stroke cycles (D) for both the forelimbs (LF) and hindlimbs (LH) decreased with age (Fig. 1). For example, there was an initial sharp decrease in D_{LF} during the first 8 days from a mean initial duration of 729 ms (1.37 Hz) until a plateau of approximately 300 ms (3.33 Hz) was reached during the second week. The analysis of variance showed that there was a significant linear decrease in D_{LF} (linear component of days: $F = 153$, d.f. = 1, 12, $P < 0.001$) over days 1–22. Results for D_{LH} were similar ($F = 33.01$, d.f. = 1, 12, $P < 0.001$).

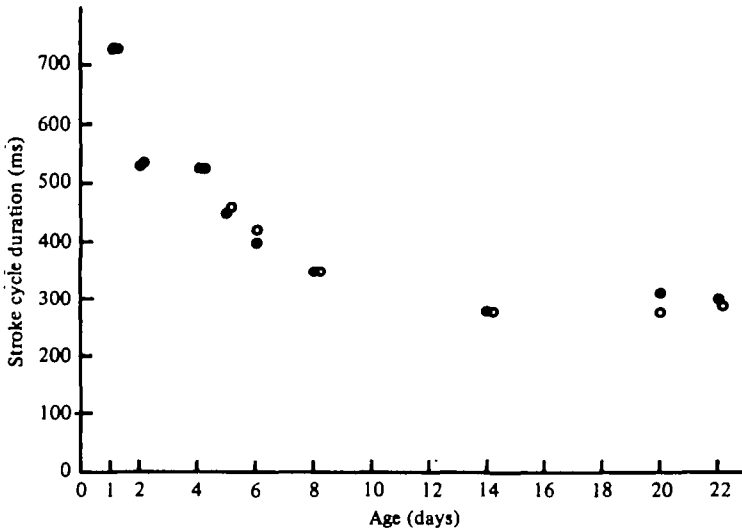


Fig. 1. Mean stroke duration plotted against postnatal age of the rat pups. ●, Left forelimb; ○, left hindlimb.

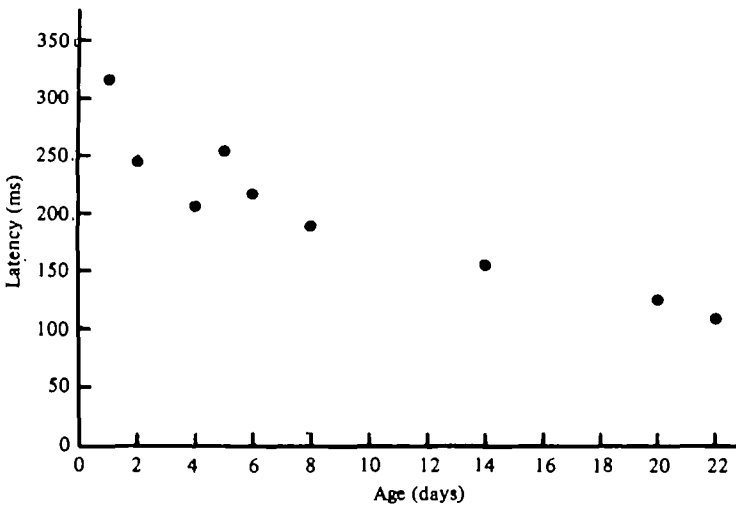


Fig. 2. Mean latency of right forelimb with respect to left forelimb plotted against postnatal age of the rat pups.

Latency

Latency from the beginning of a stroke cycle in one limb to the beginning of a stroke cycle in another limb also decreased with age (Fig. 2). This result was found for both homologous and homolateral pairs. Statistical analysis showed that there was a significant linear decrease over days (linear component of days for $L_{RF, LF}$: $F = 35.30$, d.f. = 1, 12, $P < 0.001$; for $L_{RH, LH}$: $F = 40.82$, d.f. = 1, 12, $P < 0.001$; for $L_{LH, LF}$: $F = 20.75$, d.f. = 1, 12, $P < 0.001$).

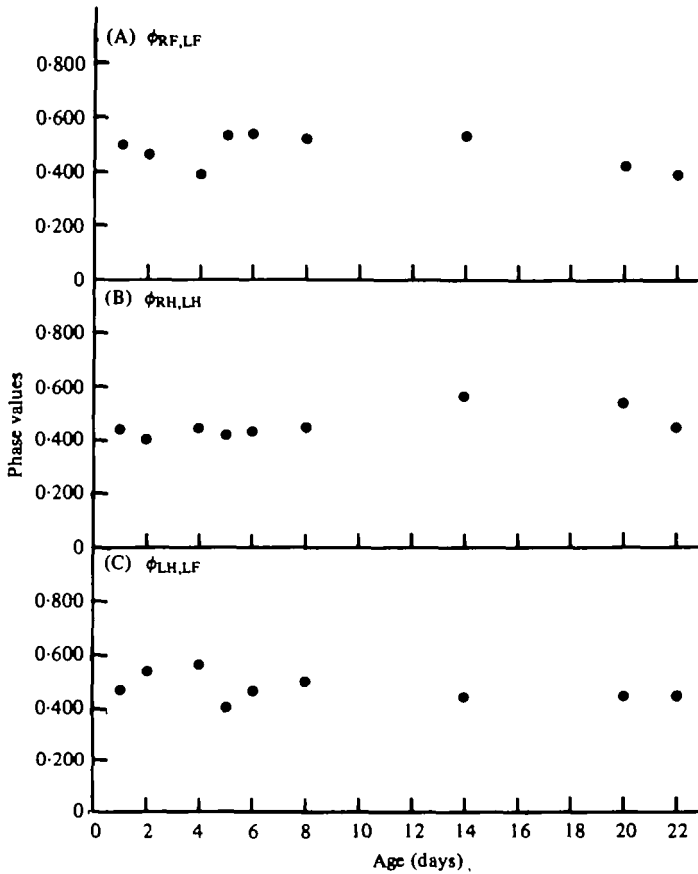


Fig. 3. Mean phase values plotted against postnatal age of the rat pups. (A) Phase values for the homologous forelimb pair. (B) Phase values for the homologous hindlimb pair. (C) Phase values for the homolateral left limb pair.

Phase

While both duration and latency changed markedly with age, phase did not (Fig. 3). On day 1 the mean \pm S.E.M. value for $\phi_{RF, LF}$ was 0.544 ± 0.056 , for $\phi_{RH, LH}$ 0.444 ± 0.062 , and for $\phi_{LH, LF}$ 0.549 ± 0.059 . Statistical analysis showed that the linear component of days failed to reach significance for $\phi_{RF, LF}$ and $\phi_{LH, LF}$. For $\phi_{RH, LH}$ it just reached significance ($F = 6.83$, d.f. = 1, 12, $P < 0.05$).

One-, two-, and three-legged swimming

Several cases in which fewer than four limbs were used during swimming were analysed in 1-day-old rats. It was possible to find sequences in which interlimb co-ordination of three limbs (always involving both forelimbs and one hindlimb) showed normal phase relationships. For example, in one sequence of 22 limb stroke cycles in which RH did not participate, $\phi_{RF, LF} = 0.498 \pm 0.026$ and $\phi_{LH, LF} = 0.470 \pm 0.020$. Stroke cycle duration was normal.

Sequences in which only the two forelimbs participated also showed normal phase

relationships. Perhaps more surprising were analyses of cases in which only one homolateral pair of limbs participated in swimming. For example, in one sequence of 16 limb stroke cycles in which only RF and RH were active in a 1-day-old rat pup, $\phi_{RH, RF} = 0.491 \pm 0.019$. In this case stroke cycle duration was somewhat longer ($D_{RF} = 885 \pm 31$ ms) than that observed during normal 4-limb swimming in 1-day-old rats.

In one case, a 1-day-old rat pup used only one limb, RF. Stroke cycle durations were longer and more variable than normal ($D_{RF} = 1403 \pm 197$ ms).

DISCUSSION

From the results presented it is clear that, at all ages studied, the rat pups could produce a pattern of four-limb co-ordination in which diagonal limbs (LH and RF or LF and RH) began their stroke nearly simultaneously, and thus phase relationships of near 0.500 were maintained for both homologous and homolateral pairs. This pattern of interlimb co-ordination is typical of terrestrial trotting in adult quadrupedal vertebrates (see Grillner, 1975, for review; Cohen & Gans, 1975, for relevant information on rats) and of aquatic swimming in adult turtles (Zug, 1971; Lennard, 1975) and cats (Halbertsma, Miller & van der Meché, 1976). Thus the rat swims in the manner expected for a quadrupedal vertebrate. Note that although interlimb co-ordination is the same during trotting and swimming, differences in intralimb co-ordination have been found during trotting and swimming in rats (Gruner, 1978).

Since the diagonal swimming pattern of interlimb co-ordination is already present on postnatal day 1, the neural circuitry responsible for generating co-ordinated four-limb swimming has already been assembled at this early stage. The only consistent deviation from the standard diagonal pattern was a tendency for rats 8 days old or less to show mean values for $\phi_{RH, LH}$ of slightly less than 0.500. That is, RH consistently began its power-stroke slightly earlier than expected. The reason for this is unknown. No correlation with circling was seen, since in the sequences analysed the pups circled equally often to the left or right.

The major differences from adult swimming observed in 1-day-old pups are seen in the stroke cycle durations and latencies, which are over twice as long as in 22-day-old rats. This basically means that the young rats swim more slowly than older ones. A gradual increase in wingbeat frequency with time, after inter-wing co-ordination had been established, has been documented in locusts (Kutsch, 1971, 1974; Altman, 1975) and moths (Kammer & Rheuben, 1976). This increase in wingbeat frequency has also been seen in other insects (see Bentley, 1973 for review). In locusts it has been shown that practice has no effect on the time course of the increase (Kutsch, 1971; Altman, 1975). There is evidence to suggest that the increase in frequency is due either (1) to changes in the excitation of wing-associated sense organs (Altman, 1975; Kammer & Rheuben, 1976), or (2) to an increase in the intrinsic oscillation frequency of the flight pattern generator (Kutsch, 1974). The present data do not allow us to distinguish between these possibilities in the rat. It is known, however, that the muscle spindles in the hindlimb of the rat are immature at birth. The full complement of intrafusal fibres is not found until postnatal day 4 and the fibres are not fully dif-

ferentiated until postnatal day 12 (Barker & Milburn, 1972; Milburn, 1973). During swimming adult stroke frequencies are reached between postnatal days 8 and 14 (see Fig. 1), suggesting a possible correlation with developing sensory input.

These results emphasize the importance of studying the development of co-ordination under permissive conditions. As pointed out by Fentress (1978), general problems such as balance, body weight and muscle weakness may prevent the expression of behavioural sequences despite the presence of the necessary neural circuitry. On a hard substrate, clear evidence for co-ordinated four-limb walking is usually not seen in rat pups until near the beginning of the second postnatal week (Tilney, 1933; Stelzner, 1971; Altman & Sudarshan, 1975). Prior to that only the forelimbs show co-ordinated movements; the hindlimbs are often dragged. Since our results show that the neural basis for diagonal four-limb co-ordination is already developed on postnatal day 1, it seems reasonable to suggest that this capability is not expressed on land because the relatively weak muscles of young rat pups cannot support their body weight during attempts at locomotion on a hard substrate.

Although it was less common to see forelimbs uncoupled than hindlimbs, there were numerous cases in young rat pups in which only one homolateral limb pair was active. Overall, forelimbs were more tightly coupled than hindlimbs in young rat pups, but in older animals forelimbs were less tightly coupled. This has also been observed in mice (Fentress, 1972, 1978). The results of the present study clearly suggest that each limb has a separate neural control centre, as has been suggested for other limbed animals (for reviews see Grillner, 1975; Stein, 1976). The right forelimb can, for example, perform stroke cycles alone, in alternation with the left forelimb, in alternation with the right hindlimb, or in co-ordination with two other limbs or with all three. Under experimental conditions, these results can be obtained in adult turtles (Lennard & Stein, 1977; P. S. G. Stein, personal communication) and cats (Kulagin & Shik, 1970). Although at certain stages it was common to see one or more limbs remain inactive while others performed co-ordinated swimming cycles, it was relatively rare to see a moving limb which was not cycling in co-ordination with the other moving limbs. Thus the neural elements responsible for interlimb co-ordination did not appear to have a threshold substantially higher than the neural elements controlling the movement of a single limb during swimming. Based on results obtained in high spinal cats (Miller & van der Meché, 1976) it seems likely that the neural circuitry underlying the interlimb co-ordination observed in the rats is located in the spinal cord.

Since interlimb co-ordination – as judged by maintenance of consistent phase relationships between homologous and homolateral limb pairs – is already evident on postnatal day 1, it would appear that the underlying neural circuitry develops prenatally. We suggest, therefore, that it may be profitable to re-examine interlimb co-ordination in rat fetuses using quantitative analyses of videotape or film records. As mentioned earlier, several qualitative studies have failed to detect patterns of interlimb co-ordination in rat fetuses (Angulo y Gonzalez, 1932; Tilney, 1933; Windle *et al.* 1935; Narayanan, Fox & Hamburger, 1971; A. Bekoff, unpublished observations). This may indeed represent a case in which, on a behavioural level, prenatal antecedents to a postnatal behaviour (locomotion) cannot be found (see Hamburger, 1973; Oppenheim, 1973). One possibility is that this behaviour is in-

hibited during prenatal life. Inhibition of specific co-ordinated behaviour patterns during ontogeny has been shown to occur in several invertebrate larvae and pupae (Bentley & Hoy, 1970; Truman, 1976; Reingold & Camhi, 1978), in a fish embryo (Pollack & Crain, 1972) and in the kitten (DeGroat *et al.* 1975).

On the other hand, it is also possible that sequences of interlimb co-ordination do not occur prenatally because this type of behaviour is expressed only during wakefulness. The phase of the wake-sleep cycle can significantly affect behaviour (Precht, 1965, 1972; Chase, 1972). At the earliest stage which has been studied, postnatal day 2, periods of wakefulness, quiet sleep and active sleep can be recognized in rats (Gramsbergen, Schwartz & Precht, 1970; Jouvet-Mounier, Astic & Lacote, 1970). However, the periods of wakefulness are quite short and comprise a relatively small part of the wake-sleep cycle. Thus the state we identify as wakefulness may be rare or non-existent in the rat before birth.

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