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THE STRIDE CYCLE OF THE CAT:

THE MODELLING OF LOCOMOTION
BY COMPUTERIZED ANALYSIS OF AUTOMATIC RECORDINGS

by

JÛNT HALBERTSMA

DELFT & STOCKHOLM 1983

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ABSTRACT

The present study gives a general description of the locomotor patterns of the intact cat. Overground and treadmill locomotion were studied by means of automatic recordings of limb movements, ground reaction forces and electromyograms. The data processing and automatic recording techniques which were used are described; one recording technique is based on a television system, another on the Selspot I system. The data were processed and analysed interactively with a computer, which allows a statistical analysis of many strides in a fast and accurate way. The amplitudes and time course of movements in different joints and different limbs were studied at different velocities of locomotion and correlated to each other and to parameters such as the onset and termination of electromyographic activity in different muscles.

— No element of the stride cycle was found to be constant: The amplitudes of joint angles and limb excursions as well as the durations of the different phases of the stride cycle can be adapted to maintain an appropriate coordination between the limbs.

— The durations of all phases of the stride cycle decrease with increasing speed of locomotion. The durations of the support and extension phases change proportionally more than those of the swing and flexion phases and they all appear to be linearly related to the stride cycle duration.

— The relations of the flexion duration with the stride cycle duration for the different joints are usually different from each other and after a disturbance of the movements of a forelimb the duration of knee and ankle flexion of the homolateral limb can increase and the first extension phase of knee and ankle decrease, whereas they usually increase or decrease together. This further supports the hypothesis that every joint is controlled by a flexion and extension unit pattern generator.

— The amplitude of the joint angle excursions during the different phases of the stride cycle are better controlled than the absolute joint angles at the onset and termination of these phases.

— The position of the toe at touch-down was studied at different velocities of locomotion and was found to remain comparatively constant. There is a correlation between hip, knee and ankle joint angles at touch-down, which was found to be of importance for the precise positioning of the foot.

— During alternating locomotion, such as walking and trotting, all events of the stride cycle are shifted approximately half a cycle with respect to the corresponding events on the contralateral side. The limbs remain coordinated even when large asymmetries in the stride cycle are induced by letting the left and right pairs of limbs locomote at different speeds on two separate treadmill belts. This mimics walking along a circular path. In contrast to other parts of the stride cycle, an event just preceding the support phase or at its onset is always shifted approximately half a cycle with respect to the corresponding event on the contralateral side during split belt locomotion with a 1:1 rhythm.

— At a certain speed difference between the two belts, the asymmetries become too large and the limbs stepping on the belt with the higher speed will take two strides when the limbs stepping on the slower belt take only one. The two strides of the limb stepping on the 'fast' belt are asymmetric with respect to limb positioning, time course of different phases and electromyographic activity. Characteristic interactions occur between the limbs on the 'slow' and 'fast' side.

— The coordination between forelimbs and hindlimbs is not very strict. Intervals may change gradually with increasing speed of locomotion and no fixed values were observed. At the same velocity of locomotion the same interval could vary considerably between trials.

The locomotor system is described in a quantitative way under different constraints, which reveal some properties which the relevant neuronal networks and feedback mechanisms must have, which generate this pattern of behaviour. This information, together with the present neurophysiological and anatomical knowledge, should allow new insights concerning the neural control system for locomotion.

Key words: cat locomotion, speed adaptation, movement patterns, interlimb coordination, intralimb coordination, electromyography, automatic recording techniques, computer analysis.

CONTENTS

INTRODUCTION

In most animals locomotion is an important pattern of behaviour which is necessary to satisfy their needs, such as to survive in a hostile environment. The neural control of locomotion can be divided into three conceptually different tasks, **1** to generate the stereotype locomotor movements and to coordinate them, **2** to adapt these movements to the intentions of the animal and the environment and **3** to maintain the equilibrium of the animal. In natural situations the stereotyped and coordinated locomotor movements are almost constantly adapted and corrected. The aim of the present study is to describe the locomotion of intact cats and in particular the adaptation of the stereotyped locomotor patterns to speed and to the environment under a variety of experimental steady-state conditions.

Eichhorst and Naunyn (1874), Freusberg (1874) and Goltz and Freusberg (1874) reported that dogs with a spinal cord transection in the lower thoracic region (low spinal preparation) could support themselves and that they showed rhythmic locomotor like flexor and extensor movements of the hindlimbs. The movements appeared in response to various nonrhythmic stimuli and they occurred spontaneously if the animal was held in the air with the limbs extended (mark time reflex). Phillipson (1905) analysed this phenomenon and the locomotion of low spinal dogs (spinal stepping) in detail with the aid of the chronophotographic method (film analysis) and compared them with the locomotion of intact dogs. He showed that during spinal stepping the movements of the hindlimbs were coordinated in the alternating way as in walking and trotting or in the more synchronous way as in galloping. These low spinal dogs were able to locomote overground, bearing the weight of their own hindquarters. Phillipson concluded that the coordination of the locomotor movements is an exclusive function of the spinal cord. The similarity of spinal locomotion to normal walking was questioned by many investigators (Magnus 1924, ten Cate 1932). Later investigators were able, by stimulation with drugs and using different training procedures, to improve the walking movements in different kinds of chronic spinal animals (Hart 1971, Shurrager and Dykman 1951, ten Cate 1940, 1962). Recent experiments by Forssberg et al. (1980a), comparing the locomotor movements and electromyograms of spinal kittens and intact cats, have demonstrated that the spinal cord with its reflex machinery can still generate even subtle details of the basic walking movements.

Sherrington (1910) investigated reflex stepping and standing in decerebrate cats and dogs and also in decapitate (high spinal) and low spinal preparations in his elegant studies on limb reflexes. He stressed the similarities between the flexion reflex with its accessory reactions and reflex stepping. Remote tonic stimulation of skin receptors or the spinal cord at C1 level could induce a stepping reflex, consisting of a rhythmic alternating excitation of flexor and extensor muscles. It was also noted that an extension of the hip (but not knee and ankle) was important to start spinal stepping. Exteroceptive ($\simeq$skin) receptors did not appear to play any role. The proprioceptors (muscle, joint and deep fascia receptors) can only be a contributing factor because a unilateral deafferentation of a limb does not stop its movements. Sherrington concluded that the rhythm generation of the stepping reflex is central in its seat, because only a tonic stimulation could elicit it. But he believed that reflex activity from the proprioceptive receptors of the ipsilateral or contralateral limb were essential to generate stepping.

Brown, however, promoted the idea of a complete central generation of the stepping movements (Brown 1911, 1912, 1914). He noted that stepping movements could also occur under deep anaesthesia, when peripheral reflexes were abolished. He proved that alternating rhythmic activity of an ankle flexor and an ankle extensor muscle could be generated by the isolated spinal cord after bilateral transection of the lumbosacral dorsal roots. Brown postulated that there exist neuronal networks in the spinal cord, one centre for each limb. These centres would be divided into two antagonistic 'half-centres', one for flexors and the other for extensors. These half-centres would inhibit each other mutually and synaptic fatigue could be responsible for the rhythmic phenomenon.

Jankowska et al. (1967a, 1967b) injected the noradrenergic precursor DOPA in spinal preparations. This activated a network of neurons that generated reciprocally organized, long lasting discharges in flexor and extensor nerves. Lundberg (1969, Engberg and Lundberg 1969) suggested that this network, as postulated by Brown (1911), could generate alternating locomotor activity to flexor and extensor motoneurons. The finer details of the motor activity could be regulated by proprioceptive reflex activity. But after deafferentation (dorsal root transection) of the mesencephalic walking cat (Grillner and Zangger 1975, cf. Grillner 1981), neither the flexors nor the extensors of different joints behave as one unit. This is just as in intact animals. This observation was subsequently extended to acute and chronic spinal cats (Grillner and Zangger 1979). Curarisation, which excludes all movement related feedback, and stimulation with drugs of decorticate (Perret and Cabelguen 1980) and acute spinal cats (Grillner and Zangger 1979) showed also a rhythmic activity (fictive locomotion) which was more complex than flexor-extensor alternation. Thus there indeed exist centres in the spinal cord that can generate the motor output for locomotion. These centres are referred to as central pattern generators (CPGs). In low spinal animals the spinal cord can coordinate the limbs in the alternating way as in walk or trot and in the more synchronous way as in gallop (Forssberg et al. 1980b, Phillipson 1905). Also high spinal cats can locomote with the appropriate coordination between the forelimbs and hindlimbs (Miller and van der Meché 1976). It follows that every limb therefore is controlled by a separate CPG.

Although these centres can generate a motor output by themselves, they are affected both by peripheral feedback and from supraspinal structures. For example a stretching of the contracting ankle extensors, in order to load these muscles above a certain level, may block the initiation of flexor activity (Duysens and Pearson 1980). Grillner and Rossignol (1978) showed in chronic spinal cats that the hip position is an important factor determining the initiation of the swing phase in that leg. The spontaneous efferent burst pattern of acute spinal and curarized cats (fictive locomotion) can be influenced by passive hip movements (Andersson et al. 1978). The locomotor rhythm will be entrained by the hip movements over a certain range below and above the spontaneous one. Short ramp-formed movements of the hip can also influence the duration of the locomotor cycle (Andersson and Grillner 1981). Receptors in and around the hip joint are responsible for these effects. The central pattern generator itself can also exert a phasic gating of certain reflex pathways from the dorsum of the foot (Forssberg 1979). Supraspinal structures also interact with the locomotor circuitry. Descending control can initiate locomotion, correct ongoing movements and influence the coordination between the limbs (Orlovskii 1972, Shik et al. 1966, 1967, 1968). Ascending pathways supply the higher structures with information of different receptor systems and they relay an efference copy of the generator activity (Arshavskii et al. 1972a, 1972b). (For further references see Grillner 1981, Shik and Orlovskii 1976, Stein 1978 and Wetzel and Stuart 1976).

Brown's theory assumes that there exists one CPG for every limb. This assumption could explain the coordination of the limbs in the various ways of locomotion. But walking backwards changes the coupling between hip and knee, while that between knee and ankle remains unchanged (Edgerton et al. 1976). Rhythmic alternating activity can occur in one group of flexors (e.g. knee) with a tonic efference discharge in other flexors (e.g. ankle) (Grillner and Zangger 1979). These findings suggest at least a subdivision of the CPGs in units that control one joint. However, in the above preparations with rhythmic alternating activity at one joint, the extensor burst may occasionally become progressively smaller in amplitude and duration. The flexor burst on the contrary will occupy a successively larger part of the cycle. This suggests a further subdivision in separate units for flexors and extensors at a joint. This leads to the following working hypothesis (Grillner 1981): *A group of unit pattern generators (unit CPGs) in the spinal cord controls each leg. Each unit controls a group of close synergists at one joint (e.g. ankle flexor muscles), and is reciprocally coupled to the unit that controls the antagonist muscles (e.g. ankle extensors).*

The unit CPGs have not yet been identified in vertebrates, but their behaviour has been documented in different kinds of locomoting preparations (see above). Less is known about how they behave in intact locomoting animals. Traditionally descriptions of tetrapod locomotion have been based on support and footfall patterns (Hildebrand 1966, Howel 1944, Marey 1901, Muybridge 1957). They lead to the classification of many different gaits, but they do not give any information about the actual movements of the limbs. The movements of the forelimb and hindlimb joints of one or several strides at a few different speeds have been analysed in detail and they are sometimes supplemented with synchronously recorded muscular activity (Engberg and Lundberg 1969, English 1978, Goslow et al. 1973, Miller and van der

Meché 1975, Phillipson 1905). But there exists no systematic analysis of how the locomotor movements of intact cats change with speed and stride duration. An obvious reason for this lack of information is the laborious character of the commonly used photographic methods. More information is available of the coordination between the limbs (English 1979, Miller et al. 1975a, 1975b, Wetzel et al. 1975). Recent developments in electronics enable an accurate and automatic recording of the positions of markers on moving limbs (Furnée 1967, Furnée et al. 1974, Halbertsma 1980a). Computerized processing and reduction of large amounts of data, from the recorded and digitized positions of markers and from the digitized data of synchronously recorded electromyograms, make it possible to analyse many strides in a fast and accurate way and to treat the data statistically. This report deals mainly with the adaptation of the unit CPGs to speed, the coordination of the unit CPGs in a limb and the interaction of the CPGs of the four limbs of intact locomoting cats. The present phenomenological approach of analysing joint angles and electromyograms is limited; it cannot reveal the underlying neuronal circuitry. This model approach gives a general description of the locomotor pattern in the intact animal. As such it is a necessary supplement to the neurophysiological and the anatomical description of the neuronal networks.

Brief accounts have been published previously (Halbertsma 1976, 1978, 1980b, 1981).

MATERIAL AND METHODS

General procedures

Experiments have been performed on intact adult male and female cats stepping on the ground or on a motor-driven treadmill. Nine cooperative cats were selected and they were trained at least two weeks before a series of experiments started. Only positive conditioning procedures were used, e.g. food rewards and handling by the experimenter. Four cats were trained to step on a plate equipped with force transducers (force plate) that was mounted in a level walkway (3 m long with adjustable transparent perspex sheets to guide the cats). The experiment was so performed that only homolateral limbs could hit the force plate.

All nine cats were trained to step on a treadmill. Two different treadmills were used, each with a different recording technique. A motor driven treadmill of 1.5 m length, 0.3 m width and with walls 0.6 m high was used with the television technique (see below). One long wall was made of transparent perspex to enable the recording of movements of the homolateral limbs. The wall in front of the cats head contained a window through which the experimenter could see the cat, and a drawer through which food rewards could be given. Another treadmill of 1.0 m length, 0.2 m width and with 0.4 m walls was used with the Selspot recording technique (see below). All walls were made of transparent perspex to enable recordings from the two opposite sides. The front wall also contained a window through which food rewards were given. The treadmill consisted of two parallel moving belts. Both could be driven at the same speed or the left one could be disconnected from the motor and manually operated while the right belt was still driven by the motor. With these split belts the limbs on the left side could step with another speed than the right limbs. During the training and recording sessions the velocity of the treadmill belt was kept constant for periods of 30 to 90 seconds. After each session a short pause was introduced to avoid fatigue. The cats were trained to step in the middle or front part of the treadmill. Four cats were recorded with the television system (cats FR, PI, PD and KJ; weight 3.5, 4.5, 5.5 and 2.5 kg respectively) and five cats with the Selspot system (cats SN, SI, ZW, BL and GR; weight 2.8, 3.2, 2.4, 2.4 and 2.8 kg respectively). The movements were presumed to take place in a parasagittal plane.

Television system

The movements of the limbs of one side have been recorded with the television technique developed by Furnée (1967) with a 9 bit horizontal and vertical resolution (Furnée et al. 1974). In this technique of video to digital conversion the positions of small white paper discs (5.5 mm diameter) glued to the skin above the bony landmarks are digitized with an error less than ½% of the total field of view. The sampling rate of the video-to-digital converter is the scan frequency of 60 Hz. Before each scan a special stroboscope is triggered to expose the subject to U.V. light for 1 ms. Under the recording conditions used the displacements of the markers during this exposure time was always smaller than the displacement corresponding to one least significant bit, which was also the noise level of this system. The markers were glued on the elbow, wrist, hip, knee and ankle joint and on the pelvis (iliac crest). Two markers on the scapula were stitched to its spine to give a better estimate. Synchronized with the clock of the video to digital converter 4 channels of amplified, rectified and low-pass filtered electromyograms (EMG) were digitized at a sampling rate of 240 Hz each. Chosen portions of the position and EMG data, stored on digital magnetic tape during the experiment, were analysed off line with a mini-computer (IBM 1130; 8k core memory, disc and storage oscilloscope display). The angles of the scapula, elbow, hip and knee joint were calculated after recognition, corrections for the movements of the skin with the markers above the joints, interpolation and software filtering of the position-data. The EMG-data were also subjected to software filtering before the onset and cessation of the EMG activity were computed. More details are given by Halbertsma (1975).

Selspot system

The movements of the limbs on both sides have been recorded with a modified Selspot I system (Selcom AB, Partille, Sweden). Markers were placed on the hip, knee, ankle and tarsometatarsal joint (toe of the hindlimb) and on the iliac crest (pelvis) of the ipsilateral and contralateral side. In some experiments they were also placed on the carpometacarpal joints (toe of the forelimb). The markers are active (see below), which is a disadvantage over the passive markers used with the television system. The active ones are heavier and require wiring, which influences the locomotion. Cats, which could gallop on the treadmill, when nothing was fixed to the shaved skin, refused to trot fast and gallop with all the markers and EMG electrodes attached. The Selspot system consists of two opto-electronic cameras and processing hardware which can detect the positions of the infra-red 'light' emitting diodes (LEDs, type: 1A48PC) with a horizontal and vertical resolution of 10 bits. Since the system can only measure the midpoint of all infra-red radiation, the LEDs (maximum 20) are pulsed sequentially. Every 100 μs a marker is pulsed for 50 μs and the scan rate is 312 scans/s for every LED. Hardware was developed **1** to reduce the scan rate to 156 scans/s (only every second scan is used), **2** to synchronize an analogue-to-digital converter (ADC) with the Selspot system (see below), and **3** to multiplex the data and interface it with a mini-computer (HP 21MX). Frequency analysis of the markers recorded with the television and Selspot system showed, even for the fastest cat and human locomotor movements recoded, that above 15 Hz no frequency components of the signal exceeded the noise level. The noise level was estimated from the frequency spectrum between ¼ to ½ the scan rate (i.e. 39 to 78 Hz), which always showed a flat appearance. Hence, it is likely that there exist no significant frequency components above 15 Hz and that the scan rate of the television and Selspot system is sufficient for a kinematic analysis.

An 8 channel ADC (improved type SEL 896, Selcom AB) with a resolution of 12 bits was synchronized with the Selspot system. The channels were sampled in sequence at 30 μs intervals, each with a sampling rate of 312 Hz. The signals of a piezo-electric force plate (Kistler, model 9261A) and the rectified EMGs were low-pass filtered with a fifth-order Bessel filter to avoid aliasing effects (frequency folding effect, due to unsufficient sampling rate) (Halbertsma and de Boer 1981). A —3 dB cutoff frequency of 45 Hz has been used to attenuate frequencies above 156 Hz (half the sampling frequency) by at least 40 dB. The time lag of these linear phase filters is equal for all frequencies (9 ms) and has been compensated for in the software when these signals were compared with the data from the position recording system.

Properties of the Selspot system. **1** The Selspot system measures the midpoint of all infra-red radiation with wavelengths between 0.8 and 1.1 μm. One must avoid interference from other radiators which contribute in that range, like the sun and strong artificial light sources. Contributions from bodies radiating with a temperature under 100° C, like test subjects, can be neglected. Reflections of the LEDs from the floor and walls should also be avoided. The reflections from the floor were reduced more than 99.7% with a brown poliamid carpet (type Tarkett Jasmin, Rönneby, Sweden; thread length 12 mm, 95000 threads/m^2). Interference from reflections from the walls and ceiling were prevented with a PVC screen. The screen (1×1 m) had a square hole in the middle in front of the camera. The hole was adjusted so that it just limited the field of view to avoid internal lens reflections. **2** The linearity of the system was tested with a grid of 11×11 points that covered 90% of the field of view in both horizontal and vertical directions (cf. Woltring 1977). The aberrations have been calculated from the extrapolated central image which was assumed to be distortion free. Both cameras and processing electronics showed irregular pincushion-like distortion, The maximal distortion found was 5% of the field of view in both directions, which can lead to length changes of 25% between the center and the edges. Corrections were made in the software for these distortions (see below).

Most of the distortions could be attributed to the Canon TV-16 lens† (1:0.95/50), because the nonlinearity of the detector and the amplifiers is less than ± 1% according to the manufacturer. **3** The noise level of the detected position is dependent on the intensity of the received radiation of the markers. The Selspot system was modified to reduce the accepted range between the low and high intensity level from 64 to 7 times by increasing the accepted low intensity level. In this way low intensity images were avoided, for instance from a reflection only. The standard deviation of the noise was now 0.05% and 0.1% of the field of view in both directions at the high and low intensity level respectively. The noise level did not change significantly with the position of the image of the LED. The correlation of the noise was investigated with the aid of three stationary points, recorded with two cameras. No significant correlation (number of observations = 100; level of significance = 0.05) was found between the noise of the horizontal positions of the different markers recorded with the same camera, nor between those of the same marker recorded with different cameras. The same was true for the noise of the vertical positions. Also the serial auto and cross correlation of the noise of the above mentioned combinations were calculated for time shifts from 1 to 200 frames (6 ms to 1.3 s). The serial correlations found were not significant, except for 2 to 7% of the time shifts, where the correlation was very low. **4** Also apparent position changes, due to intensity changes of the markers, were reduced by the modification of the intensity range. The apparent position changes were now 0.2% and 0.5% of the total field of view in the center and corners respectively. **5** The detected position of the marker could jump over a certain area every 32 least significant bits (LSBs) in the horizontal and vertical direction. This is due to a malfunction of the dividing ADC of the Selspot I system. These jumps were not present at the highest intensity level, but could be 10 to 23 times the LSB, which is 1 to 2% of the field of view at the modified low intensity level.

The Selspot II and III systems are equipped with a specially designed low distortion 50 mm lens and a feedback system to keep the intensity of the markers constant. Many of the above-mentioned problems could be solved, but difficulties with reflections and interference with other infra-red radiators will remain.

EMG processing

The electrical signals of the muscle, picked up by intramuscular electrodes and a ground electrode, were differentially preamplified with a Grass P-15 (bandwidth: 10 Hz to 3 kHz). The electrodes were made of insulated copper wire of 100 or 150 μm diameter. One to two mm of the insulation were removed from the tips of the recording electrodes and 10 to 20 mm from the ground electrode. The recording electrodes were inserted into the desired muscles with hypodermic needles (Engberg and Lundberg 1969). The correct position was checked by stimulation of each electrode against the ground electrode, which was placed subcutaneously at the back, and simultaneous palpation of the contracting muscle. Movement artefacts of the recorded signals were reduced with a fifth order high-pass Bessel filter with a —3 dB point of 50 Hz. It will suppress frequencies below 10 Hz with more than 48 dB and it will not remove a significant part of the EMG frequency spectrum. After further amplification the signal was full-wave rectified, low-pass filtered and digitized (see above). More details of the EMG processing are given by Halbertsma and de Boer (1981).

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† A wide angle Leitz Summilux 1:1.4/35 lens seems to be a much better choice. Besides the smaller aperture, it has a maximal nonlinearity of 0.5% (90% of the field of view covered) and it has a considerably larger field of view with the same camera-object distance (approximately 40%).

Software

A modular software package of 10,000 Assembler and Fortran IV statements was written to collect, process and interactively analyse the movement, the EMG and the force plate data. Cat and human locomotion, and other motor behaviour could be studied with a rearrangement of the software modules†. This software package is an extension and improvement of the earlier package used to analyse the data recorded with the television system.

Data collection. The data of the Selspot system and the ADC were multiplexed and enter the computer through one interface channel. In this way the data were placed in one of the two software buffers, of 3k 16-bit words each, with one of the two direct memory access (DMA) modules. When one of the buffers was filled with data, the other DMA module started to fill the other buffer. During that time the first buffer was written onto disk (type HP 7900A) with the first DMA module. This went on until the disk was completely filled or the experimenter interrupted this process. The maximal measuring length was 140 s when recordings were made with one camera (data transfer rate: 8748 (16 bits) words/s). It took 82 s with two cameras (data transfer rate: 14988 words/s). After a successful recording, with a typical duration of 20 s, the data were transferred to magnetic tape. The data of these recordings were preceded with an identifier which contained among other things a record counter, the subject's name and optional comments of the experimenter. After storage of these data for later off-line analysis a new recording could start.

Data processing. The raw data, stored on magnetic tape, could be displayed on a graphics terminal (Tektronix 4006 or 4010) to select a part of a recording for analysis. Sections of at the most 10.6 s were temporary stored on disk before the data were sorted and stored in 20 position files (a file for every recorded marker) and in 8 files for the 8 channels of the ADC. The record number in the files was used as frame count. A record contained the x and y coordinates of a marker of one frame in a position file, or two samples of one ADC channel recorded during one frame in an ADC file. An identifier was stored in the first record of every file. In the position files it indicated which camera recorded the marker and it gave the number of the marker. The identifier in the ADC files indicated from which channel the data were originating. Also a flag was set here to avoid mistakes like no correction or double correction of the data. During the sorting the data were checked for errors (e.g. too low or high intensity for position data and wrong channel address for ADC data). A correction program restored missing data by linear interpolation. The position data were corrected for oblique camera positions with the aid of a previously recorded calibration triangle. They were also corrected for distortions of the lenses, detectors and processing electronics, with the aid of the test grid (see above). If a recorded position was situated in between four points of the test grid (with known aberrations), the correction was calculated from the weighted sum of the four correction terms. If a recorded position was situated outside the field covered by the test grid (90%), it was calculated from the closest test points on the edges. The maximum distortion in horizontal and vertical direction was reduced from 5% to 0.8% of the total field of view for lens apertures between 0.95 and 2.0. In the horizontal as well as in the vertical direction 80% of the field was covered in this test. This method is somewhat more accurate than the method used by Gustafsson and Lanshammar (1977). After the corrections the position and ADC data were smoothed with 33-point finite impulse response filters (Rabiner and Gold 1975). The ADC data were always smoothed with a filter with a pass-band from 0 to 29 Hz and a stop-band from 49 to 156 Hz. The position data were smoothed with filters with a pass-band from 0 to 5, 10 or 15 Hz, depending on the frequency components found in the markers on a cat locomoting at a corresponding speed. The stop band of these filters was from 15, 20 and 24 Hz respectively to 78 Hz. The deviations from the pass-band of all filters were less than -52 dB. The attenuation of the stop-band of these filters was at least 32 dB. The position of the knee joint was calculated from the distance between the markers of hip and ankle joint and the length of tibia and femur, owing to the skin slippage over the knee joint. The horizontal

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† Listings of the software are available from the Prosthetics Control Laboratory,
Lorentzweg 1, Delft, The Netherlands.

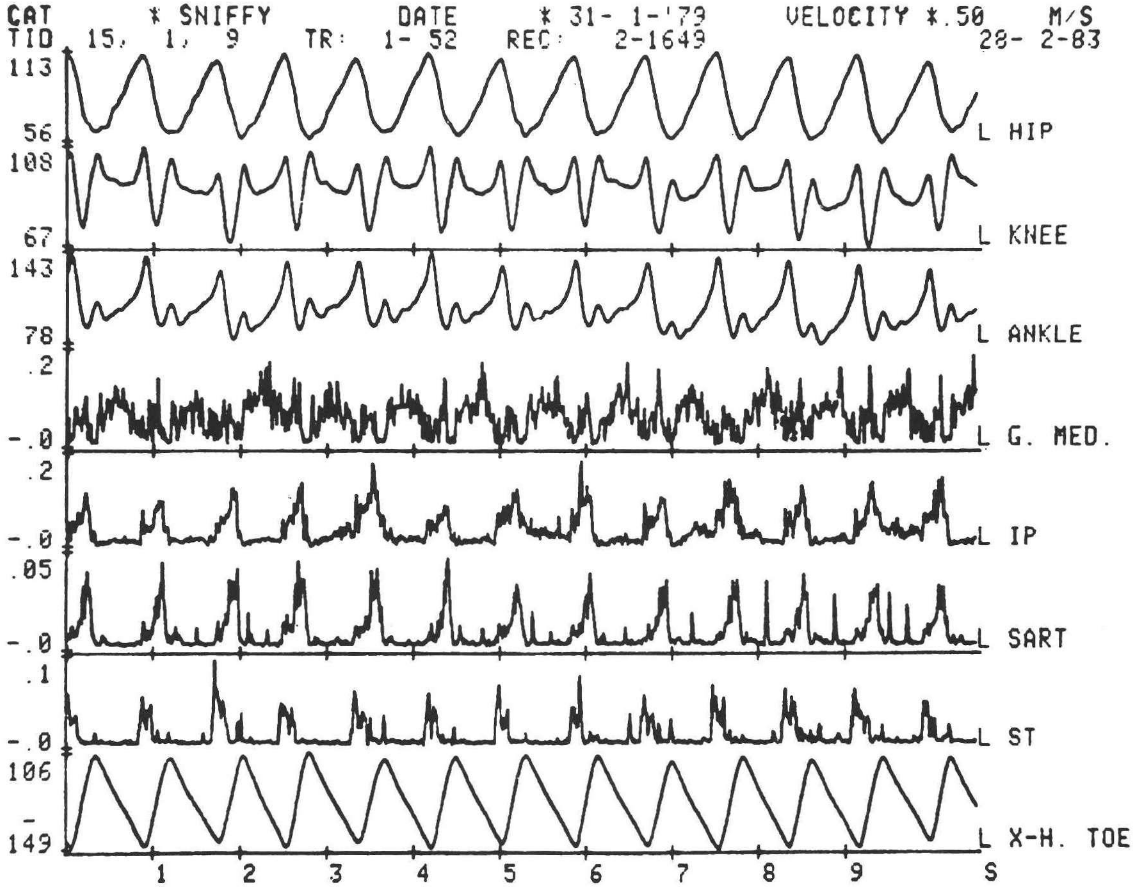

Fig. 1. Display of 10.5 seconds of locomotion. The joint angles (in degrees) of the hip, knee and ankle, the rectified and filtered electromyograms (in mV) of gluteus medius (G.MED.), iliopsoas (IP), sartorius (SART) and semitendinosus (ST), and the horizontal displacements (in mm) of the toe of the hindlimb (X-H. TOE, upward deflection indicates forward movement of the foot) are drawn on a Tektronix graphics terminal. The curves are scaled automatically and the minimum and maximum values are indicated on the left of the curves. Data concerning the test subject, the date of the experiment, the belt velocity, the part of the tape analysed, and the date of the analysis are indicated on the top. Data are from the left hindlimb of cat SN.

or vertical distances between two markers or the horizontal and vertical displacements of one marker could be calculated. The data were stored in one of ten result files. Also the joint angles calculated from the positions of markers were stored in these files. The record number of the files was also a frame count, as in all other data files. For scaling purposes the minimum and maximum values of the data in these and the ADC files were stored in records following the data, together with an alphanumerical identification. The time of onset of different phases of joint angles and displacements could be determined interactively with the aid of a graphics terminal. A cursor or cross hair was set manually to a certain level in the curves. A maximum and minimum were automatically recognized for every downgoing slope which passed through this level. Possible submaxima and subminima between the earlier determined extrema were also detected. These events in the stride cycle could also be determined by hand with the aid of cursor or cross hair. Wrongly determined turning points could be deleted. The frame number from each turning point and the value of the joint angle or displacement at this point were stored for further analysis, as was the velocity calculated from the displacements during the support phase. Also the onset and cessation of the electromyographic activity could be determined manually or automatically. With the latter method a coarse onset and cessation was determined first, as follows. An onset of the rectified and filtered EMG (RFEMG) burst was found when the level was at least 15% of the maximum level of the observation interval and 40% of the 15 succeeding frames were above that level. A cessation was recognized as soon as the level of the burst and 90% of the 15 succeeding frames were below that 15% level. These points were marked in the curves and erroneous ones could be deleted. Then the average base line was calculated between these cessations and onsets. The final times of onset and cessation of a burst were found by searching a level of the burst which was 5% of the maximum burst level above the base line. Also in this stage obvious erroneous points could be deleted. With this method short lasting artefacts were skipped and the times of onset and cessation of the bursts were recognized with less bias and effort than the manual method, where every event has to be indicated by hand. The mean, peak and integrated level of every burst were calculated and they were stored together with the timing information. The joint angles, displacements and RFEMGs were displayed on a disired time scale (fig. 1) or superimposed and averaged after normalisation of the cycle duration. The superimposition was triggered from one of the events of the stride cycle (fig. 10, 11). The mean and standard deviation of different parameters of the stride were calculated from the stored data. The data were stored elsewhere before they were replaced by data of the next observation interval. The data of all observations could be plotted and treated statistically (see below). It takes approximately 45 minutes to analyse an interval of 10.6 seconds of locomotion (HP 1000 system). The major part is occupied by the selection of the portion to analyse, by the interactive recognition, and by the plotting of the averaged curves.

Statistical treatment of data. The pooled data of a cat locomoting at different velocities were treated statistically with standard techniques (de Jonge 1964). Several curve fitting methods were used to describe relationships of different gait parameters with speed and cycle duration.

The nonlinear relationship between the stride cycle duration (T_C) and the velocity (v) was described with the model: $T_C = a/v^b$. The Maquard method was used to estimate the parameters a and b (Nag Library 1978). The variance of these parameters was estimated by calculating the Cramér-Rao lower bound (CRLB) or minimum variance bound (Kendal and Stuart 1967). The cycle durations were calculated from eight different events in the stride cycle. In order to avoid the correlation of errors in successive cycle durations the data for each event were placed alternately into two groups. This ensured that each group contained uncorrelated data. The mean and standard deviation of the parameters were calculated from eight groups, one group only for each event. These standard deviations were in the same order as those calculated from the CRLB of the individual groups. This nonlinear relationship was also described with the model : $T_C = (a/v^b) + c$. However, simulations and computations of the data showed that **1** the standard deviation of c was in the same order as c itself and **2** the correlation coefficients between the parameters were almost -1 or $+1$ (Dingemans 1980). Hence we concluded that the latter model is not adequate to describe this relationship.

The parameters of the linear relationships between the durations of the phases of the stride (e.g. swing and flexion) and the stride cycle duration were estimated with the maximum-likelihood method, because both variables contain (correlated) errors (fig. 2; Acton 1959). Linear regression analysis will lead to biased results in this case (Lindley 1947). The correlation between the errors in consecutive strides was, also in this case, avoided by dividing the data into two groups and using the means of the parameters of the groups. The standard deviations of these mean parameters were estimated from the CRLBs of the parameters of the two groups. These CRLBs were treated as if they were not covariant, although the errors in the data of the two groups are correlated and thus also these CRLBs. The slopes of the linear relationships were tested with Creasy's method as to whether they differ significantly from zero (Kendall and Stuart 1967). The stride cycle duration was calculated from another event in the stride than the one for which the slope was tested and the data were divided into two groups, as this test does not allow correlated errors in the variables. The linearity of the relationships was checked by inspection of the residues (i.e. the deviations of the measured points from the most likely position on the fitted relationship). Serial correlation of the residues did not indicate that the linear approximation was insufficient.

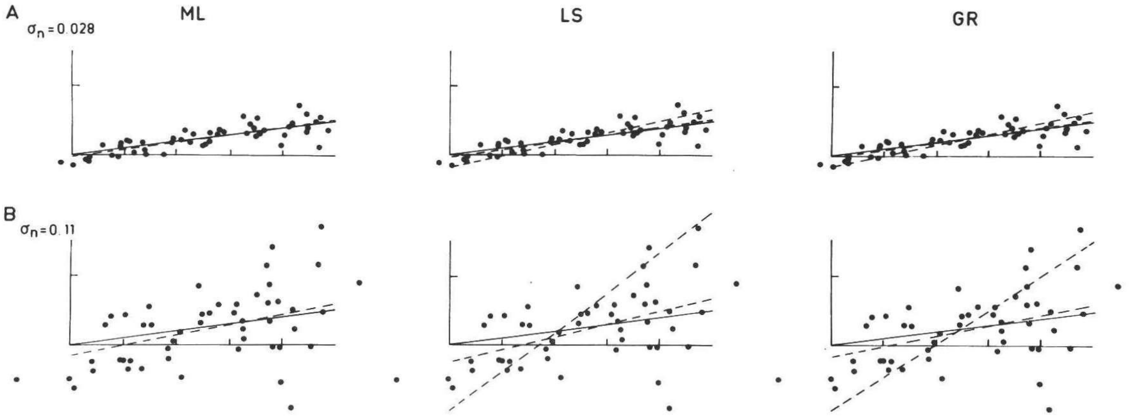

Fig. 2. Comparison of three methods to estimate the parameters of a linear relationship. The maximum-likelihood method (ML, left panels; Acton 1959) is compared with the least square method with errors only in one variable assumed (first order regression analysis; LS, middle panels), and compared with the grouping method (data divided into three groups; GR, right panels; Bartlett 1949). Covariant and normally distributed noise is superimposed on the x and y values of 50 equidistant intervals on a straight line ($y=ax+b$, $a=0.01$, $b=0.0$; the variance of the noise on x equals the variance of the noise on y, the coefficient of correlation between the noise on x and y $=0.5$). This is the same situation where the onsets of two phases are common and the terminations of the phases are different (e.g. the duration of the flexion phase and the stride cycle duration). The relationship $y=ax+b$ is indicated with a continuous line, the data points, with noise superimposed, are indicated with dots and the fitted lines are indicated with interrupted lines. The divisions on the x and y axis indicate intervals of 0.2 arbitrary units. Two different lines are fitted to the data points with the least square method, assuming **1** only errors in y and **2** only errors in x. The same is done for the grouping method where the data is divided into three groups, sorted on **1** increasing x and **2** increasing y. In *A* the standard deviation of the noise superimposed on x and y equals 0.028 and in *B* 0.11 arbitrary units. Repeated simulations with different realisations of the noise show that the parameters a and b estimated with the grouping method and with the least square method (with erroneous assumptions of the noise in the variables x and y) are more biased and have a higher variance than the parameters estimated with the maximum-likelihood method.

A level of significance of 0.05 was used in all tests.

Accuracy of the Selspot recording system

There are three types of factors influencing the accuracy of the different gait parameters: The measuring technique, the measuring system and the data processing.

The technique of gluing markers to the skin over the respective bony landmarks is one source of error. **1A** Misplacement of them could result in systematic errors of the joint angles. The distal joints (toe, ankle) are easier to recognize than the proximal ones, which is partly due to the anatomy and partly to the looser skin attachment to these joints. A 10 mm rostral or caudal placing of the hip marker will result in a maximum error of the hip joint angle of 10°. This will also influence the knee position correction (see page 14) and thus the knee and ankle joint angles. The maximum errors in these joints become 12° and 6° respectively. **1B** It has been reported that the skin remains closely related to the bony landmarks used except at the knee. The skin slippage influences the joint angles and not the timing of the phases within the stride (Miller et al. 1975a). But the skin in the pelvic area could be looser in one cat than another and slippage of the hip marker will influence the knee position correction (see page 14) and thus all joint angles of the hindlimb. An estimated horizontal or vertical shift of both pelvis and hip marker of 5 mm will result in maximum errors of 4° of these joint angles.

The following error sources are the result of the Selspot measuring system. **2A** The distortions due to the lens and to the detector and processing electronics can also influence the joint angles and displacements. In a typical recording situation, where the hip marker was situated in the centre of the measuring plane of 820 by 820 mm, the recorded positions of the ankle and toe markers were lower than the true positions, at the most by 3.5 mm. Due to these aberrations the three joint angles will increase less than one degree only. The errors in the horizontal displacements of the toes will be smaller than 2 mm. The timing of the phases of the stride cycle could also be influenced by the distortions, but this effect is smaller (after software corrections) than that due to the noise of the recorded positions (see **2C** below). **2B** The apparent position changes, due to intensity changes of the images of the LEDs (see page 13), gave similar distortions as those due to the above described aberrations. The errors were estimated to be of the same magnitude also. **2C** The noise of the recorded positions can influence the joint angles and displacements as well as their timing in the stride cycle. Simulations with superimposed, normally distributed and uncorrelated noise on the horizontal and vertical coordinates of the respective markers showed that the standard deviations of the three joint angles increased approximately from 0.8° to 1.8°, when the noise of the markers increased from the lowest (0.6 mm) to the highest (1.4 mm) level. The noise of the joint angles and displacements could obscure their turning points, especially when they changed slowly (e.g. at low speeds of locomotion). In a simplified model the angular changes of flexion and extension were simulated. The angle decreased and increased linearly over a given range during a given duration. Normally distributed noise was superimposed on the angles, and the deviations from the known onsets were calculated. This was repeated 100 times. Similar simulations were performed for the displacements. These simulations showed that the standard deviation of a joint angle at a turning point was equal to or smaller than the standard deviation of the noise of the joint angle. This was due to the fact that an extreme value of the angle was selected, which reduces the variability, but which changes the position of the mean systematically. The total error will be at most 2° and 4° with low and high noise level respectively. Similar effects occur with the displacements, where the maximum error will be 2 and 4 mm under these conditions. The standard deviation of the time of onset of the two phases of the hip joint angle at a walking speed of 0.2 m/s were simulated and turned out to be 12 and 24 ms with low and high noise level respectively. The figures reduced to 4 and 6 ms at a speed of 1 m/s. Similar results were obtained for the phases of the knee and ankle joint, except for the onsets of the slowly changing E_3 phases (third extension phase, see fig. 3). The standard deviation of the onset of the ankle E_3 phase could be more than 50 ms during slow locomotion with maximal noise, but decreased to 11 ms during locomotion at 1 m/s. The standard deviations of the time of onset of phases determined from the horizontal displacements of the marker on the toe of the forelimb were 2 and 4 ms at a speed of 0.2 m/s with low and high noise level respectively. It increases to approximately 3 and 6 ms when the displacements are calculated from the positions of two markers. At 1 m/s the standard deviation is not significantly different from 1.9 ms in all cases, which is the lower bound of this standard deviation. This lower bound can be calculated when we assume that the deviations from the known points of time are uniformly distributed within a range of ±½ sampling interval. In that case the standard deviation equals the sampling interval divided by $2/\sqrt{3}$. The means of the time of onset could be biased significantly in the direction of the slowest changing phase, but almost always less than one standard deviation. **2D** The jumps of the detected positions of the markers (see page 13) could influence the joint angles and displacements as well as the timing of their turning points. The distortions of the signals will be the strongest when the actual positions of the markers change little. This is true for the hip and pelvis LED when the measurements were made on the treadmill. In the actual recording situation jumps of 5 times the LSB can be expected. This corresponds to position changes of 6 mm. For instance, the hip joint angle can change 6° when the vertical position of the pelvis changes that much. If such a jump occurs just before or after a turning point, it can influence the measurement. At very slow walking speeds the measured hip extension phase could start 120 ms too late and end 120 ms too early in the worst case. This maximum error is reduced to only 20 ms for walking at 1 m/s. The errors in the onset of the E_3 phase of knee and ankle are of the same order. But in the F and E_1 phases (flexion and first extension; see fig. 3) the angles of these joints change rapidly and the errors in the onsets of these phases are estimated as no greater than 20 ms at low speeds of locomotion. **2E** The positions of the different markers are sampled in sequence at intervals of 100 μs. With the arrangements of diodes used the joint angles and displacements are calculated from positions of markers that are sampled over a maximum interval of 0.8 ms. The maximum displacement of markers in that time equals the resolution of the system. The time shift between different joint angles or displacements is at most 1 ms.

The data processing can also have undesirable influences on the data. **3A** Smoothing the data can influence the amplitude of angles, displacements and EMGs as well as their timing. The 10% value of a square wave test signal smoothed with the software filter used for the ADC data was reached 6 ms too early and the 90% value 6 ms too late. This can be considered as a maximum error, because the real signals change more slowly. Also the hardware filters, which smooth the signals before sampling (see page 12), introduce similar timing errors of maximum 4 ms. The mean duration of the hip flexion phase of a cat locomoting at 0.9 m/s decreases by 3 ms when the positions, from which the angle is calculated, are smoothed with a a filter with a cutoff frequency of 5 Hz instead of 10 Hz. The effects of stronger smoothing on durations of other joints is smaller and typically 1 ms. Simulations showed (see **2C** above) that reducing the noise level, which is the aim of smoothing, could partially explain the reduction of the durations. Stronger smoothing could reduce the amplitudes significantly more than could be expected from the reduction of the noise. The largest effects could be observed in the mean support length and ankle joint angle at the onset of flexion, which decreased 4 mm and 3° respectively. The results obtained with the 10 Hz filter do not differ significantly from those obtained with the less effective 15 Hz filter.

In conclusion, the placement of markers on the skin and the skin slippage over the joints introduce the largest errors in the amplitude of the joint angles. The jumps in the measured positions of the markers, due to the malfunction of the dividing ADC (see page 13), can influence both the amplitude and timing of joint angles and displacements considerably. The noise of the position measurements influences them to a lesser extent. But for accurate measurements it is important to record with the highest possible intensity from all LEDs, because this will minimize both the noise and the jumps.

Notation and abbreviations

The following notation is used: Joint angle at the onset of phase X, a_X; excursion of the joint angle during phase X, A_X; relative position of the limb at the onset of phase X, l_X; excursion of the limb during phase X, L_X; time of midpoint of phase X, mp_X; time of onset of phase X, t_X; duration of phase X, T_X.

Subscripts used: stride cycle, C; (first, second and third) extension, $E_{(1,2,3)}$; flexion, F; support, SU; swing, SW; step, S; forelimb, f; hindlimb, h; ankle, an; elbow, el; hip, hi; knee, kn; scapula, sc.

Superscripts used: Left limb, l; right limb, r.

Examples: T^l_{E2an} is the duration of the second extension phase of the left ankle joint, which is calculated from the onset of the second extension phase to the onset of the third extension phase of the left ankle joint ($T^l_{E2an} = t^l_{E3an} - t^l_{E2an}$). A^l_{E2an} is the excursion of the left ankle joint angle during the E_2 phase of the ankle ($A^l_{E2an} = |a^l_{E2an} - a^l_{E3an}|$). If possible, the superscripts l and r and the subscripts h and f are omitted.

The following abbreviations are used: Analogue to digital converter, ADC; central pattern generator, CPG; Cramér-Rao lower bound, CRLB; electromyogram, EMG; light emitting diode, LED; least significant bit, LSB; rectified and filtered EMG, RFEMG; standard deviation, sd; velocity, v; m. (musculus) iliopsoas, Ip; m. gastrocnemius lateralis, LG; m. sartorius, Sart; m. soleus, Sol; m. semitendinosus, St; m. vastus lateralis, VL.

RESULTS AND DISCUSSION

1. The stride at different velocities of locomotion

Two commonly accepted ways to subdivide the stride cycle are used: **1** The division into swing and support phases, defined by contact of the foot with the ground, and **2** the division into flexion and (first, second and third) extension phases, defined by the joint movements (Phillipson 1905). The well-known gaits such as walk, trot and gallop were investigated with an aural study of the pounding of horses hooves already in 1779 (Goiffon and Vincent 1799, cited by Gambaryan 1974). They used bells with a specific ring attached to the four limbs. Muybridge (1957) photographed different locomoting animals in 1887 and developed a footfall schematic to characterize different types of gaits. Marey (1901) extended these schematics to contact patterns. Phillipson, who analysed Marey's photographic recordings of a walking, trotting and galloping dog, supplemented these patterns of the hindlimbs with the movements of different joints. He divided the stride cycle into a flexion phase (decreasing joint angle) and three extension phases. After extension of the hip, knee and ankle joint, the limb is lifted off ground (fig. 3). This is the onset of the swing phase (SW) and the flexion phases (F) of the three joints. While the hip is still flexing and the limb is brought forward, the knee and ankle start to extend, and this constitutes the onset of the first extension phase (E_1). Afterwards the hip also starts to extend and the limb touches ground, initiating the support phase (SU). After contact the joint angle movements in the knee and ankle joint reverse (yield), this is the onset of the second extension phase (E_2). At the end of this yield the knee and ankle joints start to extend together with the still extending hip joint: The third extension phase (E_3). This phase ends when the foot is lifted off the ground and a new cycle starts. This schematic has been used for both the hindlimbs and forelimbs of cats (Engberg and Lundberg 1969, Miller and van der Meché 1975). However, this subdivision of the stride needs to be modified, since the onsets of the flexion phases in hip, knee and ankle do not always occur simultaneously. Nor do they have to coincide with the onset of the swing phase (fig. 3B, D, fig. 9A, B, C). The same can be argued for the onset of the E_2 phases of the knee and ankle and the onset of the support phase (fig. 9E, F). The onset of the E_1 phase of the knee occurs before that of the ankle and the onsets of the E_3 phases of these joints do not necessarily coincide (fig. 3B, D; cf. however Goslow et al. 1973). The Phillipson stride cycle remains useful when the flexion and extension phases refer to specified joints (Wetzel et al. 1975), and when the support and swing phases refer to ground contact.

Velocity changes can be the origin of changes in the duration of different phases and changes in the amplitudes of movements (see below). However a cat is able to influence these parameters independently of speed to a certain degree. For instance the excursion of the ankle joint during E_1 is very small and atypical in fig. 3D, but it is more pronounced a few recordings later at almost the same speed (2.6 m/s). Although valuable data can be derived from cats stepping overground, a serious drawback is that only a limited number of steps can be recorded and that the velocity of progression can vary.

On the treadmill the velocity of locomotion can be controlled better and a large number of strides can be recorded to enable a statistical analysis of the different gait parameters. There is no biomechanical difference between treadmill and overground locomotion, except for the air resistance, as long as the velocity of the belt is constant and a coordinate system is used which moves with the belt (this last condition does not influence the kinematic analysis) (van Ingen Schenau 1980). The visual feedback during treadmill and overground locomotion differs, e.g. birds move their heads forward and backward in relation to their body during overground locomotion but not on a treadmill (Frost 1978), but such effects were not observed in the present experiments.

It has been argued by Wetzel et al. (1975) that in treadmill locomotion, with both walking and trotting, the knee begins to extend before the ankle; and that this is not the case in overground stepping. However, this conclusion is contradicted by their own data, which show a statistically significant difference in timing of knee and ankle extension in both situations. In the present study, forty strides from cats stepping

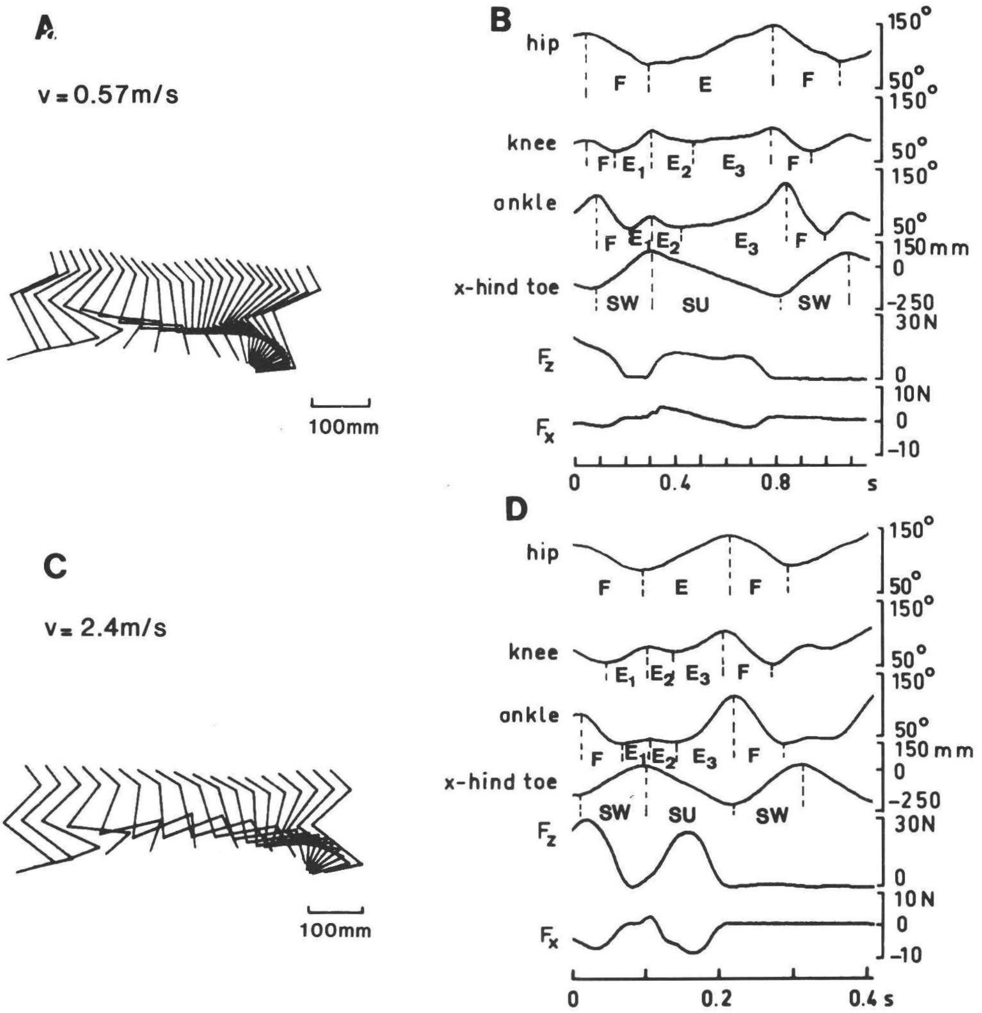

Fig. 3. Movements of a hindlimb during alternating locomotion overground. The positions of the left hindlimb are presented as 'stick' figures at 32 ms intervals during walking (0.57 m/s) in *A* and at 13 ms intervals during trotting (2.4 m/s) in *C*. The direction of progression if from right to left. These strides are also presented in *B* and *D* as angular movements of the hip, knee and ankle together with the horizontal displacements of the toe with respect to the hip (x-hind toe), and the vertical (F_z) and horizontal ground reaction force (F_x, opposite to the direction of progression). The flexion and different extension phases are indicated in the angular movements, and the swing and support phase in the x-hind toe trace (see text). The ground reaction force, due to hindlimb support, is preceded by a part of that of the left forelimb and hindlimb. Note in F_x that the forward-directed impulse is much smaller than the backward directed impulse during the first support phase in *D*. During that time the cat is accelerating from 2.3 to 2.6 m/s. The time scale at the bottom is divided into 100 ms intervals. Data are from cat ZW.

overground from 0.3 to 2.8 m/s showed that t_{E_1kn} starts 13 to 130 ms before t_{E_1an}; in only one stride did they start simultaneously. No clear differences could be recognized between overground and treadmill locomotion of the same cat, but differences between cats were obvious in both situations (see below).

The treadmills used were not fitted with force plates to detect the support phases of the limbs. Therefore the onsets of hindlimb support and swing were estimated from the extrema of the horizontal displacements of the toe (foot) of the hindlimb with respect to the hip (x-hind toe). No significant differences were found between these extrema and the onsets of support and swing calculated from the vertical force for

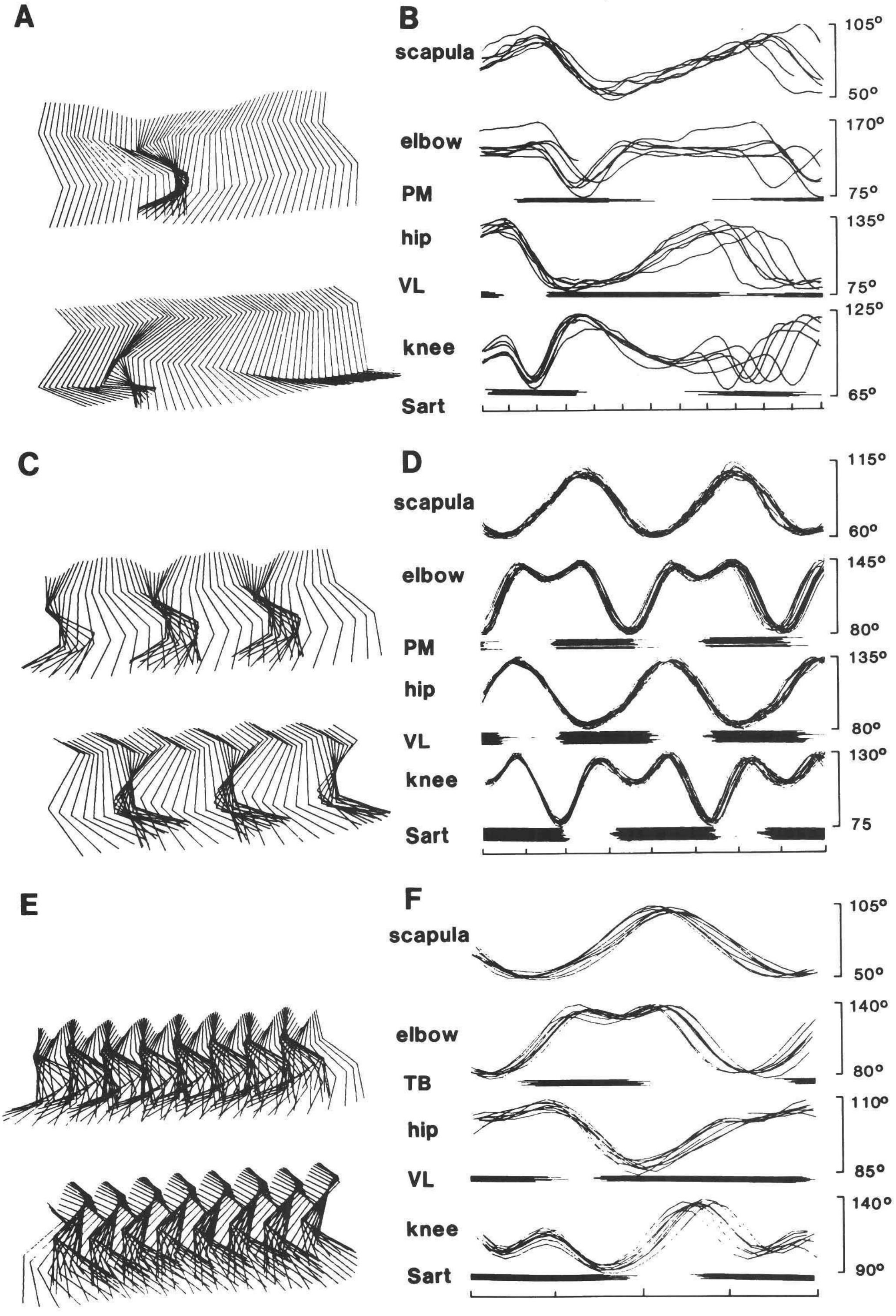

Fig. 4. Movements of the homolateral limbs and muscular activity during treadmill locomotion. The positions of the left forelimb (top) and left hindlimb (bottom) are presented as 'stick' figures at 16 ms intervals during walking (0.5 m/s) in *A*,

during trotting (2.1 m/s) in *C* and during galloping in *E*. In this reconstruction the horizontal position of the dorsal scapula marker is shifted the same distance to the left every successive stick. The pelvis of the first hindlimb stick starts at the same horizontal position as the dorsal scapula marker and uses it as a reference further on. Superimposed angular movements of scapula, elbow, hip and knee and muscular activity of VL and Sart from the same recordings as those of the stick figures are presented in *B* (0.5 m/s), in *D* (2.1 m/s) and in *F* (galloping). The muscular activity of pectoralis major (PM) is indicated in *B* and *D* and the activity of triceps brachii (TB) in *F*. The superimposition is triggered from the onset of knee flexion and the drawing starts approximately 80 ms before that. The muscular activity is represented as a bar when the muscle is active and bars of successive strides are plotted under each other. The time scale at the bottom is divided into 100 ms intervals. Data are from cat FR and were recorded with the television system.

each of the four walking and trotting cats (cf. however Wetzel et al. 1976). The differences in 20 strides were smaller than 13 ms, only two lift-offs occurred 26 ms before and after the extreme in the x-hind toe (different cats). The onsets of forelimb support and swing are estimated from the extrema of the horizontal displacements of the toe marker of the forelimb (x-fore toe) (English 1978).

Alternation between the limbs of the same girdle is the most common type of coordination for adult cats locomoting slower than approximately 3 m/s. The movements of one limb are delayed about half a cycle with respect to the homologous limb. In the lowermost region of speeds cats commonly walk (fig. 4A) and in the middle region they trot (fig. 4C). In walking there is always at least one foot on the ground and trotting is a gait in which the diagonal pair of limbs touches ground more or less at the same time (Howell 1944). In fast trotting the homolateral limbs move in opposite directions for the larger part of the stride. They convert to a gallop mode of locomotion at the upper region of speeds (fig. 4E), where the movements of the homologous limbs are more synchronized (Eisenstein et al. 1977, Miller et al. 1975b, Norgren et al. 1977). The maximum vertical movements of the hindquarters increase from approximately 10 to 20 mm during walking with speeds between 0.3 and 1.2 m/s (see also Carlson et al. 1979). They remain approximately constant above the latter speed until the cats converts to galloping, where they are about threefold (60 mm) of that during fast walking and trotting (fig. 4A, C, E; see also Wetzel et al. 1976).

Formal description of the duration and amplitude of the locomotor movements

Duration of the stride and its components in alternating gaits. The stride cycle duration T_C decreases when a cat increases the speed of locomotion v (fig. 5, Goslow et al. 1973, Halbertsma 1976 and Arshavskii et al. 1965 for dog). The relation of T_C with v resembles a hyperbola and can be described with:

$$T_C = \frac{a}{v^b} \qquad (1)$$

The values of the parameters a and b are given in table 1 for different cats. No data of galloping cats were used to estimate these parameters, since regular gallops at different speeds could not be recorded.

The support phase duration T_{SU} and swing duration T_{SW} decrease with v, although T_{SU} decreases much more than T_{SW} (fig. 5; Goslow et al. 1973, cf. Arshavskii et al. 1965). Similar adjustments in the stride cycle have been observed for chronic low spinal cats (Forssberg et al. 1980a). The relation of T_{SU} with v is non-linear, but its relation with T_C appears to be linear (fig. 6; Afelt and Kasicki 1975). This relation can be described with:

$$T_{SU} = cT_C - e \qquad (2)$$

The values of the parameters c and e are given in table 2. Table 2 also shows that the slope (c) of T_{SU} of the forelimbs (T_{SUf}) is steeper than that of the hindlimbs (T_{SUh}). T_{SUf} is longer than T_{SUh}, in the normal range of T_C (0.3 to 2 s), which was also shown by Afelt and Kasicki (1975).

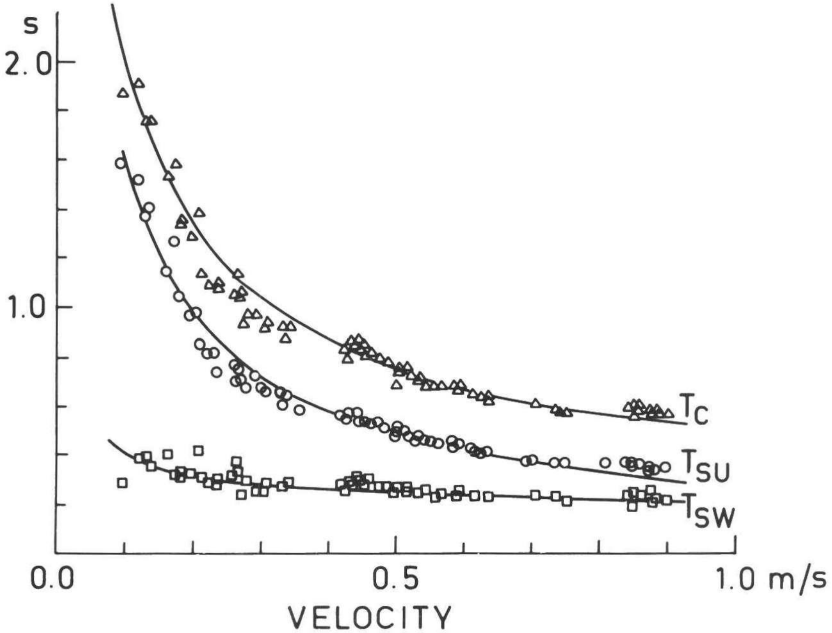

Fig. 5. Adjustments in the stride cycle with speed. The stride cycle duration (T_C, triangles), the support phase duration (T_{SU}, circles) and the swing phase duration (T_{SW}, squares) are plotted versus the velocity of locomotion. Each symbol represents a single interval. The curve in the T_C data points was fitted to those points and the curves for T_{SW} and T_{SU} were calculated (see text). Data are from the left hindlimb of cat SN stepping on a treadmill.

cat	a	sd	b	sd
FR	.544	.004	.54	.02
KJ	.512	.004	.57	.03
PI	.568	.008	.59	.04
PD	.608	.007	.585	.019
SI	.54	.02	.65	.05
SN	.495	.015	.62	.03

Table 1. The means and standard deviations (sd) of the estimated parameters a and b of the relationship between the cycle duration (T_C, in s) and the velocity (v, in m/s): $T_C = a / v^b$. The velocity for cats SI and SN was calculated for every step from the limb movements (recorded velocity range from 0.1 to 1.0 m/s). For the other cats the belt velocity was used (recorded velocity range from 0.3 to 3.0 m/s). The Maquard method was used to estimate a and b (see Methods).

The relation of T_{SW} with T_C also appears linear (fig. 6) and can either be fitted (table 3) or it can be calculated from relation (2):

$$T_{SW} = T_C - T_{SU} = (1-c)T_C + e \tag{3}$$

The relationship of T_{SW} with v can be calculated by substituting relation (1) in (3):

$$T_{SW} = (1-c)T_C + e = a(1-c) / v^b + e \tag{4}$$

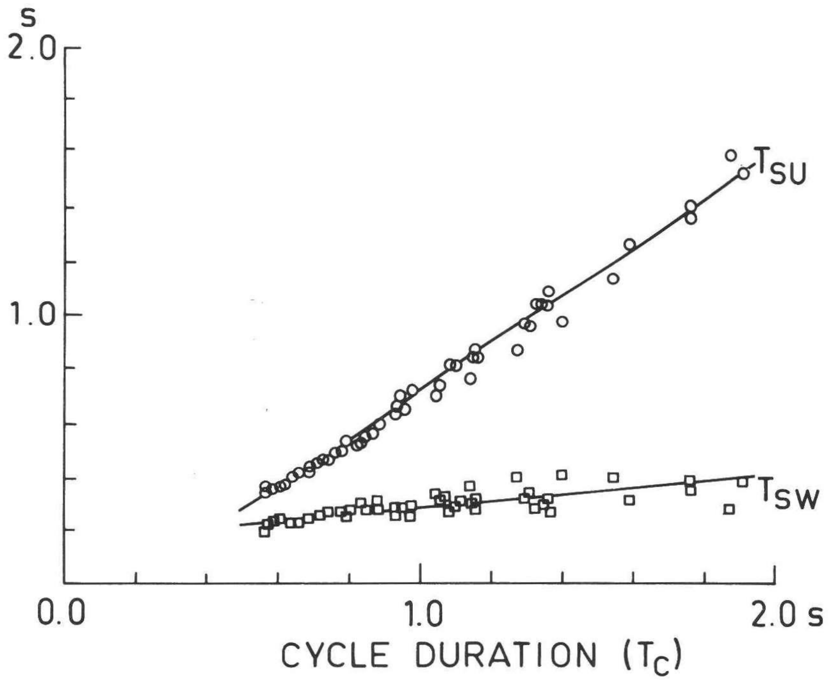

Fig. 6. Adjustments of the support (T_{SU}, circles) and swing (T_{SW}, squares) phase duration with the stride cycle duration (T_C). Each symbol represents one interval. The straight lines were fitted to the data. Data are from the left hindlimb of cat SN.

cat	limb		c	sd	e (s)	sd (s)
SI	hind	left	.885	.009	.170	.003
	hind	right	.834	.009	.133	.003
SN	fore	left	.943	.006	.172	.002
	fore	right	.951	.007	.185	.002
	hind	left	.888	.009	.173	.003
	hind	right	.932	.006	.175	.002

Table 2. The estimated parameters c and e of the linear relationship between the support phase duration (T_{SU}, in s) and the cycle duration (T_C, in s); $T_{SU}=cT_C-e$. The parameters for the hindlimbs of cat SI and for the forelimbs and hindlimbs of cat SN are given with their standard deviations (sd). A maximum-likelihood method was used to estimate c and e (see Methods).

The same can be done for T_{SU}:

$$T_{SU}=cT_C-e=ac/v^b-e \tag{5}$$

Both calculated relationships are drawn into the data points of fig. 5.

The relationships to the cycle duration of the different flexion and extension phases of the joints can also be approximated as linear (fig. 7) and the slopes and intercepts are given in table 3 and in the Appendix (table I). The slopes of all linear relations are significantly different from zero (see methods), except for T_{Fhi} and T_{Fkn} in one cat (KJ), which however appeared to walk in a stiff manner. Hence none of the stride cycle phases is constant with T_C and v (except possibly for KJ) (cf. however Goslow et al. 1973).

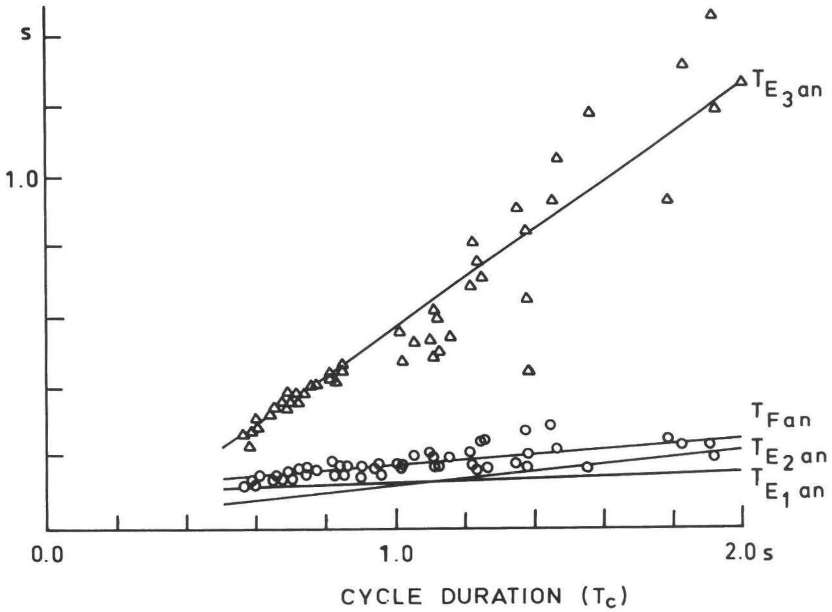

Fig. 7. Adjustments of the phases of the ankle joint with the stride cycle duration. The duration of the flexion phase (T_{Fan}, circles) and of the third extension phase (T_{E_3an}, triangles are plotted. Each symbol represents one interval. The straight lines were fitted to these data and to the data of the duration of the first (T_{E_1an}) and second (T_{E_2an}) extension phase (data points are not drawn for sake of clarity). Data are from the left hindlimb of cat SN, see the Appendix, table I, for more data of this and other cats.

cat	phase	a	sd	b	sd
				(s)	(s)
FR	Fsc	.228	.011	.081	.002
	Fel	.099	.004	.0775	.0008
	Fhi	.212	.010	.089	.002
	Fkn	.040	.004	.0830	.0008
SN	SWf	.052	.007	.177	.002
	SWh	.128	.009	.160	.003
	Fhi	.134	.012	.165	.004
	Fkn	.026	.006	.114	.002
	E_1kn	.114	.006	.061	.002
	E_2kn	.81	.04	-.382	.011
	E_3kn	.07	.03	.188	.009
	Fan	.077	.007	.098	.002
	E_1an	.047	.005	.0652	.0016
	E_2an	.10	.02	.022	.006
	E_3an	.699	.016	-.123	.005

Table 3. The estimated slopes (a) and intercepts (b) of the linear relations between the duration of phases of the stride and the cycle duration. Only the results of the left limbs are given with their standard deviations (sd). All slopes are significantly different from zero. A maximum-likelihood method was used (see Methods). More data are given in the Appendix, table I.

	T_F(meas.)			$T_F(T_C)$
	$\bar{x}$ (ms)	sd (ms)	n	(ms)
sc	152	7	7	151*
el	109	4	7	108*
hi	110	7	8	154
kn	71	4	8	95

Table 4. Duration of flexion phases during galloping. The mean duration ($\bar{x}$) of the scapula (sc), elbow (el), hip (hi) and knee (kn) flexion phases (T_F(meas.)) with their standard deviation (sd) and the number of strides (n) are given in the first three columns. The respective flexion duration, calculated from its relations with the cycle duration during alternating locomotion, is given in the last column ($T_F(T_C)$). An asterisk indicates that the calculated value is not significantly different from the measured one (level of significance = 0.05). Data are from cat FR (T_C = 308 ms, sd = 7 ms, n = 7).

From the tables it follows that the flexion phases of the proximal joints - scapula and hip - are longer than those of the more distal ones - elbow, knee and ankle. Furthermore corresponding phases of the left and the right limb can have different durations, although T_C is the same for both sides, and corresponding phases of different cats can differ considerably. Thus pooling of data from different cats can obscure the existing relationships.

Galloping. The coordination between the homologous limbs in the galloping mode of locomotion is very different from that in alternating gaits (see above). It was reported by Miller et al. (1975b) that the durations of the flexion and extension phases of the leading hindlimb differ from those of the trailing hindlimb. The same is true for the forelimbs. T_{Fsc} and T_{Fel} of the gallop of fig. 4F equal the durations which one should expect from T_C during alternating gaits (table 4). But T_{Fhi} and T_{Fkn} are longer. Although it is not known which is the trailing or leading limb (only one side was recorded with the television system), it is clear that durations of flexion phases can be modified. This could be an effect of the different coordination between the limbs (see Results, section 6).

Amplitude of the limb movements. The support length L_{SU} is the distance the body travels during the contact phase, if the pelvic movements are neglected and it is obtained by measuring the positions of the limb in relation to the body or by multiplying T_{SU} with the velocity of locomotion. The relation of L_{SU} with v can be calculated by multiplying relation (5) with v:

$$L_{SU} = vT_{SU} = acv^{1-b} - ev \tag{6}$$

L_{SU} is thus a measure of the overall movements of a limb during the support phase (fig. 8). Only in the support phase can it propel the body and a long L_{SU} is thus advantageous (Grillner 1981).

Relation (6) is the sum of a monotonically increasing and a linearly decreasing function (cf. Grillner 1975, 1981, Arshavskii et al. 1965). It has an extreme when its first derivative with respect to the velocity $\partial L_{SU} / \partial v$ equals zero:

$$\frac{\partial L_{SU}}{\partial v} = ac(1-b)v^{-b} - e = 0$$

or at a velocity of:

$$v = [ac(1-b)/e]^{\frac{1}{b}} \tag{7}$$

Substituting the parameters in equation (7) gives a maximum at approximately 1 m/s for cats SI and SN, which is at the border of the recorded velocity range for these cats (Selspot recording system used). Therefore no extreme is observable in fig. 8. The relation of L_{SU} with the velocity of locomotion appears rather linear in the example of fig. 8. This is not always the case for other limbs and cats (cf. Grillner 1981).

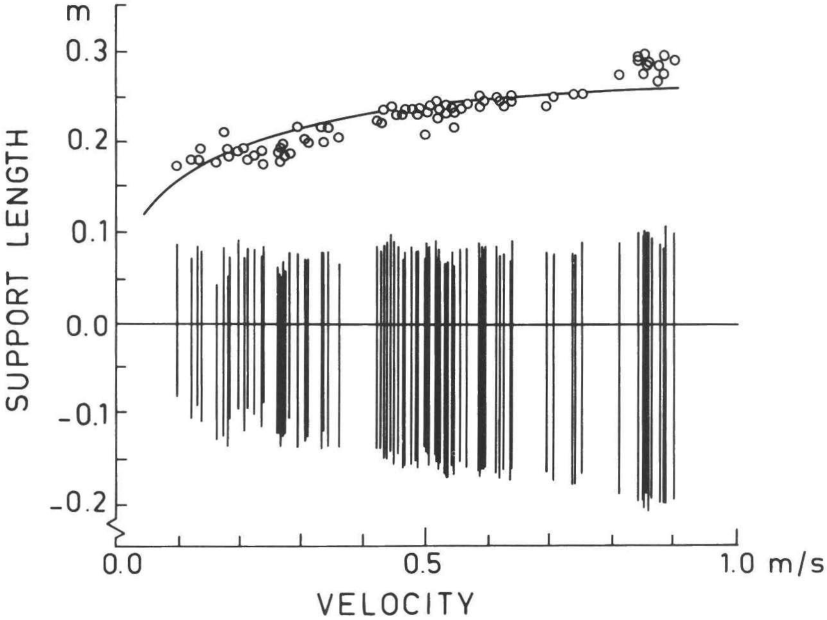

Fig. 8. Adjustment of the amplitude of the limb movements — the support length — with speed. The support lengths are plotted as circles. The horizontal positions of the toe with respect to the hip during the support phase are plotted as bars. The top and bottom of the bars indicate the toe position at touch-down and lift-off respectively. The support lengths are calculated from these positions. Each symbol represents data from a single stride. Approximately coinciding symbols are omitted for sake of clarity. The curve in the support length data points is calculated (relation (6), see text). Data are from the left hindlimb of cat SN.

From the different durations of T_{SU} of the forelimbs and hindlimbs it follows that L_{SUf} is greater than L_{SUh}. In galloping the hindlimbs move more or less synchronously and they can be positioned very close to each other. In that way the back can also contribute effectively in the propulsion phase, while the back movements also increase L_{SU} (Grillner 1981).

The step length L_S is defined as the distance a limb is put in front of the other limb of the same girdle. It characterizes how the limbs interact. The step duration T_S is defined as the time between the touchdowns of these two limbs. In alternating gaits T_S equals $T_C/2$ and L_S can be calculated from relation (1):

$$L_S = vT_S = vT_C/2 = av^{1-b}/2 \qquad (8)$$

Thus L_S increases monotonically with v to the power of approximately 0.4. This is also true for the commonly used stride length L_C (cf. Grillner 1975):

$$L_C = vT_C = av^{1-b} \qquad (9)$$

Coordination within a limb

The sequence of most events within a limb hardly changes when the speed of locomotion increases, even when the animal converts to galloping (fig. 4). The onsets of scapula and elbow flexion phases, t_{Fsc} and t_{Fel}, in the forelimb and t_{Fhi} and t_{Fkn} in the hindlimb occur almost at the same point of time (fig. 9A, Appendix table II). Significant differences exist, but they are small: less than 12 ms. The measured timing of the extrema of the joint angles will be influenced by the noise of the recording system and the effect is strongest

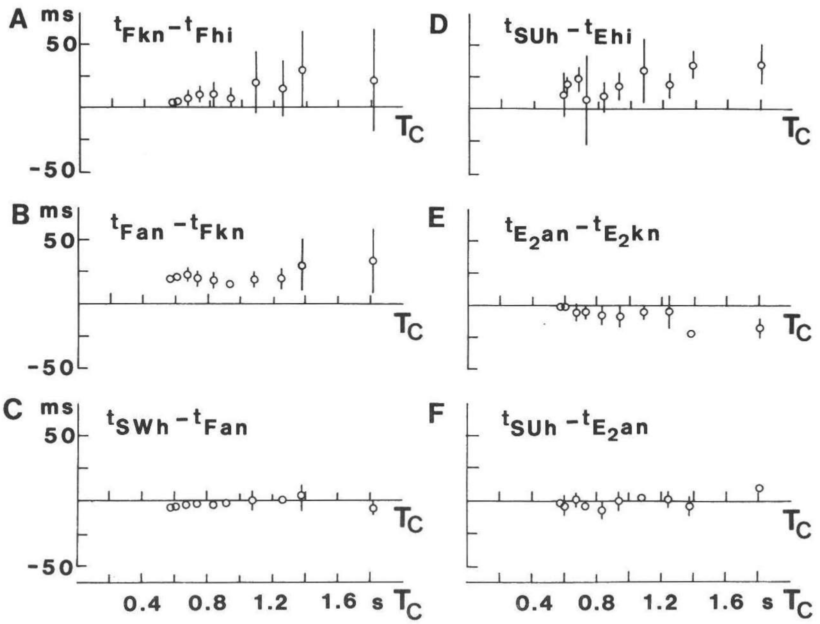

Fig. 9. Coordination of different events of the stride within a hindlimb. The mean intervals related to the onset of the swing phase (t_{SWh}) are plotted in *A*, *B* and *C* and those related to the onset of the support phase (t_{SUh}) in *D*, *E* and *F*. Every symbol represents a mean interval (n = 3 to 14) and the standard deviation is indicated with a bar when it exceeds the symbols. The standard deviation of the stride cycle duration is not indicated for sake of clarity. Data are from the left hindlimb of cat SN, see the Appendix, table II, for data of other cats.

at low velocities of locomotion (see page 18). The mean onsets of the hip and knee flexion will be shifted in the direction of the most slowly changing phase (extension) and the effect in t_{Fhi} will be greater than in T_{Fkn}, since the last part of the E_3kn usually increases more rapidly than the last part of the Ehi phase (fig. 10). The positive values of the $t_{Fkn} - t_{Fhi}$ interval, pronounced at low velocities of locomotion, could be a result of this bias (fig. 9A). The ankle flexion follows t_{Fkn} after approximately 20 ms (fig. 9B) and it almost coincides with t_{SWh} (fig. 9C). The durations of flexion of the proximal joints are longer than those of the distal joints (see above), thus t_{E_1el} precedes t_{Esc} (fig. 4) and t_{E_1kn} and t_{E_1an} precede t_{Ehi} (fig. 3). The knee flexion is shorter than the ankle flexion and it starts before t_{Fan}, thus t_{E_1kn} will start before t_{E_1an}. The timing of movements within the limb is a function of the cycle duration. For example the interval from the onset of the E_1 phase of the knee to the onset of the E_1 phase of the ankle can be calculated with the aid of table 3 and the Appendix (table II, cat SN):

$$t_{E_1an} - t_{E_1kn} = t_{Fan} + T_{Fan} - (t_{Fkn} + T_{Fkn}) = t_{Fan} - t_{Fkn} + T_{Fan} - T_{Fkn} = .020 + .051T_C - .016 = .051T_C + .004 \text{ s}$$

This agrees well with the measured relation of $.054T_C + .000$ s.

The hip extension, which leads to the support phase, starts approximately 20 ms before ground contact (fig. 9D). The knee and ankle yield when the limb touches ground, but not always at the same point of time; the knee yields after the ankle (fig. 9E). This could be due to the fact that the knee torque is smaller than that of the ankle at touch-down (Manter 1938), and that the ankle extensor LG is much more active than the knee extensor VL (fig. 11B). But bias in the measured timing of the extrema, due to the noise of the recording system (see page 18), cannot be excluded. The touch-down, estimated from the difference between the horizontal displacements of toe and hip, occurs almost simultaneously with the ankle yield (fig. 9F). The difference between these onsets is significant, however (Appendix, table II). This cannot be explained by the recording noise (see page 18), which would tend to shift mainly t_{SU} in the direction of the support phase, leading to a positive interval between $t_{SUh} - t_{E_2an}$ and not to a negative one. The onsets of knee and ankle E_3 phases are rather variable (fig. 7), and they are generally not starting at the same point of time (fig. 3, cf. however Goslow et al. 1973). It can be calculated from table 3 and the Appendix (table II) that the interval between the onsets of knee and ankle E_3 phases is dependent on the cycle duration, and thus also on the velocity. The measurements on cat SN show that t_{E_3an} starts around 500 and 50 ms before t_{E_3kn} at locomoting velocities of 0.2 and 0.9 m/s respectively. At higher speeds t_{E_3an} can start later than or simultaneous with t_{E_3kn} (fig. 3D).

2. The relation between electromyographic activity and movements in some hindlimb muscles

The activity in each group of muscles depends on the sum of all inputs to each motoneurone, which are the central pattern generator, a variety of segmental feedback mechanisms and different descending actions. The central pattern generator produces a coordinated motor pattern without feedback or descending control. This pattern is more complicated than alternating flexor and extensor bursts (Grillner and Zangger 1974, 1975, 1979, Perret and Cabelguen 1980). The exact effect which different muscles exert on the movements is not clear. To understand the functional significance of the motor pattern, we need to know the joint movements and torques around the joints, in order to estimate the force development in muscles acting on these joints. The relationships between electromyographic activity, muscle length and force, and also the electromechanical delays must be known (Grillner 1972). The nonhomogeneous distribution of motor units in a muscle further complicates the interpretation of the electromyographic activity (Burke and Edgerton 1975).

The amplitude of the rectified and filtered electromyograms (RFEMG) can nevertheless be used as an indication of the overall level of muscle activity and the RFEMG-burst as an indicator of the total activity of the muscle in one cycle, provided that the electrodes used are large and nonselective to exclude that the activity in a few nearby muscle fibres dominates. The patterns found in dogs (Wentink 1976, Tokuriki 1973a, 1973b, 1974), mesencephalic (Gambarian et al. 1971, Grillner and Zangger 1975) and intact cats (Engberg 1964, Engberg and Lundberg 1969, Forssberg et al. 1980a, Rasmussen et al. 1978) are as a rule incomplete because only one or a few speeds are used or different animals and/or different speeds are normalized and averaged which increases the variability of the results. Detailed information is also available from the chronic low spinal cat (Forssberg et al. 1980a). The flexors and extensors are defined according to Sherrington (1910) and the actions of the muscles analysed are summarized in the beginning of each subsection.

Flexor activity

M. iliopsoas (Ip; hip and spine flexor) starts gradually 0 to 75 ms before t_{SW} and is most active in the end of the hip flexion phase, around $t_{E_1 an}$ (fig. 10, 12A; Wetzel 1981). The termination is around t_{Ehi}, i.e. before t_{SU}, except for the longest cycle durations (fig. 12A, cf. however Engberg and Lundberg 1969). The duration of the Ip burst is thus changing in a similar way as T_{SW} (fig. 13A). The timing agrees with most other studies (see above), only Tokuriki (1973a) reports Ip activity after t_{SU} for dogs (where no consistent Ip activity was found in cat SN).

Anatomically Ip acts also as a spine flexor, but it is usually not active during spine flexion in the E_3an phase, however the end of Ip activity coincides with the beginning of the spine flexion around t_{SU} (Carlson et al. 1979). This suggests that Ip acts mainly as a hip flexor, throughout T_{Fhi} and that it aids the control of the foot placing on ground in the velocity range investigated ($v < 1.0$ m/s).

M. sartorius (Sart, electrodes placed in the lateral part, but 'pick-up' from the medial part cannot be excluded; hip flexor and knee extensor) starts gradually at approximately the same time as Ip and at most 50 ms before t_{SW} at velocities of locomotion below 1.1 m/s. Occasionally Sart activity appears to start after t_{SW}, which may be due to difficulties in determining the onset of the bursts (fig. 10, 12B). The peak of Sart activity coincides approximately with that of Ip or it may occur somewhat later (fig. 10). The Sart activity ends, like Ip, around t_{Ehi} and as a rule before t_{SU}. The Sart burst duration changes like T_{SW} with the cycle duration (fig. 13B).

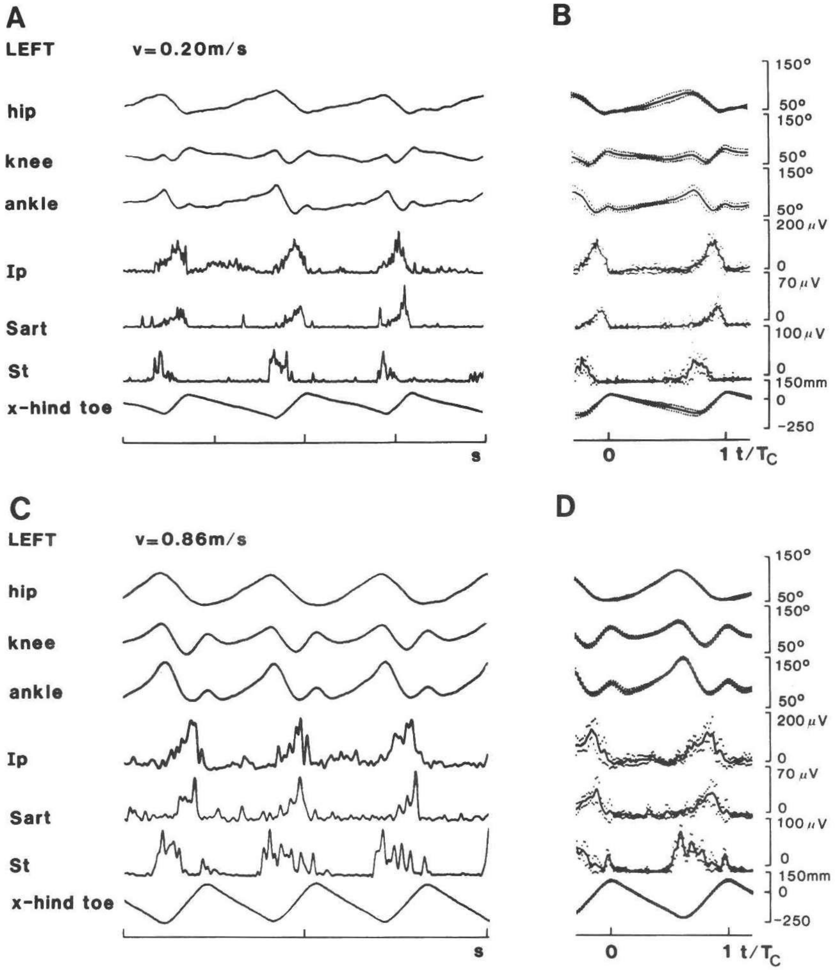

Fig. 10. Angular movements and electromyographic activity during two different speeds of locomotion. The angles of the hip, knee and ankle, joint, the rectified and filtered electromyograms of Ip, Sart and St, and the horizontal displacements of the toe of the hindlimb with respect to the hip (x-hind toe) are shown during slow (0.20 m/s, *A* and *B*) and moderate (0.86 m/s, *C* and *D*) walking speeds. The curves are drawn against real time in *A* and *C* (divisions in s) and in *B* and *D* average curves are plotted after normalization of the cycle duration to 1. The cycle starts (0) and ends (1) at the onset of the support phase of the left hindlimb. The mean is indicated as a continuous line and the standard deviation as a dotted one. Seven cycles are averaged in *B* and 8 cycles in *D*. Upward deflection of the x-hind toe curve indicates the swing phase and downward deflection the support phase. Calibrations are to the right of each curve. Data are from the left hindlimb of cat SN.

Low intensity Sart activity, observable before the main burst at speeds of locomotion around 1 m/s, becomes more pronounced at higher speeds ($1.0<v<2.5$ m/s). Within this speed range the Sart activity starts much earlier, 130 (cat FR) and 170 ms (cat PD) before t_{Fhi}, than in the lower speed range. (The Sart activity, of the main burst only, starts 30 to 80 ms before t_{Fhi} in the lower speed range for these cats.) At the highest speeds of locomotion Sart can start only 50 ms after t_{Ehi} and even before t_{SU} (fig. 4D, Rasmussen et al. 1978). The Sart activity ends in this speed range earlier than in the lower speed range and it occurs around 25 ms after T_{E_1kn} and always before t_{Ehi} and t_{SU} (fig. 12B, cf. however Tokuriki 1973b). Similar observations as during level walking and trotting were made at corresponding stride durations for the Sart activity during uphill and downhill locomotion and during galloping (fig. 4F). A distribution into

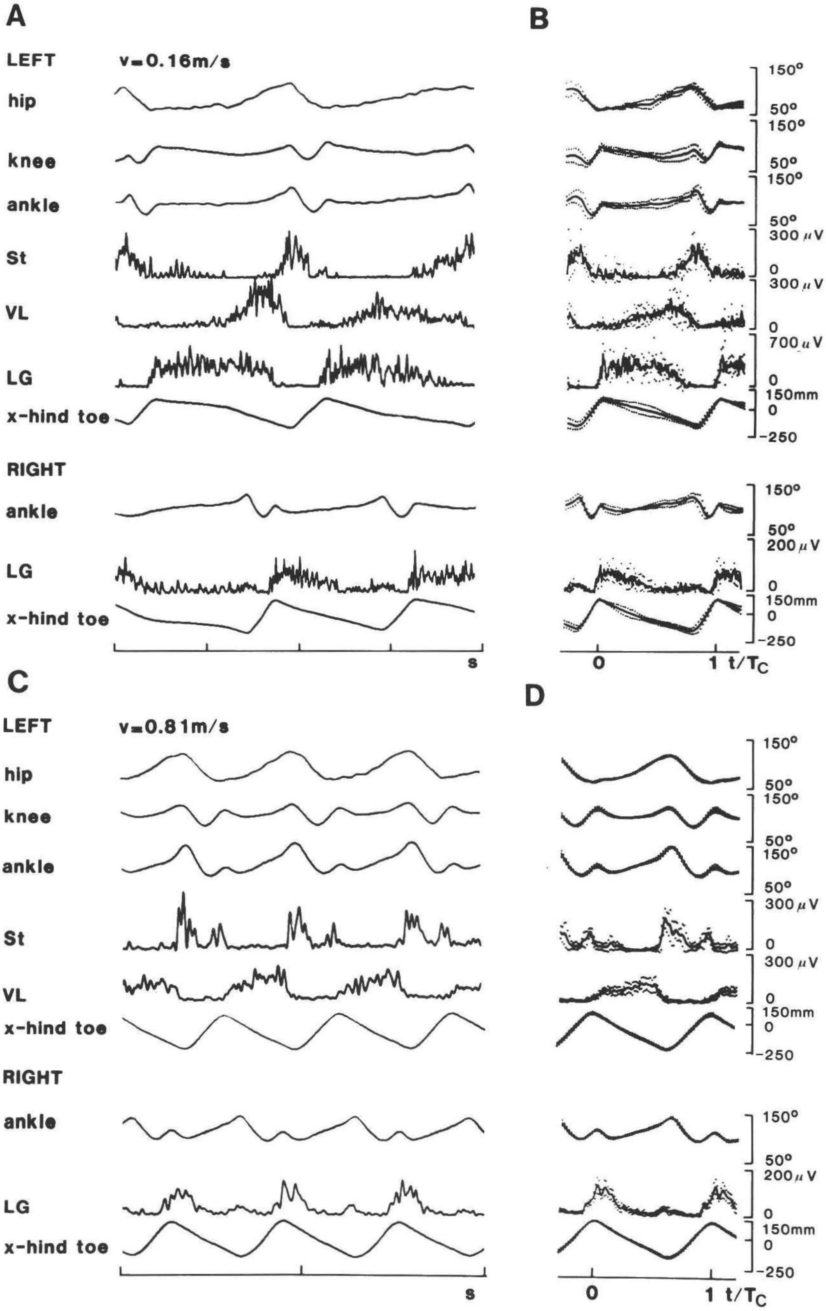

Fig. 11. Angular movements and electromyographic activity during two different speeds of locomotion. The angles of the hip, knee and ankle joint, the rectified and filtered electromyograms (RFEMG of St, VL and LG, and the horizontal displacements of the toe (foot) of the hindlimb with respect to the hip (x-hind toe) of the left hindlimb are shown, along with the ankle joint angle, the RFEMG of LG and the x-hind toe of the right hindlimb during slow (0.16 m/s, *A* and *B*) and moderate (0.81 m/s, *C* and *D*) walking speeds. The left LG activity is not illustrated in *C* and *D*. The curves are drawn agains real time in *A* and *C* (divisions in s) and in *B* and *D* average curves are plotted after normalization of the cycle duration to 1. The cycle starts (0) and ends (1) at the onset of the support phase of the left and right hindlimb for the averaged curves of the left and right limb respectively. Three cycles are averaged in *B* and 15 cycles in *D*. Data are from cat SI.

two bursts per stride was not observed here in walking, trotting, or galloping (cf. however Engberg and Lundberg 1969 and Orlovskii 1972). The Sart activity of the mesencephalic and chronic low spinal cat shows similar patterns to those of the intact cat during walking and galloping (Forssberg et al. 1980a, Gambarian et al. 1971).

At low velocities of locomotion ($v \leq 1.0$ m/s) Sart is active during the end of the support phase and most of the swing phase, where it could act as a hip flexor to assist the lift-off and bring the limb forwards. The activity in the last part of the swing phase could be a combined hip flexor and knee extensor action to delay the placing of the foot on the ground. But at higher speeds ($1.0<v<2.5$ m/s) Sart is active only during the major or whole part of the support phase where it could function as a knee extensor to support the body. Only in the end of the support phase and beginning of the swing phase could it act as a hip flexor and aids in the initiation of lift-off.

M. semitendinosus (St; knee flexor and hip extensor). The activity of St consists of two bursts every cycle: One larger burst (first) with a sudden onset and a shorter burst (second), which is not always present at very low speeds of locomotion (fig. 10, 11). The first St burst (St') starts before Ip and Sart and 50 to 250 ms before t_{SW} (fig. 12C). Note the marked difference in onsets in the two cats at longer cycle durations. The peak of St' activity occurs around t_{Fkn} (fig. 10, 11). In both cats the cessation of the St' burst is before t_{Ehi} and 60 ms before to 30 ms after t_{E_1kn} (fig. 12C). In one experiment on cat SN the activity sometimes ended 10 to 20 ms before and sometimes 10 to 30 ms after t_{E_1kn}; in another experiment with the same cat St' always ended 15 to 60 ms before t_{E_1kn}. One explanation could be that different parts of the muscle show small differences in timing or another that the behavioural situation was somewhat different. Also differences between cats can be observed. The St' burst duration of cat SN is increasing less with T_C than that of cat SI and the latter is increasing more than T_{Fkn} (fig. 13C).

The second St burst (St") starts 50 to 90 ms before t_{SU} (and thus before t_{Ehi}) and ends in most cases 0 to 20 ms before t_{SU} with rare observations in the interval 10 ms after t_{SU} (fig. 12D). Sometimes variable St activity could be observed after t_{SU}, which could become pronounced during split belt locomotion (fig. 18, 21). The duration of the second St burst is short (80 to 100 ms) and rather constant for both cats (fig. 13D).

The timing of the first St burst is similar to what was found by other authors (see above), but the early onset of St compared with those of Ip and Sart has only been reported in the mesencephalic preparation (Grillner and Zangger 1975). The first St burst is active before and during F_{kn}, suggesting a knee flexor and not a hip extensor action.

The second burst, which was not observed by Tokuriki (1973a, 1973b), starts after t_{SU} according to Wentink (1976) and ends after t_{SU} according to Rasmussen et al. (1978) and in the recordings of Engberg and Lundberg (1969). The second St burst coincides with the last part of Fhi and the first part of Ehi. This could be a combined hip extensor action that would in addition decelerate the knee extension to guarantee a soft contact with the ground (cf. however Engberg and Lundberg 1969).

Extensor activity

M. vastus lateralis (VL; knee extensor) starts before t_{SU} (fig. 12E), as was demonstrated elegantly by Engberg and Lundberg (1969), and usually VL is most active in the later part of the E_3kn phase (fig. 11). The VL activity starts almost always after t_{E_1kn}, even in the fast trot, and it coincides with t_{E_1kn} during galloping, but the timing can differ considerably between different cats and with different T_C (fig. 4D, 4F, 12E). However, in the low spinal cat the VL activity starts 10 to 60 ms before t_{E_1kn} at higher speeds of locomotion (Forssberg et al. 1980a). A separate small burst before the main activity, as emphasized by Engberg and Lundberg (1969) and Wetzel (1981) for the intact cat and described at higher speeds of locomotion in the spinal cat (Forssberg et al. 1980a), was rarely observed during walking in cats SN, SI and PD

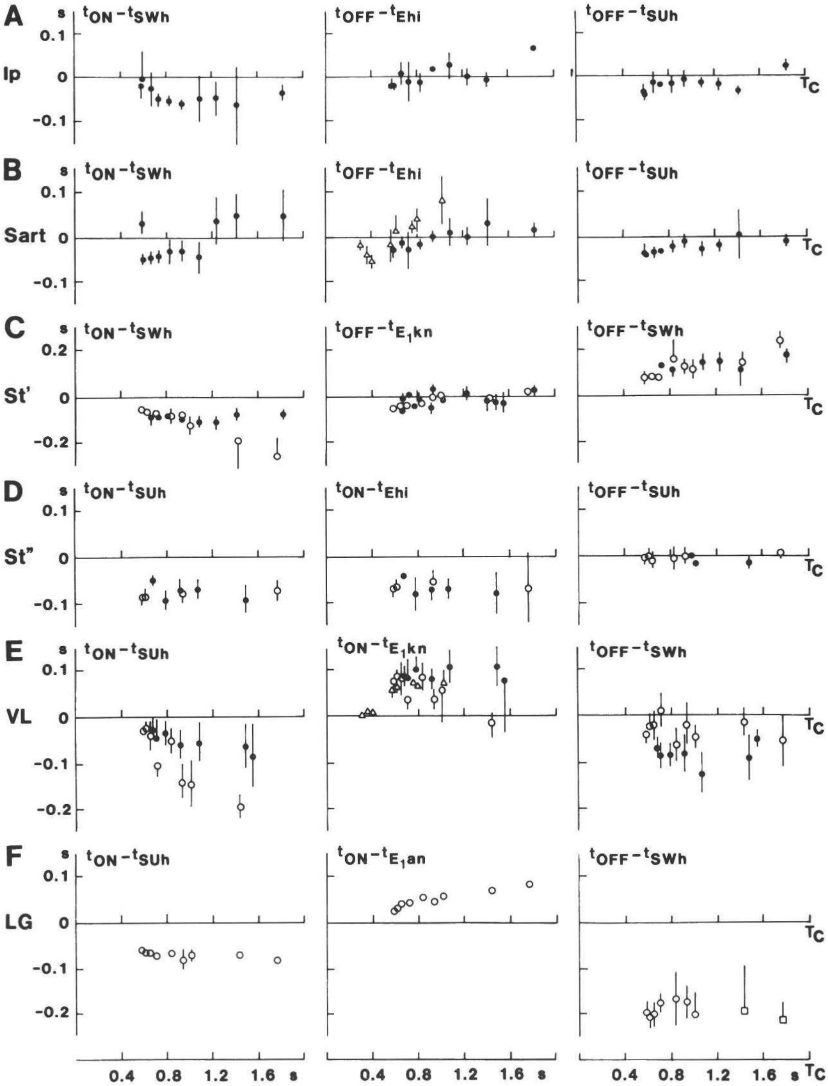

Fig. 12. The timing of electromyographic activity in relation to phases of the stride cycle. The means of the interval from the onset of a phase to the onset (t_{ON}) or termination (t_{OFF}) of the RFEMG burst of a muscle are plotted against the cycle duration. At the vertical axis of every plot the interval is indicated and on the left side of every row the muscle. Closed circles are data from the left limb of cat SN, open circles and squares from the left and right limb of cat SI respectively. The triangles are data from the left limb of cat FR. For reasons of clarity some data are not included in the figure as the data points came too close to each other. Note the different scale in *C*. The standard deviation of the mean value (n = 2-17) is indicated with a bar when it exceeds the symbol.

(fig. 11). Other cats (FR and KJ) show this small VL burst inconsistently from slow walking (0.3 m/s) to fast trotting (2.5 m/s) and galloping. In most cases it is not clearly separated from the main burst. The VL activity terminates abruptly and almost always before t_{SW} (fig. 12E). Also in trot and gallop it ends around t_{Fkn} (mean values: 20 ms before and 12 ms after respectively) and thus probably before t_{SW}. The duration of the VL burst is thus following T_{SU} (fig. 13E). The timing of VL activity during uphill and downhill locomotion corresponds to that during level locomotion at corresponding cycle durations.

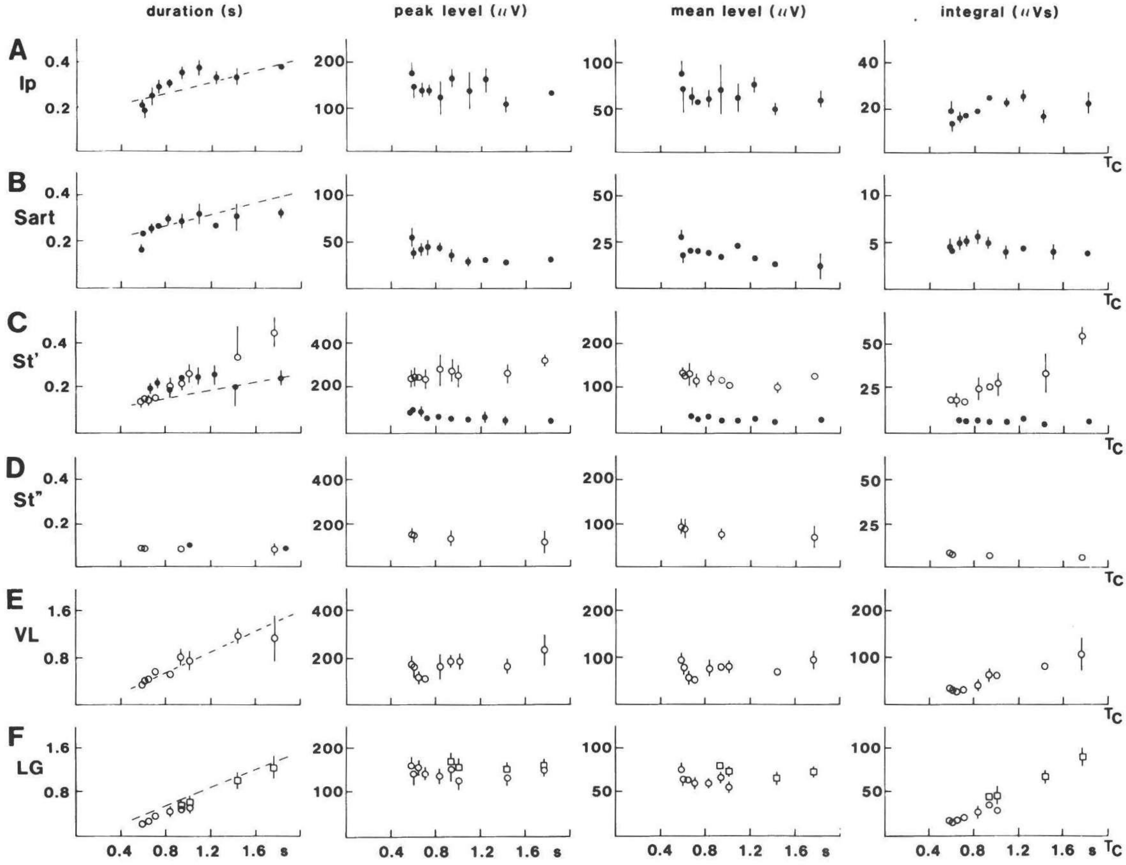

Fig. 13. Properties of the bursts of electromyographic activity. The mean values of the duration of the RFEMG burst (first column), the peak (second column) and mean (third column) level of the RFEMG burst, and the time integral of the RFEMG burst (fourth column) are plotted against the cycle duration for the different muscles in *A* to *F*. Same symbols used as in fig. 12. The units of the different properties of the bursts are given above each column. The peak and mean level, and the integral of the right LG burst (squares) are divided by 4 to fit in the figure of the left LG burst. (No separate scaling was used for the St' activity from cats SN and SI in *C*.) The estimated linear relationships with T_C of T_{SWh} (cat SN) are drawn as broken lines in the first column of *A* and *B*, of T_{FKn} (cat SI) in *C*, and of T_{SUh} (cat SI) in *E* and *F*. The standard deviation of the data points ($n=2\text{-}17$) is indicated with a bar when it exceeds the symbol.

VL is thus active just before and during the major part of the support phase. This suggest a supporting function and it could propel the animal during the last part of its activity.

M. lateral gastrocnemius (LG, ankle extensor and knee flexor) has an intense onset after $T_{E_1 an}$ and 60 to 80 ms before t_{SU} (fig. 12F). The activity drops gradually and terminates before the VL activity around 200 ms before t_{SW} (fig. 11, 12F). The duration of the LG burst is thus shorter than T_{SU}, and it will increase at the same rate as T_{SU} (fig. 13F). A similar timing was also found by other authors (see above), although Tokuriki (1973a) found a main burst around t_{SU} followed by a smaller burst in the support phase and around t_{SW}. Similar LG activity was observed in the right LG of cat SI, but not in the left LG of the same cat (fig. 11).

LG is active during the first part of the support phase, which suggests that LG supports the body after touch-down. LG is not active during the last part of the support phase, the propulsive phase, where the knee extensors are still active. The delay between the electromyographic activity and the force development in the muscle could be responsible for the substantial ankle torque, which is needed during this phase

(Manter 1938). The lack of LG activity during knee flexion suggests that there is no knee flexor function in the velocity range investigated ($v < 1.0$ m/s).

Level of activity

It is striking that the peak and mean level of the bursts of activity of the hip and knee and ankle flexors and the knee and ankle extensors change so little over a more than threefold range of T_C (fig. 13). Differences between cats can be observed in the peak level of the first St burst, where one is increasing and the other decreasing with T_C (fig. 13C). The total activity (integral) of the muscle, which is the duration of the burst multiplied by the mean level of activity, reflects mainly the changes in the duration of the bursts, because the latter is rather constant. This means that the integral of the extensor activity is increasing with T_C (fig. 13E, 13F) and that the integral of the flexor activity is rather constant, with the exception of the St' burst of cat SI (fig. 13A-D). Still it is well possible that the level of activity increases at the smallest cycle durations (300 to 400 ms), where cats usually trot and gallop (Smith et al. 1977). Unfortunately the hip extensors were not investigated here, although they are of importance for the propulsion.

3. The effect of speed on the movements in different joints

The horizontal position of the toe, with respect to the hip at touch-down, shows only minor changes with increasing speed, but at lift-off the limb becomes considerably more extended (fig. 8). The lift-off occurs just after the onset of hip and knee flexion and around the onset of ankle flexion and the joint angles at the onsets of flexion of the hip, knee and ankle increase significantly with speed (fig. 14, 9).

The joint angles of the knee and ankle at the onset of the E_1 phase, during the swing phase, is approximately constant at different velocities. The hip joint angle at the onset of the extension phase (a_{Ehi}), just before touch-down, also remains approximately constant. The a_{E_2kn} and a_{E_2an} values, at touch-down, increase slightly with speed or remain constant. This is consistent with the small changes of the toe position at touch-down. However, the same toe position can be obtained with different combinations of joint angles, because a change in one joint - within certain limits - can be compensated by another (see below). The a_{E_3kn} and a_{E_3an}, during the support phase, show clear differences. Where a_{E_3kn} always increases significantly with speed, a_{E_3an} may decrease slightly or remain constant. Based on similar findings (a_{E_1kn}, a_{E_1an}, a_{Ehi}) for the shoulder and elbow joints of dogs, Orlovskii and Shik (1965) suggested that these joints have to flex up to a definite finite angle irrespective of the initial angle. This is not always the case since deviations can be observed during split belt locomotion (fig. 20E).

Previous studies in cats have not dealt with speed induced changes in joint angles (Engberg and Lundberg 1969, Goslow et al. 1973). With dogs, Orlovskii et al. (1966) reported an increase of the amplitude of the elbow, knee and hip joint angle. In the present study the range of velocities of locomotion analysed included very low values. The increase of the joint angles above 1 m/s is rather small. For instance, with an increasing velocity from 1.5 to 2.5 m/s, a_{Fkn} increases from 128° to 133° (maximum values during observation intervals of 6.5 s of locomotion of cat FR).

The angular excursions of the hip joint during its flexion phase ($A_{Fhi} = |a_{Fhi} - a_{Ehi}|$) increases significantly with speed ($v<1$ m/s, fig. 15A). The same applies for knee (A_{Fkn}) and ankle (A_{Fan}). It is the result of changes in a_{Fhi}, a_{Fkn} and a_{Fan} with speed and the relatively small changes in a_{Ehi}, a_{E_1kn} and a_{E_1an} respectively. Changes in A_{E_1kn} and A_{E_1an} were either not significant or small (either increasing or decreasing). These reflect small changes in a_{E_1} and a_{E_2} of both joints. The yield of the knee (A_{E_2kn}) is somewhat decreasing with speed, but A_{E_2an} is constant for cat SI but increases for cat SN. The changes in A_{E_3}, like those of A_F, are mainly the result of changes in a_F with speed.

Covariance between the joint angles at the onset and cessation of the phases of the stride cycle

The variabilities of the ankle joint angle at the onset and at the cessation of the E_1 phase seem to be much greater than the variability of the excursion of the joint angle during that phase (fig. 15B). To quantify this supposition the following method was used. The residues were calculated, i.e. the deviations of the joint angle from the approximated linear relationship of that joint angle with speed at every measured velocity. This was done for the onset and the cessation of the three joint angles and for the excursions of these angles during their corresponding phases. These residues were further analysed since the effects looked for are obscured by the speed dependency of the joint angles; this increases the sensitivity of the method. The variances (sd^2) of the residues of the joint angles and the excursions were calculated.

If the ankle joint angle at the onset of the E_1 phase is independent of the joint angle at the termination of that phase, then the sum of the variances of the residues of these phases ($sd^2(a_{E_1an}) + sd^2(a_{E_2an})$) should

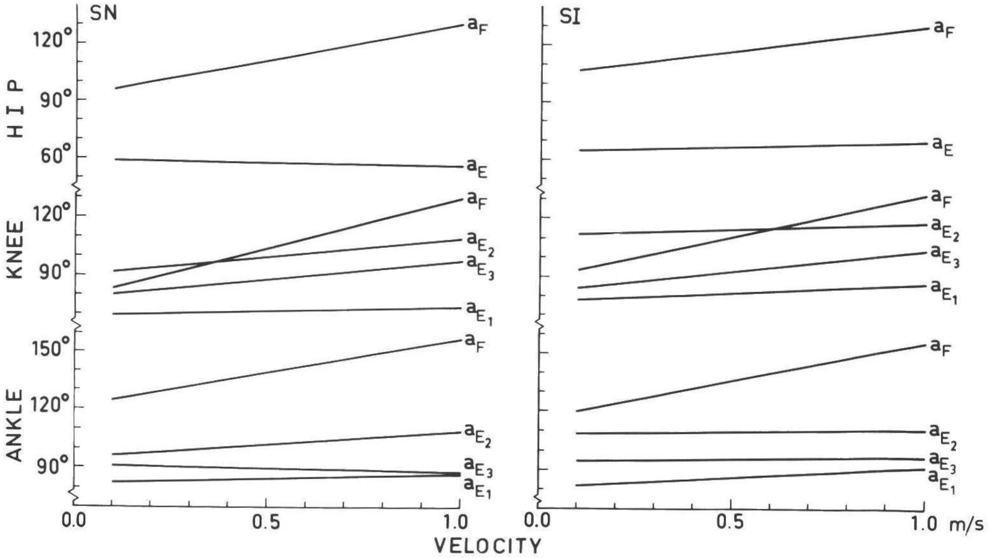

Fig. 14. Adjustments of joint angles with speed. The relations with speed of the angles of the left limbs of cat SN (left) and SI (right) of the hip, knee and ankle joint were approximated with first order regression analysis. The joint angles of the hip at the onset of the flexion (a_F) and extension (a_E) phase and the joint angles of the knee and ankle at the onset of the flexion and the first (a_{E_1}), second (a_{E_2}) and third (a_{E_3}) extension phases are illustrated. The slopes of a_{Ehi}, a_{E_1kn}, a_{E_1an} and a_{E_3an} for cat SN, and a_{E_2an} and a_{E_3an} for cat SI are not significantly different from zero. Each line fits data from 79 to 104 strides.

equal the variance of the residues of the excursion of the E_1an phase ($sd^2(A_{E_1an})$). In that case:

$$sd^2(A_{E_1an}) = sd^2(a_{E_1an} - a_{E_2an}) = sd^2(a_{E_1an}) + sd^2(a_{E_2an})$$

but $sd^2(A_{E_1an})$ is significantly smaller than $sd^2(a_{E_1an}) + sd^2(a_{E_2an})$ (table 5). This means that the residues are not independent; a_{E_1an} and a_{E_2an} are covariant. The same effect was observed in all other phases of the three joints of the hindlimbs of cats SN and SI and the differences were significant for all but the knee flexion phase of cat SI. In other words: *the excursions of the joint angles during the phases of the stride are better controlled than the joint angles themselves at the onset and termination of these phases.*

This finding could be explained by central mechanisms without feedback from the periphery. With the same degree of muscle activation and the same time interval the limb will be moved through roughly the same excursion whether it starts slightly more flexed or somewhat more extended. However, feedback can also play a role. A variety of sensory mechanisms are utilized to correct the execution of the different phases of the stride, the trajectory of the foot during the swing phase (Forssberg 1979, cf. Orlovskii and Shik 1965), the hip movements (Andersson and Grillner 1981, 1983, Grillner and Rossignol 1978) and the load on the limb extensors (Duysens and Pearson 1980). The correlations found in the joint angles could also be explained by the properties of the mechano-receptors activated by the movements or by the properties of the neuronal networks processing the sensory information.

Let us consider some different receptor types that might be important. One class is the joint receptors, but little is known how they behave under dynamic conditions like locomotion (Loeb 1981, Skoglund 1957). Furthermore it is still not clear to what extent the discharge of joint receptors is limited to extreme joint positions rather than providing signals throughout the entire range of joint angles (Grigg 1975, Ferrell 1980). Another class consists of muscle receptors like the muscle spindles, since the lengths of the muscles change with joint angle. Spindle afferents with primary and secondary endings can detect changes of muscle

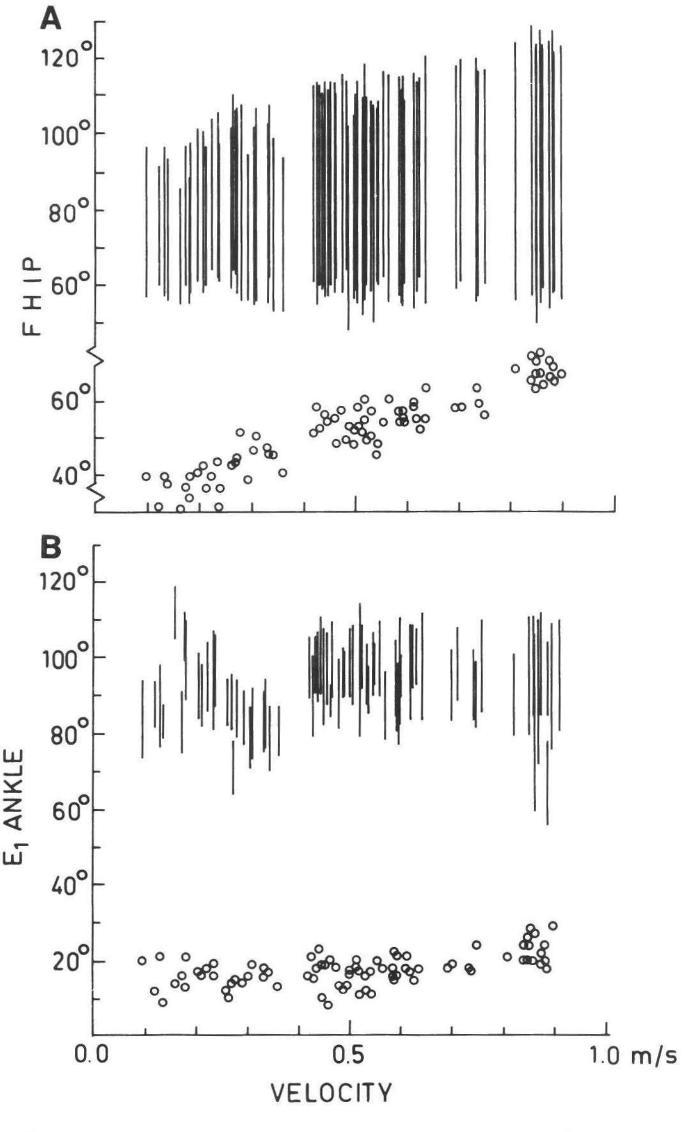

Fig. 15. Adjustments of joint angles and excursions with speed. *A* The angles of the hip joint during the flexion phase are plotted as bars, the excursions of the hip joint angle during this phase as circles. The top and bottom of the bars indicate the joint angle at the beginning and end of the flexion phase respectively. The length of the bar is the excursion of the angle. *B* The angles of the ankle joint during the E_1 phase of the ankle are plotted as bars, the excursions as circles. The bottom and top of the bar indicate the joint angle at the beginning and end of the E_1 phase respectively. In both illustrations the variances of the residues (see text) of the excursions of the joint angles during the phases are significantly smaller than expected from the sum of variances of the joint angles at the beginning and end of those phases. Every symbol represents one measurement. Approximately coinciding symbols are omitted for sake of clarity. Data are from the left hindlimb of cat SN.

$sd(a_{Fhi})$	$sd(a_{Ehi})$	$sd(A_{Fhi})$	$[sd^2(a_{Fhi})+sd^2(a_{Ehi})]^{1/2}$
4.4	3.3	3.9	5.5
$sd(a_{E_1an})$	$sd(a_{E_2an})$	$sd(A_{E_1an})$	$[sd^2(a_{E_1an})+sd^2(a_{E_2an})]^{1/2}$
6.6	6.9	3.3	7.7

Table 5. Standard deviations of the residues of the hip joint angle at the onset of the flexion ($sd(a_{Fhi})$) and the extension phase ($sd(a_{Ehi})$) and of the residues of the excursion of the hip joint angle during its flexion phase ($sd(A_{Fhi})$). Also the standard deviation of A_{Fhi} was calculated from the residues of a_{Fhi} and a_{Ehi}, supposing that these residues were independent (fourth column). The same was done for the residues of a_{E_1an}, a_{E_2an} and A_{E_1an} in the second row. The variance of the residues of the excursions is significantly smaller than the sum of the variances of the residues of the joint angles at the onsets of the phases from which the excursions were calculated (F-test, level of significance = 0.05). The number of observations from which the standard deviations of the residues were calculated is approximately 80 and the standard deviations are expressed in degrees. Data are from the left hindlimb of cat SN.

lengths during walking; they may be active during a part or almost the whole stride (Loeb and Duysens 1979, Prochazka et al. 1976, 1977, 1979, Wand et al. 1980). Changes in the alpha-gamma coactivation may change the working range of the spindles and thus the muscle length, provided that the assumed servo assistance is strong enough. The alpha-gamma coactivation is probably relative weak during walking in intact cats (Prochazka et al. 1976, 1977). Thus a change of the length of the muscles could be controlled better than the length itself, which may explain the above described findings in the joint angles. However, a combination of central mechanisms and peripheral feedback from different receptors seems also a likely explanation.

4. The positioning of the foot at touch-down and lift-off

The single most important event in the stride cycle is the placement of the foot at touch-down. A good control over this phase is important to avoid obstacles and holes in the terrain and to ensure a stable support. The animal should also avoid contact between the forelimbs and hindlimbs and a limb should be placed or lifted at an appropriate moment in relation to the other limbs for reasons of stability.

In this section the coordination of the joints is analysed at the moments of touch-down and lift-off of the foot (toe). With the same methods as used in the previous section, the residues of the measured hip, knee and ankle joint angles at touch-down and lift-off are calculated. This was also done for the horizontal position of the toe of the hindlimb with respect to the hip (x-toe) and for the vertical position of the hip with respect to the toe (y-hip).

At touch-down the coefficient of correlation between the residues of the knee and ankle joint angles is very high (table 6, r(knee-ankle)). Hence the coefficients of correlation of the residues of one of the distal joint angles (knee or ankle) with the residues of the hip joint angle, x-toe and y-hip are not very different from those of the other distal joint angle. For example, r(hip-knee) is very similar to r(hip-ankle). The correlation between the residues of the x-toe and y-hip is not significant at touch-down. The residues of the distal joint angles are better correlated with those of the height of the animal (y-hip), than are the residues of the hip joint angle. The only residues which are moderately correlated with the residues of the horizontal position of the foot (x-toe) at touch-down are those of the distal joint angles of cat SI.

Simulations have been performed to investigate the functional significance of the correlation between the different residues. In a simplified model the position of the toe, with respect to the hip at touch-down, was calculated as a function of the height of the hip above the surface of the ground, the dimensions of the leg and the knee and ankle joint angles. The movements of the phalanges and digits were neglected. The movements of the pelvic girdle were restricted to vertical ones (fig. 16). From this initial position small changes were made in the joint angles and a new position of the toe was calculated. Any vertical deviation of the toe from the horizontal surface was translated into a vertical change of the hip position. The calculations were repeated 100 times with different values of the joint angles, distributed around chosen mean values. The variations of the joint angles were normally distributed and the standard deviation of the variations of every joint angle was set to a value corresponding to the measured standard deviations. In this model the variations (residues) of the joint angles were constructed in such a way that the coefficients of correlation between the variations of the knee and ankle joint angle and between the variations of the hip and ankle joint angle could be changed independently. The coefficient of correlation between the variations of the hip and knee joint followed from the multiplication of the other two coefficients of correlation. These coefficients did not differ significantly from the measured ones, which validated the simplifications made in the model.

The simulations were performed with or without correlation between the residues of the hip, knee and ankle joint angles. The coefficients of correlation used were measured from the pooled data. Initial limb positions and residues of the joint angles, measured at three different speeds of locomotion, were used. The simulations, with the proper coefficients of correlation between the residues of the three joint angles, did not show a significant difference between the measured and simulated standard deviation of the horizontal variations of the toe (table 7, first and second row). The simulations show further that the standard deviation of the horizontal variations of the toe increases significantly when the three joints are not covariant (table 7, third row). *Thus the covariance found between the residues of the hip, knee and ankle joint reduces the variance in the horizontal position of the foot.* This suggests that the system that positions the limb at touch-down controls the hip, knee and ankle joint angles in a way which results in a more precise placement of the foot, suggesting a position control of the foot at touch-down.

Similar results can be obtained simulating the lift-off of the toe. But the increase in the variability of x-toe is smaller and not always significant, when the simulations with and without covariant residues are compared. A good position control of the foot at lift off is not as important as at touch-down, because the

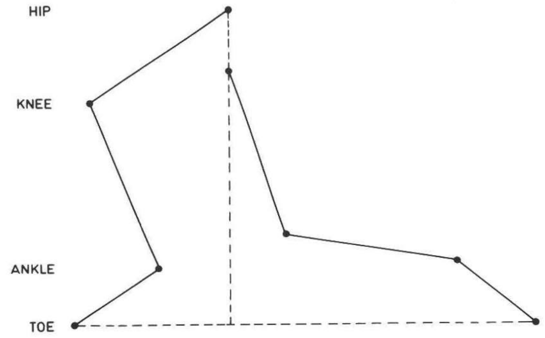

Fig. 16. Diagram of the simplified model (see text) simulating the limb position at touch-down and lift-off. In this model the movements of the phalanges and digits are neglected and the movements of the pelvic girdle are restricted to vertical ones. The positions of the limb at touch-down and lift-off are drawn at the left and right side respectively. Position data are from mean values of cat SN locomoting at a velocity of 0.9 m/s.

	touch-down		lift-off	
	SN	SI	SN	SI
r(hip — knee)	.43	.24	.12°	.83
r(hip — ankle)	.52	.34	.29	.76
r(knee — ankle)	.95	.90	.79	.92
r(hip — x-toe)	.21	-.03°	-.68	-.88
r(knee — x-toe)	.19°	.73	-.49	-.90
r(ankle — x-toe)	.29	.74	-.44	-.83
r(hip — y-hip)	.43	.48	-.17°	-.08°
r(knee — y-hip)	.91	.75	.84	.21
r(ankle — y-hip)	.87	.70	.65	.26
r(x-toe — y-hip)	-.16°	.15°	-.02°	.22

Table 6. Coefficients of correlation at touch-down and lift-off for cats SN and SI. The coefficients of correlation (r) of the residues of the joint angles of the hip, knee and ankle and of the residues of of the horizontal displacements of the foot (toe) with respect to the hip (x-toe) and the vertical displacements of the hip with respect to the toe (y-hip) are given for the left limbs of both cats at touch-down first two columns) and lift-off (last two columns). The coefficients of correlation are calculated from approximately 100 paired observations. Those which are not significantly different from 0 are indicated with a ° sign (level of significance = 0.05).

limb has only to be brought upward and forward and there is no supporting function.

The coefficients of correlation between the residues of the hip, knee and ankle joint angles during a whole stride cycle are illustrated in figure 17 for a constant velocity of locomotion. It is clear that the coefficients of correlation between the knee and ankle remains high during the major part of the support phase. It decreases around the transition from the E_3 to the F phase of knee and ankle. In this part of the cycle the extensor activity ceases and the flexor activity starts (see section 2) and the flexion of the knee precedes that of the ankle (fig. 9). The same can be observed in the last part of the ankle flexion phase, where the coefficient of correlation also decreases. In this part of the stride cycle the flexor activity ceases and the knee starts to extend while the ankle still flexes. Similar results can be observed for the coefficients of correlation between the residues of the hip and knee joint angles and between the residues of the hip and ankle joint angles. But the coefficients reverse in sign in the later part of the hip flexion phase where the knee and ankle starts to extend. Note that the coefficient of correlation between the residues of the knee and ankle joint angle remains very high during the E_2 phases of these joints, even when the ankle begins to extend and the knee still yields (flexes). *The coefficients of correlation between the residues of the joints are thus high during the periods of muscle activity of extensors only or of flexors only and low in transition phases.*

Let us consider the different factors, which could effect the observed covariance of the residues of the hip and especially those of knee and ankle joint angles at touch-down and lift-off. Measuring noise in the positions of the markers could lead to this covariance. For instance variations in only the horizontal

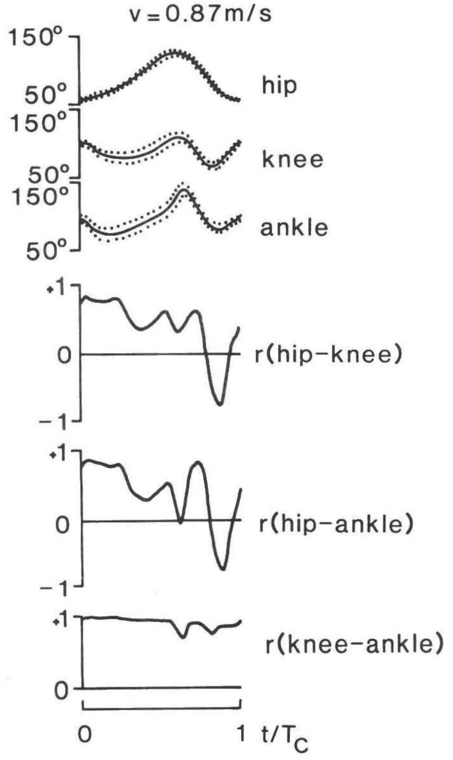

Fig. 17. Normalized and averaged joint angles with their coefficients of correlation. The duration of the stride cycle is normalized to 1 and the joint angles of the hip, knee and ankle are averaged (upper three traces). The standard deviations of the mean joint angles are indicated with dots. The coefficients of correlation (r) between these joints are calculated from the deviations of the normalized joint angles from the average curves and are plotted in the lower three traces. Note that the number of strides averaged is 15, which makes r not very reliable, e.g. an r of 0.5 is not significantly different from 0 (level of significance = 0.05).

velocity	(m/s)	.18		.45		.87	
sd(x-toe)							
measured	(mm)	18	(7)	7	(13)	11	(15)
simulated with covariant variations of the joint angles	(mm)	12*		7*		13*	
simulated with independent variations of the joint angles	(mm)	24*		13		23	

Table 7. The variations in the horizontal position of the foot (toe) of the hindlimb at touch-down. The measured standard deviations (sd) of the horizontal position of the toe, with respect to the hip (x-toe), is given in mm for cat SN locomoting at three different velocities (first row). The number of steps is given in parenthesis. The variations in the position of the toe, due to superimposed normally distributed variations in the hip, knee and ankle joint angles, were simulated 100 times (see text). The sd of the simulated x-toe was calculated. The simulations were performed **1** with the measured sd of the variations of the hip, knee and ankle joint angles at the different velocities and the measured coefficient of correlation between them from the pooled data (second row) and **2** with independent variations of the joint angles (third row). In the latter case the sd of the x-toe increased significantly. An asterisk indicates that the simulated sd is not different from the measured sd (level of significance = 0.05).

	case			
	1	2	3	4
sd(y-hip)	0.0	0.0	11.7	11.7
sd(x-toe)	9.8	0.0	0.0	9.8
sd(hip joint angle)	0.0	3.4	0.0	3.4
r(hip-knee)	.040	.993	.083	.638
r(hip-ankle)	.068	-.996	.082	.131
r(knee-ankle)	.301	-.978	.996	.434

Table 8. Simulations to investigate the coefficients of correlation between the residues of the hip, knee and ankle joint angles at touch-down. With the aid of simulations (see text) the coefficients of correlation are calculated, due to variations in the vertical position of the hip (y-hip), in the horizontal position of the toe (x-toe) and in the hip joint angle, for cat SN locomoting at a constant speed. Only the y-hip, or only the x-toe or only the hip joint angle is varied in case 1, 2 and 3 respectively. In case 4 the variations in the three parameters are combined with the appropriate coefficients of correlation between them. In this case the coefficients of correlation between the variations of the hip and ankle joint angles and between the knee and ankle joint angles are significantly different from the measured ones of .519 and .954 respectively (level of significance = 0.05). Simulations at other speeds and for cat SI gave similar results. The standard deviations are values from the pooled data and are expressed in mm for the positions of the toe and hip, and in degrees for the hip joint angle.

position of the knee will lead to a perfect correlation between the residues of the three joint angles. However, noise occurs in both horizontal and vertical position measurements and simulations show that the independent normally distributed noise superimposed on the horizontal and vertical positions of the limb markers (the knee correction performed, see Methods) results in low or very low coefficients of correlation between the residues of the three joint angles. The mechanical connections of double joint muscles could not lead to this covariance, since they will flex in one joint as they extend another, which would give opposite results (negative coefficients of correlation). A third possibility could be that the constraints imposed by the anatomy of the limb leads to the correlations found. For example the knee and ankle joint could compensate the variations in the hip joint or other parameters. These possibilities were tested in the model used above (see page 42). The vertical position of the hip (y-hip), the horizontal position of the toe (x-toe) and the hip joint angle could be varied and new joint angles were calculated. This was repeated 100 times and the coefficients of correlation between the variations (residues) of the joint angles were calculated. Variations of only the horizontal position of the toe, thus keeping the hip joint angle and the hip height fixed, will lead to a very low coefficient of correlation between the residues of the knee and ankle joint angle at touch-down (table 8, case 1). (When the hip joint angle was 'fixed', very small variations of the hip joint angle were introduced in order to avoid overflow and underflow in the calculations of the simulations. This leads to small and insignificant coefficients of correlation between the residues of the hip and other joint angles.) Variations of only the hip joint angle will lead to very high coefficients of correlation, but not with the proper sign (table 8, case 2). Only variations of the y-hip will lead to the very high coefficients of correlation between the knee and ankle (table 8, case 3). If all three parameters are varied together, with the appropiate coefficients of correlation between them, then the coefficient of correlation between the residues of the knee and ankle joint angle is significantly different from the measured one of 0.95 (table 8, case 4). The same results were obtained simulating locomotion at different velocities. Hence the covariance cannot be explained by anatomical constraints. This conclusion was sustained by comparable simulations for cat SI.

At lift-off the measured coefficients of correlation between knee and ankle could be explained by these constraints for one cat (SN) but not for the other (SI).

In conclusion, the covariance in ankle and knee joints at touch-down is advantageous for the accuracy, and must be generated by neural mechanisms. These are presumably part of the position control system, which guides the placement of the foot at touch-down. This system is critical for the adaptation of movements to the environment, i.e. the anticipatory control of the limb placement. The exact neural mechanisms has not yet been studied in direct experiments.

5. Adaptation of limb movements during split belt locomotion

Split belt locomotion of the intact cat

The movements of the limbs of the same girdle are shifted with half a cycle in alternating gaits, as walk and trot, but are more synchronized in non-alternating gaits, as gallop. The interlimb coordination is achieved by interactions between independent neuronal centres controlling each limb (see next section). Another form of interlimb coordination occurs when an animal walks along a circular path and the outer limbs have to cover a longer distance (i.e. walk faster) than the inner ones. This situation can be mimicked and driven to an extreme by using a treadmill with two belts so that the left and right pair of limbs have to locomote at different velocities. The low spinal and the mesencephalic cat can deal with such a situation by adaptations of the stride cycles on the two sides (Forssberg et al. 1980b, Kulagin and Shik 1970).

Also the intact cat is able to locomote with different velocities of the left and the right pair of limbs, and even when only one limb has a different speed. The cycle durations of all limbs remain equal (1:1 rhythm, fig. 18) until the differences between the durations of the phases of the stride cycle become sufficiently large, then the 'fast' limbs will take one stride per cycle more than the 'slow' limbs (2:1 rhythm, fig. 21). The basic movement pattern of a given limb remains the same as if both belts were tied together, i.e. t_{Fhi} is followed by t_{Fkn} and t_{Fan}, t_{E_1kn} occurs before t_{E_1an} and the onsets of the E_2 phases of knee and ankle practically coincide. On the other hand, the durations and the joint angle amplitudes of the different phases of the stride can differ strikingly (fig. 18, 21).

Split belt locomotion with a 1:1 rhythm

Cycle duration. The duration of the stride (T_C) decreases with speed (fig. 5). If T_C were determined by the belt velocity only, limbs walking on belts with different speeds should step with different frequencies. This is not the case for a wide range of velocity combinations (fig. 18, 19A). Usually T_C of the 'fast' limb is prolonged and that of the 'slow' limb shortened, as found in spinal and mesencephalic cats (Forssberg et al. 1980b, Kulagin and Shik 1970).

In most cases T_C is close to the value appropriate to the average speed of all four limbs (T_C(v mean), table 9). If only one hindlimb or both homolateral limbs are stepping on the 'fast' belt, then T_C is longer than T_C(v mean), but shorter than the cycle duration would have been if all limbs were walking with the 'slow' speed (T_C(v 'slow')). When only one hindlimb is stepping on the 'slow' belt, T_C lies between T_C(v mean) and T_C(v 'fast'). The relative influence of the forelimbs and hindlimbs on T_C was estimated when both forelimbs were walking on the same belt. The relative influence of the hindlimbs varies unpredictably between 13 and 51% with the velocity combinations used ('slow' speed is 42 to 56% of the 'fast' speed). Also a linear weighting of the velocities with their support phase durations does not give consistent results. It seems that T_C is determined by a nonlinear average of the velocities of all limbs during their respective support phases.

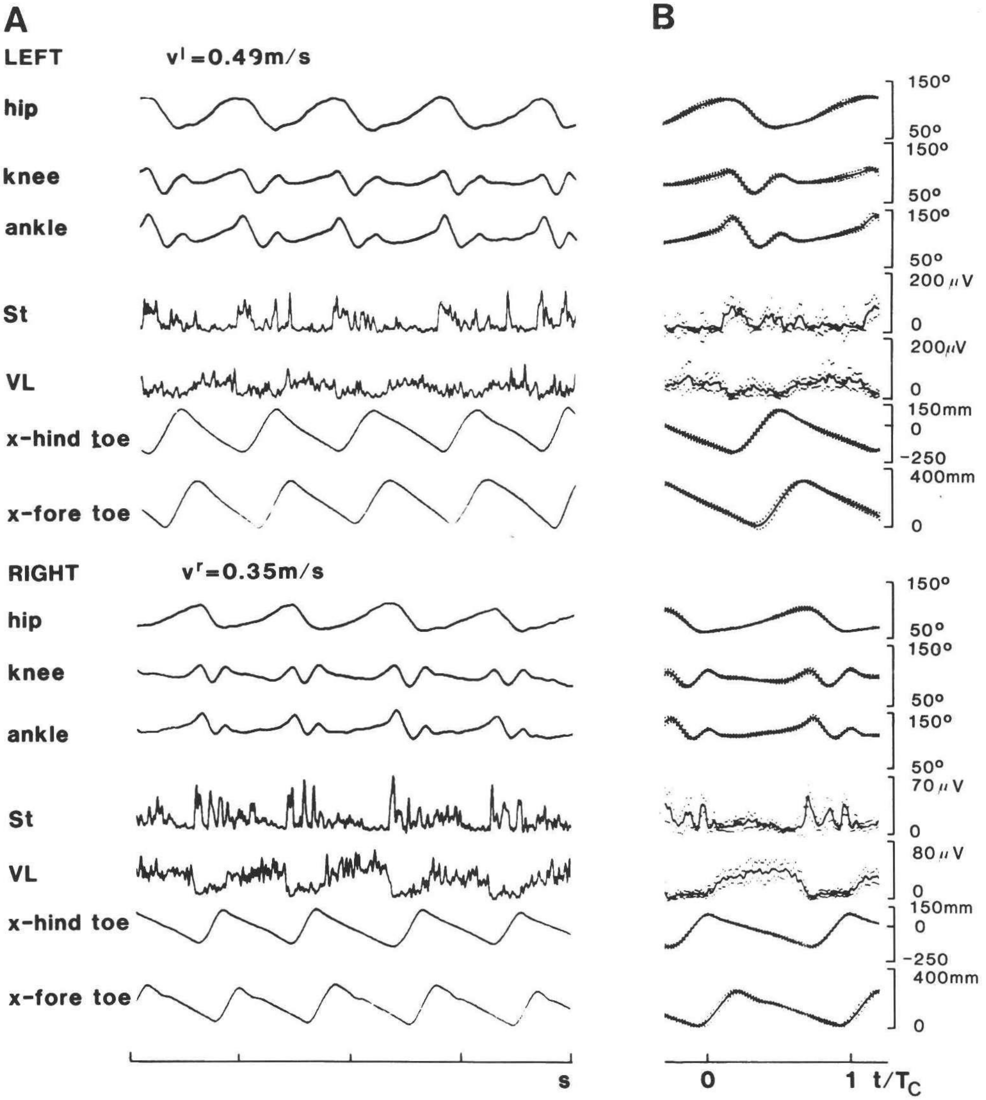

Fig. 18. Locomotion on split belts with a 1:1 rhythm. The joint angles of the hip, knee and ankle, the synchronously recorded RFEMGs of St and VL, and the horizontal displacements of the toe (foot) of the hindlimbs with respect to the hip (x-hind toe) and that of the toe of the forelimb (x-fore toe) are shown for the left and right side. The belt on the left side was driven at 0.49 m/s (sd = 0.05 m/s) and that on the right at 0.35 m/s (sd = 0.01 m/s). The curves are drawn against real time in *A* (divisions in s) and in *B* average curves (11 strides, including those of A) are plotted after normalization of the cycle duration to 1. The cycle starts (0) and ends (1) at the onset of the support phase of the right hindlimb. The mean is indicated as a continuous line and the standard deviation with dots. Upward deflection of the horizontal displacements indicates the swing phase and downward deflection the support phase. Calibrations are to the right of each curve. The most caudal position of each forelimb toe is used as an origin for that displacement. Data are from cat SN.

forelimbs on	v^l (m/s)	sd (m/s)	v^r (m/s)	sd (m/s)	T_C (ms)	sd (ms)	n	$T_C(v^l)$ (ms)	$T_C(v^r)$ (ms)	T_C(v mean) (ms)
A different belts	.32	.04	.47	.03	934	54	10	1003	791	880
	.66	.08	.50	.03	701	25	14	640	761	694*
	.92	.10	.50	.05	667	51	15	521	761	612
B 'fast' right belt	.25	.03	.48	.01	817	37	12	1169	780	844*
C 'slow' left belt	.25	.02	.46	.03	1079	68	9	1169	801	1039*

Table 9. Modifications of the stride cycle duration during split belt locomotion with a 1:1 rhythm. The velocity of the left (v^l) and right (v^r) belt, with their standard deviations (sd) are given in the left columns. The measured cycle duration (T_C) with its standard deviation and the number of observations (n) are given together with the calculated cycle durations, to be expected when all limbs should walk on the left belt ($T_C(v^l)$), when all limbs should walk on the right belt ($T_C(v^r)$), and when they all should walk on a belt with the average velocity of the belts on which the four limbs walk (T_C(v mean)). In *A* the right and left pair of limbs walk on the right and left belt respectively and in *B* and *C* both forelimbs walk on the 'fast' and 'slow' belt respectively. An asterisk indicates that the calculated value is not different from the measured value (level of significance = 0.05). It is assumed that the variance of the calculated value is negligible with respect to the variance of the measured value. Date are from cat SN.

Duration of the phases of the stride

'Slow' limb. If T_{SU} were determined by the velocity only, all limbs could still step with the same T_C by adjusting T_{SW}. However, T_{SU} of the hindlimb walking on the 'slow' belt is shorter (but not always significantly) than expected from the slower belt velocity. On the other hand T_{SU} is longer than, or equal to, the value expected from T_C (fig. 19B; table 10). Consequently T_{SW} is shorter than, or equal to, the value expected from T_C. But it is also shorter than, or equal to, the value expected from the belt velocity (fig. 19C; table 11). Similar adaptations of T_{SU} and T_{SW} occur in spinal and mesencephalic cats (Forssberg et al. 1980b, Kulagin and Shik 1970). The decrease of T_{SW} is achieved by decreasing both T_{Fkn} and T_{E_1kn} (fig. 19D, 19E) and T_{Fan} and T_{E_1an} are decreasing in a similar way (fig. 18). The spinal cat, however, reduces T_{SW} mainly by decreasing the flexion phase duration (Forssberg et al. 1980b).

'Fast' limb. The T_{SU} of the hindlimb stepping on the 'fast' belt is usually longer than expected from the faster belt speed (fig. 19; table 10), but shorter than expected from T_C (table 10). Exceptions can be observed when T_C is close to T_C(v 'fast'), i.e. two forelimbs stepping on the 'fast' belt or small velocity differences between the belts. T_{SW} will be too long for T_C when T_{SU} is too short, but in these cases T_{SW} is also longer than expected form the belt speed (table 11). This increase of T_{SW} is achieved by an increase of both T_{Fkn} and T_{E_1kn} (fig. 19D, 19E) and of T_{Fan} and T_{E_1an} (fig. 18). The adaptations of T_{SU} and T_{SW} to the belt speed are similar in the mesencephalic cat (Kulagin and Shik 1970), the spinal cat, however, does not appear to lengthen T_{SU} of the 'fast' limb (Forssberg et al. 1980b).

The same observations can be made for T_{SU} and T_{SW} of the 'slow' and 'fast' forelimb (Appendix table VI). The adaptation of T_{SU} and T_{SW} of the right and left forelimb should be the same, when they both are stepping on the same belt, if there is no influence of the hindlimbs on the forelimbs. But the differences between T^r_{SUf} and T^l_{SUF} are greater than expected from the natural asymmetries between the forelimbs (table 12). In most cases T_{SUf} on the side of the 'slow' hindlimb is smaller than T_{SUf} on the other side. Thus, besides the forelimb cycle duration (see above), also the durations of the phases of the forelimb stride are influenced by the hindlimbs (cf. however Shik and Orlovskii 1965).

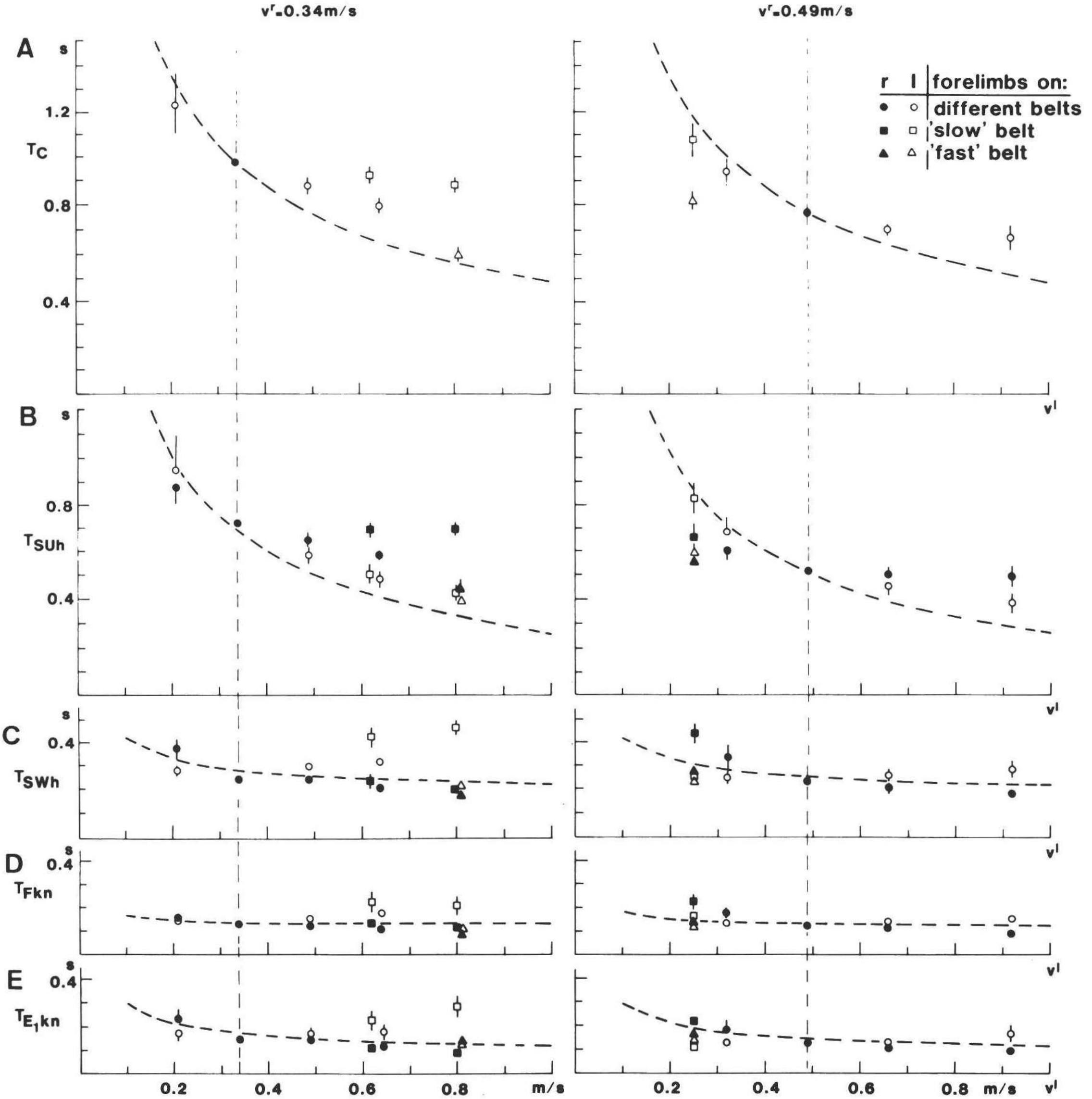

Fig. 19. Adjustments of the duration of the stride cycle and its phases during split belt locomotion. The velocity of the right motor driven belt was kept constant and the other one was driven at various speeds. The velocity of the right belt (v^r) is given at the top of each column, the speed of the left belt (v^l) is given along the abscissa in each plot. The open and closed symbols correspond to the durations of the phases of the left and right limb respectively. The circles, triangles and squares correspond to the experimental situations where the forelimbs are on different belts, on the 'fast' belt and on the 'slow' belt respectively. The standard deviation of the mean value (n = 8 — 15) is indicated with a bar when it exceeds the symbol. In *A, B, C, D* and *E* the durations of the stride cycle (T_C, measured from the successive t^l_{SUh}), the support phase of the hindlimbs (T_{SUh}), the swing phase of the hindlimbs (T_{SWh}), the flexion phase of the knee (T_{Fkn}) and the first extension phase of the knee (T_{E_1kn}) are plotted versus the speed of the left belt. The relations of the parameters with speed for this cat locomoting on tied belts are indicated with an interrupted curve for the left limb and with a dot for the right limb (fixed speed) on the vertical interrupted line (see fig. 5). Note that the right limb is the 'fast' one and the left limb the 'slow' one to the left of the vertical line and the other way around to the right of the vertical line. The durations of the flexion and extension phases of the ankle change in a similar way as those of the knee. They are not indicated here. Data are from cat SN.

forelimbs on	v^l (m/s)	v^r (m/s)	T^l_{SU} (ms)	sd (ms)	n	T^r_{SU} (ms)	sd (ms)	n	$T^l_{SU}(T_C)$ (ms)	$T^r_{SU}(T_C)$ (ms)	$T^l_{SU}(v^l)$ (ms)	$T^r_{SU}(v^r)$ (ms)
A both belts	.32	.47	687	62	10	601	39	11	656*	695	717*	561
	.66	.50	451	34	14	498	26	14	449*	478	395	533
	.92	.50	383	40	15	490	45	15	419	447	269	533
B 'fast' right belt	.25	.48	590	39	12	554	19	12	552	586	864	552*
C 'slow' left belt	.25	.46	828	64	9	655	58	9	785*	831	864*	571

Table 10. Adaptations of the hindlimb support phase duration during split belt locomotion with a 1:1 rhythm. The velocity of the left (v^l) and right (v^r) belt and the measured support phase duration of the left (T^l_{SU}) and the right (T^r_{SU}) hindlimb are given together with their calculated values, to be expected from the cycle duration ($T^l_{SU}(T_C)$ and $T^r_{SU}(T_C)$) and belt velocity ($T^l_{SU}(v^l)$ and $T^r_{SU}(v^r)$). Data of *A*, *B* and *C* are from the same experiments as in table 9A, 9B and 9C respectively and are presented in a similar way.

forelimbs on	v^l (m/s)	v^r (m/s)	T^l_{SW} (ms)	sd (ms)	n	T^r_{SW} (ms)	sd (ms)	n	$T^l_{SW}(T_C)$ (ms)	$T^r_{SW}(T_C)$ (ms)	$T^l_{SW}(v^l)$ (ms)	$T^r_{SW}(v^r)$ (ms)
A both belts	.32	.47	246	23	11	336	52	10	280	239	288	231
	.66	.50	255	25	14	205	18	14	250*	224	242*	229
	.92	.50	284	31	15	178	11	14	245	222	226	229
B 'fast' right belt	.25	.48	227	8	12	269	15	11	265	231	309	230
C 'slow' left belt	.25	.46	251	14	9	430	42	8	298	248	309	231

Table 11. Adaptations of the hindlimb swing phase duration during split belt locomotion with a 1:1 rhythm. The experiments and presentation are the same as in table 10.

forelimbs on	v^l (m/s)	v^r (m/s)	T^l_{SU} (ms)	sd (ms)	n	T^r_{SU} (ms)	sd (ms)	n	$T^l_{SU}(T_C)$ (ms)	$T^r_{SU}(T_C)$ (ms)	$T^l_{SU}(v^l)$ (ms)	$T^r_{SU}(v^r)$ (ms)
A 'fast' belt	.25	.48	535	12	12	557	12	12	598	592	564	557*
	.81	.34	383	22	8	339	27	7	395*	387	360	352*
B 'slow' belt	.25	.46	837°	79	9	809°	84	8	845*	841*	931	927
	.62	.35	707	25	9	679	26	9	698*	693*	723*	718
	.80	.34	683°	33	11	654°	36	10	662*	656*	740	734

Table 12. Adaptations of the forelimb support phase durations during split belt locomotion with a 1:1 rhythm and both forelimbs on the same belt. The velocity of the left (v^l) and right (v^r) belt and the measured support phase duration of the left (T^l_{SU}) and right (T^r_{SU}) forelimb are given together with the calculated durations, to be expected from the cycle duration ($T^l_{SU}(T_C)$ and $T^r_{SU}(T_C)$) and from the belt velocity on which both forelimbs are walking ($T^l_{SU}(v)$ and $T^r_{SU}(v)$). In *A* both forelimbs walk on the 'fast' belt and in *B* on the 'slow' belt. A zero indicates that the means of the measured left and right T_{SU} are equal. An asterisk indicates that the calculated T_{SU} is equal to its measured value (level of significance = 0.05). Data are from cat SN.

Foot position at touch-down and lift-off and joint angles

At touch-down. The limb stepping on the 'fast' belt usually has a long T_{SW} compared to the tied belt situation (fig. 19C). Thus there is more time to place the limb on the belt and it is placed approximately in the position expected for that speed or even in front of that position (fig. 20A). Conversely, less time is available during the short T_{SW} of the 'slow' limb (fig. 19C) and the toe is then often placed in a more caudal (backward) position than during locomotion on tied belts (fig. 20A).

The hip angle at the onset of the extension phase - just before touch-down - and the knee and ankle angles at the onset of the E_2 phase - at touch-down - should reflect the position of the toe at touch-down (fig. 20C, 20F). Trigonometric calculations show that an increase of 1° in the hip, knee and ankle joint angles will lead to a horizontal displacement of the toe with respect to the hip of -3 (caudal), +2 and -1 mm respectively. Thus the hip joint influences the position of the toe 1.5 times more, and in an opposite direction, than the knee joint. There is no unique combination of hip, knee and ankle angles for any given toe position. For instance a more caudal position of the 'slow' left limb has been achieved with an increase in the hip angle only (fig. 20A, 20C, 20F, right panels) and a more rostral position of the 'fast' right limb actually with an increase in both hip and knee angles (fig. 20A, 20C, 20F, left panels).

At lift-off. The position of the toe of the 'fast' limb at lift-off (l_{SW}) is not very different from the value expected from the speed during locomotion on tied belts (fig. 20A). More caudal positions are related to the longer durations, where T_{SU} is longer than in the tied belt situation (e.g. forelimbs on the 'slow' belt; fig. 20A, right panel). More rostral positions are related to the shortest cycle durations, where T_{SU} is approximately the same as during locomotion on tied belts (fig. 19A, 19B). The more rostral positions at lift-off are accompanied by more rostral positions at touch-down (e.g. forelimbs on the 'fast' belt; fig. 20A, left panel).

The adaptations of the 'slow' limb are more marked than in the 'fast' limb. An extreme example occurs when both forelimbs step on the 'fast' belt. The support phase becomes shorter than expected from the speed and the lift-off takes place in a more rostral toe position (fig. 20A). On the other hand, if both forelimbs step on the 'slow' belt, then T_{SU} of the 'slow' hindlimb will not be different from the value expected from the velocity in the tied belt situation. The toe lift-off is now in a more caudal position (fig 20A), but the position at touch-down is also more caudal.

The hip and knee joint angles just before lift-off, a_{Fhi} and a_{Fkn}, reflect the position of the toe at lift-off (l_{SW}). They tend to be larger when the toe lifts off in a more caudal position and vice versa (fig. 20A, 20B, 20D). Trigonometric calculations show that an increase of 1° of the joint angles of knee and ankle will lead not only to a horizontal displacement of -3, +1 and -1 mm respectively, but also to a vertical displacement of +3, -3 and +1 mm respectively. Thus mainly the hip and knee compensate each other to keep the vertical position of the toe constant. The horizontal position is mainly influenced by the hip angle.

The knee joint angle at the onset of the E_1 phase (a_{E_1kn}) seems to be mainly a function of T_{Fkn}. A long T_{Fkn} is related to a small a_{E_1kn} and a short T_{Fkn} to a large a_{E_1kn}, but not for the longer cycle durations (fig. 19D, 20E). In the latter situation the total level of activity seems to be reduced and the relations with speed seem to be less strict. Note for instance a_{E_1kn} of the 'fast' right hindlimb when both forelimbs step on the 'slow' belt (fig. 20E, right panel).

The knee joint angle at the onset of the E_3 phase does not show a clear relation with speed or T_{SU}. But the deviations from the values expected from the velocity of both the 'slow' and 'fast' limb are similar. It seems that the change of the overall stiffness of the limb extensors is the same with the homologous limbs. The joint angles of knee and ankle behave in a similar way and are not discussed separately.

In conclusion, during split belt locomotion with a 1:1 rhythm the duration of phases of the stride cycle, the limb positioning at touch-down and lift-off, and the joint angles can be adapted. Usually the duration of both the swing and support phase of the limbs on the 'slow' side are shortened and T_{SU} and T_{SW} of the limbs on the 'fast' side lengthened with regard to the velocity of the respective belts. The positioning of the 'fast' limb at lift-off and touch-down is not very different from the limb positioning during locomotion on tied belts. Conversely, the limbs on the 'slow' side have often a more caudal position at touch-down and a

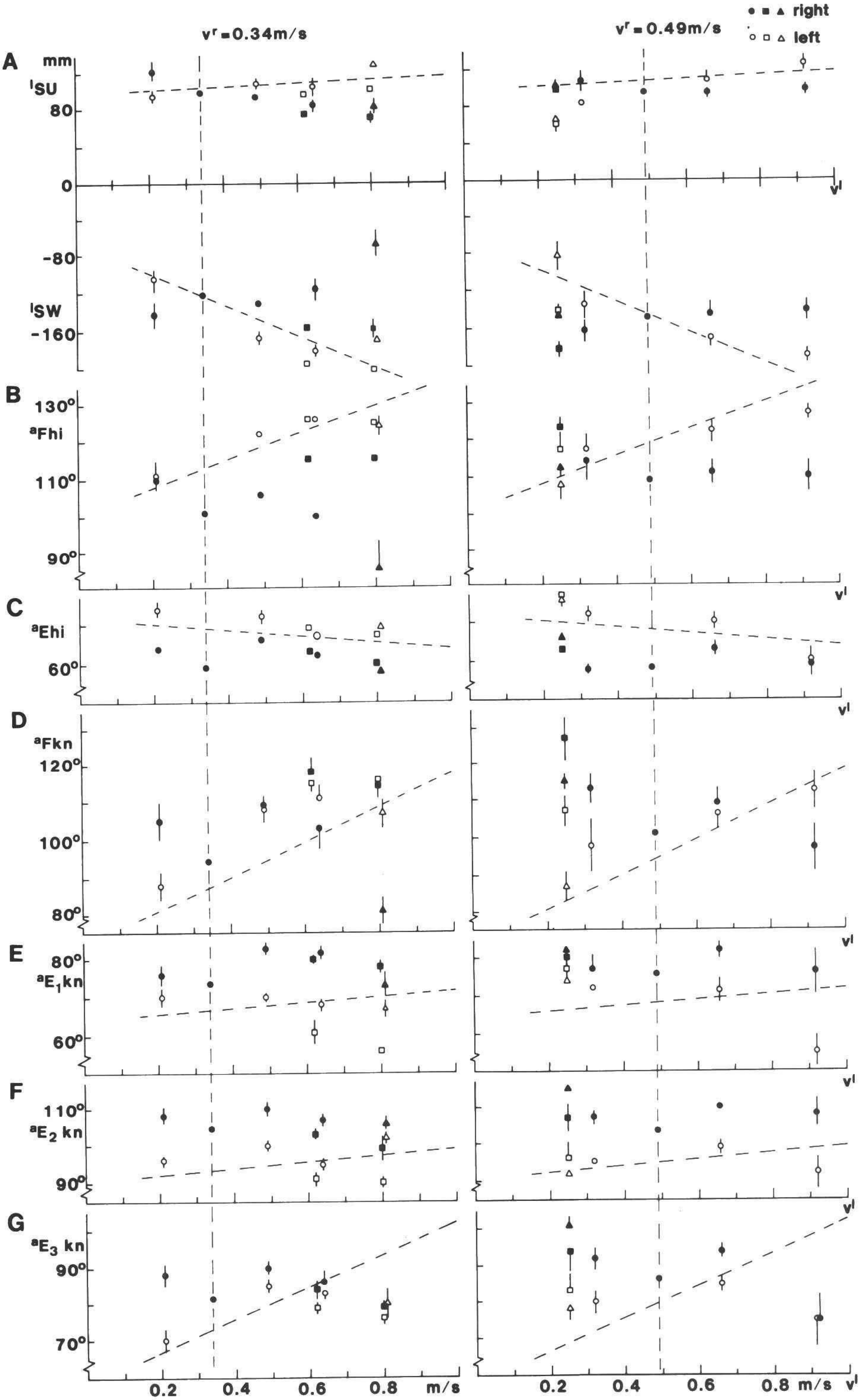

Fig. 20. Adjustments of the position of the toe (foot) and joint angles during split belt locomotion. The same experimental paradigm and the same symbols as in fig. 19 are used. In *A* the position of the toe of the hindlimb with respect to the hip

at touch-down (l_{SU}) and at lift-off (l_{SW}) are plotted for both limbs. In *B* and *C* the hip joint angles are plotted at the onset of the flexion (a_{Fhi}) and the extension phase (a_{Ehi}) respectively. The knee joint angle at the onset of the flexion (a_{Fkn}), the first extension (a_{E_1kn}), the second extension (a_{E_2kn}) and the third extension phase (a_{E_3kn}) are plotted in *D, E, F* and *G* respectively. The relations of these parameters with speed for this cat locomoting on tied belts are approximated with first order regression analysis. They are indicated with interrupted lines for the left limb and with a dot on the vertical lines for the right limb (fixed speed). Data are from cat SN, same experiment as in fig. 19.

more rostral position at lift-off, which results in a shorter support length than during locomotion on tied belts. Generally, the joint angles are adapted together with the foot position, although considerable deviations can be observed, during both the swing and the support phase. Thus no standard elements of the stride could be observed, neither in the amplitude of the limb movements nor in their timing (cf. however Orlovskii and Shik 1965, cf. Orlovskii et al. 1966).

Split belt locomotion with a 2:1 rhythm

If the speed difference between the belts increases, the differences between durations of corresponding phases of the stride become larger. At a certain point the 'fast' limb does not prolong its T_{SU} and T_{SW} any longer, but it takes an extra step. Usually this happens in both the forelimb and hindlimb (fig. 21). The point at which 2:1 stepping occurs turns out to be a function of the individual speeds of the two belts. Higher rhythms, like 3:1 and 4:1, were not observed in intact cats and in the mesencephalic preparation, but could be obtained in the chronic low spinal cat and during fictive locomotion (Forssberg et al. 1980b, Grillner and Zangger 1979, Kulagin and Shik 1970).

'Fast' limb. During locomotion with a 2:1 rhythm the two strides of the 'fast' limb are usually different. One stride of the 'fast' limb, partially occurring during the swing phase of the 'slow' limb, has a longer duration and is larger than the subsequent stride, as was also sometimes observed in the low spinal cat. A stride is defined from t_{SU} to the next t_{SU}, as the position of the limb at t_{SU} varies less than at t_{SW} (fig. 21; table 13).

The T_C, T_{SU} and T_{SW} of the large stride of the 'fast' limb are longer, although not always significantly longer, than expected from the belt velocity (table 13). In contrast, in the small stride of the 'fast' limb the T_C, T_{SW} and T_{SU} are shorter than expected from the belt speed. At the onset of the small stride of the 'fast' limb the hindlimb toe is placed in a more rostral position than expected from the belt speed. This occurs after the long T_{SW} of the large stride of the 'fast' limb. The toe is lifted much earlier during the short stride of the 'fast' limb, and L_{SU} is shorter than expected from the belt speed. Although T_{SW} of the small stride is short, the sway of the limb is small and the hindlimb toe is also placed more rostral than expected from the velocity, i.e. at the beginning of the large stride.

'Slow' limb. The stride duration of the 'slow' limb can be somewhat shorter or longer than expected from the belt speed, which is the result of small adaptations of T_{SU} as well as T_{SW} (table 13; cf. Kulagin and Shik 1970). Both the touch-down and the lift-off of the 'slow' limb occur more caudally than expected from the belt velocity. Sometimes this is also the case with split belt locomotion with a 1:1 rhythm (fig. 20A).

The unusually deep yield of the of the knee and ankle of the 'slow' limb (fig. 21), during the long contralateral swing phase, is accompanied with an extra St burst (knee flexor and hip extensor), which could also be observed during split belt locomotion with a 1:1 rhythm (fig. 18). This yield may result from the combined action of an increased load on the slow limb during the contralateral swing phase and the activation of the knee flexor. A second yield, without consistent St activity, can be observed in knee and ankle of the 'slow' limb during the next swing phase of the 'fast' limb. This is presumably at least partially due to the increased load on the 'slow' limb.

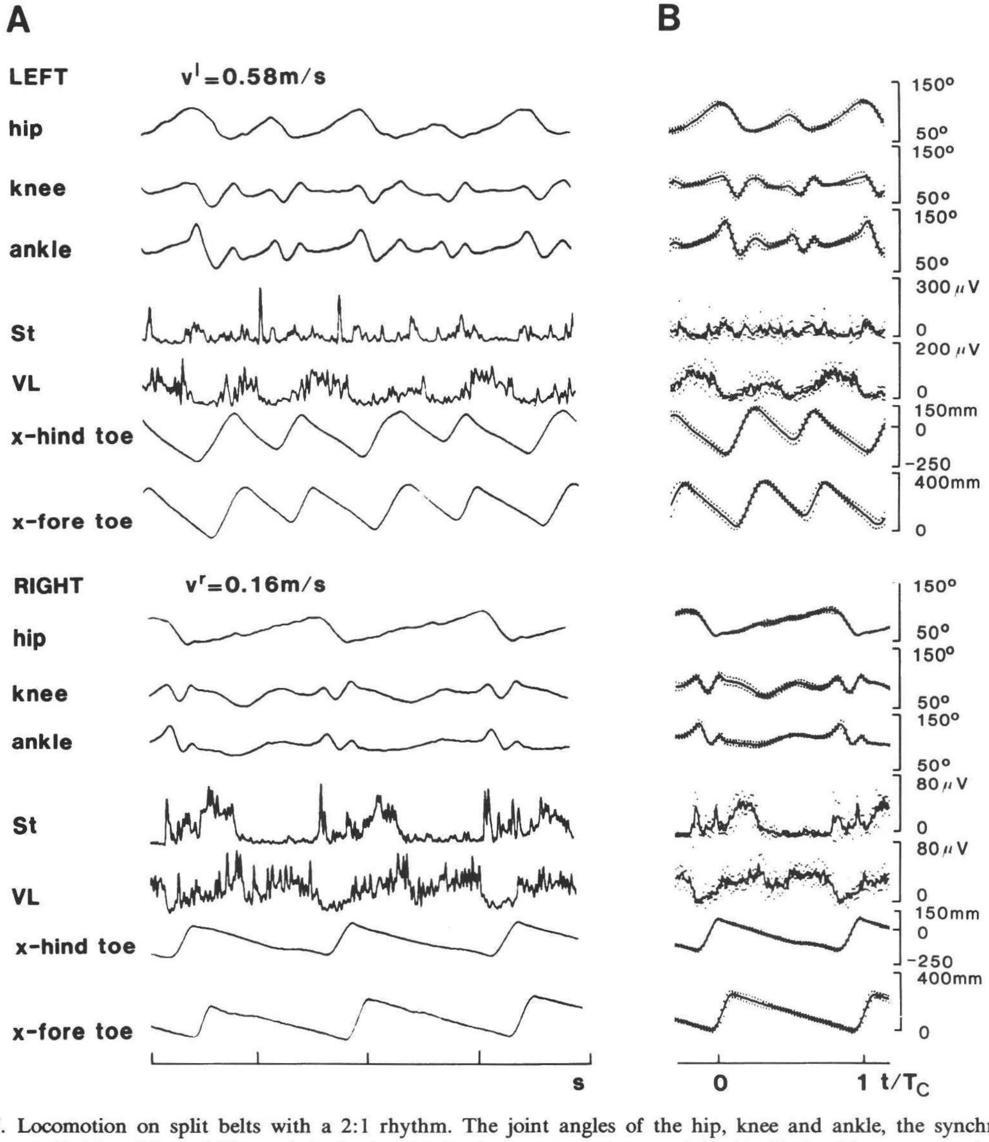

Fig. 21. Locomotion on split belts with a 2:1 rhythm. The joint angles of the hip, knee and ankle, the synchronously recorded RFEMGs of St and VL, and the horizontal displacements of the toe of the hindlimb with respect to the hip (x-hind toe) and that of the toe of the forelimb (x-fore toe) are shown for both sides. The belt of the left side was driven at 0.58 m/s (sd = 0.07 m/s) and that on the right at 0.16 m/s (sd = 0.01 m/s). Details as in fig. 18, but the average curves in *B* are calculated from 7 strides. Note the right St activity during the E_2 phase, which was not present during preceding sessions of locomotion on tied belts. Note also the slowing down of the left hindlimb in the last part of the third swing phase, which could be observed occasionally. Numerical data are presented in table 13. Data are from cat SN, same experiment as in fig. 18.

The amplitude of the VL activity (knee extensor) of the 'fast' limb is often smaller during the short stride, which coincides with the contralateral support, than during the long stride during the contralateral swing phase. Conversely, the VL activity of the 'slow' limb is reduced during a part of the short support phase of the 'fast' limb. The reduction in EMG activity could be due to a reciprocal interaction of the CPGs, but also to feedback signals related to the different loads these muscles are exposed to, when one or both hindlimbs provide support. Similar effects were observed in the low spinal cat (Forssberg et al. 1980b).

			fast		slow	fast		slow
			short	long		short	long	
v	(m/s)		0.41	0.41	0.16	0.58	0.58	0.16
T_C	(ms)	mean	591	995	1629	603	854	1450
		sd	69	39	25	36	57	41
		n	4	3	4	6	7	6
$T_C(v)$	(ms)		860	860	1542	701	701	1542
T_{SW}	(ms)	mean	194	363	293	211	317	224
		sd	16	38	45	19	35	11
		n	4	3	4	6	7	6
$T_{SW}(v)$	(ms)		270	270*	278*	249	249	278
$T_{SW}(T_C)$	(ms)		236	287*	282*	237	269	271
T_{SU}	(ms)	mean	397	655	1335	393	537	1226
		sd	78	49	56	37	37	45
		n	4	4	4	7	7	6
$T_{SU}(v)$	(ms)		590	590*	1261*	449	449	1261*
$T_{SU}(T_C)$	(ms)		352*	711*	1343*	362*	585	1176
l_{SU}	(mm)	mean	119	117	81	141	115	85
		sd	10	10	16	5	7	5
		n	4	4	5	7	7	7
$l_{SU}(v)$	(mm)		91	91	99*	88	88	99
l_{SW}	(mm)	mean	-41	-136	-139	-75	-158	-124
		sd	21	25	12	29	10	11
		n	4	4	4	7	7	6
$l_{SW}(v)$	(mm)		-134	-134*	-90	-161	-161*	-90
L_{SU}	(mm)	mean	160	253	218	215	272	208
		sd	12	30	9	31	10	11
		n	4	4	4	7	7	6
$L_{SU}(v)$	(mm)		226	226*	189	249	249	189

Table 13. Two examples of regular split belt locomotion with a 2:1 rhythm. Data of the short and long stride of the 'fast' limb and of the 'slow' limb of the two velocity combinations are given in the successive columns. With the 'slow' belt set to a speed of 0.16 m/s, 2:1 stepping could be obtained within a range of the 'fast' belt speed from 0.32 to 0.85 m/s. A stride is defined from the onset of the support phase to the subsequent one. Mean measured values are given with their standard deviation (sd) and the number of observations (n). Also values are given calculated from the estimated relations with the velocity (v) and cycle duration (T_C) during locomotion with tied belts. The speeds are expressed in m/s, the durations of the phases in ms and the position of the toe with respect to the hip in mm. An asterisk indicates that the calculated value is equal to the measured one (level of significance = 0.05). It is assumed that the variance of the calculated value is negligible with respect to the variance of the measured value. Note that the values of the measured L_{SU} of the 'fast' limb deviate from the calculation $L_{SU} = v \times T_{SU}$. This is mainly due to insignificant velocity variations of the belt during the long and short strides. Data are from cat SN.

In conclusion, during split belt locomotion with a 2:1 rhythm the two strides of the limbs stepping on the 'fast' belt are asymmetric with respect to limb positioning, time course of different phases and electromyographic activity. The longer stride of the 'fast' limb coincides with the swing phase of the 'slow' limb and the shorter stride of the 'fast' limb with the support phase of the 'slow' limb, which optimizes the support of the animal. Thus the movements of the limbs are influenced by the contralateral limb in a characteristic way.

6. Interlimb coordination

Von Holst (1934, 1935, 1939) demonstrated that the coordination between different fins during fish locomotion could be very strict or exhibit large variations. In the latter case one fin could move with twice or thrice the fin frequency of another fin. Von Holst suggested that this coordination somehow resulted from an interaction between independent neuronal centres (central pattern generators) controlling each fin. Subsequent experiments suggested that the coordination of the limbs in mammals might follow the same principle (von Holst 1938, 1939). Interneurones, which may be responsible for the coordination between the CPGs have been identified in two invertebrate motor systems, one controlling walking in the cockroach and the other the swimmeret system of the crayfish (Pearson and Iles 1973, Stein 1971,1974, 1976). These interneurones are active during a segmental motor burst and provide the next ganglion with an efference copy, which is presumably used to produce intersegmental coordination. In cats a part of the ascending neuronal activity to the cerebellum provides efference copy signals (Arshavskii et al. 1972a, 1972b). Such signals could also be utilized to coordinate the CPGs (Grillner 1981). The spinal cord itself can coordinate the hindlimbs in an alternating mode, such as walk and trot, and a non-alternating mode, such as gallop, and it can also coordinate the forelimbs with the hindlimbs (Forssberg et al. 1980b, Grillner and Zangger 1979, Miller and van der Meché 1976).

Coordination between limbs at the same girdle

The movements of the homologous pairs of limbs are shifted half a cycle in alternating gaits (Arshavskii et al. 1965). Miller and co-workers stressed the strict nature of this type of coordination in the forelimbs and in the hindlimbs (Miller et al. 1975b, Halbertsma et al. 1976), whereas English (1979) emphasized the variability. However, he pooled data from alternating gaits, non-alternating gaits and transitions between them which increases the variability (English 1979, English and Lennard 1982). In the non-alternating gaits the homologous limbs move in a more synchronous fashion (Miller et al. 1975b, Norgren et al. 1977, Eisenstein et al. 1977).

Treadmill locomotion. Not all homologous events of the stride of the left and right limbs are shifted half a cycle, i.e. have a 180° phase interval (fig. 22, left panels). This must be expected, since corresponding phases of the left and right limbs may have different durations (see page 27). The variability off all intervals is higher at low velocities of locomotion ($v<0.4$ m/s) and all corresponding events of the stride of the left and right limbs have phase shifts different to 180° at the lowest speeds.

Split belt locomotion with a 1:1 rhythm. During split belt locomotion the cat has to adapt the different phases of the stride cycle in order to step in the same rhythm with all limbs (see page 48). Hence, not all events of the stride can have a phase interval of 180° (fig. 22, middle and right panels).

The onset of the support phases of forelimbs and hindlimbs are in most cases closer to a 180° phase interval than the onset of the swing phases (fig. 22A, 22B, middle and right panels). Usually, when measuring from the 'fast' to the 'slow' limb, the phase interval for t_{SU} is smaller than 180° and the phase interval for t_{SW} is larger than 180° (e.g. fig. 22B, middle panel). Hence it appears that there exists a point with a phase interval of 180° between the two sides in both the swing and support phase. This point in the swing phase is rather well approximated with the midpoint of the knee E_1 phases for one cat (SN, fig. 22C) and with the onset of the support phases for another cat (SI). In most cases the midpoint of the E_1kn phase or the onset of the support phase is closer to a phase interval of 180° than are other events in the swing phase, including the onset and midpoint of the ankle E_1 phase. Similar observations were made for low spinal cats (Forssberg et al. 1980b). The midpoints of the ankle E_2 phases come close to a phase interval of 180° in the support phase, but not as close as the above phase intervals in the swing phase. In some cases a phase interval of all events of the stride smaller or larger than 180° was observed during split belt locomotion (fig. 22, middle panels). This effect is not dominated by the left or right limb, but it depends on whether the

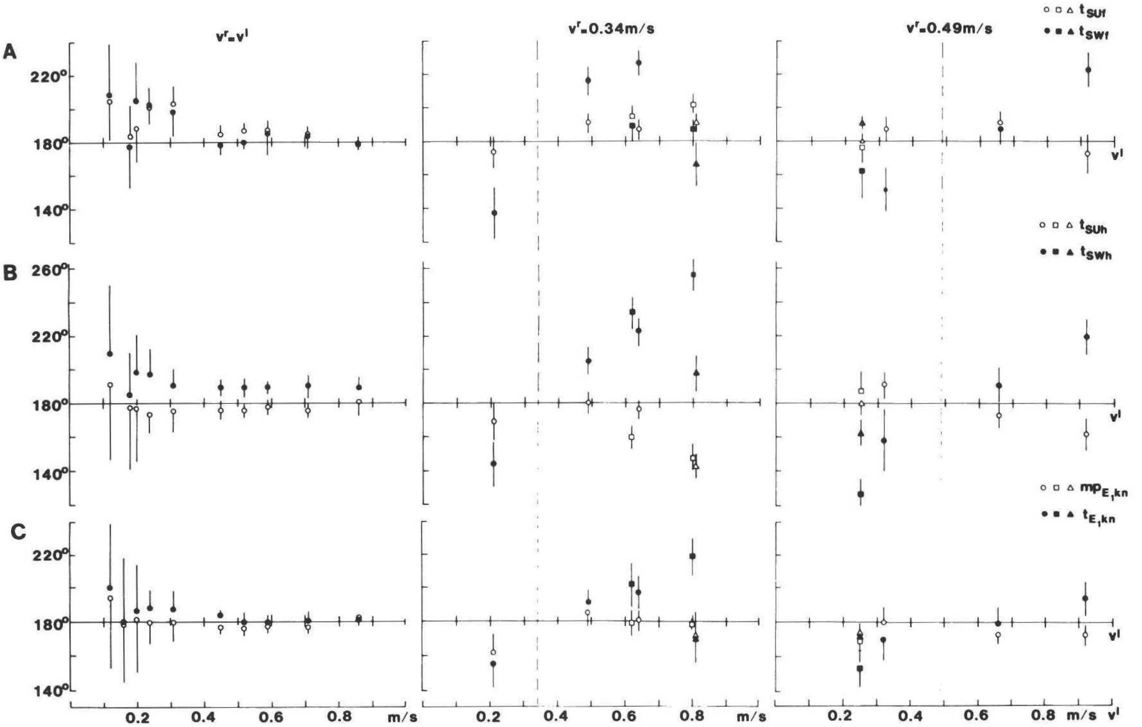

Fig. 22. Coordination between the homologous limbs when the belts are tied (left panels) and during split belt locomotion (middle and right panels). The right motor driven belt was kept at a constant velocity (v^r, indicated at the top of the panels) and the speed of the left belt (v^l) varies as indicated along the abscissa in each graph. The relative shifts, expressed in degrees ($360° \times \text{interval} / T_C$), are calculated from the left to the right corresponding event. For the middle and right panels the circles, triangles and squares correspond to the forelimbs on different belts, both on the 'fast' belt, and both on the 'slow' belt respectively. (The hindlimbs are always on different belts.) *A* Shifts between t_{SUf} (open symbols) and T_{SWf} (closed symbols). *B* Shifts between t_{SUh} (open symbols) and between t_{SWh} (closed symbols). *C* Shifts between mp_{E_1kn} (open symbols) and between t_{E_1kn} (closed symbols). The standard deviation is indicated with a bar when it exceeds the symbol ($n = 3 - 16$). Data are from cat SN.

limb is on the 'fast' or on the 'slow' belt. The effect disappears with decreasing cycle durations.

Split belt locomotion with a 2:1 rhythm. The four limbs are coordinated in a characteristic way when the limb on the 'fast' belt steps twice, but the limb on the 'slow' side only once (fig. 21). In the 'slow' limb the onset of the hindlimb support phase lies approximately in the midway between the corresponding events on the 'fast' side. This is also true for the midpoint of the knee E_1 phase (table 14A). In the 'fast' limb the onsets of the hindlimb support phases and the midpoints of the knee E_1 phases of the two strides are not positioned equally in between the corresponding events of the 'slow' limb. Nevertheless the midpoints of these events of the two strides on the 'fast' side occur approximately midway between the corresponding events on the 'slow' side (table 14B). The forelimbs behave similarly (table 14).

In conclusion, a fixed interval between certain events or phases of the right and left limb can be discarded as a possible mechanism for coordination during alternating locomotion, since the durations of all phases decrease with speed. A tendency for a concurrence of one phase on one side with a different phase of the other side might appear as a possible mechanism but this was not observed during split belt locomotion with a 1:1 or 2:1 rhythm. An event in the stride close to the midpoint of the E_1 phase of the knee and the onset of the support phase is always shifted approximately half a cycle with respect to the corresponding event on the contralateral side during split belt locomotion with a 1:1 rhythm. This event of the stride

			v^l	v^r	t_{SUf}			t_{SUh}			mp_{E_1kn}		
			(m/s)	(m/s)	mean	sd	n	mean	sd	n	mean	sd	n
A	from fast to slow stride	$360^\circ \times T_0 / T_A$	.41	.16	177*	21	4	162	10	4	169*	9	3
	from fast to slow stride	$360^\circ \times T_0 / T_A$	.58	.16	202	10	7	176*	14	7	188*	13	5
B	from slow to first fast stride	$360^\circ \times T_1 / T_B$	.41	.16	102	7	4	121	8	4	116	9	3
	from first to second fast stride	$360^\circ \times T_2 / T_B$	.41	.16	143	9	4	131	17	4	146	15	3
	from second fast to slow stride	$360^\circ \times T_3 / T_B$	.41	.16	114	10	4	108	12	4	100	6	3
	midpoint of the two fast strides	$360^\circ \times T_4 / T_B$	.41	.16	174*	8	4	186*	5	4	187	2	3
C	from slow to first fast stride	$360^\circ \times T_1 / T_B$	.58	.16	89	6	6	105	7	6	98	5	4
	from first to second fast stride	$360^\circ \times T_2 / T_B$	.58	.16	156	12	6	150	13	6	150	12	4
	from second fast to slow stride	$360^\circ \times T_3 / T_B$	.58	.16	114	7	6	105	9	6	111	7	4
	midpoint of the two fast strides	$360^\circ \times T_4 / T_B$	.58	.16	167	2	6	180*	5	6	174	1	4

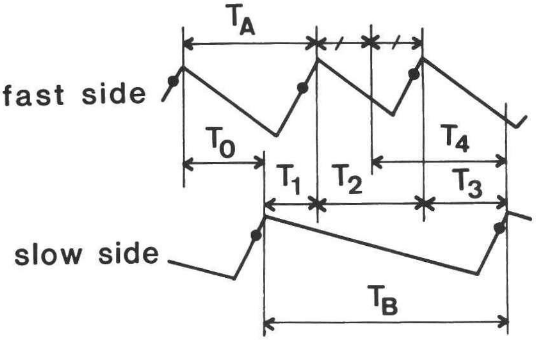

Table 14. Relative shifts between corresponding events of the strides of the homologous limbs during split belt locomotion with a 2:1 rhythm. The results are expressed as phase intervals and are given in degrees for the onset of the forelimb support phases (t_{SUf}, first column), for the onset of the hindlimb support phases (t_{SUh}, second column) and for the midpoint of the first extension phases of the knee (mp_{E_1kn}, third column) (sd is the standard deviation and n the number of observations). The inset illustrates the different intervals for the onset of support phases. The midpoints of the first extension phases of the knee are indicated with dots. *A* The position of events of the stride on the 'slow' side (slow stride) in between events on the 'fast' side (fast stride) for two velocity combinations. A cycle is defined from successive events on the 'fast' side (T_A). *B* The position of events of the two strides on the 'fast' side in between events on the 'slow' side. A cycle is defined from successive events on the 'slow' side (T_B). An asterisk indicates that the mean phase interval is not different from 180° (level of significance = 0.05). Data are from cat SN.

of the 'slow' limb is also positioned symmetrically in between the corresponding events of the 'fast' limb during split belt locomotion with a 2:1 rhythm. A 'reciprocal inhibition' between the neurons generating corresponding events or phases on the two sides could thus explain the coordination in alternating gaits. A switch to non-alternating gaits could be achieved by switching from a pathway generating reciprocal inhibition between the networks to one that mediates excitation (Forssberg et al. 1980b, Grillner 1981).

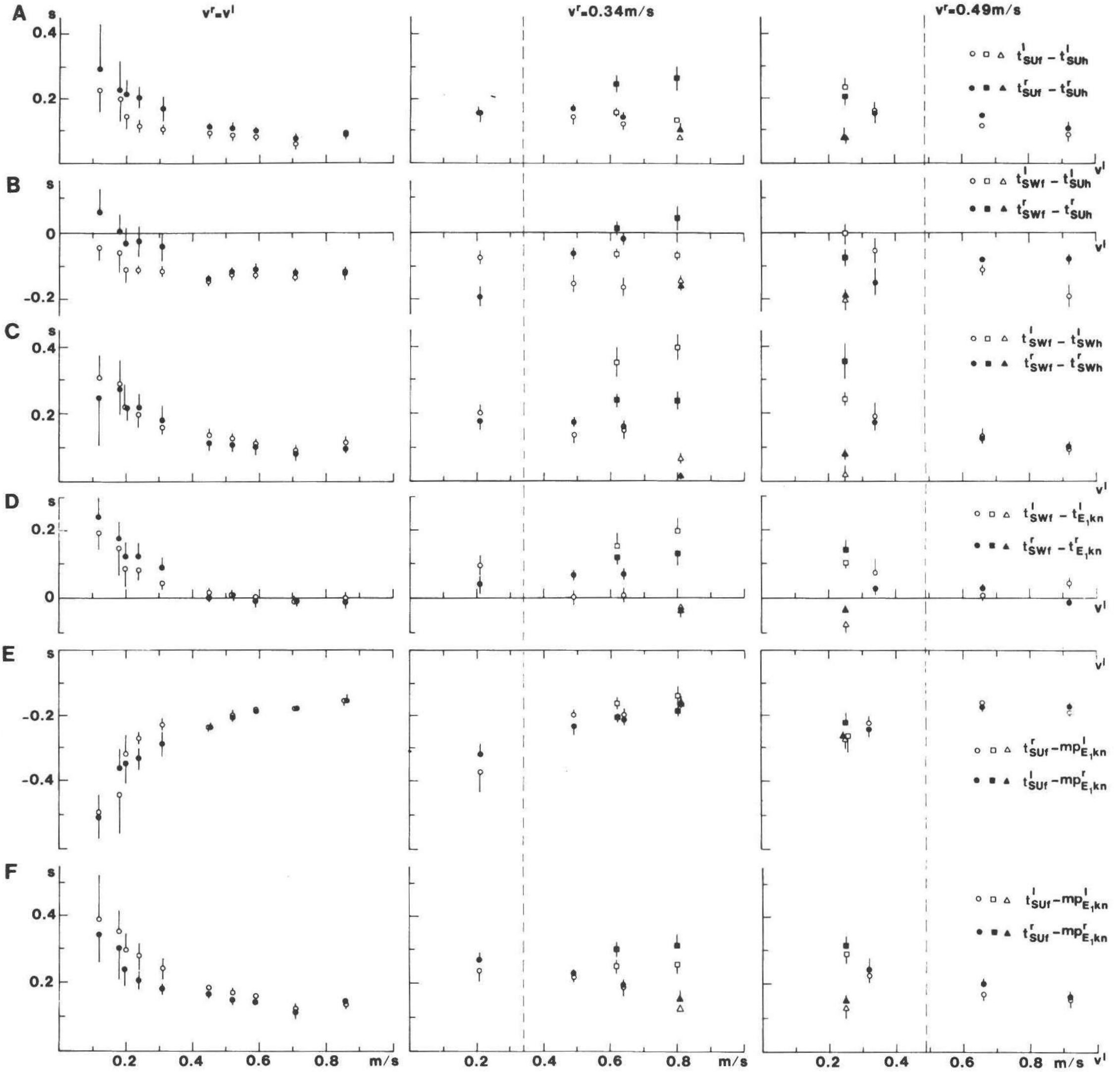

Fig. 23. Coordination between forelimbs and hindlimbs when the belts are tied (left panels) and during split belt locomotion (middle and right panels). The experimental set up is the same as in fig. 22. Tn *A* to *D* and *F* the intervals on the left (open symbols) and the right side (closed symbols) are represented. Same symbols used as in fig. 22. In *E* the crossed intervals from the left to the right (open symbols) and from the right to the left (closed symbols) are represented. The mean and standard deviation are indicated (n = 3 - 16). Data are from cat SN.

Coordination between the forelimbs and hindlimbs

It has been reported that the values of intervals between certain events of the strides of the forelimbs and of the hindlimbs are restricted to a narrow range for all speeds of alternating locomotion (Arshavskii et al. 1965, Miller and van der Burg 1973). Later it was noted that the interlimb intervals can be divided into two groups of nearly constant intervals, one group related to lower velocities of alternating locomotion and the other group related to higher velocities (Coss et al. 1978, Halbertsma et al. 1976, Miller et al. 1975a). However, the interlimb intervals are dependent on environmental conditions and training procedures, which

				'fast' left limb						'slow' right limb		
				short stride			long stride					
	interval	v^l (m/s)	v^r (m/s)	mean (ms)	sd (ms)	n	mean (ms)	sd (ms)	n	mean (ms)	sd (ms)	n
A	$t_{SUf}-t_{SUh}$	.41	.16	91*	40	4	144*	24	4	171	42	3
		.57	.16	79	21	7	105	14	6	141	13	6
	$t_{SWf}-t_{SUh}$	.41	.16	-202	63	4	-34	25	4	-72	14	4
		.57	.16	-206	33	6	-106	11	6	-60	32	6
	$t_{SWf}-t_{SWh}$	.41	.16	162*	34	4	152*	41	3	209	50	3
		.57	.16	104*	15	7	111*	9	7	164	32	7
	$t_{SWf}-t_{E_1kn}$	.41	.16	110	36	4	15	49	4	77	22	4
		.57	.16	39	15	7	-18	8	6	63	29	5
	$t_{SWf}-mp_{E_1kn}$	.41	.16	208*	27	4	200*	34	4	262	38	4
		.57	.16	173*	16	6	164*	20	7	199	15	5
B	$t^r_{SUf}-mp^l_{E_1kn}$	.41	.16	718°	38	4	-256°	25	4			
		.57	.16	623	47	6	-202	29	7			
	$t^l_{SUf}-mp^r_{E_1kn}$	.41	.16	717°	52	4	-244°	7	3			
		.57	.16	562	35	5	-261	43	5			

Table 15. Intervals between forelimbs and hindlimbs during split belt locomotion with a 2:1 rhythm. *A* Homolateral intervals of the short 'fast' strides (first column), of the long 'fast' strides (second column) and of the 'slow' strides (third column) for two velocity combinations. *B* Crossed interlimb intervals from the mp_{E_1kn} of the short stride (first column) and of the long stride (second column) of the 'fast' left hindlimb to t_{SUf} of the 'slow' right forelimb ($t^r_{SUF}-mp^l_{E_1kn}$) and intervals from the mp_{E_1kn} of the 'slow' right hindlimb to t_{SU} of the short stride (first column) and of the long stride (second column) of the 'fast' left forelimb ($t^l_{SUf}-mp^r_{E_1kn}$). An asterisk indicates that the means of the homolateral intervals of the short and long stride of the 'fast' limb equal each other (for *A*) and a ° sign indicates that the mean of the crossed interval from the left to right equals the one from right to left (for *B*, level of significance = 0.05). Data are from cat SN.

seem to favour certain types of gaits (Lockhard et al. 1976, Wetzel et al. 1975). Halbertsma (1976) did not observe a tendency for any constant interlimb interval between the movements of the forelimbs and hindlimbs during treadmill locomotion.

Treadmill locomotion. Usually the values of interlimb intervals change with the speed of locomotion (fig. 23, left panels), most steeply at the lowest velocities ($v<0.4$ m/s), and there is no tendency to assume certain values. The timing within a limb is determined by the stride duration and thus by the speed of locomotion. Consequently all interlimb intervals can be expressed as another interlimb interval plus an interjoint interval and/or a combination of linear relations with T_C (see page 28, Halbertsma 1976). For instance

$$t_{SWf}-t_{SUf}=t_{SWf}-(t_{SWh}+T_{SWh})=t_{SWf}-t_{SWh}-(1-c)T_C-e=t_{SWf}-t_{SWh}-a(1-c)/v^b-e$$

(see page 24, fig. 23B, 23C). Thus if distinct clusters of the values of one interlimb interval between movements of the limbs are not observable, they cannot be observed for another interlimb interval, since there are no discontinuities in the interjoint intervals and the relations of T_C with the speed of locomotion (fig. 5, 9). The same applies for the diagonal (crossed) intervals during alternating locomotion, which equal the corresponding homolateral interval plus the duration of half a cycle.

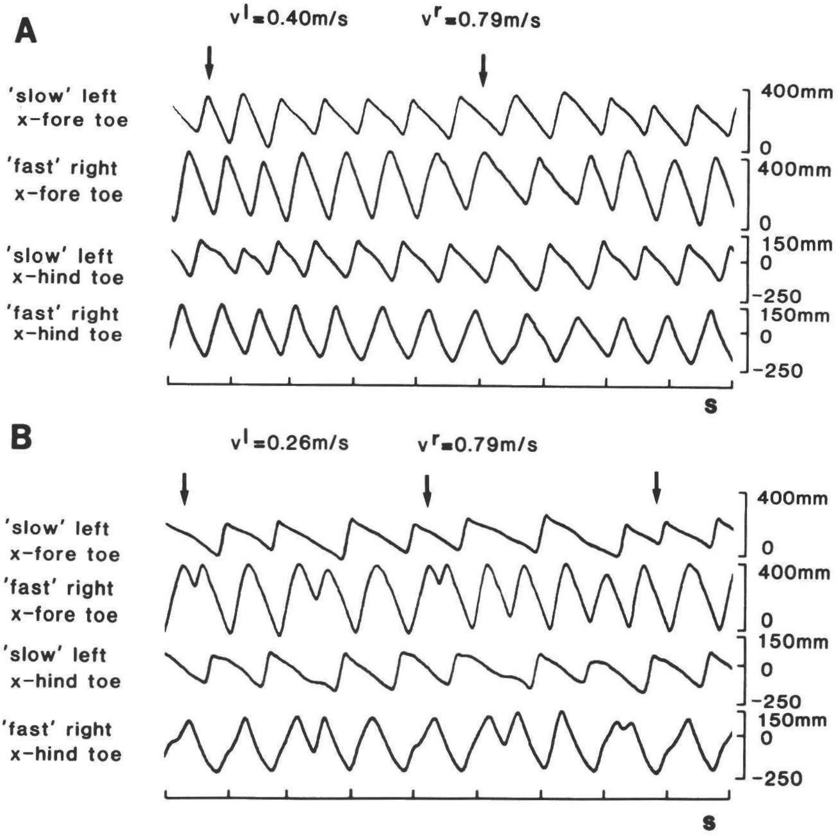

Fig. 24. Coordination between the limbs during split belt locomotion with transition effects. The horizontal displacements of the toes of the forelimbs (x-toe fore) and the toes of the hindlimbs with respect to their hip positions (x-hind toe) are plotted. The most caudal positions of the forelimbs are used as zero references for these limbs. Downward deflection corresponds with the support phase. *A* Split belt locomotion where the 'slow' left forelimb takes two steps on the 'fast' right belt (first arrow) and where the 'fast' right forelimb takes two steps on the 'slow' belt (second arrow). *B* Irregular split belt locomotion where the 'fast' limbs occasionally take an extra step (see text). Data are from cat SN.

Split belt locomotion. During split belt locomotion the durations of phases of the stride on the 'slow' and 'fast' side differ considerably (fig. 19). Consequently homolateral interlimb intervals on the 'slow' and 'fast' sides will usually not be equal (fig. 23A-D, middle and right panels). The only homolateral interlimb intervals which will be equal on the two sides for all cycle durations are intervals between an event in the forelimb which is 180° out of phase with the other forelimb, and an event in the hindlimb which is likewise 180° out of phase with the other hindlimb. The same applies for the crossed interlimb intervals. The events which do have a homologous phase interval of approximately 180° are the midpoints of the knee E_1 phase for the hindlimbs and the onsets of the support phase for the forelimbs (cat SN; fig. 22C, 23E, 23F). Thus the interlimb intervals between t_{SUf} and mp_{E_1kn} are approximately equal on the two sides for both homolateral and crossed limbs. Small differences may be due to asymmetries of the limbs.

During split belt locomotion with a 2:1 rhythm the limbs on the 'fast' side take a long and a short stride for every stride on the 'slow' side (fig. 21). This allows comparison between interlimb intervals on the same side under different conditions. The homolateral interlimb interval between mp_{E_1kn} and T_{SUf} of the short 'fast' strides equals the interval of the long 'fast' stride. This is not the case for most other homolateral intervals (table 15A). The crossed intervals do not always have equal durations in this case, but this may be because intervals between different pairs of limbs are being compared (table 15B).

Transition effects. The split belt coordination discussed above was studied under steady state conditions. Transition effects are also important. In figure 24A the 'slow' left forelimb takes two steps on the 'fast' belt (first arrow) and, a few strides later, the 'fast' right forelimb take two steps on the 'slow' belt (second arrow; see Appendix, table VII for numerical data).

The support phase duration of the 'slow' left forelimb is suddenly shortened when it steps on the 'fast' belt (fig. 24A, first arrow) and the swing phase duration is prolonged. The other three limbs reduce the durations of both their swing and support phases. This reduction is very marked in the 'slow' left hindlimb.

The reverse effects can be observed when the 'fast' right forelimb steps on the 'slow' belt (fig. 24A, second arrow). The right forelimb reduces its swing phase for a partial compensation of the prolongation of its support phase. The 'slow' left forelimb prolongs its support phase and the succeeding swing phase to maintain the coordination with the right forelimb. Adaptations in the movements of the 'slow' left forelimb can be observed 153 ms after the right forelimb steps on the 'slow' belt; at that moment the 'slow' left forelimb prolongs its support phase instead of lifting (Appendix, table VII). Both hindlimbs prolong their support phases gradually, the right hindlimb even when the right forelimb is stepping back on the 'fast' belt. The swing phase of the 'slow' left hindlimb is also prolonged gradually, even after the right forelimb has stepped back on the 'fast' belt. The swing phase duration of the 'fast' right hindlimb remains approximately constant, although T_{Fkn} and T_{Fan} are prolonged, and T_{E_1kn} and T_{E_1an} are shortened within the first stride after the 'fast' right forelimb steps on the 'slow' belt.

Complicated coordination patterns of the four limbs are illustrated in fig. 24B. The 'fast' right forelimb and hindlimb occasionally take an extra stride (2:1 rhythm). Sometimes the 'fast' forelimb takes two strides, when the 'fast' hindlimb steps only once (fig. 24B, first and second arrow). A strong homolateral interaction is observable when the 'slow' left forelimb is lifted earlier, to restore the appropriate coordination with the 'slow' left hindlimb, and the forelimbs switch from a 2:1 coordination pattern to a 1:1 pattern (fig. 24B, third arrow).

In conclusion, a fixed homolateral or crossed interlimb interval between the forelimbs and hindlimbs could not be observed, nor a switch at a certain speed from one interval to another. The homolateral interlimb intervals between events just before or at touch-down (t_{SU} and mp_{E_1kn}) are speed dependent during locomotion with tied belts. However, they are rather similar on the two sides during split belt locomotion, although the limbs on the two sides step with different speeds. It appears that the interlimb coordination is organized so that the timing of the phases just before or at touch-down is controlled. This coordination is achieved by adaptations of the durations of all phases of the stride or, in extreme situations, by taking an extra stride. The adaptation in the homologous limbs is quicker than in the homolateral limbs, where the adaptation seems to be gradual and not completed within one stride.

GENERAL DISCUSSION

Locomotion of intact cats has been studied by means of automatic recordings of limb movements, ground reaction forces and electromyograms (see methods). The data have been processed and analysed interactively with a computer which allows an analysis of many strides in a fast and accurate way and allows the data to be treated statistically. The analysis has been focused on the timing and amplitudes of stride cycle phases, limb movements and electromyograms as a function of the velocity of locomotion. This gives a more complete view than studies in which only one of these parameters was investigated, which are sometimes hard to interpret (e.g. electromyograms, see page 31). The present phenomenological approach gives a general description of the locomotor pattern. As such it is a necessary supplement to the neurophysiological and anatomical description of the neuronal networks.

The analysis has mainly been limited to treadmill locomotion under a variety of steady-state conditions, since the speed adaptations are less obscured in this way, and the sensory information from auditory, vestibular and visual systems remains approximately constant. However, in more natural surroundings the locomotor pattern is constantly adapted to the terrain and goals of the animal and the visual information is basically different (see page 20).

Accurate coordination between the limbs and between the joints within a limb are essential in locomotion. Appropriate coordination will ensure the dynamic stability of head and trunk, will prevent stepping of limbs on one another, will allow a smooth contact against ground for each limb, and will reduce oscillatory movements of head and trunk, thus decreasing the energy needed for locomotion.

Coordination between limbs

The movements of a limb must be adapted not only to the velocity of locomotion (see results, section 1), but also to the other limbs (see page 51 and 62). Both the duration of each phase of the stride and the amplitude of the joint and limb movements can be modified. No element of the stride cycle is constant (see page 53).

After a disturbance of the movements of one limb, the restoration of the appropriate coordination seems to be faster between homologous limbs than between other pairs (see page 62). A systematic analysis of the interaction between limbs could be performed in cats locomoting on a treadmill with four different belts where sudden speed changes of one of the limbs could be induced, and in curarized preparations during fictive locomotion where forced movements of different limbs can influence the efferent burst pattern.

The coordination between forelimbs and hindlimbs is not very strict. No clustering of intervals around certain values could be observed in relation to the velocity of locomotion or the stride duration (see page 60). However, the intervals between events at or just preceding the onset of the support phase change less than other intervals with speed of locomotion and during split belt locomotion (see page 61).

A mutual inhibition† occurring around the onset of support phases between the two sides during alternating locomotion could explain the observation that events at or just preceding the onset of support phases remain shifted approximately half a cycle in respect to the corresponding contralateral events (cf. Williams 1980). This also holds during split belt locomotion with a 1:1 rhythm (see page 57). During locomotion with a 2:1 or higher rhythm, this mutual inhibition could explain the observation that the ‘fast’ limb always steps with a multiple of strides of the ‘slow’ limb (see fig. 21 and page 57, Forssberg et al. 1980b, Kulagin and Shik 1970). The long and short strides of the ‘fast’ limb during split belt locomotion with a 2:1 rhythm (see fig. 21) could be explained by a decreasing tendency for the ‘slow’ side to counteract the onset of the

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† Inhibition is used in a general sense which could be a removal of excitation as well as an active inhibition. The converse applies for excitation.

swing phase in the 'fast' limb (e.g. if the tendency were proportional to hip extension of the 'slow' limb), combined with an increasing tendency of the 'fast' limb to start its swing phase (e.g. if the tendency were proportional to the hip extension of the 'fast' limb).

Coordination within a limb

The basic coordination between the joint movements within a limb during overground and treadmill locomotion is not different from that during split belt locomotion with a 1:1 or a 2:1 rhythm. The order of onset of flexion and extension phases remains unchanged, although the duration of phases can differ considerably (see page 46).

The durations of all phases of the stride cycle decrease with increasing velocity of locomotion. The durations of support and extension phases change proportionally more than those of swing and flexion phases. All durations of phases appear to be linearly related with the stride duration. This is a common feature throughout the animal kingdom, including man (Grillner et al. 1979). In more primitive animals than mammals the relationships often intersect the origin, but not in cat and man (see page 24 and 25, Grillner 1974, Williams 1977). These common features suggest similarities in the neuronal networks generating the phases of the stride in many species of animals including man.

The hypothesis that every joint is controlled by a flexion and an extension unit pattern generator (Grillner 1981, see page 9) is further supported by the observations **1** that the relations of the flexion duration with the stride cycle duration for scapula and elbow in the forelimb, and for hip, knee and ankle in the hindlimb are different from each other (see page 27) and **2** that after a disturbance of the movements of the homolateral forelimb the duration of knee and ankle flexion can increase and the first extension phase of knee and ankle can decrease, whereas they usually increase or decrease together (see page 62).

The more the swing phase coincides with the last part of the contralateral support phase and/or the beginning of the contralateral swing phase, the more it shortens. This happens with increasing speed (see fig. 5) or during split belt locomotion ('slow' limb, see fig. 19C). The apparent linear relation of the swing phase duration with the stride cycle is thus not necessarily an exclusive property of the generators that produce the swing phase; it could also be the result of mechanisms coordinating the limbs. This could be further studied with combinations of forced movements of limbs in preparations during fictive locomotion.

The support phase duration decreases markedly with increasing velocity of locomotion. If the limb is always put down and lifted up at identical positions, the hip angle at touch-down and lift-off should be approximately constant (see page 51). However, the hip angle at lift-off increases considerably in the low velocity range ($v<1$ m/s, cf. fig. 15A). Afferents in and around the hip joint can induce flexion (swing phase) at a well extended hip joint angle (see page 39). Suppose that the initiation of the swing phase occurs when an excitation, which is dependent on the hip position (excitation = EX), becomes greater than a linear decreasing time dependent inhibition, possibly influenced by the contralateral limb (inhibition = IN $=a-bt$, a and b are constants, t is time with $t=0$ at the onset of hip extension; cf. Grillner 1981). The excitation from the hip position could be proportionally related to the hip joint angle above a certain value (Grillner and Rossignol 1978). The hip joint angle increases approximately linearly during extension with a rate dependent on the velocity of locomotion (v). This excitation could thus be described by $EX=cvt-d$ (c and d are constants). If the swing phase is initiated when $EX=IN$, the support phases duration will be given by the value of t for which this is true, $T_{SU}=(a+d)/(cv+b)$. This is a hyperbolic relation with the speed v (cf. relation (5), page 25), and hence with this simple model the observations during treadmill locomotion can be reasonably described (see fig. 5). However, the effects from the homolateral limbs (see page 51) and the possible effects from loading the extensors (Duysens and Pearson 1980) are not included (see page 39).

Joint angles and positioning of the limb

The excursions of the joint angles during the phases of the stride cycle are better controlled than the joint angles themselves at the onset and termination of these phases. The physiological basis of this control is unknown, but both central mechanisms and peripheral information could be utilized (see page 39). Possibly there exist different control systems for posture and locomotion. The posture control system could regulate the average joint angles and the locomotor system could superimpose excursions of joint movements, which will produce locomotion.

The positioning of the limb during placement on ground is the most important event in the stride cycle: The foot should not be placed in holes or on unstable surfaces. Consider for instance the time constraints and the precision needed in a fast gallop in uneven terrain. Therefore,it is not surprising that there is a correlation between the joint movements which results in a position control of the foot during its placement on ground (see page 42). The central organisation, which supplies common signals to the muscles controlling joints during touch-down, is unknown (see page 45). Anatomical and electrophysiological methods are needed to elucidate how such networks operate.

Modelling the mechanisms that produce locomotion remains speculative until the elements of these mechanisms and their interactions are identified (Miller and Scott 1977, Willis 1980). Nevertheless through models more insight can be gained about the consequences of different possible configurations of elements that are assumed to generate the motor pattern. This work provides a detailed knowledge about the motor pattern of locomotion under a variety of conditions, sometimes with severe constraints. A model used must be able to account for the entire motor pattern observed. Studies of simpler networks that produce locomotion in for instance lower vertebrates and invertebrates, will probably provide a more detailed understanding (Grillner 1981, Stein 1978, Wallén 1982). An investigation of these networks may also lead to a better understanding of more complex systems that produce locomotion in mammals and ultimately lead to a better understanding of human locomotion.

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APPENDIX

cat	phase	left limb				right limb			
		a	sd	b (s)	sd (s)	a	sd	b (s)	sd (s)
KJ	F_{sc}	.28	.03	.062	.004				
	F_{el}	.081	.017	.089	.002				
	F_{hi}	.09	.03	.152	.004				
	F_{kn}	.075	.018	.082	.002				
PI	F_{sc}	.241	.013	.095	.003				
	F_{el}	.095	.007	.0803	.0012				
	F_{hi}	.262	.012	.069	.003				
	F_{kn}	.122	.008	.0659	.0016				
PD	F_{sc}	.273	.009	.0664	.0014				
	F_{el}	.164	.007	.0553	.0012				
	F_{hi}	.205	.009	.0944	.0015				
	F_{kn}	.074	.009	.0968	.0015				
SI	SWh	.122	.009	.165	.003	.179	.011	.125	.003
	Fhi	.14	.018	.145	.004	.163	.016	.136	.004
	Fkn	.041	.007	.1067	.0013	.084	.007	.070	.002
	E_1kn	.0909	.0017	.072	.002	.105	.008	.069	.002
	E_2kn	.62	.03	-.233	.009	.49	.03	-.115	.007
	E_3kn	.24	.03	.055	.007	.30	.03	-.013	.008
	Fan	.056	.007	.116	.002	.087	.009	.086	.003
	E_1an	.067	.006	.0521	.0016	.073	.007	.054	.002
	E_2an	.31	.02	-.114	.006	.218	.017	-.052	.005
	E_3an	.57	.02	-.053	.006	.59	.02	-.065	.006
SN	SWf	.052	.007	.177	.002	.045	.007	.189	.002
	SWh	.128	.009	.160	.003	.062	.007	.181	.002
	Fhi	.134	.012	.165	.004	.106	.009	.168	.003
	Fkn	.026	.006	.114	.002	.034	.004	.0917	.0014
	E_1kn	.114	.006	.061	.002	.058	.004	.0829	.0014
	E_2kn	.81	.04	-.382	.011	.71	.02	-.260	.007
	E_3kn	.07	.03	.188	.009	.19	.02	.091	.007
	Fan	.077	.007	.098	.002	.036	.005	.099	.002
	E_1an	.047	.005	.0652	.0016	.026	.004	.0681	.0014
	E_2an	.10	.02	.022	.006	.280	.011	-.078	.004
	E_3an	.699	.016	-.123	.005	.645	.014	-.080	.005

Table I. The estimated slopes (a) and intercepts (b) of the linear relations of phases of the stride and the cycle duration. The results are given with their standard deviations (sd). All slopes are significantly different from zero, except for T_{Fhi} and T_{Fkn} of cat KJ. A maximum-likelihood method was used (see Methods).

cat	interval	mean (s)	sd (s)	n	≠0	slope
	$t_{Fel}-t_{Fsc}$					
FR		-.006	.012	128	+	—/—
KJ		-.009	.019	30	+	—/+
PI		.006	.016	102	+	+/+
PD		-.006	.017	90	+	—/—
	$t_{Fkn}-t_{Fhi}$					
FR		-.001	.012	123	—	—/+
KJ		-.012	.011	27	+	—/—
PI		-.001	.015	102	—	+/+
PD		-.012	.014	94	+	+/+
SI		.003	.016	103	—	—/—
SN		.009	.015	111	+	—/+
	$t_{Fan}-t_{Fkn}$					
SI		.016	.009	106	+	—/+
SN		.020	.009	111	+	—/+
	$t_{SWh}-t_{Fan}$					
SI		.002	.005	104	+	—/—
SN		-.002	.006	108	+	—/+
	$t_{SUh}-t_{Ehi}$					
SI		.02	.02	111	+	—/+
SN		.017	.019	103	+	—/+
	$t_{E_2an}-t_{E_2kn}$					
SI		-.002	.005	98	+	—/—
SN		-.006	.007	101	+	+/+
	$t_{SUh}-t_{E_2an}$					
SI		-.005	.005	104	+	—/+
SN		-.003	.007	105	+	—/+

Table II. Coordination of events in the stride cycle within a limb. The mean, standard deviation (sd) and the number of observations (n) of different intervals of the left limbs are presented for different cats. The means were tested whether they were significantly different from zero (+) or not (-). The data were divided into two groups and the slopes of the linear relationships between the interval and the cycle duration were calculated. Creasy's method was used to test whether the slope in each of the two groups is significantly different from zero (+) or not (-). A significant slope indicates a trend in the data with T_C which may bias the mean and standard deviation of the pooled data. The slope could be caused by systematic errors due to measuring noise (see page 18).

forelimbs on	v^l (m/s)	sd (m/s)	v^r (m/s)	sd (m/s)	T_C (ms)	sd (ms)	n	$T_C(v^l)$ (ms)	$T_C(v^r)$ (ms)	T_C(v mean) (ms)
A different belts	.21	.02	.30	.02	1231	135	8	1303	1044	1155*
	.49	.05	.35	.01	882	32	11	770	949	848
	.64	.05	.34	.03	794	24	10	653	966	770
B 'fast' left belt	.81	.06	.34	.02	601	27	8	564	966	622*
C 'slow' right belt	.62	.06	.35	.01	923	27	11	666	949	851
	.80	.06	.34	.01	884	24	11	568	966	807

Table III. Modifications of the stride cycle duration during split belt locomotion with a 1:1 rhythm. The velocity of the left (v^l) and right (v^r) belt, with their standard deviations (sd) are given in the left columns. The measured cycle duration (T_C) with its standard deviation and the number of observations (n) are given together with the calculated cycle durations, to be expected when all limbs should walk on the left belt ($T_C(v^l)$), when all limbs should walk on the right belt ($T_C(v^r)$), and when they all should walk on a belt with the average velocity of the belts on which the four limbs walk (T_C(v mean)). In *A* the right and left pair of limbs walk on the right and left belt respectively and in *B* and *C* both forelimbs walk on the 'fast' and 'slow' belt respectively. An asterisk indicates that the calculated value is not different from the measured value (level of significance = 0.05). It is assumed that the variance of the calculated value is negligible with respect to the variance of the measured value. Date are from cat SN.

forelimbs on	v^l (m/s)	v^r (m/s)	T^l_{SU} (ms)	sd (ms)	n	T^r_{SU} (ms)	sd (ms)	n	$T^l_{SU}(T_C)$ (ms)	$T^r_{SU}(T_C)$ (ms)	$T^l_{SU}(v^l)$ (ms)	$T^r_{SU}(v^r)$ (ms)
A both belts	.21	.30	950	142	8	871	63	7	920*	972	980*	796
	.49	.35	587	34	11	644	26	11	610*	647*	510	709
	.64	.34	480	28	10	587	17	9	532	565	406	725
B 'fast' left belt	.81	.34	392	17	8	493	36	5	361	385	327	725
C 'slow' right belt	.62	.35	500	39	11	690	31	10	647	685*	417	709*
	.80	.34	420	24	11	689	33	10	612	649	331	725

Table IV. Adaptations of the hindlimb support phase duration during split belt locomotion with a 1:1 rhythm. The velocity of the left (v^l) and right (v^r) belt and the measured support phase duration of the left (T^l_{SU}) and the right (T^r_{SU}) hindlimb are given together with their calculated values, to be expected from the cycle duration ($T^l_{SU}(T_C)$ and $T^r_{SU}(T_C)$) and belt velocity ($T^l_{SU}(v^l)$ and $T^r_{SU}(v^r)$). Data of *A*, *B* and *C* are from the same experiments as in table IIIA, IIIB and IIIC respectively and are presented in a similar way.

forelimbs on	v^l (m/s)	v^r (m/s)	T^l_{SW} (ms)	sd (ms)	n	T^r_{SW} (ms)	sd (ms)	n	$T^l_{SW}(T_C)$ (ms)	$T^r_{SW}(T_C)$ (ms)	$T^l_{SW}(v^l)$ (ms)	$T^r_{SW}(v^r)$ (ms)
A both belts	.21	.30	276	25	7	371	38	7	318	257	326	246
	.49	.35	295	22	11	237	19	10	273	236*	258	240*
	.64	.34	309	18	9	203	15	8	262	230	243	242
B 'fast' left belt	.81	.34	210	13	7	172	5	5	237	218	232	242
C 'slow' right belt	.62	.35	422	43	10	229	27	10	278	238*	245	240
	.80	.34	464	33	10	195	18	10	273	236	232	242

Table V. Adaptations of the hindlimb swing phase duration during split belt locomotion with a 1:1 rhythm. The experiments and presentation are the same as in table IV.

forelimbs on	v^l (m/s)	v^r (m/s)	T^l_{SU} (ms)	sd (ms)	n	T^r_{SU} (ms)	sd (ms)	n	$T^l_{SU}(T_C)$ (ms)	$T^r_{SU}(T_C)$ (ms)	$T^l_{SU}(v^l)$ (ms)	$T^r_{SU}(v^r)$ (ms)
A both belts	.21	.30	994	115	8	885	35	7	989*	986	1057*	809
	.49	.35	567	28	11	649	26	11	660	654*	555*	718
	.64	.34	515	29	9	602	26	9	577	570	444	734
B both belts	.32	.47	712	77	11	624	38	11	709*	703	775	567
	.66	.50	480	47	14	483	30	14	489*	482*	432	539
	.92	.50	391	44	15	485	51	14	457	449	320	539

Table VI. Adaptations of the forelimb support phase durations during split belt locomotion with a 1:1 rhythm. The left and right forelimb step on the left and right belt respectively. Same presentation as in table IV. The data in *A* are from the same experiments as the data in table IIIA of this appendix and the data in *B* are from the same experiments as the data in table 9A of section 5 (split belt locomotion).

	mean	sd	n	stride			
				1	2	3	4
	(ms)	(ms)			(ms)		
left hindlimb							
T_{SU}	568	16	3	608	628†	506†	
T_{SW}	179	10	4	199(58)	218†	231†(0)	154†
T_{Fkn}	93	4	4	109†	122†	141†	83†
T_{E_1kn}	98	11	4	96	90	102	77
T_{Fan}	106	15	4	115	135	147†	83
T_{E_1an}	80	9	4	77	77	77	64
$t^l_{SUf}-mp^l_{E_1kn}$	167	5	4	279†	231†	122†	141†
$mp^r_{E_1kn}-mp^l_{E_1kn}$	373	24	4	452†	442†	327	352
right hindlimb							
T_{SU}	407	12	4	429(-90)	474†	493†(-167)	397
T_{SW}	337	20	3	391	339	243†	
T_{Fn}	169	16	3	250†	192	154	
T_{E_1kn}	192	11	3	154†	167	128†	
T_{Fan}	207	29	3	295†	250	167	
T_{E_1an}	133	10	3	102†	102†	90†	
$t^r_{SUf}-mp^r_{E_1kn}$	173	11	4	224†	237†	83†	
$mp^l_{E_1kn}-mp^r_{E_1kn}$	352	13	3	388	372	417†	339
left forelimb							
T_{SU}	544	32	4	653†(-391)	557	608(-449)	544
T_{SW}	170	8	4	224†	218†	141†	
$t^r_{SUf}-t^l_{SUf}$	378	23	4	397	449†	288†	
right forelimb							
T_{SU}	444	22	4	679†	651†	359†	474
T_{SW}	282	22	4	205†	211†	231	
$t^l_{SUf}-t^r_{SUf}$	348	11	4	487†	378†	301†	397†

Table VII. Durations of phases of the hindlimbs and forelimbs and of interlimb intervals during split belt locomotion with transition effects. The results of an observation interval of regular locomotion are given (in ms) in the first column (mean; standard deviation: sd; number of observations: n). The durations of single successive phases and intervals are given when the 'fast' right forelimb takes two steps on the 'slow' belt (stride 1 and 2) and steps back on the 'fast' belt (stride 3 and 4). The results of these support and swing phases are positioned in a way to give a rough indication of their spacing in time. The onsets of the velocity changes of the right forelimb are indicated with two vertical lines and the interval from the onset of the velocity changes to the onset of the particular phase is given in parenthesis behind these phases. A † indicates that the value is greater than or smaller than the the mean of the preceding part (t-test on two means, where one mean consists of a single observation. Variances are assumed equal. Level of significance for this single-tailed test is 0.05). The velocity of the left and right belt is 0.40 and 0.79 m/s respectively. Data are from cat SN and are illustrated in fig. 24A.

Stellingen behorende bij het proefschrift van J. M. Halbertsma

1. Wetenschappelijk medewerkers, die niet gemiddeld minstens één maal per jaar een citaat hebben in de Science Citation Index, behoren ontslag te nemen voor dat gedeelte van hun dagtaak dat zij geacht worden aan wetenschappelijk onderzoek te besteden.

2. Om het parameterschatten te populariseren is het aan te bevelen om te spreken van het 'inschatten' van parameters in plaats van het 'schatten' van parameters.

3. Door haar eenvoud en didactische kwaliteiten wordt eerste orde regressie analyse, bij het schatten van de parameters van een verondersteld lineair verband, vaker toegepast dan is toegestaan.

4. De gevleugelde uitspraak 'Meten is Weten' heeft door de toenemende computerisering van meetsystemen en de daarbij behorende grote hoeveelheden meetgegevens, pas gebruikswaarde na het schrijven en het zorgvuldig uittesten van de programmatuur om deze gegevens te verwerken.

5. Jumping to conclusions is slow progression.

(Furnée 1975)

6. Het is onlogisch dat de courtage van een makelaar, die voor een koper optreedt, een bepaald percentage van de koopsom bedraagt.

Delft, mei 1983