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THE EFFECT OF FILMING SPEED ON THE INTERPRETATION OF ARTHROPOD LOCOMOTION

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SUMMARY

Films of spider locomotion taken at about 270 frames per second (f.p.s.) were reanalysed to give effective filming speeds of 100, 50 and 25 f.p.s. Reanalysis of the data shows that mean values and variance for phase lag, period, stepping frequency and protraction/retraction ratios depart from the control values (270 f.p.s.) at slower sampling rates. Guidelines are presented for filming arthropod locomotion with high stepping frequencies and high or low *p*/*r* ratios. Most film analysis of arthropod locomotion has had insufficient time resolution to examine resolution-sensitive parameters such as the *p*/*r* ratio. Filming speeds giving sampling rates greater than 40 frames per step do not increase accuracy.

INTRODUCTION

Apart from the novel techniques used by Wendler (1966) cinematography has been the basis of most investigations of arthropod locomotion. The most commonly used filming speeds have been 32–64 frames per second (f.p.s.) (Wilson, 1967; Burns, 1973; Spirito & Mushrush, 1979) although filming speeds as low as 16 f.p.s. (Hughes, 1952) and as high as 500 f.p.s. (Delcomyn, 1971) have been used. More recently television or 'video' has been used but the effective filming speed is limited to 25 f.p.s. or, with loss of half the vertical resolution, to 50 f.p.s.

This report results from an investigation into locomotory gaits in burrowing and vagrant wolf spiders (Ward & Humphreys, 1981). Initial analysis of film taken at 64 f.p.s., which is a high filming rate for this type of work, showed that the sampling rate was too low. Here the effect of analysing the films at different filming speeds is discussed with respect to the interpretation that may be placed on the data. In addition guidelines are proposed for minimum filming speeds for animals with different stepping frequencies and protraction/retraction ratios.

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MATERIALS AND METHODS

The materials, methods and definitions together with the statistical treatment of the data used in this study have been presented elsewhere (Ward & Humphreys, 1981). In that report an effective filming speed of about 270 frames per second (f.p.s.) was used. Here two runs were taken to represent high and low stepping frequencies for each of the species of wolf spider studied [*Lycosa tarentula* (Linné, 1758) and *Trochosa ruricola* (DeGeer, 1778) Araneae: Lycosidae]. The runs were reanalysed to give effective filming speeds of 100, 50 and 25 f.p.s.

RESULTS

Stepping pattern diagrams (Fig. 1) show that subtle differences occur at all sampling rates. At 25 f.p.s. the period (τ) is sometimes lengthened considerably (Fig. 1) compared with the period at 270 f.p.s. The most general feature is that at lower filming speeds the overlap of protraction between adjacent ipsilateral and contralateral legs is abolished and alternate ipsilateral leg pairs appear to function in precise synchrony.

For reanalysis phase lag data were pooled in two groups; alternate ipsilateral legs and all other pairings of legs, based on the expected values for phase lag of 0 and 0·5 respectively (Ward & Humphreys, 1981). The data have been presented in terms of frames per step and deviation from the value at 270 f.p.s. so that the four runs reanalysed may be compared directly.

Generally the mean values for period, phase lag and protraction/retraction ratio change erratically over the range of sampling rates used (Fig. 2) with a tendancy for greater deviations at the lower filming speeds. The mean p/r ratio changes with sampling rate in a similar manner for all the runs analysed despite the variation in stepping frequency within and between the two species (Fig. 2).

Generally the standard errors decrease as the sampling rate (frames per step) increases (Fig. 3). The circular standard errors change more for alternate ipsilateral phase lag than for the other phase comparisons (Fig. 3). Standard errors close to zero occur for phase lag, frequency and p/r ratio when the number of frames per step is small (< 3). The standard errors fluctuate rather little when more than 10 frames per step are analysed.

DISCUSSION

Analysis at different filming speeds shows that the precision generally is directly related to filming speed. However, the variance in the data should not necessarily be taken as an indication of accuracy, especially over short stepping sequences, since low variance occurs at low filming speeds for all the parameters examined (phase lag, stepping frequency and p/r ratio). Spider gaits are rarely precisely coordinated so variances close to zero should be suspected of inaccuracy. For other animals with less variable stepping patterns, erroneous values may not be detected as easily.

Manton (1973) placed great importance on the p/r ratio, especially in the way it changed with speed. The p/r ratio is based on the smallest measurements and is therefore the parameter most sensitive to a decrease in the number of samples used

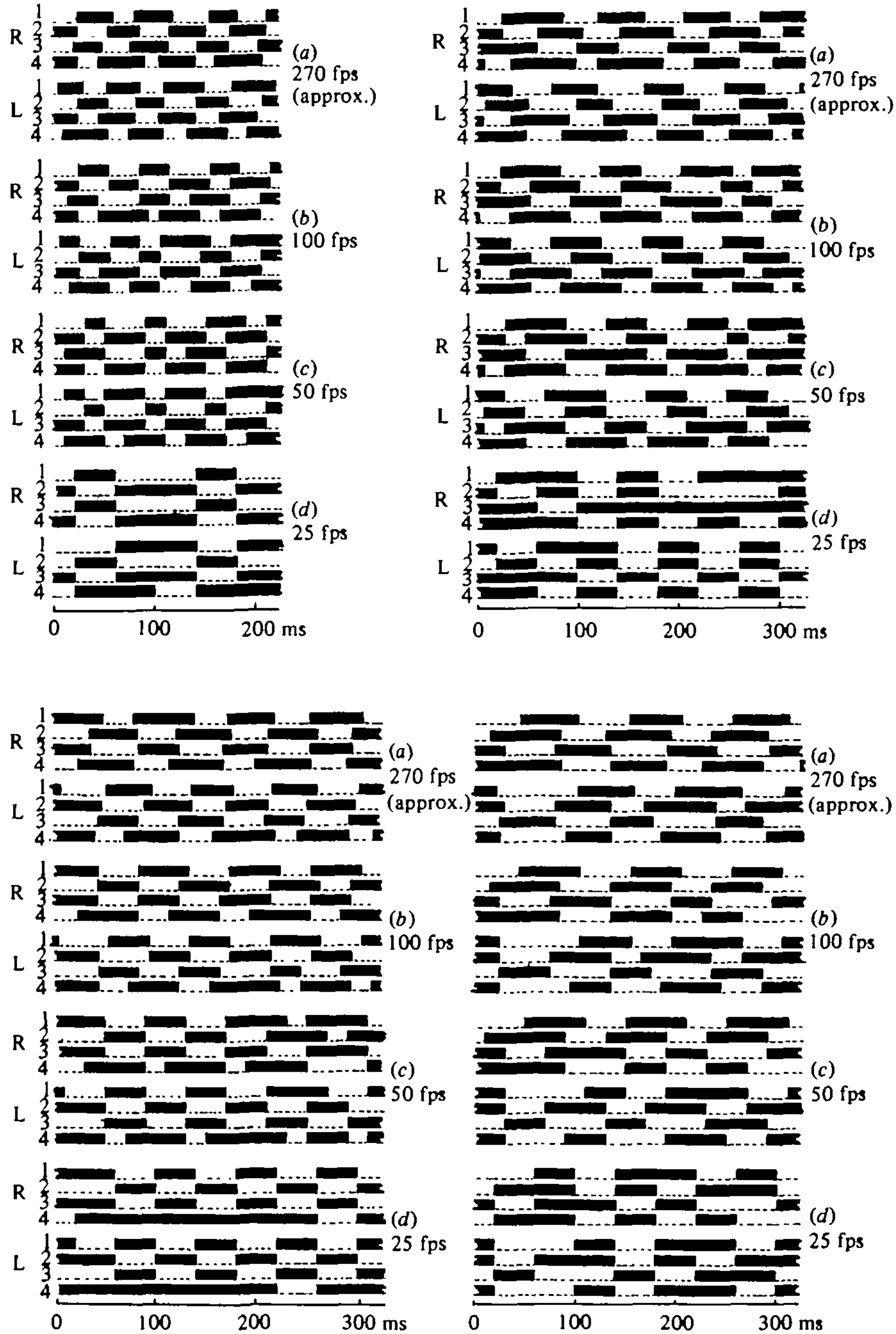

Fig. 1. Stepping pattern diagrams of spiders moving at different speeds. Solid bars denote protraction. The diagrams were created from the same film taken at ≃ 270 f.p.s. and reanalysed using effective film speeds of 100, 50 and 25 f.p.s. Upper left – *T. ruricola* at 16·8 steps s^{-1}; lower left – *T. ruricola* at 12·8 steps s^{-1}; upper right – *L. tarentula* at 11·8 steps s^{-1}; lower right *L. tarentula* at 9·5 steps s^{-1}. Gross changes occur in the apparent stepping pattern at the lower film speeds.

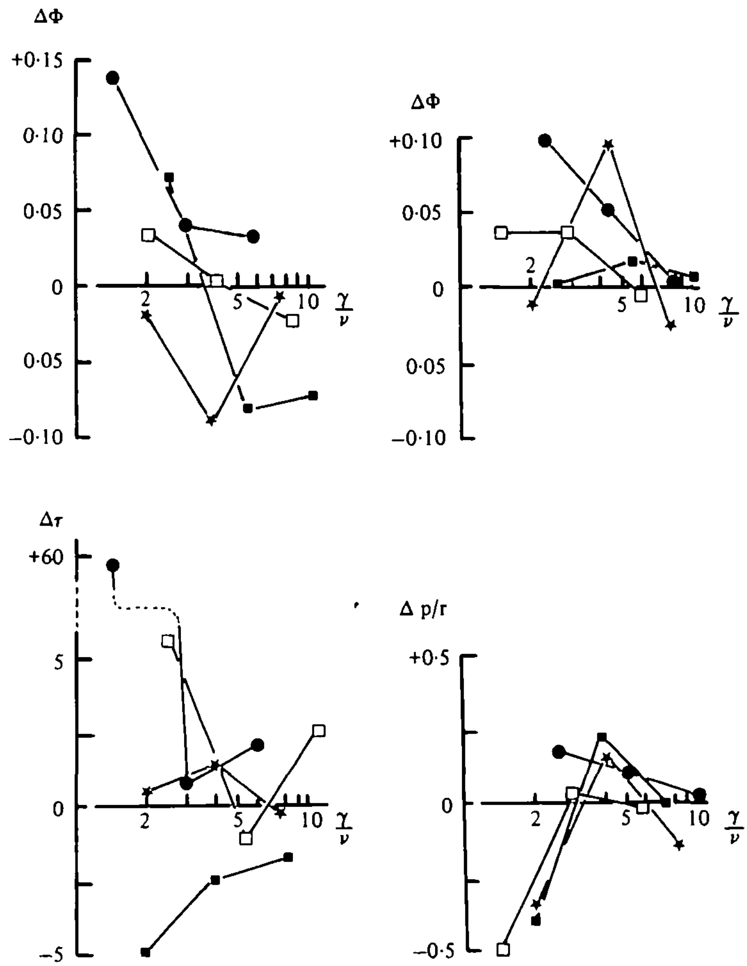

Fig. 2. Deviation from the mean of a number of measured parameters, as measured at 270 frames s^{-1}, for a range of values of number of frames per step ($\gamma\nu^{-1}$). The four separate runs analysed are recorded separately on each diagram. Upper left – deviation from mean phase lag ($\Delta\Phi$) in contralateral and adjacent ipsilateral leg pairs; upper right – the same ($\Delta\Phi$) for alternate ispsilateral leg pairs; lower left – deviation from mean period ($\Delta\tau$); lower right–deviation from mean p/r ratio ($\Delta p/r$).

to define each step. When there are fewer than two samples per step p/r ratios will tend to unity because only lengths of film showing either protraction or retraction on alternate frames could be analysed. Other sequences would show either prolonged retraction or protraction depending on the sampling rate, the p/r ratio and the point in the cycle where sampling began. Interestingly Manton (1973) notes that spiders have a p/r ratio tending to unity at higher stepping frequencies (her sampling rate at the higher frequencies was about 2 frames per step).

At low sampling rates, especially if the true p/r ratio deviates from unity, gross inaccuracies will occur at high stepping frequencies because there is a greater chance of missing either the protraction or the retraction phase of the stepping cycle, which ever is shorter. The changes in interpretation resulting from different filming speed

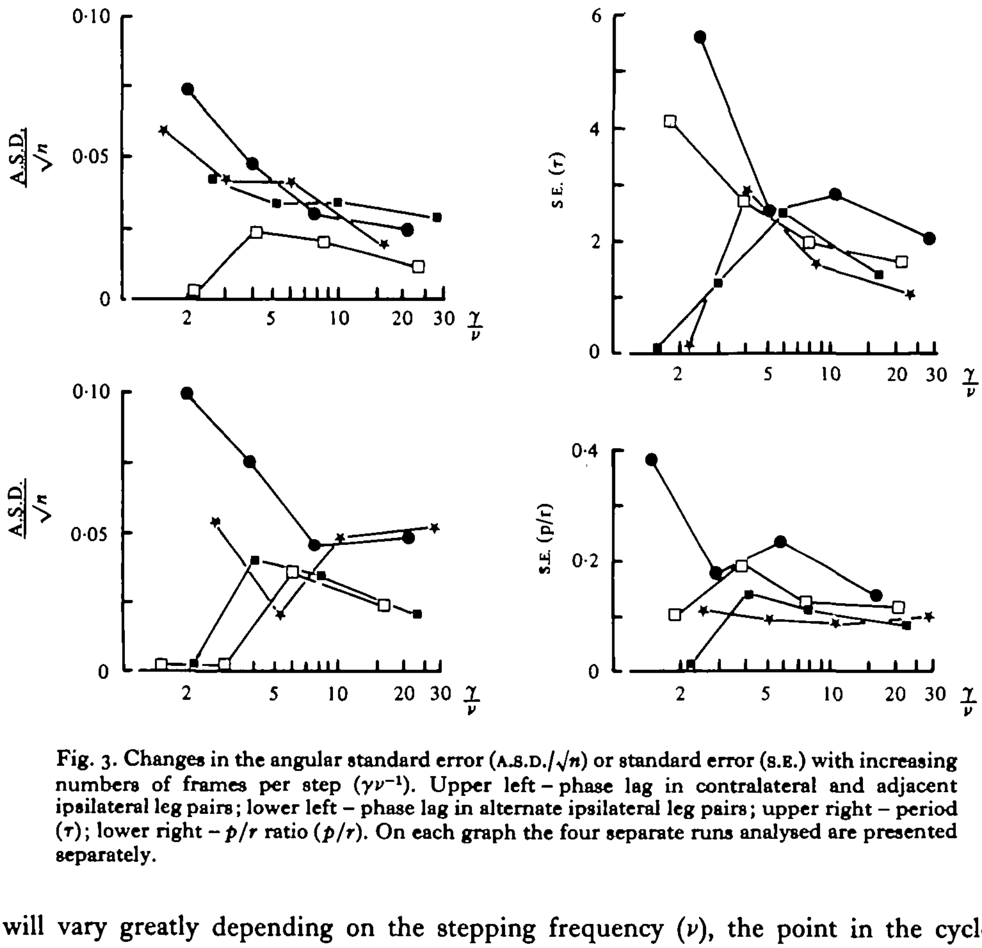

Fig. 3. Changes in the angular standard error (A.S.D./$\sqrt{n}$) or standard error (S.E.) with increasing numbers of frames per step ($\gamma\nu^{-1}$). Upper left – phase lag in contralateral and adjacent ipsilateral leg pairs; lower left – phase lag in alternate ipsilateral leg pairs; upper right – period (τ); lower right – p/r ratio (p/r). On each graph the four separate runs analysed are presented separately.

will vary greatly depending on the stepping frequency (ν), the point in the cycle where sampling begins and on the p/r ratio. For any combination of filming speed (γ) and p/r ratio, it is possible to predict the maximum possible error from the true times of lift-off and touch-down of the legs. With repeated sampling the average error would be half the maximum possible error. Conversely it is possible to calculate the filming speed required to produce a stated maximum error. These values may be determined from the equations derived below.

If the stepping pattern diagrams are constructed according to the rule that the position of the leg during sampling defines its position for half the sampling interval (the time between successive samples) the maximum possible error from the true time of touch-down or lift-off is plus or minus half the sampling interval. The maximum possible error (α) is expressed as a percentage of the period. Thus: since period (τ) = $1/\nu$,

$$\alpha = \frac{50\nu}{\gamma},$$

where; ν = stepping frequency (Hz), α = maximum error (% period), γ = filming speed (f.p.s.). To ensure that at least one frame shows protraction and another

Table 1. *Minimum filming speeds* (γ_{min}) *to ensure that at least one frame shows protraction and one shows retraction in each step, for a range of stepping frequencies* (α) *and p/r ratios*

(Maximum errors (α) are also shown and expressed as a percentage of the step period.)

ν (Hz)	p/r ratio	α (%)	γ_{min} (f.p.s.)
2	0·5	16·7	6
2	1	25	4
2	3	12·5	8
4	0·5	16·7	12
4	1	25	8
4	3	12·5	16
8	0·5	16·7	24
8	1	25	16
8	3	12·5	32
16	0·5	16·7	48
16	1	25	32
16	3	12·5	64

retraction in each step, 2α must be less than the smallest of either the protraction or retraction times. Thus:

for $p/r > 1$ $$\gamma_{min} = \nu(p/r+1),$$

for $p/r < 1$ $$\gamma_{min} = \nu\left(\frac{1}{p/r}+1\right),$$

where γ_{min} is the value of γ required to ensure that at least one frame shows protraction and another shows retraction in each step. γ_{min} for a range of stepping frequencies and p/r ratios is shown in Table 1.

It should be stressed that γ_{min} represents the minimum filming speed that is required to identify the *stepping frequency* within plus or minus 50%. To determine the other parameters (phase lag and p/r ratios) extremely large samples would be required. γ_{min} should be regarded as the absolute *minimum* sampling frequency. The filming speeds required to produce a range of values of α for given stepping frequencies and p/r ratios are given in Fig. 4.

Theoretically, higher filming speed results in greater accuracy but there is an upper limit in accuracy set by the ability of the analyst to detect leg movement between successive frames. The use of low angle lighting to cast bold shadows of the legs assists in determining leg movement. Despite this the moment of leg touch-down is spread over several frames during the slowest runs (lowest stepping frequency) and this occurred at a sampling rate of about 80 frames per step which suggests that greater sampling rates yield no increase in sensitivity. Since at 80 frames per step the moment of touch-down was spread over at least two frames, half this sampling speed would give the same sensitivity, giving a best maximum error (α) of about 1%. The plateau in the graphs of standard errors (Fig. 3) shows that at about 12 frames per step ($\alpha = 4$%) stable values were reached.

The above considerations show that the useful range of filming speeds are between

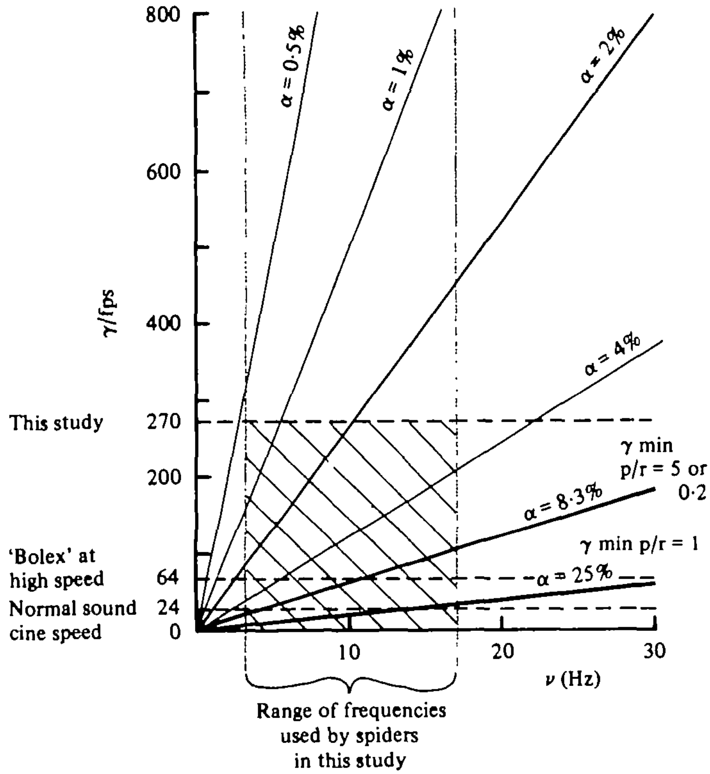

Fig. 4. Filming speeds (γ frames s^{-1}) required to give a range of maximum errors (α; see text) over a range of stepping frequencies (ν s^{-1}). The graph also shows the minimum filming speeds (γ_{min}) required to ensure that at least one frame shows protraction and one retraction in each step for p/r ratios of 0·2, 1 and 5.

12 and 40 frames per step (α 4% to 1%). Unless radically different experimental techniques are used α values of less than 1% are impractical. While the optimal filming speed will vary between species, between runs and between legs, α values of less than 4% are needed to avoid gross misinterpretation of stepping patterns; a filming speed about fifteen times the stepping frequency should be satisfactory.

In the investigation reported here and elsewhere (Ward & Humphreys, 1981) filming speeds of about 270 f.p.s. had α values of less than 2% when stepping frequencies were < 10 Hz but for greater stepping frequencies the α values were between 2–4%.

Table 2 shows the range of stepping frequencies and filming speeds used in some other investigations of arthropod locomotory patterns. In some, filming speeds were below γ_{min} (Manton, 1973; Hughes, 1952) required for the higher stepping frequencies. In only three cases (Delcomyn, 1971; Graham 1972; Ward & Humphreys, 1981) were filming speeds in excess of the values required for α4%.

This analysis makes it clear that detailed comparative studies of arthropod locomotion have commonly relied on analytical techniques having insufficient resolution.

Table 2. *Stepping frequencies and filming speeds in investigations of arthropod locomotion*

(Also shown are the minimum filming speeds (γ_{min}) to ensure that at least one frame shows protraction and one shows retraction in each step and filming speeds for maximum errors (α) of 4 %. Note that γ for α 1 % = 50 ν.)

Investigator	Subject	Filming technique	Filming speed (f.p.s.)	Stepping frequency (Hz)	γ min, p/r = 1 (f.p.s.)	γ for α = 4 %, p/r = 1 (f.p.s.)
Barnes (1975)	Crab	Cine	64	10 (max)	20	125
Bowerman (1975)	Scorpion	Video	50	2–8	4–16	25–100
Burns (1973)	Grasshopper	Cine	64	1–9	2–18	13–112
Delcomyn (1971)	Cockroach	Rotating prism	200, 500	1–25	2–50	13–225
Graham (1972)	Stickinsect	Cine and video	18–70	0·7–5	2–10	13–63
Graham (1978)	Grasshopper	Video	50	1–4	2–8	13–50
Harris & Ghiradella (1980)	Cricket	Cine	48–80	2–9	4–18	25–113
Hughes (1952)	Cockroach	Cine	16–32	2–17	4–34	25–213
Hughes (1957)	Cockroach	Cine	24–32	3–9	6–18	38–113
Manton (1973)	*T. ruricola*	Cine	32	14 (max)	28	175
	Galeodes	Cine	32	17 (max)	34	214
	Scorpion	Cine	32	8 (max)	16	100
	Pseudo-scorpion	Cine	32	30 (max)	60	375
	Mite	Cine	32	6 (max)	12	75
Spirito & Mushrush (1979)	Cockroach	Cine	64	2–7	4–14	25–88
Wilson (1967)	Tarantula	Cine	24, 32	0·3–7	1–14	13–88
This study	*T. ruricola*	Rotating prism	≃270	9–17	18–34	113–213
	L. tarentula	Rotating prism	≃270	3–11	6–22	38–138

Even in some of the high time-resolution studies (Ward & Humphreys, 1981) parameters which are particularly sensitive to resolution, such as the p/r ratio, have to be interpreted with caution.

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