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Context-dependent changes in strength and efficacy of leg coordination mechanisms

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Summary

Appropriate coordination of stepping in adjacent legs is crucial for stable walking. Several leg coordination rules have been derived from behavioural experiments on walking insects, some of which also apply to arthropods with more than six legs and to four-legged walking vertebrates. Three of these rules affect the timing of stance–swing transition [rules 1 to 3 (*sensu* Cruse)]. They can give rise to normal leg coordination and adaptive responses to disturbances, as shown by kinematic simulations and dynamic hardware tests. In spite of their importance to the study of animal walking, the coupling strength associated with these rules has never been measured experimentally. Generally coupling strength of the underlying mechanisms has been considered constant rather than context-dependent.

The present study analyses stepping patterns of the stick insect *Carausius morosus* during straight and curve walking sequences. To infer strength and efficacy of coupling between pairs of sender and receiver legs, the likelihood of the receiver leg being in swing is determined, given a certain delay relative to the time of a swing–stance (or stance–swing) transition in the sender leg. This is compared to a corresponding measure for independent, hence uncoupled, step sequences. The difference is defined as coupling strength. The ratio of coupling strength and its theoretical maximum is defined as efficacy.

Irrespective of the coordination rule, coupling strength between ipsilateral leg pairs is at least twice that of contralateral leg pairs, being strongest between ipsilateral hind and middle legs and weakest between contralateral middle legs. Efficacy is highest for inhibitory rule 1, reaching 84–95% for ipsilateral and 29–65% for contralateral leg pairs. Efficacy of excitatory rules 2 and 3 ranges between 35–56% for ipsilateral and 8–21% for contralateral leg pairs. The behavioural transition from straight to curve walking is associated with context-dependent changes in coupling strength, increasing in both outer leg pairs and decreasing between inner hind and middle leg. Thus, the coordination rules that are thought to underlie many adaptive properties of the walking system, themselves adapt in a context-dependent manner.

Key words: leg coupling, coupling strength, context dependence, stick insect, *Carausius morosus.*

Introduction

The coordination of step cycles between legs is of prime importance to the control of walking. Appropriate leg coordination ensures static and dynamic stability and accounts for synergistic action of the legs to propel the body. The two objectives of the present study are to introduce a measure of coupling strength that can be interpreted directly as the efficacy of inter-leg coordination mechanisms, and to determine relative coupling strength associated with the three most important coordination rules in different leg pairs and in two behavioural contexts.

The step cycle sequence of each walking leg consists of alternating swing and stance modes. As the body weight is supported during stance only, transitions between the support and non-support states immediately affect static stability. There is a qualitative difference between the two possible types of state transition: whereas the swing–stance transition, i.e. touch-down of the leg, adds support to the body, the stance–swing transition, i.e. lift-off of the leg, reduces support and, therefore, potentially destabilises the animal. Thus, appropriate timing of lift-off is particularly important to stability. Indeed, behavioural experiments on different insect species have gathered evidence for three coordination mechanisms that affect timing of the stance–swing transition during walking (reviewed by Cruse, 1990). Throughout this study, they will be referred to as rules 1 to 3, *sensu* Cruse et al. (1995), where rule 1 postulates an inhibitory mechanism acting on anterior and contralateral neighbour legs, rule 2 postulates an excitatory mechanism acting on anterior and contralateral neighbour legs, and rule 3 postulates an excitatory mechanism acting on posterior and contralateral neighbour legs.

On the basis of a number of kinematic simulations (Dean, 1991b, 1992b; Müller-Wilm et al., 1992; Cruse et al., 1995, 1998) and robot hardware tests (Espenschied et al., 1993; Pfeiffer et al., 1995) it is well established that behaviourally derived coordination rules are sufficient to generate natural hexapod gaits that are robust against perturbation (Dean, 1992a; Kindermann, 2002). Moreover, theoretical analyses (Dean, 1991a,b; Calvitti and Beer, 2000) and sensitivity analyses in software (Dean, 1992b) and hardware tests (Espenschied et al., 1993) have highlighted the importance of the three coordination mechanisms that affect the timing of stance–swing transitions. In contrast to the parameter ranges derived from theoretical and engineering studies, coupling strengths associated with coordination rules 1 to 3 have never been determined experimentally. Rather, coupling between adjacent legs is typically quantified by measures of relative coordination (Holst, 1943), expressing the phase lag of the step cycle in a receiver leg within the step cycle of the sender leg. The resulting phase histograms and corresponding circular statistics measures quantify the coherence of two rhythmic patterns (eg. Clarac and Chasserat, 1986; Cruse and Knauth, 1989) but they cannot be related to any of the proposed leg coordination rules in particular.

The present study supplies the first empirical values of coupling strengths associated with individual mechanisms. Taking a stochastic view of leg coordination, the strength of each one of three competing coordination mechanisms is assessed by its likelihood of enforcing a stance–swing transition. The likelihood of a receiver leg being in swing mode depending on the time relative to a state transition in the sender leg is determined for each coupled pair of legs, and in a specific way for each one of the three major coordination rules.

The rules under investigation are associated with putative neural mechanisms, one inhibitory and two excitatory. Wilson (1966) deduced the existence of an inhibitory mechanism from observations on insects. The associated rule 1 states that lift-off in a receiver leg is suppressed while the sender leg is in swing. This rule was also proposed for walking scorpions (Bowerman, 1975), suggesting that it is widespread among arthropods. Careful analysis of irregular stepping patterns in grasshoppers (Graham, 1978b) and direct evidence from perturbation experiments on stick insects (Cruse and Epstein, 1982) unequivocally demonstrated the existence of rule 1 in insects. Rules 2 and 3 have been derived from studies on walking stick insects, based on perturbation experiments (Cruse and Schwarze, 1988) and observations on mechanically uncoupled steps of contralateral neighbours (Cruse and Knauth, 1989). Rule 2 states that an excitatory mechanism favours stance–swing transition in a receiver leg shortly after the sender leg commences stance. Rule 3 refers to a position-dependent excitatory mechanism that favours swing–stance transition in a receiver leg with increasingly posterior tarsus position of the sender leg. Similar rules have been described for walking crayfish (Cruse and Müller, 1985) where they mainly affect swing–stance transition.

Based on the experimental data of the accompanying paper (Dürr and Ebeling, 2005), the present study measures coupling strength and efficacy associated with coordination rules 1–3 in all four ipsilateral and three contralateral leg pairs. Whereas coupling strength supposedly indicates the strength of the underlying neural mechanism, coupling efficacy expresses the relative effect of this mechanism on the prevalent gait. Context-dependent modulation of coupling strength is shown to occur during the behavioural transition from straight to curve walking. Due to the specificity of the analysis to individual coupling mechanisms, the results require postulating adaptive modulation of leg coordination mechanisms and demand changes to current hexapod walking models. In addition, the relative differences of coupling strength between leg pairs and coordination rules provide a behavioural reference for further neurophysiological investigations. Preliminary results have been published by Dürr (2002).

Material and methods

Experimental procedures have been explained in detail in the accompanying paper (Dürr and Ebeling, 2005) and will be only reiterated briefly here.

Experimental animals and set-up

Experiments were carried out on eight adult female stick insects of the species *Carausius morosus* Brunner. Stick insects walked on the surface of a hollow Styrofoam sphere that floated on an air cushion. The sphere was covered by evenly spaced patches of reflective foil, the movement of which was recorded by an optic tracking system. Animals were tethered to a balsa wood support above the sphere, restricting any horizontal displacement relative to the set-up. A balancing system ensured that animals needed to carry their own weight and adjust their body height. Walking stick insects rotated the sphere underneath them. The resulting walking path was reconstructed from the displacement readings of the tracking system. All three degrees of freedom of horizontal walking could thus be measured: forward and sideward translation and yaw rotation around the vertical axis. Additionally to the tracking system, a monochrome CCD video camera was mounted 1.4 m above the set-up. All walking sequences were videotaped using standard PAL video equipment.

The tracking system was centred in a motor-driven paper drum that was lined with a black-and-white grating of wavelength 24° (Fig. 1A). The pattern was diffusely illuminated from the outside (contrast of 90%, luminance 60 cd m^{-2}) and rotated around the tracking system at 38.1 deg. s^{-1}.

The tracking system, video system and stimulus drum were connected to a personal computer *via* a data acquisition board (stimulus drum and synchronisation signals) and the parallel port (tracking system). The camera synchronisation signal was used to trigger a single data acquisition cycle on the PC. Light-emitting diodes within view of the camera indicated the start and end of a measurement sequence, allowing matching of single frames of the video tape to the data logged on the computer.

Experimental procedure

Single trials lasted 22.5 s and were divided into three periods of equal duration. Following a pre-stimulus period of 7.5 s, during which the drum stood still, the drum was rotated for 15 s. This stimulus period was divided into an early transition phase and a late steady-state phase. The large-field visual motion stimulus reliably elicited an optomotor turning response in the direction of stimulus motion. All analyses presented in this study compare leg coordination during straight walking in the pre-stimulus period, to that during curve walking in the late stimulus period.

Direction of stimulus motion was randomised and leftward and rightward turns were pooled, assuming bilaterally symmetric animals. According to the location of the legs relative to the turning direction, they are denoted as inner legs (I1 to I3) and outer legs (O1 to O3) throughout this study (Fig. 1B). In total, 33 out of 321 trials from eight animals were selected according to steadiness of forward walking and maximum diameter of the walked curve (see Fig. 1C).

Step sequences of each leg were recorded manually from digitised video files, using a custom-written program. Only the timing of touch-down and lift-off was considered here, as these transition times are equivalent to the beginning of stance movement, i. e. power stroke, and swing movement, i.e. return stroke, respectively. Representative step sequences are shown in Fig. 1C.

Data analysis and terminology

Coupling strength and efficacy was determined for pairs of step sequences of sender and receiver legs, where the leg that exerts the effect is called the ‘sender’ and the leg being influenced is called the ‘receiver’. Mathematically, step sequences were treated as functions of a discrete state variable over time, assuming value 0 during stance and value 1 during swing movement. State transitions were considered as triggering events, and the effect of these events upon adjacent legs was quantified as the likelihood of a receiver leg to be in state 1, given a particular time delay relative to the transition event in a sender leg, e.g. $P(S=1|t-t_{\mathrm{trans10}}|)$, where S is a state variable and P is probability. According to their sign, transitions are called ‘trans01’ for the stance–swing transition and ‘trans10’ for the swing–stance transition. The peak likelihood minus its baseline value is a measure of ‘coupling strength’, where the ‘baseline’ is calculated by shuffling step sequences from independent, hence uncoupled, pairs of trials. As expected, the resulting baseline likelihood is time-invariant. It can be interpreted as the average probability of the receiver leg to be in swing or, equivalently, as the average ratio of swing duration over step period. The fraction of step cycles consistent with a given coordination rule is defined as ‘coupling efficacy’. Accordingly, efficacy is equal to (peak–baseline)/(1–baseline) for rules 2 and 3 and (baseline–minimum)/baseline for rule 1. The rationale underlying these formulae will be explained in more detail in relation to Figs 2 and 5. Note that if a coordination rule is violated in a fraction of steps, this does not imply that the associated neural coordination mechanism is not present. Rather, it suggests that it is being overridden by other competing mechanisms or noise. Thus, coupling efficacy indicates how strongly a mechanism affects the gait of the animal.

Local differences in likelihood were considered statistically significant if the 95% confidence intervals for proportions (Hayes, 1988, p. 240) did not overlap. A pair of legs is considered to be coupled according to a given coordination rule, if the distance of peak likelihood to baseline is beyond 0.086. This threshold difference is equivalent to the largest 95% confidence interval of any determined likelihood value.

Results

Trial variability and free gait

As the stepping patterns of insects are typically classified as tetrapod or tripod gaits, eight examples of gait patterns observed in the present study are shown in Fig. 1C. A pure tetrapod gait is characterised by a minimum number of four legs being on the ground at any time (hence the name tetrapod) and by the presence of back-to-front waves of ipsilateral step cycles. An example of tetrapod-like gait is illustrated in the pre-stimulus period in Fig. 1Ci, where the right legs are stepping in a back-to-front wave (red diagonal lines, legs denoted as inner legs I1–I3 in clockwise curve). Note, however, that this wave is not so regular in the left legs (outer legs O1–O3). A pure tripod gait, on the other hand, is characterised by a minimum number of three legs being on the ground at any time (hence the name tripod) and by the presence of alternating tripods of ipsilateral front and hind legs and their contralateral middle leg. An example of a brief tripod-like gait phase is illustrated in Fig. 1Cvii, where ipsilateral hind and front legs step in synchrony and in counter-phase with their ipsilateral middle leg (vertical blue lines). Alternating tripods occur during the second half of the pre-stimulus period. The fact that the tetrapod gait is only present on one side of the animal in the first example, and that the tripod gait only lasts for some 5 or 6 alternating tripods in the second example, shows that stepping patterns in stick insects vary considerably in time. This is true for both the straight walking sequences of the pre-stimulus period (left third of gait plots in Fig. 1C) and for the curve walking sequences of the late stimulus period (right third of gait plots in Fig. 1C). In conclusion, when stick insects walk on a surface rather than on a treadwheel or narrow bridge, gaits often cannot be identified unequivocally. Even if they can, they may change readily. This is not only true for the transition phase between straight and curve walking, but also for the more steady behavioural states of straight and curve walking, in which the walked path does not change much.

Accordingly, gaits may not be a helpful concept for describing leg coordination in all walking arthropods, because often the prevalent gait is discernable for a short period of time only. This situation may be called a free gait, a term frequently

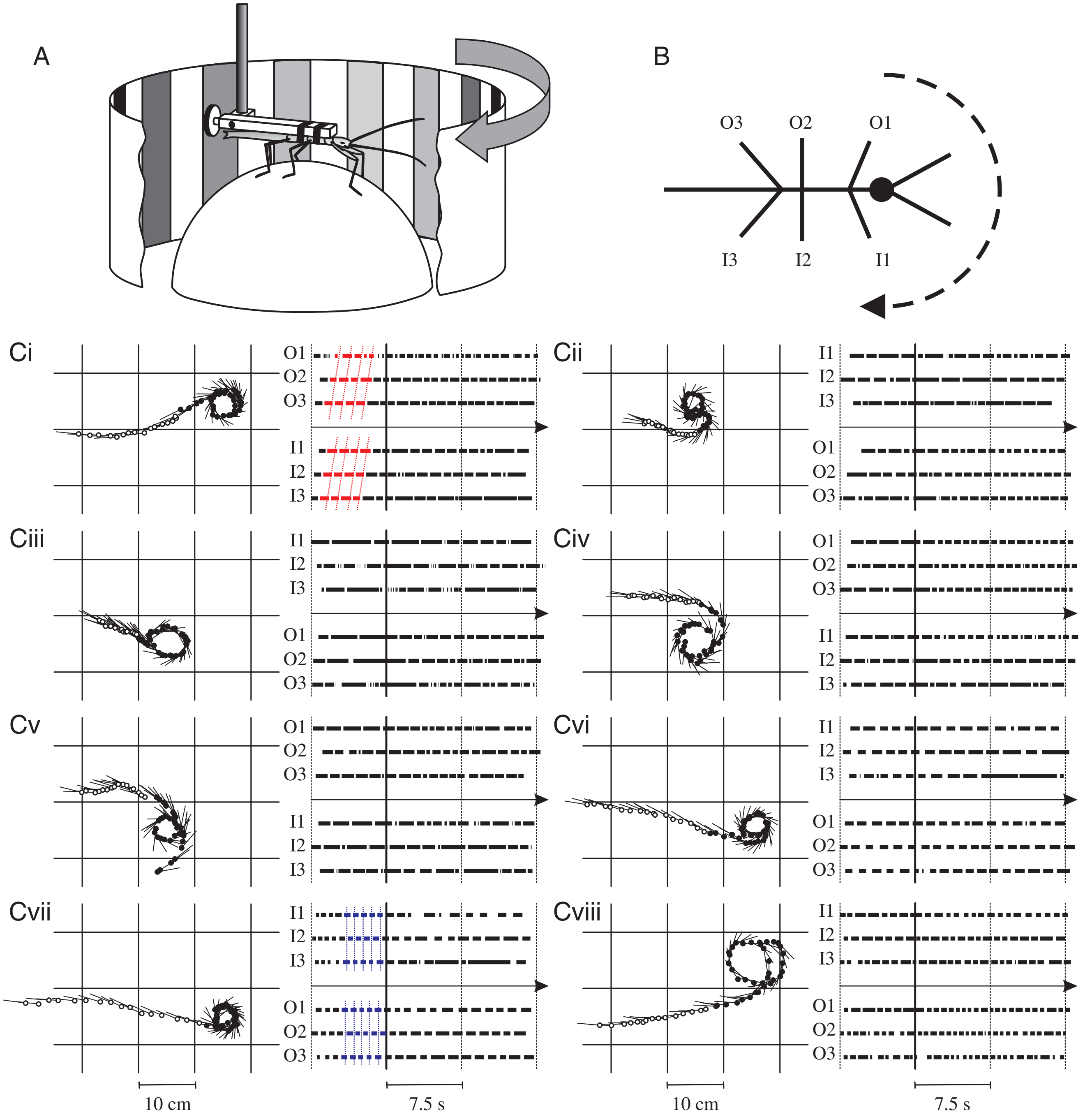

Fig. 1. Optomotor-induced curve walking behaviour. (A) Stick insects walked on the apex of a light-weight sphere that floated on an air cushion. Animals were tethered to a support that required them to carry their own weight by adjustment of body height, but restricted horizontal translation and rotation. A vertical stripe pattern was rotated around the animal, reliably eliciting an optomotor turning response in the direction of stimulus motion. (B) Walking legs are denoted as outer legs (O1 to O3) and inner legs (I1 to I3), depending on turning direction (broken arrow). For example, in clockwise rotations left legs are outer legs and right legs are inner legs. (Ci–Cviii) Examples of walking paths (left) and corresponding gait patterns (right) of each one of the eight animals used in this study. Walking paths: Head position (circles) and orientation of the body axis (line segments) are indicated for every 20th record of the tracking system. Open and filled symbols indicate the pre-stimulus period (first 7.5 s) and stimulus period (last 15 s), respectively. Width of the scale grid, 10 cm. Path curvature is always such that a loop in the path remains within one field of the grid. Gait patterns: Stance phases (power strokes) of each leg are indicated by a row of black bars. Rows from top to bottom show left front, middle and hind leg, followed by right front, middle and hind legs, respectively. Time runs from left to right, with vertical lines spaced by 7.5 s, indicating the pre-stimulus, transition and curve-walk period of each trial. The bold vertical line marks stimulus onset. Gait patterns are sometimes time-varying within single stimulus periods and vary strongly between animals, even if the walked path is fairly similar (e.g. compare Ci, Cvi and Cvii). Red diagonal lines highlight back-to-front waves of step cycles during tetrapod-like gait, blue vertical lines highlight in-phase step cycles of ipsilateral front and hind legs during tripod-like gait.

used by engineers that design step controllers for legged machines. It expresses the fact that the step cycle of each leg depends on a number of internal and context variables, and that a stable repetitive pattern is not always produced. Fig. 1 shows that a free gait was observed for each one of eight walking stick insects.

The lack of a stable repetitive pattern, however, poses severe problems for the quantification of leg coordination. As the cycle periods change continuously, relating the step cycle of a given leg to the step cycle of its neighbour would be appropriate to quantify the coherence of two step rhythms, but coherence is a result of several interacting physiological coordination mechanisms and does not indicate the efficacy of any known mechanism in particular. Although phase analyses are a powerful descriptive tool, they do not relate the timing of a step to an observable event or a measurable state variable and, therefore, provide only indirect information about causal coordination mechanisms. In order to quantify the coupling strength of a coordination mechanism, it is desirable to determine the significance of a given event or state variable for entrainment or reset of a given pattern. For this reason, the following analysis introduces measures of coupling strength and efficacy that are directly related to coordination rules derived from behavioural experiments on walking arthropods (reviewed by Cruse, 1990).

The role of touch-down as a coordinating event

From behavioural experiments on stick insects, three coordination rules have been proposed to act between ipsilateral legs. In two of these, rules 1 and 2 *sensu* Cruse et al. (1995), the sender leg is posterior to the receiver leg, i. e. hind legs affect middle legs and middle legs affect front legs (Fig. 2A). Rule 1 states that stance–swing transition in the receiver leg is inhibited during swing movement of the sender leg. Rule 2 states that stance–swing transition in the receiver leg is excited for a brief period after the sender leg begins or resumes stance movement (the typical case after touch-down). Note that inhibition does not imply prevention of lift-off, and excitation does not imply that lift-off is invoked. Rather, both of these rules affect the likelihood of a stance–swing transition in the receiver leg, depending on the time relative to touch-down of the sender leg (Fig. 2B). Moreover, by affecting the likelihood of a stance–swing transition, the rules have a sustained effect on the likelihood of a leg to be in swing mode. This is because swing phases typically last for at least 200 ms, and stance phases last even longer. Accordingly, the likelihood to be in swing mode is zero for some time before a given stance–swing transition, and one for some time after the transition.

A useful measure of coupling strength can be obtained by calculating how reliable the effect of a coordination rule is. For example, coupling strength of rules 1 and 2 can be determined by looking up each touch-down event in a sender leg and

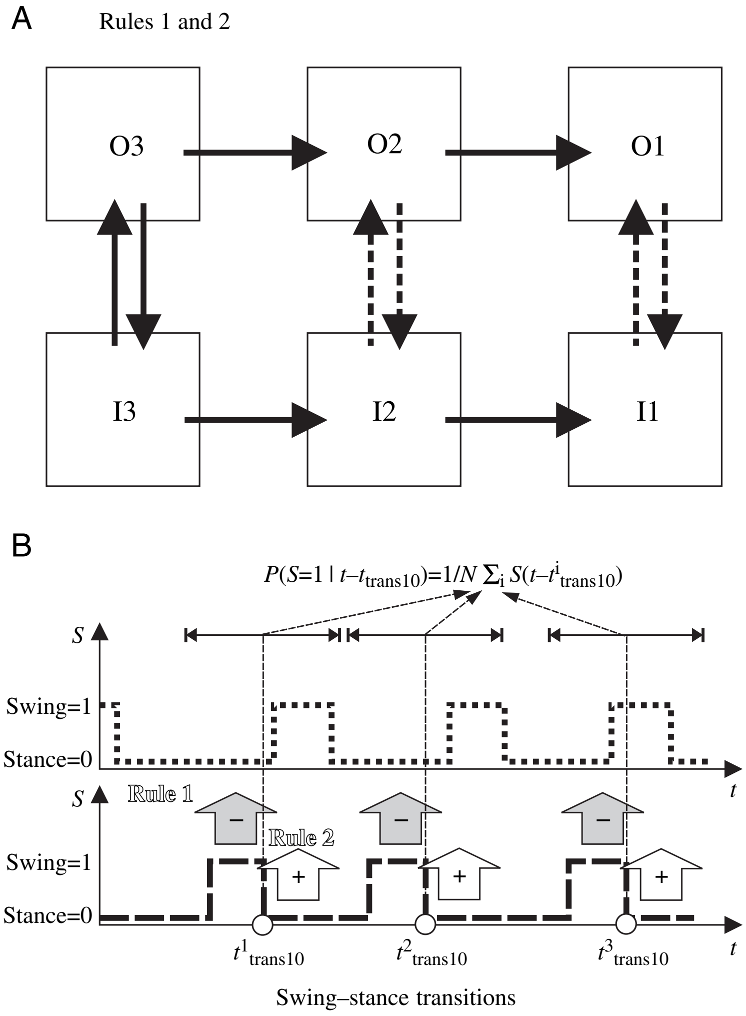

Fig. 2. Leg coordination rules 1 and 2. (A) Leg coordination rules 1 and 2, *sensu* Cruse et al. (1995), act ipsilaterally in an anterior direction and contralaterally between intrasegmental leg pairs (arrows point from sender to receiver leg). Rule 1 supposedly does not act between middle and front legs (broken arrows). Legs are labelled according to the standardised clockwise turning direction. (B) Quantification of coupling strength associated with rules 1 and 2. Step cycle timing of a leg is considered a sequence of alternating, mutually exclusive states S over time t, assuming value 0 for stance and value 1 for swing. In an ipsilateral leg pair, rule 1 inhibits stance–swing transition in the anterior leg (dotted line, receiver leg) whenever the posterior leg (broken line, sender leg) is in state 1 (large grey arrows). In the same leg pair, rule 2 excites stance–swing transition in the anterior leg soon after swing–stance transition of the posterior leg. Thus, if rules 1 and 2 were effective, the receiver leg should undergo a stance–swing transition at the time of a swing–stance transition of the sender leg (trans10). Coupling strength is calculated by summing the state of the receiver leg for a given time bin (t–t_{trans10}) within a time window (horizontal arrows between stops) for each one of N steps belonging to the same stimulus period. Division by N gives the likelihood of the receiver leg to be in state 1, given a particular time delay relative to the swing–stance transition in the sender leg. If coupling according to rules 1 and 2 is strong, values are expected to be close to zero before t_{trans10} (rule 1) and close to unity after t_{trans10} (rule 2).

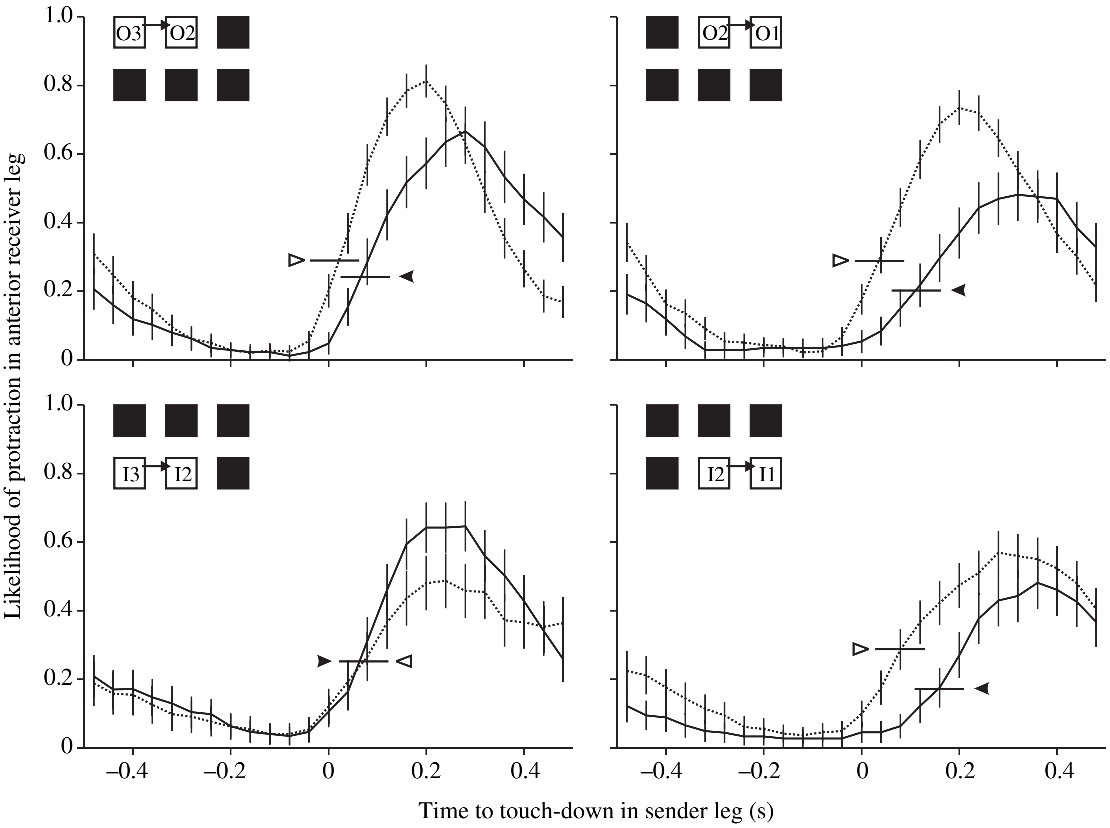

Fig. 3. Coupling strength of rules 1 and 2 between ipsilateral legs. Likelihood of protraction in anterior legs (receiver legs) relative to t_{trans10} (see Fig. 2), i.e. time of touch-down in posterior legs (sender legs). Coupling strength is plotted for the straight walking sequence of the pre-stimulus period (solid lines) and the curve walking sequence of the second half of the stimulus period (dotted lines). Error bars indicate 95% confidence intervals. Inserts indicate the leg pair concerned (see Fig. 1B). Horizontal line segments marked with arrowheads indicate the baseline, i.e. the level expected without any coordinating influences (solid arrowheads: straight walking; open arrowheads: curve walking). The latter was evaluated from step sequence pairs taken from independent trials. Rule 1 is always acting strongly, as values prior to touch-down are close to zero and significantly below the baseline. Values are similar for straight and curve walking. Coupling strength associated with rule 2 changes with the behavioural context of the animal. During curve walking it increases in outer legs and decreases or remains similar in inner legs.

calculating the fraction of events in which the receiver leg was in swing mode within some time window before and after the event. The corresponding mathematical equation is:

$$P\,(S = 1 \mid t - t_{\mathrm{trans10}}) = 1 / N\, \Sigma_{\mathrm{i}}(t - t^{\mathrm{i}}_{\mathrm{trans10}})\ ,$$

(see also Fig. 2B), where the state variable S at time $t - t_{\mathrm{trans10}}$ is averaged for each one of N trans10 transitions. Since the state variable is 1 during swing mode and zero during stance mode, the result equals the likelihood of the receiver leg to be in swing mode, given a certain delay to touch-down in the sender leg.

If rule 1 was deterministic rather than stochastic and applied to each single step cycle, the likelihood of the receiver leg to be in swing mode would be zero before touch-down because swing was inhibited each time. If rule 2 applied to each single step cycle, likelihood would equal one soon after touch-down. If neither of these rules ever applied, the likelihood would equal the expected value for independent step sequences. Essentially, the latter is equal to the average fraction of the step cycle period in which the receiver leg is in swing mode. This baseline value typically lies between 0.15 and 0.3 in *Carausius morosus*. The coupling strength of the coordination rule can thus be defined as the difference between the observed coupling strength and its respective baseline value. Extreme values of the likelihood functions are tabulated in Table 1, listing their magnitude, time of occurrence as well as the corresponding baseline.

Ipsilateral leg pairs

Much as predicted above, ipsilateral coupling strength due to rules 1 and 2 is clearly below or above baseline, respectively (Fig. 3). Each one of the eight curves in Fig. 3 have minimum values between 0.012 and 0.041, occurring 0.08–0.24 s before touch-down of the posterior leg, indicating a strong effect of rule 1. Peak likelihood lies between 0.482 and 0.813, occurring 0.2 to 0.36 s after touch-down of the posterior leg (Table 1), indicating a strong effect of rule 2. For comparison, baselines range between 0.174 and 0.291. During straight walking, coupling strength according to rule 2 is stronger between hind and middle legs (0.646 to 0.667) than between middle and front

Table 1. *Coupling strengths of the three major coordination rules*

		Rule 1			Rule 2			Rule 3		
		Min	Δt	Zero	Max	Δt	Zero	Max	Δt	Zero
Ipsilateral pairs										
I3–I2	S	0.035	–0.08	0.255	0.646	0.28	0.255	–	–	–
	C	0.041	–0.08	0.255	0.487	0.24	0.255	–	–	–
I2–I3	S	–	–	–	–	–	–	0.582	–0.20	0.240
	C	–	–	–	–	–	–	0.341	–0.24	0.180
I2–I1	S	0.028	–0.04	0.174	0.482	0.36	0.174	–	–	–
	C	0.037	–0.12	0.290	0.569	0.28	0.290	–	–	–
I1–I2	S	–	–	–	–	–	–	0.580	–0.36	0.254
	C	–	–	–	–	–	–	0.504	–0.28	0.257
O3–O2	S	0.012	–0.08	0.243	0.667	0.28	0.243	–	–	–
	C	0.020	–0.16	0.295	0.813	0.20	0.295	–	–	–
O2–O3	S	–	–	–	–	–	–	0.594	–0.24	0.267
	C	–	–	–	–	–	–	0.688	–0.16	0.258
O2–O1	S	0.029	–0.24	0.202	0.482	0.32	0.202	–	–	–
	C	0.021	–0.12	0.291	0.735	0.20	0.291	–	–	–
O1–O2	S	–	–	–	–	–	–	0.514	–0.36	0.250
	C	–	–	–	–	–	–	0.729	–0.20	0.299
Contralateral pairs										
I3–O3	S	0.152	–0.08	0.262	0.420	0.28	0.262	0.406	–0.44	0.265
	C	0.122	–0.04	0.259	0.413	0.20	0.259	0.414	–0.24	0.262
O3–I3	S	0.121	–0.12	0.239	0.392	0.44	0.239	0.381	–0.48	0.239
	C	0.077	–0.08	0.178	0.247	0.36	0.178	0.269	–0.20	0.181
I2–O2	S	0.175	–0.04	0.245	0.324	0.52	0.245	0.328	–0.40	0.247
	C	0.262	–0.08	0.296	0.336	0.48	0.296	0.358	–0.48	0.298
O2–I2	S	0.170	–0.20	0.253	0.368	0.44	0.253	0.317	–0.20	0.259
	C	0.222	–0.20	0.256	0.305	0.48	0.256	0.266	–0.32	0.258
I1–O1	S	0.072	–0.12	0.199	0.363	0.40	0.199	0.364	–0.40	0.203
	C	0.135	–0.08	0.291	0.408	0.44	0.291	0.492	–0.24	0.289
O1–I1	S	0.060	–0.16	0.175	0.319	0.40	0.175	0.336	–0.40	0.180
	C	0.134	–0.08	0.290	0.452	0.24	0.290	0.374	–0.24	0.288

For a given leg pair (sender leg–receiver leg), each row lists the minimum and/or maximum of the corresponding likelihood functions shown in Figs 3, 4, 6 and 7 (min/max), the time delay relative to the transition of the sender leg (Δt in s), and the baseline level (zero) in either the straight walking context (S) or the curve walking context (C). The difference between max/min and zero is defined as the coupling strength. The efficacy of a coupling rule is defined as (max–zero)/(1–zero) for rules 2, 3 and (zero–min)/zero for rule 1 (see Fig. 8).

legs (0.482). In contrast, coupling strength due to rule 1 is very similar for all leg pairs.

The likelihood minima in Fig. 3, indicating coupling according to rule 1, are very similar during straight and curve walking. As the baseline is elevated during curve walking, coupling strength according to rule 1 increases too. In contrast, there is a clear context-dependent increase of peak likelihood associated with rule 2 in outer leg pairs. Larger peak values are accompanied by a reduced delay relative to touch-down and a moderate rise in baseline. Inner leg pairs undergo different changes during curve walking. There is a significant reduction of the peak likelihood for the rear pair of inner legs, but an increase for the front pair. However, as the baseline of the front pair rises by the same amount as the peak value, there is no change in coupling strength.

In summary, as the stick insects change from straight to curve walking, coupling strength according to rule 1 remains the same (from –0.214 to –0.220) between inner hind and middle leg, but increases in all other ipsilateral leg pairs (straight: –0.146 to –0.231; curve: –0.253 to –0.275). This increase is due to a raised baseline, accompanied by nearly constant likelihood minima. Coupling strength of rule 2 increases in outer legs (0.424 to 0.518 between O3/02, 0. 280 to 0.444 between O2/O1), remains stable between inner middle and front legs (0.308 and 0.279) and decreases between inner hind and middle leg (from 0.391 to 0.232).

Contralateral leg pairs

Rule 2 has been suggested to be active symmetrically between contralateral leg pairs as well (Cruse and Knauth, 1989), whereas rule 1 is typically claimed to be absent (but see Dean, 1991b). Naturally, the above analysis can be applied to pairs of intrasegmental front, middle and hind legs (Fig. 4), using each leg once as a sender leg and once as a receiver leg.

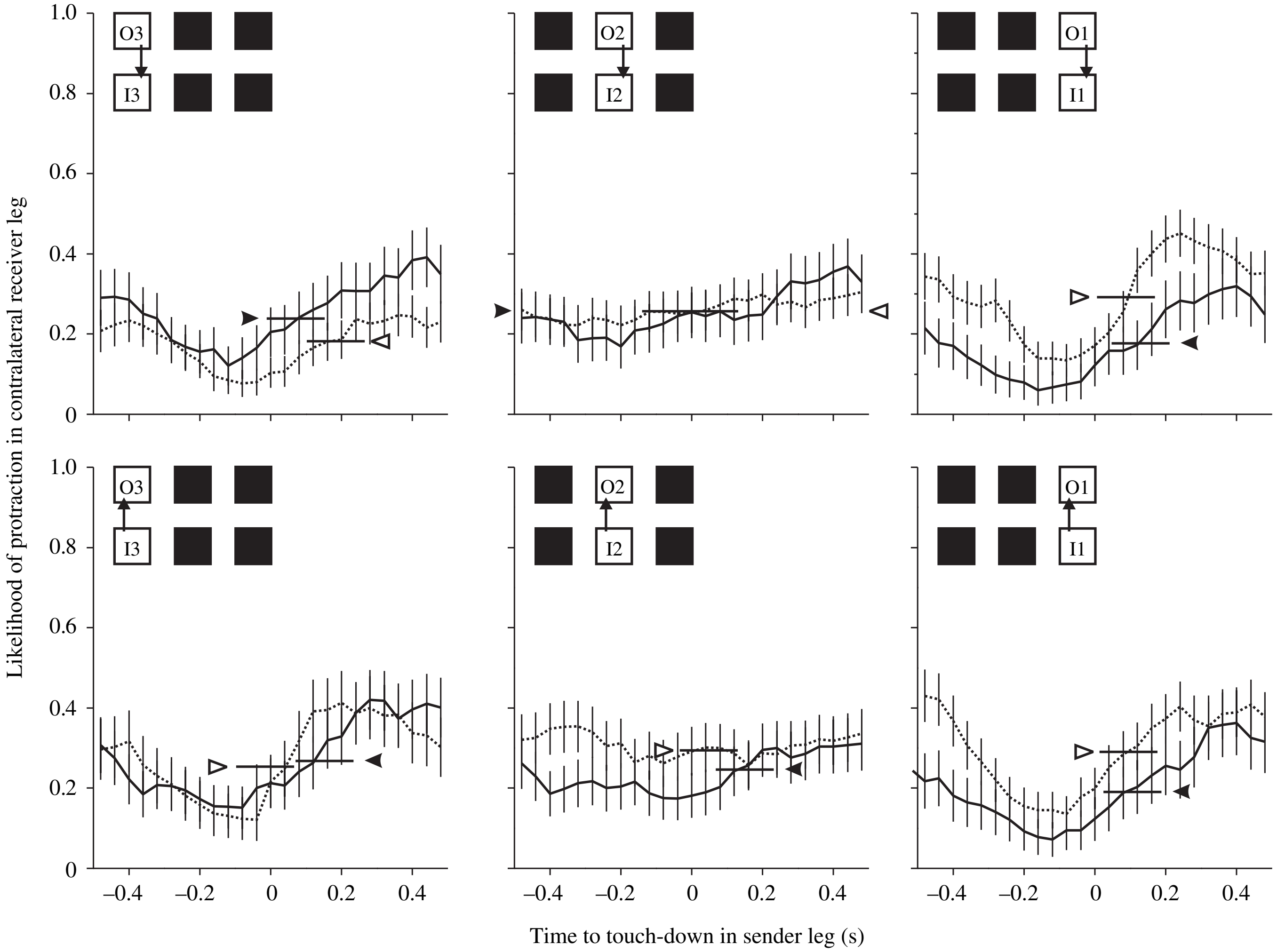

Fig. 4. Coupling strength of rules 1 and 2 between contralateral legs. Likelihood of protraction in receiver legs of one side relative to time to of touch-down (t–t_{trans10}) in sender legs of the other side. Same plot details as in Fig. 3. (Top) Outer legs are sender legs, inner legs are receiver legs; (bottom) inner legs are sender legs, outer legs are receiver legs. For middle legs, likelihood values deviate little from the baseline, indicating complete lack of contralateral coupling. Coupling strength of rules 1 and 2 between intrasegmental front and hind legs is a lot weaker than for ipsilateral leg pairs. During curve walking the observed changes are in the same range as the shift of the baseline, indicating little or no context dependence.

Compared to ipsilateral leg pairs, contralateral coupling is much weaker. The resulting plots of coupling strength do not always show a pronounced trough related to rule 1 or peak related to rule 2. Between middle leg pairs, the lack of either peak or trough suggests the absence of significant contralateral coupling.

For hind leg and front leg pairs, likelihood minima range between 0.06 and 0.152, occurring 0.04 to 0.16 s prior to touch-down of the contralateral leg. Peak likelihood lies between 0.247 and 0.452, occurring 0.2 to 0.44 s after to touch-down of the contralateral leg (Table 1). As baselines range between 0.178 and 0.291 for these leg pairs, coupling strength is in the range of –0.101 to –0.157 for rule 1 and 0.069 to 0.169 for rule 2. This is approximately half the strength of ipsilateral coupling.

When changing from straight to curve walking, peak likelihood undergoes a positive shift in front leg pairs and a negative shift in the hind leg pair O3/I3. In most contralateral leg pairs, the corresponding shift in baseline is of similar magnitude, indicating that contralateral coupling strength of rules 1 and 2 changes little or not at all in a context-dependent manner.

The role of lift-off as a coordinating event

The third leg coordination rule that affects the timing of stance–swing transitions has been described to couple ipsilateral leg pairs in a posterior direction (Cruse and Schwarze, 1988). This coordination rule will be called rule 3 *sensu* Cruse et al. (1995). Like rule 2, it has been described to act contralaterally as well (Cruse and Knauth, 1989). Apart from its direction of action (Fig. 5A), the major difference to rules 1 and 2 is that it is active during late stance. Thus, the part of the step cycle in which rule 3 is active is related to the stance–swing transition, i.e. lift-off, of the sender leg.

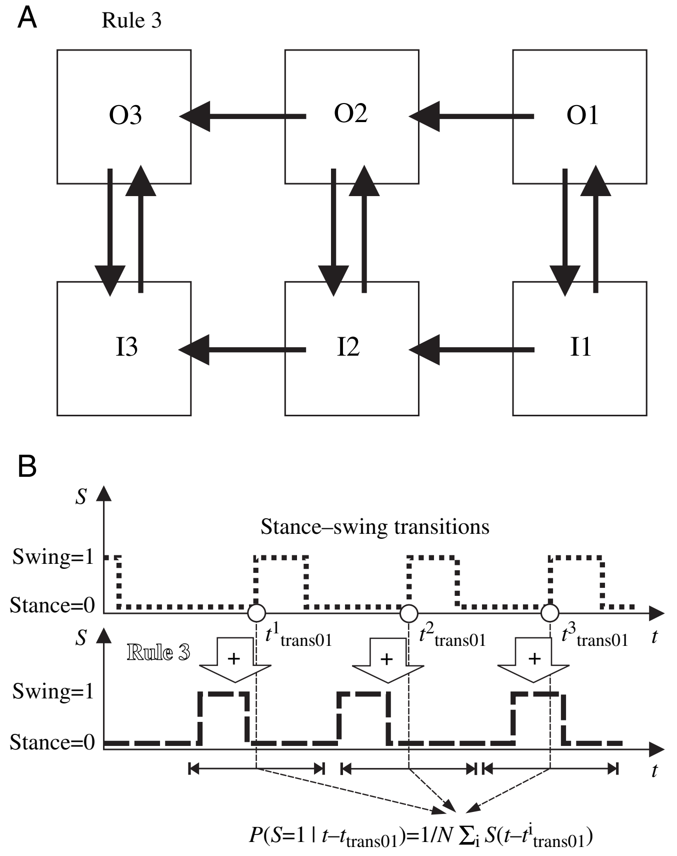

Fig. 5. Leg coordination rule 3. (A) Leg coordination rule 3, *sensu* Cruse et al. (1995), acts ipsilaterally in a posterior direction and contralaterally between intrasegmental leg pairs (arrows point from sender to receiver leg). Legs are labelled according to the standardised clockwise turning direction. (B) Quantification of coupling strength associated with rule 3. Step cycle sequences of state S over time t for an ipsilateral leg pair, as in Fig. 2. Rule 3 excites stance–swing transition in the posterior leg (broken line, receiver leg) if the anterior leg (broken line, sender leg) is close to a stance–swing transition. Thus, if rule 3 is in effect, the receiver leg should undergo a stance–swing transition prior to a stance–swing transition of the sender leg (trans01). The coupling strength of this rule is calculated by summing the state of the receiver leg for a given time bin (t–t_{trans01}) within a time window (horizontal arrows between stops) for each one of N steps belonging to the same stimulus period. Division by N gives the likelihood of the receiver leg to be in state 1, given a particular time delay relative to the stance–swing transition in the sender leg. If coupling according to rule 3 was strong, values would be expected to be close to unity before t_{trans01}.

Accordingly, coupling strength due to rule 3 must be calculated as the likelihood of a receiver leg to be in swing mode, depending on the delay relative to a stance–swing transition (t–t_{trans01}) in a sender leg. Fig. 5B shows the corresponding scheme, where an excitatory influence, that occurs during late stance of the sender leg, raises the likelihood of a stance–swing transition in a receiver leg. The corresponding equation follows the same rationale as explained in relation to Fig. 2B. If rule 3 was in effect in each single step cycle, the likelihood of receiver leg to be in swing would equal one prior to time of lift-off of the sender leg (t_{trans01}).

Ipsilateral leg pairs

Fig. 6 shows that coupling strength associated with rule 3 reaches a peak prior to lift-off, followed by a significant trough soon after lift-off. Peak values lie within 0.341 and 0.729 and these are reached 0.36 to 0.16 s prior to lift-off (Table 1). Differences are mainly due to behavioural context as peak values during straight walking vary only between 0.514 and 0.594, which is only about half the range of rule 2. Baselines range between 0.180 and 0.299. Coupling strength minima are similarly pronounced as those related to rule 1 (compare with Fig. 3), which could indicate the presence of an inhibitory effect after lift-off. Note that this would be equivalent to a posterior action of rule 1, i.e. suppressed lift-off in a posterior leg during swing mode of an anterior leg.

During curve walking, peak likelihood increases in outer leg pairs (O2/O3, 0.688; O1/O2, 0.729) and decreases in inner leg pairs (I1/I2, 0.504; I2/I3, 0.341). Also, in three of four leg pairs, peaks shift closer to time of lift-off in the sender leg. As none of these changes can be explained by equivalent shifts in baseline, they reflect changes in coupling strength. Whereas coupling strength of rule 3 is between 0.264 and 0.342 during straight walking, it decreases during curve walking to 0.161 or 0.247 in inner leg pairs, and increases to 0.430 in outer leg pairs. Thus, coupling due to rule 3 is context-dependent.

Contralateral leg pairs

When applied to contralateral leg pairs, the analysis reveals similar results for rule 3 as have been described previously for rule 2. As can be seen in Fig. 7, contralateral coupling strength is marked by relatively shallow peaks in hind and front legs. They range from 0.269 to 0.492 and occur 0.48 to 0.2 s prior to lift-off of the sender leg. No clear peak is discernable for middle legs, indicating that they are not coupled according to rule 3. Finally, during curve walking the sizes of the observed changes in peak likelihood are approximately the same as the shift of the baseline, indicating little or no context dependence.

Discussion

Leg coordination of the stick insect *Carausius morosus* was analysed to measure coupling strength and efficacy of three behaviourally derived coordination rules during straight walking and visually induced curve walking. The results show that gaits vary strongly between animals, can change readily during the 22.5 s trials, and may differ between right and left legs even during straight walking (Fig. 1). Coupling strength associated with rules 1 and 2 is calculated as the coupling-induced change in likelihood of a receiver leg to be in swing, given a delay relative to swing–stance transition in the sender leg (Fig. 2). For both rules, this measure differs between ipsilateral (Fig. 3) and contralateral (Fig. 4) leg pairs. Coupling strength associated with rule 3 was determined by a similar measure as for rules 1 and 2, but related to stance–swing

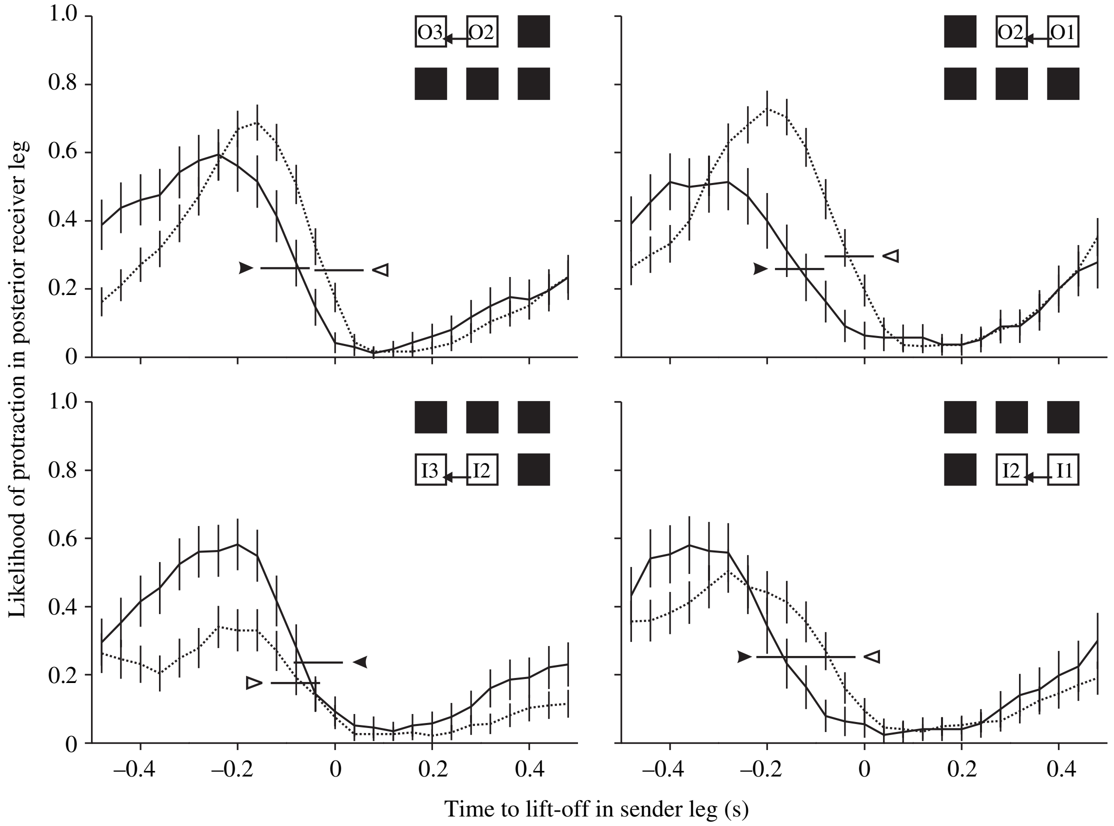

Fig. 6. Coupling strength of rule 3 between ipsilateral legs. Likelihood of protraction in posterior legs (receiver legs) relative to t_{trans01}, i.e. time to of lift-off, in anterior legs (sender legs, see Fig. 5). Coupling strength is evaluated for the straight walking sequence of the pre-stimulus period (solid lines, baseline marked by solid arrowhead) and the curve walking sequence of the late stimulus period (dotted lines, baseline marked by open arrowhead). Error bars indicate 95% confidence intervals. Inserts indicate the leg pair concerned (see Fig. 5B). Coupling strength associated with rule 3 is indicated by the peak likelihood of a receiver leg to be in swing mode prior to lift-off of the sender leg. Coupling strength changes with the behavioural context of the animal. During curve walking it increases in outer legs and decreases or remains similar in inner legs.

transition in the sender leg (Fig. 5). This rule is also stronger for ipsilateral (Fig. 6) than for contralateral (Fig. 7) leg pairs. Coupling strength associated with each of the three coordination rules differs between the two behavioural situations and is, therefore, context-dependent (see Fig. 8).

Measuring coupling strength and efficacy

The present study applies a stochastic measure to quantify the strength of a given leg coordination mechanism. Moreover, it uses transitions between swing and stance mode as reference events, rendering the analysis time-dependent. Both of these properties, its stochastic nature and its time dependence, are somewhat different from the properties of measures previously applied. Typically, coordination of adjacent legs is described by phase histograms (e.g. Holst, 1943), or circular statistics measures thereof (e.g. Cruse and Knauth, 1989; Clarac and Chasserat, 1986). Using the terminology of coupled sender and receiver legs, phase histograms relate the occurrence of a step transition in a receiver leg to the normalised step cycle period of the sender leg. Due to the variability of both the step cycle period of the sender leg and the relative timing of transitions in the receiver leg, the width of the histogram peak cannot be related to an event in the step cycle of either leg. However, since coupling mechanisms trigger discrete transitions between antagonistic actions, they must either depend on a discrete triggering event, e.g. an entraining reference clock signal, or on thresholds of one or more physiological parameters, e.g. the spike thresholds in a motoneuron pool. Phase histograms reveal dependence on discrete events or thresholds only if either the rhythm of the sender leg is very regular, or if the peak of the histogram is very narrow, i.e. shows very little variability. In the first case, the result indicates a clear temporal relation to the state transitions in the sender leg. In the second case, the result indicates the presence of a threshold that is reached at a certain phase of the sender's step cycle.

In contrast to phase histograms, the stochastic measure applied here is always time-locked to a behavioural event: lift-off or touch-down of a leg. Thus, coupling strength can be interpreted as the fraction of transition events that is attributable to a given coordination rule. Since leg mechanosensors encode changes in load and ground contact, information about transition events is supplied to the nervous system. Assuming that three distinct neural mechanisms give rise to coordination rules 1 to 3, coupling strength indicates the

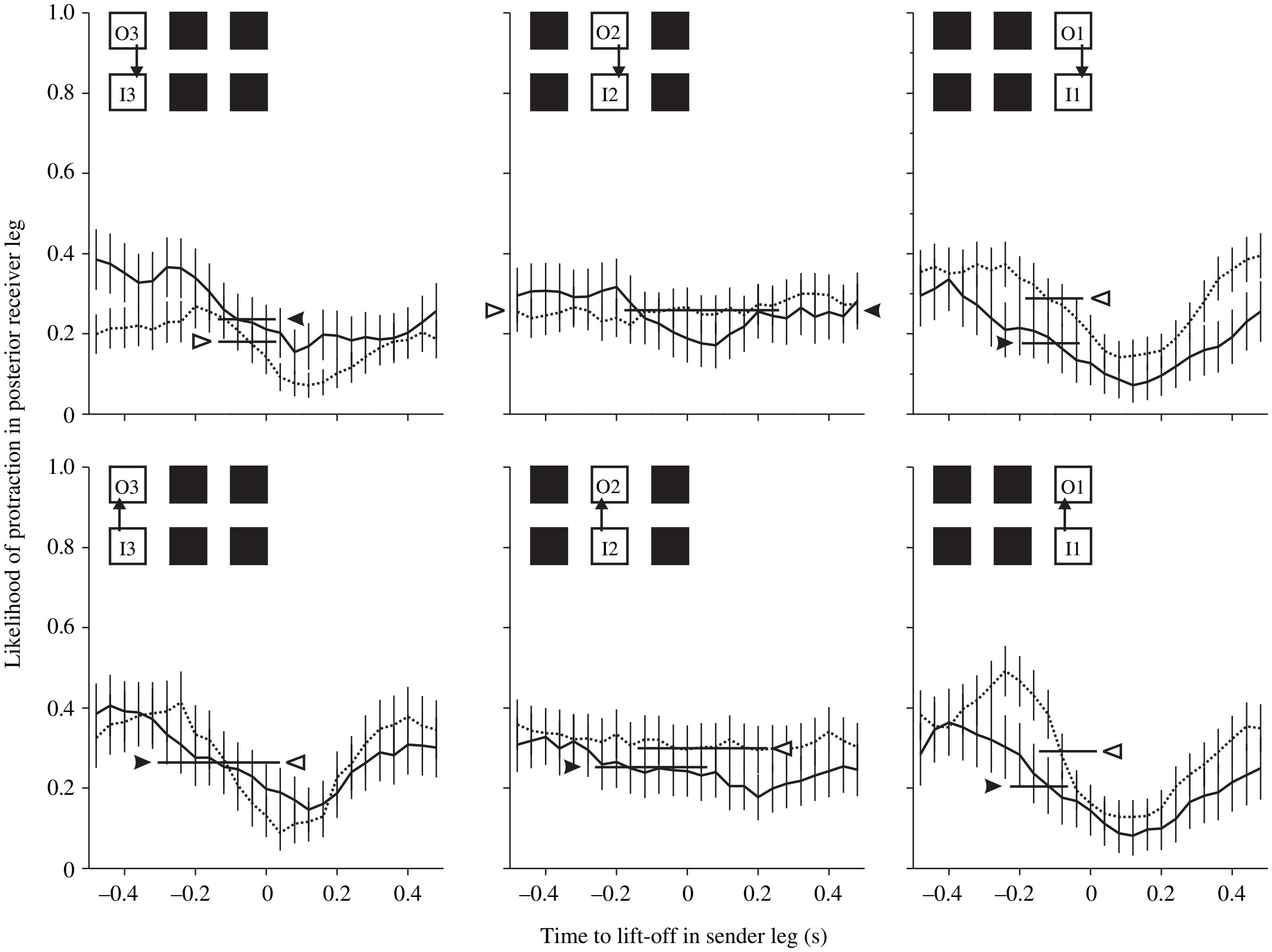

Fig. 7. Coupling strength of rule 3 between contralateral legs. Likelihood of protraction in receiver legs of one side relative to time of lift-off (t_{trans10}) in sender legs of the other side. Same plot details as in Fig. 6. (Top) Outer legs are sender legs, inner legs are receiver legs; (bottom) inner legs are sender legs, outer legs are receiver legs. Peak likelihood was close to the expected baseline for the middle leg pair, indicating complete lack of contralateral coupling. In front and hind legs, coupling strength associated with rule 3 is much weaker than for ipsilateral leg pairs. During curve walking, the observed changes are in the same range as the shift of the baseline, indicating little or no context dependence.

strength by which these mechanisms act to shift the likelihood of a transition event away from baseline. Therefore, this measure can serve as a quantitative behavioural reference value for electrophysiological studies on reduced preparations.

A further advantage of this approach is that each rule makes clear-cut predictions and, therefore, allows calculation of its efficacy. Efficacy, indicated by the arrow widths in Fig. 8, is defined as the fraction of step cycles that is consistent with a given rule. The more consistent a step pattern is with a given coordination rule, the more important must be the associated mechanism in generating the stepping pattern. Irrespective of the nature of the underlying neural mechanism, efficacy can be compared between types of rules, contralateral and ipsilateral leg pairs, and behavioural contexts.

Evidence for the three coordination rules is based on statistics of stepping patterns (Wilson, 1966; Graham, 1978a), disturbance of single step cycles (e.g. Cruse and Epstein, 1982; Cruse and Schwarze, 1988), mechanical uncoupling of left and right legs (e.g. Cruse and Knauth, 1989) or comparison of model simulations with natural step sequences (e.g. Graham, 1978a,b). Rules 1 and 2 are related in the sense that both have been postulated to be time-dependent with respect to the swing–stance transition of the sender leg. Rule 1 acts whenever the sender leg is in swing mode (Wilson, 1966; Graham, 1978a; Cruse and Epstein, 1982). Rule 2 acts for a brief period after the sender leg begins or resumes stance (Cruse and Schwarze, 1988; Cruse and Knauth, 1989). Although the excitatory effect of rule 2 immediately follows the inhibition mediated by rule 2, there is evidence that rule 2 is not just due to a post-inhibitory rebound effect: the onset of a stance can raise the probability of lift-off in the receiver leg if stance movement is resumed after an experimental interruption (Cruse and Schwarze, 1988). Other than rules 1 and 2, rule 3 is not time-dependent but position-dependent (Dean and Wendler, 1983; Cruse and Schwarze, 1988). Moreover, it is thought to increase in strength with increasingly caudal tarsus position of the sender leg. Indeed, Ludwar et al. (2005) have recently found in a stick insect preparation with a single walking front leg that the spike rate of a mesothoracic levator neuron increases during the stance phase of the ipsilateral front leg. This may be indicative of a posterior directed, position-dependent synaptic drive that increasingly facilitates lift-off in

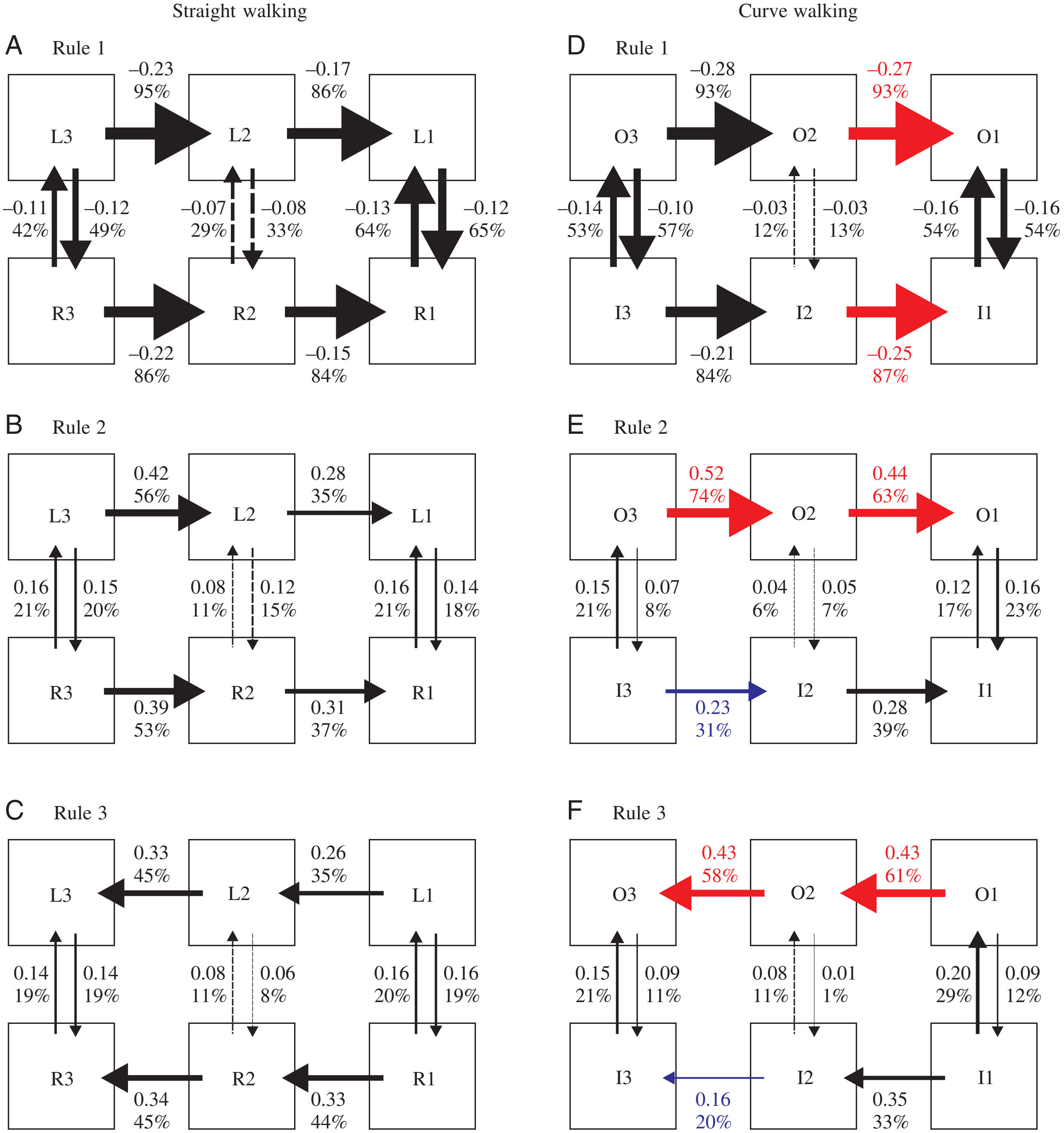

Fig. 8. Local and context-dependent differences in leg coupling strength. Coupling strength (numbers) and efficacy (percentages) of the three main coordination rules (sensu Cruse et al., 1995) known to be present in the walking stick insect. (A–C) Rules 1–3, respectively, for straight walking. L, left; R, right leg. (D–F) Rules 1–3, respectively, for curve walking. O, outer; I, inner leg. Arrows point from sender to receiver legs. Arrow size is scaled to the efficacy of the rule. Coupling strength is the difference between the likelihood maxima (rules 2 and 3) or minima (rule 1) and the baseline. Efficacy indicates the percentage of the maximum coupling strength possible, i.e. the situation if a rule held in each single step cycle. This is equivalent to the fraction of step cycles by which a given coordination rule increased (rules 2 and 3) or decreased (rule 1) the likelihood of protraction. Coloured arrows mark coordination rules for which the coupling strength changed significantly (red, increase in strength; blue, decrease in strength). Coordination strength and efficacy vary strongly between rules and between leg pairs. During curve walking, coordination rules undergo a context-dependent change in strength and efficacy. Rule 1 becomes more effective between ipsilateral front/middle leg pairs. Efficacy of rules 2 and 3 increases between outer leg pairs and decreases between inner hind and middle leg.

Table 2. *Literature values of coupling strength during straight walking*

	Ipsilateral			Contralateral		
	Rule 1	Rule 2	Rule 3	Rule 1	Rule 2	Rule 3
Dean, 1991b	–0.62	0.19 to 0.57	–0.26 to 0.26	–0.62	0.19 to 0.48	0-0.48
Espenschied et al., 1993	–0.3	0.5	0 to 0.29	–0.06	0.05	0 to 0.39
Calvitti and Beer, 2000	–0.3	0.5	0 to 0.3	–	0.05	0 to 0.45
This study	–0.23 to –0.15	0.28 to 0.42	0.26 to 0.34	–0.13 to –0.07	0.08 to 0.16	0.06 to 0.16

Rows give the coupling strength of each coordination mechanism as used by the cited studies. In all of these studies, coupling strength was implemented as a shift of the posterior extreme position, i.e. the threshold position triggering lift-off, as a fraction of the stride length. Where ranges are given, they indicate velocity dependence of rule 2 and position-dependence of rule 3. Contralateral rule 1 of Dean (1991b) acts only between hind legs.

Note that the ranges given for this study indicate differences between legs rather than dependence on position or velocity. Moreover, as coupling strength in this study is not scaled to stride length, only relative differences among rules are of interest. A scale factor may apply to successfully implement these values in simulation.

a middle leg. By measuring coupling strength associated with rule 3 as depending on time rather than on position of lift-off, the magnitude obtained is a weighted average within the range of lift-off positions. Assuming that the strength of the underlying mechanism linearly increases with position (as done by Müller-Wilm et al., 1992; Espenschied et al., 1993; Calvitti and Beer, 2000; but see Dean, 1991b), coupling strength as determined here equals the strength at the average lift-off position. An additional velocity dependence of rule 3, as suggested by Dean (1991b), would also have some effect on the coupling strength measure used here. However, because the likelihood of the receiver leg being in swing mode changes for the duration of an entire swing movement, the overlap would compensate for much of the velocity-dependence of the shift, changing location but not magnitude of the peak.

Differences between leg pairs

In the analyses shown in Figs 2–7, a leg pair is considered coupled according to a given coordination rule, if coupling-related likelihood is sufficiently different from the value expected for uncoupled step patterns. With the threshold chosen in this study, all adjacent leg pairs are coupled according to each one of the three coordination rules, the only exception being the contralateral pair of middle legs (broken arrows in Fig. 8). Coupling strength of ipsilateral leg pairs is about twice that of contralateral leg pairs. Coupling due to rule 2 also differs considerably between ipsilateral leg pairs, being stronger in the rear pair.

Comparing the three rules, coupling strength due to rule 2 is slightly larger than that due to rule 3, and yet again larger than that due to rule 1. This ranking is of functional importance where a receiver leg is influenced by several mechanisms and/or by several sender legs. This is particularly so if all mechanisms act on the same variable, which is a feature common to all leg coordination schemes suggested for insects later than that proposed by Dean (1991b). However, ranking of coordination rules looks different when considering the efficacy of each rule (arrow width in Fig. 8) rather than coupling strength. In terms of efficacy, rule 1 is about twice as strong as rules 2 and 3. In other words, 100% efficacy of rule 1 in suppressing swing-movements requires less coupling strength than does 100% efficacy of rule 2 in inducing a swing movement. This is because any leg is less likely to be in swing mode than in stance mode, as is reflected by the baselines in Figs 2–7, which are always asymmetric with respect to the two extremes. Whereas the behavioural relevance of a coordination rule is best reflected by its efficacy, the strength of an underlying physiological mechanism is best reflected by coupling strength. For instance, a neural signal from a sender leg may directly affect the likelihood of lift-off in a receiver leg, but the same signal will result in different efficacy, depending on the ratio of protraction and retraction time.

It is important to note that coupling strength as measured in this study refers to regularities in behaviour rather than to an identified neural mechanism. Because several neural mechanisms may cause inter-leg coupling either directly or indirectly (see below), the values given in Fig. 8 must be considered relative measures that can be interpreted as a summed effect of various neural mechanisms contributing to a given coordination rule. An example where an indirect effect of local sensory feedback mechanism contributes to coupling strength is rule 1. Contralateral coupling due to rule 1 has often been ruled out because contralateral legs may swing simultaneously at times, although in general they step alternately. The low coupling strength reported in Figs 5 and 8 reflects this ratio. To date, it cannot be excluded that neural inhibitory coupling of contralateral legs exists, since bilateral swing movements could occur if weak contralateral coupling was overridden by a stronger ipsilateral mechanism, e.g. if rule 3 tended to enforce lift-off in a hind leg while rule 1 tended to suppress it. On the other hand, there are local sensory feedback signals that affect the likelihood of stance–swing transitions in addition to coordinating signals from adjacent legs. For instance, increased load (Cruse, 1985) and increasingly caudal tarsus position (Bässler, 1977) have competing effects on stance–swing transition. In particular, a load-dependent inhibition of lift-off can create the same effect as a contralateral rule 1: during swing movement of a leg, the contralateral leg in stance takes on an additional load. If this load increase was sufficient to suppress lift-off, the effect of rule 1 would be caused by mechanical dependencies rather than neural connections. This effect has been documented in curve-walking stick insects (Jander, 1985). Similarly, the strong contralateral coupling according to rule 1 between hind legs in walking cats (Cruse and Warnecke, 1992) is probably mostly due to unilateral load-dependent feedback from Golgi tendon organs that prevent flexion and, therefore, lift-off (reviewed by Pearson, 1995). In stick insects, the centre of gravity lies behind the hind leg coxae, so the swing movements of a hind leg cause increased loading of the ipsilateral middle leg, though to a lesser extent than of the contralateral hind leg. Given that coupling strength due to rule 1 between ipsilateral leg pairs is twice that between hind legs, this strong effect could only be caused by a load reflex alone if the gain was much higher in middle legs than in hind legs. Similar considerations lead to the conclusion that coupling strength associated with rule 2 is partly due to unloading of a leg as a result of touch-down and corresponding load-sharing by an adjacent leg.

To date, sensitivity studies on the relative contribution of the three coordination rules to hexapod walking have been carried out in software (Dean, 1992b; Calvitti and Beer, 2000) and hardware models (Espenschied et al., 1993). All of these studies agree in that the three coordination rules are redundant in that each one of them can be deleted without failure of coordinated walking. The solutions preferred by these studies (Table 2) differ mainly in coupling strength according to rule 1, velocity dependence of rule 2 and an inhibitory branch of the rule 3 characteristic as used by Dean (1991b). Comparing the relative differences among rules between the present study and literature values for straight walking (Table 2), the present results agree best with the settings used by Espenschied et al. (1993). What is different according to the present results is the lower coupling strength of ipsilateral rule 1 and contralateral rule 3. It is interesting to note that the results of Espenschied et al. (1993) indicate that overall stability is most sensitive to coupling strength associated with rule 3.

Context dependence and functional significance

In contrast to all models of hexapod leg coordination, coupling strength differs not only between the three rules but also between ipsilateral leg pairs and between the two behavioural contexts. Curve walking naturally is an asymmetrical locomotor behaviour, as legs on the inner side of the curve have to produce different ground reaction forces than legs on the outer side of the curve. Although this asymmetry in force need not necessarily be overt in kinematic asymmetries of the leg movements, it is always accompanied by changes in stance direction and other kinematic variables (see the acccompanying paper, Dürr and Ebeling, 2005, and references therein). Fig. 8 illustrates the changes in leg coupling strength and efficacy as determined for equal periods of straight and curve walking. The four ipsilateral leg pairs stand out as being subject to context-dependent changes. Associated with the transition from straight to curve walking, rule 1 becomes stronger in both front/middle leg pairs, rules 2 and 3 become stronger for outer leg pairs and weaker between inner hind and middle leg (coloured arrows in Fig. 8). Whether or not this asymmetry in coupling alone is sufficient to give rise to a change in walking direction will have to be tested in forthcoming simulation experiments. Functionally, increased coupling strength between outer legs is likely to enhance cooperative effects on yaw rotation by coherent movement along the circular outer stance trajectory (Dürr and Ebeling, 2005). Conversely, uncoupling of the inner hind leg allows its tarsus to remain in stance for long periods and thus become the pivot around which the animal turns (see also Jander, 1985). Nevertheless, modelling studies have shown that coupling strength does not have to change to allow curve walking (Cruse et al., 1998; Kindermann, 2002) or to change walking speed (Müller-Wilm et al., 1992), results that have contributed substantially to the view that coordination rules 1 to 3 account for adaptive features of the locomotor system. Here I report a change in coupling strength that is not accompanied by a significant change in forward velocity, as shown in fig. 3 in the acccompanying paper (Dürr and Ebeling, 2005). The present results show that coupling strength and efficacy depend on behavioural context, so the underlying coordination mechanisms must be subject to modulation. Therefore, the adaptive properties of the locomotor system, which are due to these coordination mechanisms, themselves adapt.

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