

The hub as a launching platform: rapid movements of the spider *Leucauge mariana* (Araneae: Tetragnathidae) as it turns to attack prey

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Abstract. Spiders are effectively blind with respect to the lines in their webs, and they commonly use exploratory leg movements to find lines, just as a blind man finds objects using a cane. Nevertheless, a mature female *Leucauge mariana* (Keyserling 1881), which spins a relatively open, sparsely-meshed hub and whose legs I and II hold widely-spaced radii rather than dense hub lines, turns precisely and rapidly when prey strike her orb. She can turn $> 90^\circ$, finding and grasping new lines with all her legs, in as little as 0.1 s and can reach a prey several body lengths away in as little as 0.23 s after impact. The hub design and resting postures of the spider's legs allow her to sense where the prey strikes the web, generate the force necessary to turn her body rapidly, and find lines to grasp. The spider may move most (if not all) of her legs, without obtaining further guidance information once the leg has begun to move until it nears the site where it will grasp a line. The order in which legs are moved is relatively consistent, and each tarsus moves to a site where lines are relatively abundant; some then make small, quick searching movements to find and grasp lines there. When radial lines were experimentally cut near the hub in a sector in which a prey was subsequently introduced, legs I and II first made small searching movements, and then executed much larger searching movements. The rapid leg movements directed toward specific areas where lines are abundant, and the small searching movements employed at these sites suggest that the spider modifies her behavior when she is at the hub of an orb.

Keywords: Leg movements, rapid orientation behavior, orb web design

To move in an orb web, a spider must first find lines before it can grasp them. Orb weavers are likely to be unable to see the lines in their webs and are thus essentially blind with respect to the positions of these lines. This is because many species build and operate their webs in the darkness, and the eyes of orb weavers are incapable of resolving such fine lines (Foelix 1996). In addition, their eyes are placed dorsally, while the lines are generally ventral to the spider's body. In most contexts, the spider's solution is to use its legs as tactile sense organs, waving and tapping with them like a blind man using his cane (e.g., Hingston 1920, 1922; Witt et al. 1968; Eberhard 1972; Vollrath 1992). An orb weaver's task is more difficult than that of a blind man, however: it has eight different legs, and it needs to find highly localized supports (the lines in its web) to sustain its weight.

Despite these problems, orb weavers generally take only a few seconds to reach insects that strike their webs. Average response times, from the moment of prey impact until initiation of biting or wrapping, were 6.9 s in *Nephila maculata* (Fabricius 1793) and 8.7 s in *Cyrtophora moluccensis* (Doleschall 1857) responding to blowflies (Lubin 1973), about 5.5 s in *Araneus diadematus* (Clerck 1757) responding to house flies (Witt et al. 1978), and from 1.7 to 3.8 s in *Cyclosa turbinata* (Walckenaer 1842) (R. Suter pers. comm.). Execution of such rapid responses to prey is physically challenging. By following the movements and positions of a spider's legs as they touch or grasp lines, it is possible to deduce the information it has available regarding the positions of lines, just as one can deduce from the movements of a blind man's cane which objects he has succeeded in locating as he moves through the environment.

One common tactic that spiders use to locate lines is following behavior (Eberhard 1972). First a more anterior leg

explores the space in front of the spider's body by waving and tapping, and finds and grasps a line there. Then the spider moves a more posterior leg forward and grasps the same line near the site held by the anterior leg. Then the anterior leg moves forward to explore for further lines. In this way a line is passed from one leg to the next and so on, and more posterior legs do not need to search for lines. Following behavior is probably widespread. It has been seen in a nephilid (Hingston 1922), a uloborid (Eberhard 1972), a tetragnathid (Eberhard 1987a), and several araneids (Jacobi-Kleemann 1953; Eberhard 1982; W. Eberhard unpubl. data on *Micrathena duodecimspinosa*) (Cambridge 1890).

Following behavior, however, is probably too slow for a spider at the hub of its orb when a prey strikes the web. Prey often escape quickly from orbs, and in many orb weavers more than half of the prey that strike the web escape (summary in Eberhard 1990), so the spider needs to turn rapidly toward the prey. Indeed, some spiders do respond quickly and precisely; the beginning of the response of *Nephila clavipes* (Linnaeus 1797) to vibrations occurred after a delay of only 0.1 s, and the spider turned to face the prey (with a precision of $3.6 \pm 7.7^\circ$) (mean \pm standard deviation) in only 0.04 s (Klärner & Barth 1982); corresponding times for *Zygiella x-notata* (Clerck 1757) were 0.1 and 0.6 s (Klärner & Barth 1982).

How are spiders able to accomplish such rapid reactions without being able to see the lines on which they depend for support? In some orb weavers, such as *Cyclosa turbinata* and *N. clavipes* (Suter 1978; Klärner & Barth 1982), the mesh of the hub is very tight, so lines are available nearby for all of the spider's tarsi to grasp wherever they are placed. In other species, however, such as many tetragnathids, the center of the hub is open (perhaps an adaptation to increase the web's ability to sag when prey strike it – Eberhard 1987a), and the

hub itself has relatively few lines, so more precise placement of the tarsi is necessary. In this study, we used high speed video recordings and experimental manipulations of webs to address the question of how *Leucauge mariana* (Taczanowski 1881), a species with an open, loosely meshed hub, executes attacks even more rapid than those measured in other species.

METHODS

We used mature females of *L. mariana* for all observations and recorded behavior in captivity using a high-speed video camera (up to 500 frames/s) (TroubleShooter® model TS500MS Fastec Imaging Corporation - www.fastecimaging.com) connected to a computer. The camera recorded continuously, maintaining a record (buffer) of the latest 2 s in the computer's memory. By stopping the camera within 2 s after an event had occurred, we saved the recording of the event in the computer's memory.

We collected intact webs of mature females in San Pedro de Montes de Oca, Costa Rica. After removing the spider from her web and placing her in a vial, we pressed a circular styrofoam frame coated with double-sided sticky tape carefully against the anchor lines of the more or less horizontal orb; then we cut these lines free from the objects to which they were attached. We took care to minimize alterations in the tensions on the web, and if the tensions in a web seemed to have been altered, we discarded the web in favor of another. We reintroduced the spider onto her web after placing it horizontally over a strong (1000 W) light and a black background. We directed the camera downward from above, and focused on the hub of the web; all or most of the radii and hub lines were visible in the recordings.

We assigned females randomly to one of three treatments. For females in the "3 radii cut" experiment, we gently cut three adjacent radii in a sector behind the spider (between 90° and 180° from the direction in which she was oriented) in the free zone (the space lacking spirals between the hub and the inner loop of sticky spiral) with scissors while the spider rested at the hub (Fig. 1a). This manipulation (to which the spider usually gave no overt response) produced a hole in the array of radii near the hub. Given that orbs of this species have on average about 30 radii (Eberhard 1988), interradii angles averaged approximately 12°, and the hole in an orb with three adjacent radii broken was on the order of 48°. For experimental females in the "all but 5 radii cut" treatment, we cut all but five radii in the free zone, leaving five intact radii at approximately equal angles (Fig. 1b). The mean angle between adjacent intact radii was thus on the order of 72°. The orbs of control females were left unaltered.

We elicited turning reactions of spiders by gently blowing live *Drosophila melanogaster* flies from an aspirator held perpendicular to the web. The fly struck a portion of the web to the rear of the spider, between 90° and 180° from the direction in which she was oriented, and approximately half way from the hub to the frame. The fly was not always in the field of view in the recordings, but in some recordings the vibration caused by its impact was visible, and the lapse between impact and the first response of the spider could be determined.

Leg movements were presumed to function as exploration when the tarsus moved in a tapping or waving pattern until it

contacted a line, and then immediately seized and held this line (Fig. 2). Similar movements that did not result in contact with lines were also considered to be exploratory. Legs on the side of the spider toward which she turned are termed leading (or L) legs, while those on the other side are trailing (or T) legs. Means are followed by ± 1 standard deviation.

We also studied the behavior of mature females in the field in San Pedro de Montes de Oca, and near San Antonio de Escazu, Costa Rica. We recorded the resting postures of the legs of spiders in the field in two ways. We noted which radii held by legs I and II by direct observations. In addition, we used digital photos of spiders as they rested at the hub to measure the angles between adjacent legs using the program "Image J" (Image J. 2006. Image J. <http://www.uhnresearch.ca/facilities/wcif/imagej/>, Bethesda, Maryland, USA) (Fig. 3). We studied responses to prey by dropping a 2.75 mg weight (a V-shaped 1.1 cm piece of fine copper wire) onto the outer half of the sticky spiral portion of the web to the rear of the spider (90° to 180° with respect to the orientation of her body) from about 1–2 cm above the web. Mature female *L. mariana* weigh approximately 40–60 mg (Eberhard 2007), so these weights were on the order of 5% of the spider's body weight. We filmed the responses of spiders at 30 fps with a digital movie camera (Sony DCR-TRV50). Because the radii were more reliably discerned with the naked eye, we also observed the orientation of other spiders directly. We only used spiders that were on intact orbs and that were not feeding. No spider was observed more than once.

RESULTS

Resting leg positions in the field and distribution of weight.—

To aid in understanding the details of turning behavior, we first describe the spider's original position while resting at the hub. This position was relatively consistent (Table 2, Fig. 3, 0:012 in Fig. 4). Legs I and II always held radii beyond the edge of the hub, nearly always in the free zone (rarely extending into the prey capture zone), while legs III and IV usually held either radial lines or hub loops within the hub (Table 2). Legs III were directed laterally; the angle of the tarsi with the central axis of the spider averaged $89.5 \pm 9.1^\circ$ (range 72–111°). The positions of the two legs III tended to be bilaterally symmetrical, as there was a significant positive correlation between the angle of one leg III and that of the other ($R = 0.45$, $P = 0.014$). Legs IV gripped the web in approximately symmetrical positions directed posteriorly (Fig. 3). The separation between legs I was greater than that between ipsilateral legs I and II, both in terms of the angles between legs, and in terms of unoccupied radii between them (Table 2). The tip of the spider's abdomen was always in the hole in the center of the hub (Table 2), often near the center of this hole (Fig. 3).

There were three indications that legs IV, and probably also legs III, were more important in sustaining the spider's weight than legs I and II. First, the webs of *L. mariana* generally slanted somewhat with respect to horizontal (mean = $40 \pm 13^\circ$ in 66 orbs in the field – Eberhard 1987b), and undisturbed spiders on slanting webs nearly always faced downward. Thus legs IV were directed more nearly upward; their tarsi were above the others and thus probably sustained a greater portion of the spider's weight. Secondly, tarsi III and IV often

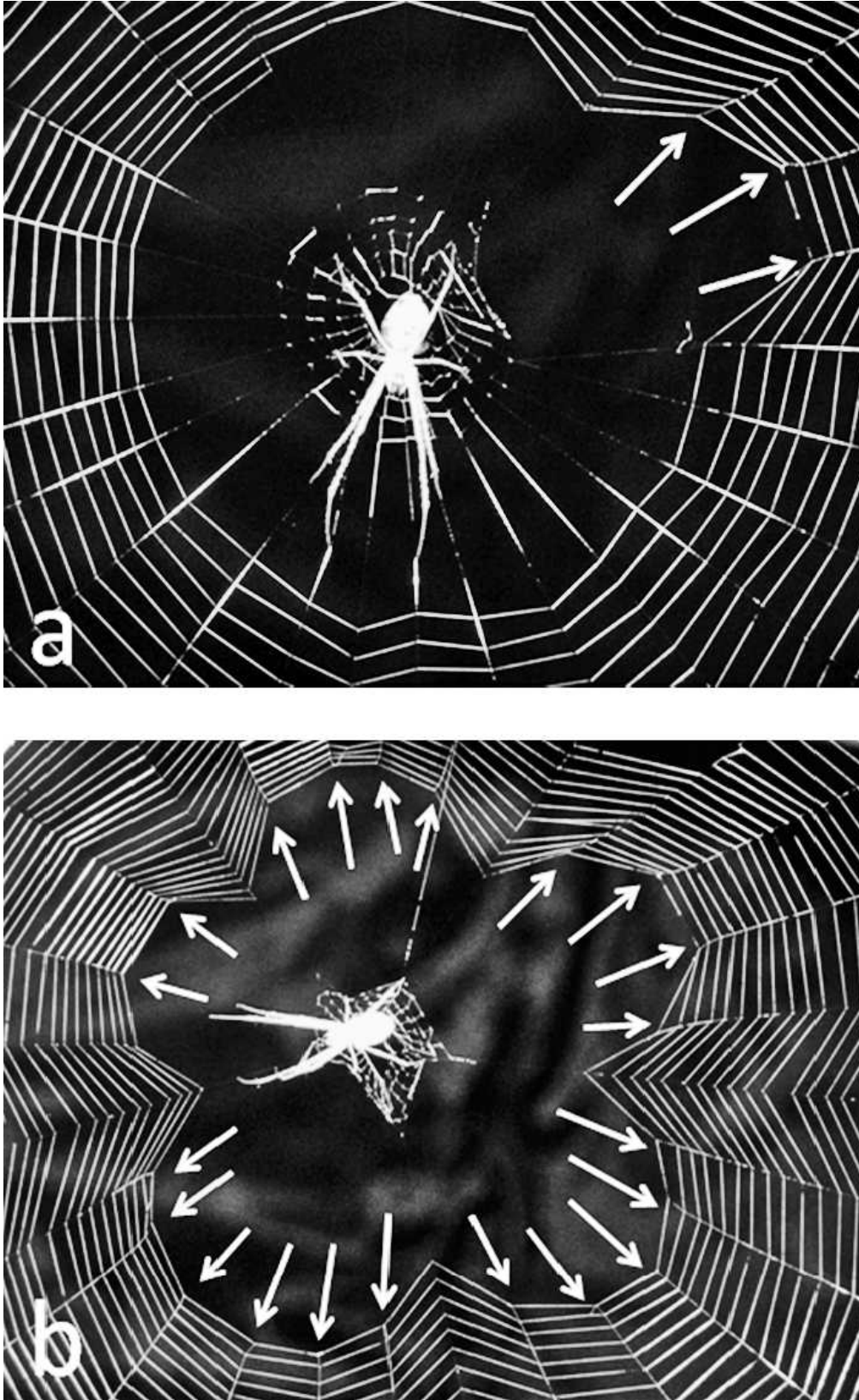


Figure 1.—Spiders resting at the hub of webs in which three radii were cut in the free zone in an area behind the spider (a), and in which all but five more or less equally spaced radii were cut in the free zone (b). Arrows indicate broken inner ends of radii (not all intact radii are clearly visible near the hub). Left legs I and II of the spider in b were held in the open space where radii had been broken, while right legs I and II held the same intact radius.

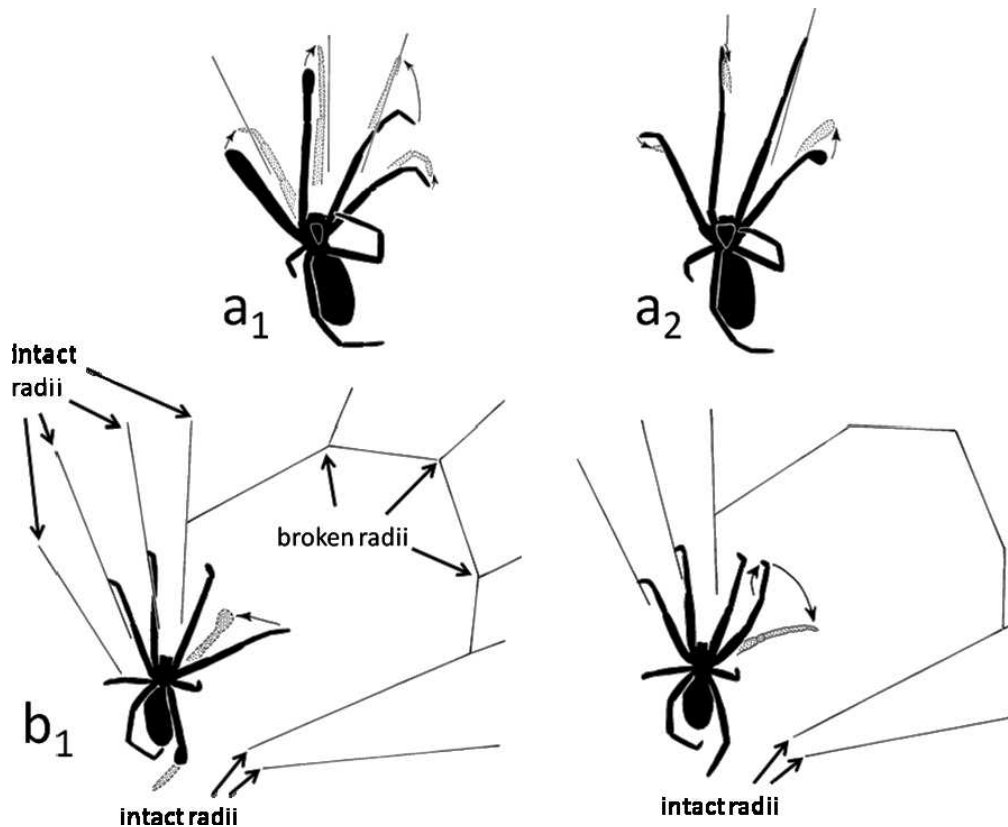


Figure 2.—Examples of movements in a small amplitude, rapid “J” (curved, thin arrows in a) and a slower, large amplitude (curved, thin arrows in b) exploratory movement in the 3 radii cut experiment. The solid image in a_2 occurred 0.002 s after the stippled image in a_1 , while the stippled images in both a_1 and in a_2 were 0.006 s after their respective solid images; the solid image in b_2 occurred 0.064 s after the stippled image in b_1 , while the solid and stippled images in b_1 and b_2 were 0.064 s and 0.144 s after their respective solid images.

pulled the lines they held into perceptible V configurations (e.g., leg TIV in frame 44 in Fig. 4), while such visible deflections of lines were rare for other tarsi. Finally, the abdomen constituted a mean of 71% of the total fresh weight of three individuals (none were obviously swollen with eggs; mean weight 36.6 mg), while the legs constituted only about 17% and the cephalothorax 12% of her weight (the percentage in the abdomen will obviously be greater in females about to oviposit). Therefore, the center of gravity of a mature female probably lies somewhere in the anterior portion of her abdomen. Usually the only legs posterior to this were legs IV; legs III were approximately lateral to the abdomen-cephalothorax junction, and thus probably somewhat anterior to the spider's center of gravity.

When the spider was at the hub, she was apparently able to distinguish intact from broken radii, perhaps on the basis of the resistance they offered when she pulled on them. When the spider was chased to the edge of the web and alternate radii were cut beyond the free zone but near the inner edge of the prey capture zone (all radii were cut less than seven loops of the sticky spiral from the innermost sticky spiral loop) in the lower portion of the web (where her legs I and II would be), legs I grasped unbroken radii in 71% of 154 radii in 77 webs, and legs II grasped unbroken radii in 67% (both significant: $P < 0.001$ with X^2 tests) when the spider returned to the hub and resumed her resting posture. Results from a second experiment in which we cut additional radii suggest that this preference for

intact radii may be due to a preference for radii that give less when the spider pulls on them. When we cut alternate radii farther from the free zone (near the frame) in 51 additional orbs, the preference for intact radii was reduced. Because orbs typically have approximately 40 loops of sticky spiral (Eberhard 1988), these radii had approximately 30 loops of sticky spiral attached to the inner intact segment of the radius that was nearest the hub. The preference of legs I for intact radii disappeared (50% of legs I were on unbroken radii), while the preference of legs II for intact radii remained, but was slightly weakened (63% on unbroken radii).

Speed of response.—Each spider performed three basic tasks as she turned at the hub in response to prey: locate and grasp the radial lines leading toward the prey with her anterior legs, pull and push on lines at the hub so as to turn her body until it faced toward the prey, and reposition all her other legs in preparation to run toward the prey. Different functions were performed by different legs. As in other orb weavers (e.g., Suter 1978; Klärner & Barth 1982), attack behavior by *L. mariana* began with the spider turning rapidly at the hub to face the prey. The mean delay between the impact of the prey and the first movement of the spider's anterior legs in high-speed video recordings in control webs was 0.055 ± 0.04 s (minimum 0.012 s) ($n = 14$). These response delays (which somewhat underestimate the spider's speed, since they do not include the flexion of legs III and IV that just preceded the movements of legs I and II – see below) were comparable to

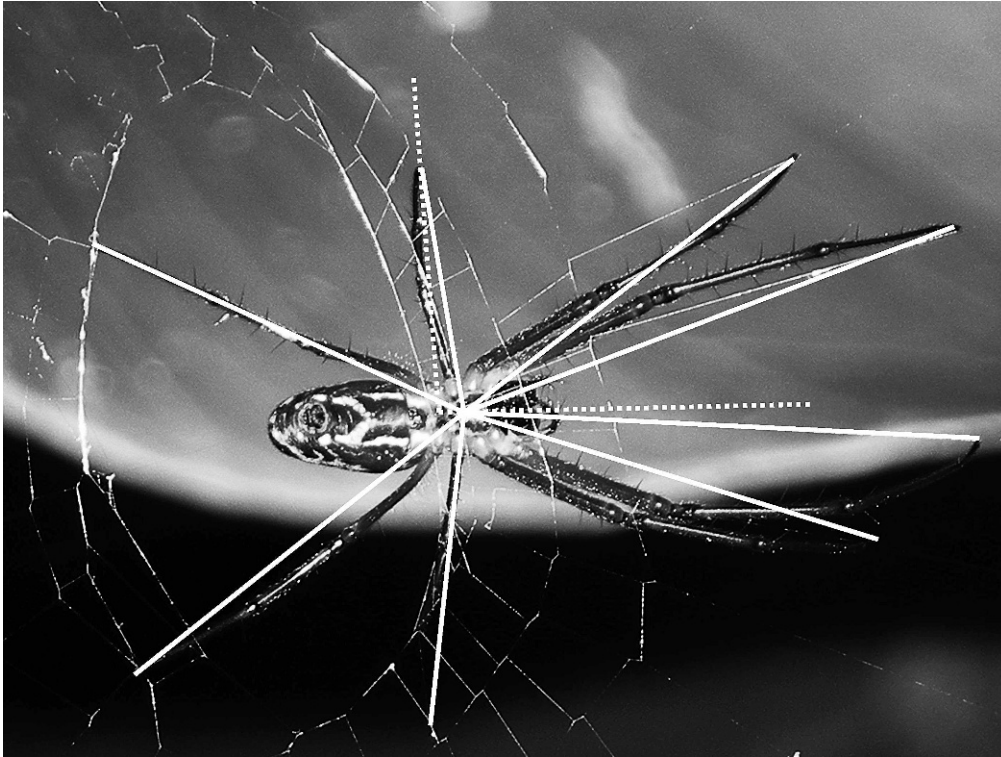


Figure 3.—An adult female *L. mariana* resting at the hub of her web. The solid lines mark the angles that were measured between her legs, and the dotted lines the angle between her longitudinal axis and one leg III.

delays seen in the field, which lasted a median of one frame in a video recording (0.03 s). Mean delays were similar in high-speed video recordings of “3 radii cut” webs (0.117 ± 0.101 s, minimum 0.028 s) ($n = 25$); but the delays were longer in “all but 5 radii cut” webs than in control webs (0.177 ± 0.115 s (minimum 0.03 s) ($n = 26$) ($P < 0.001$ with Mann-Whitney *U* Test).

In the 20 cases recorded in the field in which the spider ran to the wire, she took as little as four more frames (about 0.13 s) to move 4–5 body lengths and touch the prey with her anterior legs. Thus the shortest total delay in the field, from the impact of the wire until the spider touched the wire with her legs I, was 7 frames (about 0.23 s) (two cases) (two other spiders took only 0.33 s). Not all delays were this short, and the median was 16 frames (0.53 s). Commonly, the spider jerked the web at the hub one or more times after turning and before running toward the prey when the delay was longer. Once the spider began to run toward the prey, her mean velocity was 29.6 ± 7.7 body lengths/s ($n = 12$; the mean distance travelled in these cases was 6.5 body lengths; body length in this species is on the order of 7 mm).

Leg movements during turning behavior on control orbs.—Several details of how the spider turned to face the prey were relatively consistent in high-speed video recordings.

Early movements: The first movements were small flexing movements of legs LIII and LIV that drew the web lines held by their tarsi (and connected lines) toward the spider’s body. These just barely visible tensing movements were simultaneous, and generally preceded the first lateral movement of other legs by 0.002–0.004 s (1–2 frames of high-speed video). These tensing movements presumably helped generate the

force needed to swing the spider’s legs and body laterally and rearward (note TIV in Fig. 4, 0:044). Leg LIII continued to pull on the web (and thus probably produced a turning force) until it released its hold on the hub (and the hub lines that it had pulled on sprang back to their previous positions). Leg LIV maintained its hold much longer; it ended up being bent far under the spider’s body (Fig. 4, 0:080) before finally releasing its hold.

Legs LI and LII were usually the first to move laterally, releasing the radii they were holding, descending somewhat below the plane of the web, and swinging simultaneously laterally and rearward toward the side of the hub where the prey had landed (0:044–0:060 in Fig. 4). LII usually began to move either simultaneously or only about 0.002 s later than LI (Table 2, Fig. 5), and the two legs swung almost as a unit, with their tips remaining nearly the same distance apart during the entire lateral and rearward swing (Figs. 4, 0:044, 0:060). After reaching an orientation more or less toward the prey, the two legs moved upward and grasped new radial lines, about 0.05 s after they had begun to move (Fig. 5). Neither leg made any perceptible tapping or waving movement during the swing, and neither leg consistently ended up grasping a line that was held by any other leg; thus, the lateral swings of legs LI and LII were probably not guided by further stimuli from the web once they were initiated.

When legs LI and LII arrived in the sectors in which they would each grasp a radius, they each usually made a small, apparently exploratory movement (Fig. 2a). Usually tarsi LI and LII had not struck radii during the turn, and each was in a space between two radii; the leg was extended quickly upward and prolatally and then flexed in a small “J” movement that

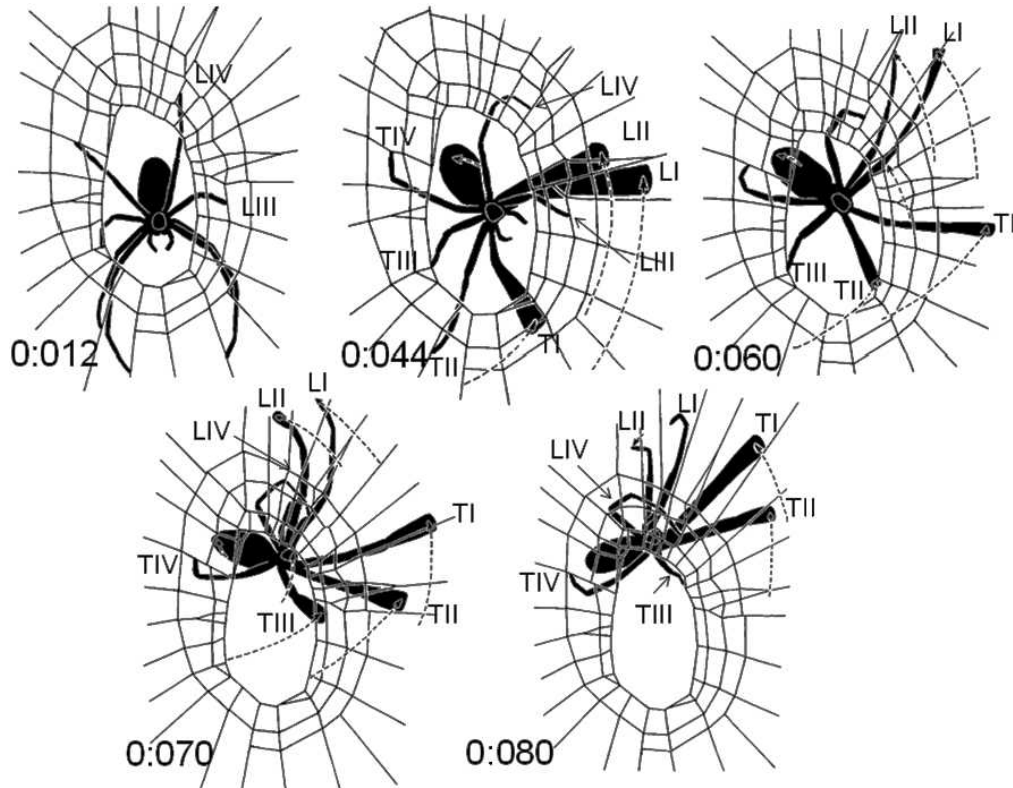


Figure 4.—A typical sequence of movements as a mature female *L. mariana* turned at the hub to face toward a *Drosophila* fly which had struck her web (traced from a view of her ventral surface from above in a high speed video). The times refer to fractions of a second elapsed following the frame of the video recording in which the first leg movement occurred. Thicker leg outlines indicate blurred images (i.e., structures moving rapidly); arrows with dotted lines represent distances that structures moved from preceding positions. Images of lines were generally not clear enough to be sure regarding deflections of lines due to tarsi pulling on them, and (other than TIV in “0:044”) deflections are not included. Leg LIII was too indistinct in several frames to draw with certainty, and was omitted.

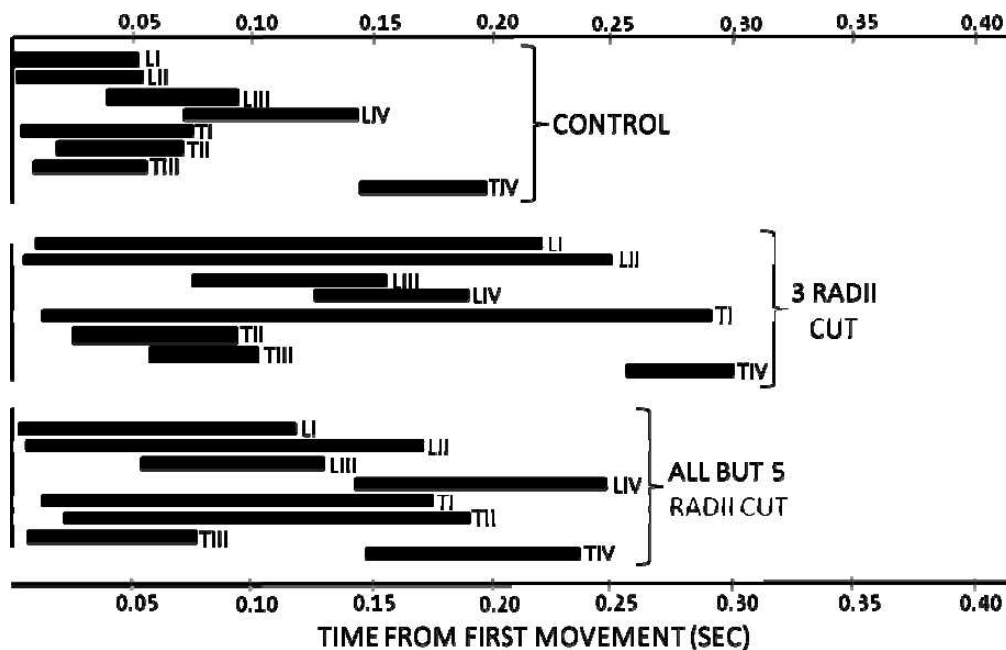


Figure 5.—Mean durations and sequences of leg movements during turns in the three treatments. Time 0 was the frame in the video in which the first leg movement occurred. The left end of each black bar represents the mean time at which the leg began to move, and the right end the mean time at which it grasped a new line. Sample sizes for the three treatments were, in order, 20, 20, and 25.

ended when the tarsus seized a radius. The leg always moved prolaterally (Fig. 2a), although the degree of extension varied. The presence and form of searching movements was flexible, and the order with which legs LI and LII seized radii apparently depended on the luck of where the tarsi arrived after the turn (how close they were to radii). "J" movements were often very small, and sometimes absent or so small as to be imperceptible. On average, LI grasped a new radius only about 0.002 s before LII (Fig. 5); sometimes leg LI was the first to grasp a line, sometimes LII, and sometimes they grasped radii simultaneously.

The radii seized by LI and LII were always adjacent to each other, for two reasons. First, the distance between the two legs was more or less constant as they were swung laterally and then began "J" movements and was similar to the distance between them before the turn began. Because the spider tended to face toward the larger part of the orb and her ipsilateral legs I and II generally held adjacent radii, only a single radius was present between them when they finished the first part of the turn. Secondly, the "J" movements of both legs were oriented prolaterally, thus eliminating the possibility that a third radius would remain undiscovered between them, which could have happened if leg II were to find a radius by moving retrolaterally while leg I found a radius by moving prolaterally. Thus, leg II always ended up seizing the radius that was between legs LI and LII after they had completed the turn. Within an average ca. 0.05 s after the turn began, LI and LII had grasped adjacent radii; usually the radius held by LI was the radius closest to the prey and would serve as the spider's attack route (below).

Soon after the anterior legs moved, leg TIII moved rapidly, crossing the hub hole to grasp a hub line near the opposite edge (Fig. 4, 0:060–0:070). This step by TIII was often quicker than that of any other leg (Fig. 5). Because legs III are relatively short, this step was necessary to allow the spider's body to turn. Associated with this movement, the tip of the spider's abdomen moved posteriorly (Fig. 4, 0:060, 0:070); subsequently, the point around which her body pivoted during the rest of the turning movement was near the tip of her abdomen (Fig. 4, 0:070–0:080).

Intermediate movements: Legs TI and TII trailed behind legs LI and LII in space and often in time. Sometimes TI began to move at the same moment when legs LI and LII moved, but more often it did not release its radius until a few hundredths of a second later (on average 0.02 s) (Fig. 5). The movement of TI began when it released the radius it was holding and swung downward and laterally across the spider's body toward the side with the prey (Fig. 4, 0:044). If its tarsus did not immediately encounter the radius adjacent to the radius held by LI, it searched with a prolatral "J" movement. In each of 30 cases the first line grasped by TI was the radius adjacent to the radius grasped by leg LI. In 27 of 30 cases TII then grasped the radius that was adjacent to the radius being held by TI.

Late movements: Legs III and especially legs IV were probably used to support the spider's body during the entire sequence. They held the web during the early stages of a turn without changing their grips as the spider's body turned and her more anterior legs were in the air moving rearward, and LIV, LIII and TIV only moved after the turn was nearly complete (Figs. 4, 5). The result was that Leg LIV became

severely contorted and crossed over much of the spider's body (Fig. 4, 0:080). The twisted position of LIV suggested that the line gripped by its claws must have been severely twisted (perhaps twisted around the tip of the spider's leg), but there was never any sign that the spider experienced any difficulty in releasing the line held by leg LIV when she finally moved it. Leg TIV generally did not change its grip on the web until LIV had moved and seized another line (Fig. 5).

Once the spider had turned her body, she often jerked the radii one or more times with her anterior legs just before running toward the prey. The number of jerks in high-speed recordings ranged from one to three (mean = 1.42 ± 0.67 s, $n = 15$). The duration of a jerk averaged 0.04 ± 0.001 s, and the total time spent jerking averaged 0.076 ± 0.06 s ($n = 21$). The most common combination of legs that jerked was both legs I and leg LII (Table 4).

Turning on experimental webs.—The responses of spiders on webs with radii that had been experimentally broken were similar in several respects to those of spiders on intact webs. The first tensing responses in the two types of experimental webs occurred 0.003 ± 0.002 s and 0.004 ± 0.002 s before the anterior legs began to move (not different from control webs). The spiders' body turned $158 \pm 11^\circ$, $147 \pm 20^\circ$, and $151 \pm 12^\circ$ in, respectively, control, "3 cut radii", and all but "5 radii cut" treatments (again not statistically different). The order in which legs then initiated lateral movements was also similar to that in the controls (Fig. 5, Table 3). When legs LI and LII arrived in the area of the broken radii, however, their behavior differed. The original "J" movements failed to contact a radius, and at least one of the two legs then executed one or more large searching movements (Fig. 2b). Much more time elapsed before the legs finally grasped radii (Fig. 5, Table 2).

The spiders' jerking behavior also differed on experimental webs. The frequency with which the turn was followed by jerking behavior was not different from that in control webs (77% of 21 turns) in webs with three radii cut (76% of 70 turns) or with all but five radii cut (70% of 30 turns). However, the number of jerks following the turn increased, compared to the number observed on control webs (mean 1.42 ± 0.67): there were 2.17 ± 1.42 jerks in webs with 3 cut radii, and 2.83 ± 1.42 in webs with all but 5 radii cut ($n = 70, 30$; $P = 0.02$ and 0.004 , respectively, compared with control values using Mann-Whitney U Tests). The mean duration of a jerk on experimental webs was not significantly different (0.046 ± 0.01 and 0.05 ± 0.013 s, respectively ($n = 70, 30$), compared with jerks on intact orbs (0.04 ± 0.001 s). Fewer legs were used to perform jerks on experimental webs than on control webs (Table 4), presumably because fewer radii were available to be jerked.

Precision of turns in the field.—Spiders observed in the field generally responded immediately to the impact of "prey" (67% of 72 cases; presumably at least some failures to respond occurred because the spider had been inadvertently frightened by the observer contacting nearby vegetation). Of the 48 spiders that responded immediately, 89.6% turned accurately to face toward the prey, with one of the spider's legs I holding the radius running most directly toward the wire. In 79.2% of the immediate responses, the spider immediately ran to the wire (in the others she turned back to her resting position, possibly because the wire "prey" did not produce further

vibrations). In 71.4% of the 21 cases in which her orientation was correct and it was possible to see this detail, leg LI rather than TI held the radius nearest the wire ($X^2 = 3.86$, $df = 1$, $P < 0.05$). Thus the turn tended to undershoot rather than overshoot the correct radius. There was a similar trend in the mistaken orientations: in three of the four cases in which this detail was noted, the spider was short of the correct radius. Because the orbs of this species generally have on the order of 30 radii (Eberhard 1988), the precision of correct turns was on the order of $\pm 12^\circ$ (the approximate angle between adjacent radii).

DISCUSSION

Speed of turns.—Compared with the webs of many orb weavers, those of *L. mariana* probably retain prey relatively briefly (Zschokke et al. 2006). Their orbs are relatively open-meshed, weak, and horizontal, and, compared with the spider's body size, have relatively small amounts of sticky material on sticky spiral lines (Opell 2002). Perhaps in association with their flimsy webs, the attack behavior of *L. mariana* is very rapid. The spider's reaction time – the time between prey impact and the first movement of her legs – was as little as 0.012 s, and averaged only 0.055 s in controls, or about half the 0.1 s reaction times of *Zygiella x-notata* and *Nephila clavipes* (Klärner & Barth 1982). The median of the total time to reach the prey in *L. mariana* (time between prey impact and the spider's legs contacting the prey) was only 0.53 s; the minimum was 0.21 s. These are substantially quicker responses than the mean of about 1.5 s reported for a combination of *L. mariana* and *L. venusta* (Walckenaer 1842) by Zschokke et al. (2006), perhaps because the prey in the present study were smaller (2.75 vs. mean of 14.4 mg in the Zschokke et al. study) and thus elicited less cautious approaches. The responses of other species of orb weavers are in general slower, with means ranging from 1.7 to 8.7 s (Lubin 1973; Witt et al. 1978; Zschokke et al. 2006; R. Suter pers. comm.). These comparisons underestimate the advantage in speed of *L. mariana*, because (in contrast with the other studies) all prey in this study hit the orb behind the spider and thus required a relatively large turn by the spider, probably slowing the speed of her attack.

Despite the speed with which *L. mariana* responded, the turn was also very accurate; in about 90% of turns of $> 90^\circ$, the spider grasped the radius nearest the prey with one leg I. The angle she turned tended to be the minimum rather than the maximum needed (the leading leg I was more than twice as likely as the trailing leg I to grasp the correct radius), perhaps an additional feature designed to increase attack speed. In sum, we speculate that raw speed probably plays an important role in the predatory strategy of *L. mariana* (see also Zschokke et al. 2006). This gives reason to analyze the leg movements that were used to turn at the hub in terms of their effects on the speed of the spider's turn.

During the 0.1 s in which the spider turned on an intact orb, she found new lines to grasp with all eight legs. The largest leg movements appeared to be blind with respect to particular lines: the legs all seized lines that were not already being held by other legs, and no leg performed any exploratory behavior until it had arrived at the site where it would grasp a line. Once at these new sites, legs either grasped lines without any

perceptible exploratory movements, or with only small “J” exploratory movements. The movements of both legs I, of both legs II, and of TIII were all initiated before any other legs had grasped a new line. If these movements of the spider's legs were not guided by further information once the leg began to move, as proposed here, they were probably guided on the basis of information obtained from the vibrations produced by the impact of the prey, conducted along the radii, and sensed by the spider's legs as they rested at the hub (Figs. 3, 4, 0:012). Probably the spider determined the direction of the prey by comparing the intensities of longitudinal vibrations of different lines (Landolf & Barth 1996), and presumably the locations of prey that struck the web behind the spider were sensed mainly by her legs III and IV, on or near the radii closest to the prey. The probable importance of radii in transmitting vibrations is supported by the nearly threefold increase in the delay before the spider began to turn when all but five radii were cut (a mean of 0.18 s as opposed to 0.055 s, $P < 0.001$ with Mann-Whitney *U* Test), perhaps due to reduced amplitude of the vibrations or a greater difficulty in localizing their source.

The positions of the spider's legs at the hub surely influenced the leg movements needed to make a turn. The most interesting possible functional consequence was that the relative positions of LI and LII (Table 1) were maintained with little variation during the entire turn. Moving these legs as a unit may increase the likelihood of their grasping adjacent radii following the turn. This meant that if the spider's turn was slightly less than that needed to put her leg LI on the radius with the prey, her leg LII would occupy the radius on which the prey was located. The especially close space between legs I and II could also function to increase the speed with which the spider located the line leading to prey. Leg TI often trailed behind leg LI, but nevertheless consistently seized the radius adjacent to that seized by LI, however, so movement as a unit is not necessary to grasp adjacent radii.

All legs were moved during turns of $> 90^\circ$, and in all cases their tarsi went directly to sites where lines were relatively closely spaced. Perhaps the most dramatic movement of this sort was that of TIII, which went directly from one edge of the hole in the center of the hub to the other (Fig. 4, 0:070). By moving her legs to sites where lines were abundant, the spider was able to find and grasp new lines with only small, quick searching “J” movements. We interpret these small “J” movements, which contrast with the large sweeping searching movements seen in other contexts, as being specially designed for web regions with abundant lines. The highly directed movements of legs to areas where lines were close together, and the use of “J” movements thus imply prior knowledge by the spider of the relative abundance of lines in different regions of the webs. The cue or cues that trigger such expectations remain to be established.

Precision of turns and motive force.—As just noted, the positions of the spider's legs as she rested at the hub probably influenced the information available from vibrations produced when the prey hit the web. Strikingly, however, the spider's legs were not positioned so as to obtain uniform coverage of vibrations from all parts of the orb. Instead, the angles between adjacent anterior legs (I and II) were much smaller than those between the posterior legs (III and IV), and the

Table 1.—Means ± standard deviations of angles and numbers of radii between adjacent legs and frequencies with which they grasped different sites for mature *L. mariana* females resting at the hubs of their orbs in the field. Values followed by the same letter and number were significantly different in Mann-Whitney *U* Tests (*P* < 0.0001).

| Legs | Mean angle (°) | <i>n</i> | Mean number of radii between legs | <i>n</i> |
|----------------------|----------------------------|----------|-----------------------------------|----------|
| I-I | 27.8 ± 7.9 c ₁ | 29 | 1.2 ± 0.95 d ₁ | 100 |
| I-II (ipsilateral) | 16.4 ± 6.4 c ₁ | 58 | 0.32 ± 0.63 d ₁ | 100 |
| II-III (ipsilateral) | 66.7 ± 12.5 c ₂ | 58 | | |
| III-IV (ipsilateral) | 55.0 ± 7.9 | 58 | | |
| IV-IV | 55.0 ± 7.2 c ₂ | 29 | | |
| III – long axis body | 89.5 ± 9.1 | 58 | | |

Lines grasped by different legs (frequency)

| Leg | Radius in free zone | Radius in sticky spiral zone | Radius in hub | Hub loop | Hub edge hole | No line | <i>n</i> |
|-----|---------------------|------------------------------|---------------|----------|---------------|---------|----------|
| I | 55 | 2 | 0 | 1 | 0 | 0 | 58 |
| II | 52 | 0 | 6 | 0 | 0 | 0 | 58 |
| III | 0 | 0 | 21 | 30 | 4 | 1 | 56 |
| IV | 0 | 0 | 34 | 14 | 7 | 0 | 55 |

Positions of other parts of body (*n* = 29)

| | Under central hole | Edge hole | Hub or beyond |
|--------------------|--------------------|-----------|---------------|
| Tip of abdomen | 29 | 0 | 0 |
| Abd/ceph. junction | 5 | 2 | 21 |

angles between her ipsilateral legs I and II were smaller than those between her two legs I (Table 1). The wide angles between the posterior legs might seem likely to reduce the spider's ability to discriminate the directions of prey hitting the rear portion of the orb. Nevertheless, the spider's responses were relatively precise, even when prey hit the web in these less well-covered positions to the rear.

Additionally in contrast to the consistent positioning of legs I and II on radii, legs III and IV held a variety of lines,

including hub lines as well as (more frequently) radii within the hub (Table 1). The variety of lines grasped by legs III and IV and of the connections between them emphasizes the apparent lack of difficulty that spiders had in sensing the location of prey with these legs. For instance, longitudinal vibrations on a radius would displace a leg III holding a hub line toward and away from the spider less than if the leg were holding the radius itself. Nevertheless, the spider obtained enough information to execute precisely oriented turns, even

Table 2.—Means ± standard deviations of duration of the movement (s) of each leg between sites where it grasped lines (A), and of recognizable searching movements during this process (B) for different legs in different treatments. Numbers followed by the same letter and number in the same row differ significantly in Mann-Whitney *U* Tests.

| | Treatment | | |
|---|---------------------|------------------|---------------------|
| | Control | 3 Radii cut | All but 5 radii cut |
| A. Movement between sites | | | |
| LI | 0.051 ± 0.009 | 0.210 ± 0.242 | 0.116 ± 0.095 |
| LII | 0.051 ± 0.09 | 0.242 ± 0.207 | 0.165 ± 0.257 |
| LIII | 0.055 ± 0.025 | 0.077 ± 0.054 | 0.077 ± 0.046 |
| LIV | 0.077 ± 0.058 | 0.065 ± 0.07 | 0.097 ± 0.109 |
| TI | 0.07 ± 0.02 | 0.276 ± 0.424 | 0.159 ± 0.150 |
| TII | 0.05 ± 0.009 | 0.069 ± 0.054 | 0.167 ± 0.154 |
| TIII | 0.048 ± 0.035 | 0.045 ± 0.024 | 0.07 ± 0.08 |
| TIV | 0.05 ± 0.05 | 0.048 ± 0.022 | 0.08 ± 0.088 |
| B. Searching movements at the new site | | | |
| LI | 0.005 ± 0.002 c1c2 | 0.18 ± 0.22 c1 | 0.094 ± 0.14 c2 |
| LII | 0.0053 ± 0.002 c1c2 | 0.13 ± 0.20 c1 | 0.14 ± 0.18 c2 |
| LIII | 0.009 ± 0.005 a1c1 | 0.018 ± 0.012 a1 | 0.041 ± 0.087 c1 |
| LIV | 0.016 ± 0.018 | 0.028 ± 0.032 | 0.068 ± 0.102 |
| TI | 0.007 ± 0.003 b1c1 | 0.12 ± 0.14 b1 | 0.17 ± 0.15 c1 |
| TII | 0.011 ± 0.018 c1 | 0.058 ± 0.091 | 0.13 ± 0.13 c1 |
| TIII | 0.026 ± 0.043 | 0.008 ± 0.012 | 0.065 ± 0.22 |
| TIV | 0.012 ± 0.016 b1 | 0.053 ± 0.097 | 0.042 ± 0.044 b1 |

Table 3.—Mean rank for each leg for the order (1–8) in which they were first moved (A) and in which they seized new lines (B) when the spider turned at the hub.

| Leg | A. Order in which the first movement of each leg occurred | | | B. Order in which seized new line | | |
|------|---|-------------|---------------------|-----------------------------------|-------------|---------------------|
| | Control | 3 Radii cut | All but 5 radii cut | Control | 3 Radii cut | All but 5 radii cut |
| LI | 1.0 | 1.15 | 1.32 | 1.8 | 3.85 | 2.92 |
| TI | 3.0 | 2.85 | 3.36 | 4.15 | 4.55 | 5.04 |
| LII | 1.45 | 1.4 | 1.36 | 1.95 | 5.1 | 3.0 |
| TII | 4.85 | | 3.76 | 4.35 | 3.05 | 4.92 |
| LIII | 5.9 | 5.1 | 4.72 | 4.45 | 4.45 | 4.40 |
| TIII | 3.4 | 3.15 | 2.64 | 2.2 | 1.70 | 2.64 |
| LIV | 6.8 | 7.05 | 7.04 | 5.75 | 4.85 | 5.44 |
| TIV | 8.0 | 7.9 | 7.84 | 7.82 | 7.0 | 6.88 |

Table 4.—Percentage of times that different legs were used to jerk the web simultaneously after turning at the hub.

| | LI TI | LI LII TI TII | LI TI LII | LI LII | LI | LII | <i>n</i> (jerks) | <i>n</i> (turns) |
|---------------------|-------|---------------|-----------|--------|----|-----|------------------|------------------|
| Control | 24 | 14 | 57 | 0 | 5 | 0 | 21 | 21 |
| 3 Radii cut | 47 | 36 | 2 | 12 | 1 | 1 | 149 | 70 |
| All but 5 radii cut | 33 | 5 | 1 | 25 | 19 | 18 | 85 | 30 |

when the legs likely involved in the orientation were relatively far apart and their placements on lines at the hub were inconsistent. The implication is that the reasons for particular leg positions at the hub probably include functions, such as supporting the spider and providing motive force to allow it to turn, in addition to sensing the site of impact of the prey. On the other hand, sensing vibrations is important, and the spiders's preference for grasping intact rather than broken radii with legs I and II while resting at the hub may function to improve her ability to sense prey vibrations with these legs.

Lines grasped by the tarsi of legs III and IV as the spider rested at the hub were more often pulled out of line than lines grasped by other legs, indicating that legs III and IV sustained an important portion of the spider's weight as she rested at the hub. The two legs IV and the leading leg III probably also provided much of the motive force used when the spider turned to attack a prey. The coordination of the movements of legs III and IV (leg TIV did not release its hold until leg LIV had grasped a new line; LIV did not release its hold until TIII had grasped a new line - Fig. 5) supports the idea that legs III and IV are especially important in supporting the spider's weight.

Responses to experimental modification of the web.—The two experiments in which radial lines near the hub were experimentally removed resulted in variable effects. Some aspects of turning, especially those involving posterior legs, were little affected. This is perhaps not surprising, because the line grasped by these legs was not altered. In contrast, the behavior of three of the anterior legs (especially LI, LII, TI) was greatly altered in these experiments, and they took much longer to find and grasp radii (Fig. 5). Probably this was because the lines these legs would have grasped were altered in the experiments. After performing small exploratory "J" movements with at least some of her legs LI, LII, and TI, the spider switched to large exploratory sweeps that were better designed to encounter more widely spaced lines. We interpret the switch from small "J" to large-amplitude waving movements on experimental webs to indicate that the spider, after failing to find the lines she expected to find, switched to

the more usual exploratory behavior that is used at sites where the densities of lines are not predictably high. In other words, spiders on orbs somehow anticipated that lines would be common in the areas to which they swung their legs I and II. The persistent large searching movements of *L. mariana* resembled the persistent searches by the araneid *Neoscona nautica* (Koch 1875) when radii were experimentally removed during radius construction (Hingston 1920); presumably the spider's persistence in both cases was due to expectations that lines would be present in the area where it was searching. Experiments of this sort can open small windows on the mental processes of orb weavers.

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