

Imprecision in the Behavior of *Leptomorphus* Sp. (Diptera, Mycetophilidae) and the Evolutionary Origin of New Behavior Patterns

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Accepted 24 August 1988; revised 20 July 1989

*The hypothesis is advanced that nervous control of behavior is imprecise and that some behavioral evolution involves a selective pruning of variants similar to that which occurs in embryological canalization. Variations documented in many previous behavioral studies may have been selectively advantageous and therefore do not provide appropriate tests for the imprecision hypothesis. The spinning behavior of individual larvae of the fly *Leptomorphus* sp. satisfies the conditions for a sufficient test. As predicted by the hypothesis, the behavior is extremely variable at several levels of organization (attachment sites, movements between sites, sequences of up to four movements, pairs of sequences, and entire trains of spinning behavior between movements forward), even when the larva is on a relatively uniform substrate. The temporal clumping of different variations, the combination of responses to large discontinuities and lack of responses to smaller discontinuities, and the improbability of selection favoring such a wide variety of responses all suggest that some of the variation in high as well as low levels of organization of behavior does not represent adjustments to irregularities in the substrate. Larvae can reduce or repress this behavioral variability, as stereotypy increased at several levels of organization when larvae encountered large irregularities in their environments. Variation in spinning by *Leptomorphus* sp. larvae may thus be due to "imprecision" in the nervous control of their behavior.*

KEY WORDS: behavioral imprecision; evolutionary model; spinning behavior; *Leptomorphus*.

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INTRODUCTION

The processes by which genetic information is translated into behavioral phenotypes are as yet unclear. Undoubtedly translations from DNA sequences to nerve networks, from nerve networks to behavior, and from behavior to nerve networks are all involved. Better understanding of these phenomena is likely to furnish new insights into the causes of behavioral evolution, just as details of embryological processes are beginning to illuminate morphological evolution (e.g., Bonner, 1982). This paper examines the hypothesis that translation from nerve networks to behavioral phenotypes is intrinsically imprecise and that an important part of the evolution of heritable behavior patterns may involve mechanisms that selectively repress or prune variations, as in the canalization of embryology.

The central question concerns the existence and patterns in behavioral variation. That variation exists is not controversial. Most students of animal behavior would probably enthusiastically endorse the proposition that animals' behavior is often disconcertingly variable. This impression is confirmed by the substantial variability uncovered even in studies of small details of behavior. Von Holst (1937; cited by Gallistel, 1980) refers to the "well-known fact" that in the intact animal no single movement is exactly like any other. Sequences of movements also show a great deal of variation (e.g., Dane and van der Kloot, 1962; Dawkins and Dawkins, 1973, 1976; Stamps and Barlow, 1973; van der Kloot and Morse, 1975; Golani, 1975; Bell, 1984, 1985).

There are two types of explanations for this variability. Variability may result from programmed abilities to make fine adjustments to different arrays of stimuli or from nervous activity designed to produce some degree of apparently random variation (see below). This type of hypothesis assumes a relatively high "reliability" or precision in the nervous system, so that a given set of neurons connected in a given way consistently produces a given behavior under a certain range of stimuli; behavioral variation would result from nervous system features designed (as a result of natural selection) to produce those variations. On the other hand, nervous system control over behavior may not be highly precise, and some behavioral variations may result from "noise" in the nervous system. Variant behavior would result from "errors" by a nervous system which was designed to produce other behavior.

Imprecision has been documented in firing rates of single neurons, where it was linked to both "synaptic noise" and random short-term changes in properties of neurons themselves (Calvin and Stephens, 1967, 1968). Design properties of a sensory system can also lead to "a minority of neurons in the CNS . . . casting the 'wrong vote' all the time" (Heiligenberg, 1987). Other possible nervous mechanisms that could generate such imprecision are discussed by Beridge and Fentress (1986). It appears, however, that careful proof that such

imprecision exists at the behavioral level, a necessary step in testing the imprecision hypothesis, is lacking. Previous authors have mentioned the possibility of noise or imprecision in behavior, but without supporting evidence (Dawkins and Dawkins, 1976; Jacobs, 1981; Bell, 1985; see, however, Berridge and Fentress, 1986).

Perhaps surprisingly, many studies which have documented the existence of behavioral variation do not permit discrimination between "reliable" and "imprecise" models of the nervous system. This is because they have generally dealt with behavior in which variation per se could have adaptive value; the observed variations may have thus resulted from nervous system activity specifically designed to produce such variation.

Behavioral variation can be selectively advantageous in several contexts. Most obviously, the stimuli eliciting and guiding a behavior may vary, producing a graded series of responses. For example, the predatory behavior of the fish *Badis badis* varies according to how tightly the prey is lodged in the substrate (Barlow, 1977). Variation in fine details of motor behavior such as the fin movements studied by von Holst could result from adjustments to small differences in body posture or water movement.

In addition, novelty per se may render occasional variants adaptive as attention-getting devices in courtship and aggressive displays that are under sexual selection (Barlow, 1977; Jackson, 1981; West-Eberhard, 1983; Eberhard, 1985). Unpredictable variation could also be advantageous during physical fights and predator avoidance because it would make one individual's behavior less predictable by the other (e.g., Jones and Leise, 1987). The capacity to make fine behavioral modifications allowing an animal to adjust its display to the particular responses of a mate or opponent is probably often favored and would also result in varied displays. Variation in exploratory or foraging behavior could be selectively advantageous by increasing the probability of discovering important objects or resources (Trivers, 1985). Apparently random turning does in fact occur under certain stimulus conditions during chemoorientation in several species (Bell and Tobin, 1982; Bell, 1984, 1985). Finally, behavioral variation in learning situations could improve the chances that an animal learns the most effective type of behavior. Taken together, these arguments suggest that animals may often be programmed to modify even relatively stereotyped behavior by either switching between different patterns or including "random" variations in selectively advantageous ways. Variations in much behavior might result from "reliable" nervous system activity.

The alternative, "imprecision" hypothesis suggests that behavioral variability occurs not because it is advantageous, but because the organism fails to suppress or eliminate irrelevant variations which are generated within its nervous system. In other words, there may be a certain amount of nonadaptive imprecision in animals' behavior. To test the imprecision hypothesis one must

check for within-individual variation in behavior in which variation per se is not likely to be selectively advantageous. Time intervals should be short enough to exclude the possibility of changes in connections in the nervous system between repetitions. This is a feasible undertaking with some variants which are selectively trivial, since the more trivial a variant (the less effect it has on the animal's reproduction), the less likely it is to be "corrected" or suppressed by mechanisms favored by natural selection. As in the evolution of neutral alleles (e.g., Kimura, 1983), the greater the selective equivalence between alternatives, the greater the probability that alternative forms (in this case, behavioral variants) will be found coexisting.

Finding test cases in which the criterion of complete or near-complete lack of advantage for variability is met is less difficult than it might seem. This is because variability may be at least slightly *disadvantageous* in some behavior. There is a widespread tendency (called the principle of least action or least effort) for regularly performed behavior to become increasingly stereotyped (Barlow, 1977). Such stereotypy occurs in activities as different as play and superstitious behavior in Skinner boxes (Barlow, 1977), probably because it makes the activity less costly to perform. Finding variability in such highly repeated behavior in which selection appears not to favor variations would represent especially strong support for the imprecision hypothesis.

The spinning behavior of larvae of the fly *Leptomorphus* sp. is especially well suited to testing the imprecision hypothesis. It is spontaneous, complex, and highly repetitive. It is also confined largely to a single plane, making it especially easy to record and analyze in detail (compare with, e.g., Golani, 1976). In addition, larvae are apparently unresponsive to minor variations in stimuli from the substrate (see Results), making it reasonable to attempt to explain fine details at both high and low levels of behavioral organization. Variation per se is probably not advantageous, since the same function (lay a patch of silk trail) is accomplished over and over as the larva moves forward, and the principle of least action is expected to be in effect.

This paper analyzes the spinning behavior of *Leptomorphus* sp. larvae at several levels of organization. First the existence of many patterns plus substantial variation is documented at all levels. Then several lines of evidence are presented which indicate that a major part of the variation results from imprecision rather than "wired in" variability. The Discussion outlines a new model of behavioral evolution based on these results.

NATURAL HISTORY OF *Leptomorphus* SP.

Larvae of the fly genus *Leptomorphus* live under more or less flat fungal fruiting bodies that grow on dead or dying wood (Eberhard, 1970, unpublished). The larva, which is about 3 cm long at maturity, spins an approximately

horizontal sheet of silk lines as a trap for fungal spores on which it feeds. The larva lives on the undersurface of the sheet and periodically eats pieces of the sheet and accumulated spores, then lays fresh sheet across the holes. The labrum has a row of eight papillae or spigots, and by swinging its anterior end from side to side and touching the spigots to the substrate periodically, the larva stretches silk lines from one point to another. Typical spinning behavior consists of a cycle of several kinds of behavior. The larva inches forward a short distance, lifts its head and anterior five or six segments from the substrate, and swings them from side to side in an apparently exploratory movement in which the head touches the sheet about 2–10 times (Fig. 1) but no silk is laid (Eberhard, 1970). After eating an approximately semicircular hole in the sheet just ahead of itself, the larva spins a fresh sheet across this hole with a series of side-to-side and forward-and-backward movements of its anterior end, then inches forward to repeat the cycle.

When a larva crawls across a surface without any sheet (an occasional occurrence in the normal life of a larva), eating movements are omitted but the other movements are consistently performed unless the larva is fleeing rapidly from a disturbing stimulus. The larva thus usually spins a swath or "trail" of silk lines when it crosses a new surface; a central band of slime is left on the trail where the rest of the larva's body passes. These trails probably serve as paths for larvae rather than as traps for spores. The larva can also inch backward

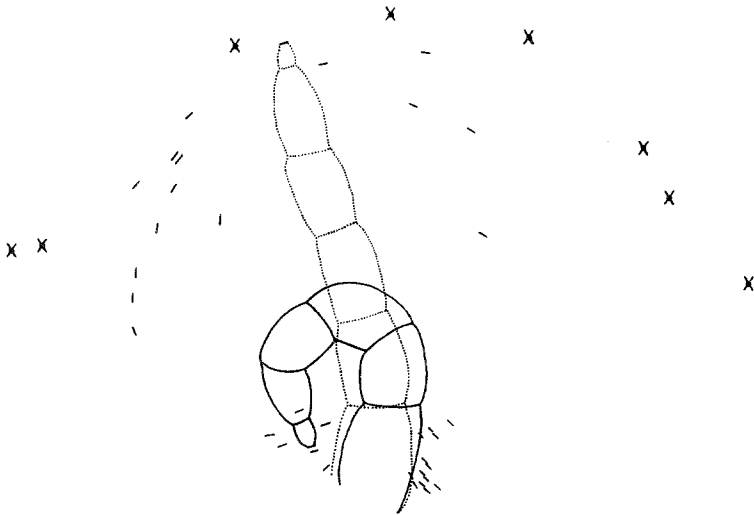


Fig. 1. Sites touched by a larva as it made exploratory swings (X) and then as it spun lines on a clean glass plate, with a diagrammatic representation of two of the larva's spinning positions. The larva's path was bearing to the left.

(not accompanied by spinning movements) or turn 180° by crawling back along its own body.

The species identity of the larvae studied cannot be determined at present due to lack of adequate taxonomic studies (R. Gagné, personal communication). Adults raised from the larvae that were observed and from others found at the same time on the same fungi are deposited in the U.S. National Museum and Museo Nacional of Costa Rica.

METHODS

Last-instar larvae of *Leptomorphus* sp. were collected in San Antonio de Escazu, San José Province, Costa Rica, and videotaped using a National "Newvicon Omnipro" camera with +6 closeup lenses on a tripod. The larvae were filmed from above as they moved on the underside of a glass plate. The glass plate, which had been cleaned with soap, then rinsed thoroughly in nonchlorinated tap water and dried, rested on a petri dish which contained a bit of moist paper towel and was backed by light blue paper. The camera was focused on the lower plane of the glass and recorded at 30 frames/s, with the time recorded automatically on each frame. A microscope lamp about 10–15 cm above and to the side of the larva illuminated both the larva and the blue paper below. Both camera and light were moved periodically to follow the larva as it moved across the plate. Detailed analyses were made of recordings from two larvae: one record (No. 1) of 50 bursts of spinning behavior (8 min 22 s) by larva A and five records (Nos. 2–7) totaling 384 bursts (30 min 24 s) by larva B. Short segments of several other records of larva B were also examined. After taping 8–10 min of behavior, I placed dots on the top of the glass over the trails the larva had produced, rendering them visible in the video images of subsequent behavior. Larva B was also taped for 10 min 20 s while spinning on the sheet of silk on the log where it was found. In this case, the log was photographed from above after being turned, so the larva was in the unnatural position of being on top of its sheet.

Videotapes were analyzed frame by frame by placing a transparent grid over the monitor screen and recording attachment sites and frames elapsed between attachments. The grid was repositioned each time the larva moved forward, using the boundary between body segments 5 and 6 and the longitudinal axis of the larva as guides (Fig. 2). The distance the grid was moved was taken as the distance the larva moved forward. Some distances could not be measured because the camera was sometimes moved forward while the larva was moving forward.

Usually the larva attached silk every three frames. Despite occasional blurring of the video image, it was possible to determine attachment sites and times (within 1–2 frames) with relatively high confidence, since the timing of attach-

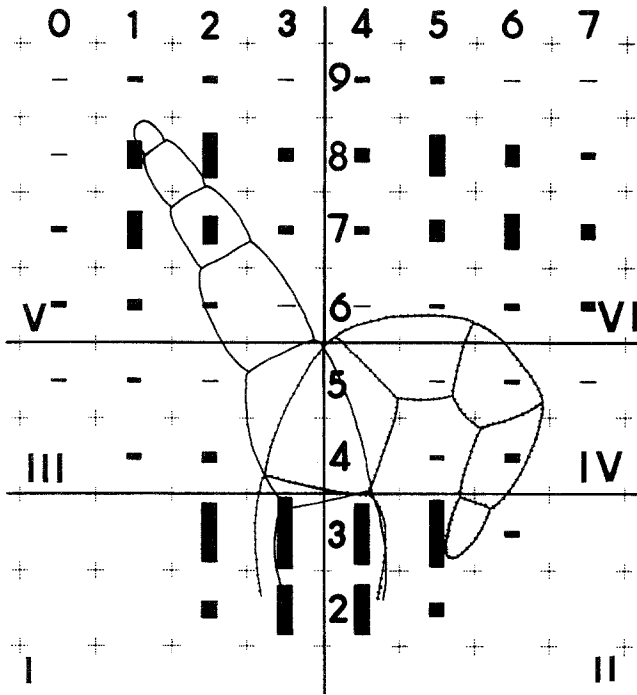


Fig. 2. Distribution of 2010 sites of attachment during 50 bursts of spinning movements of larva A (bars represent fractions of total attachments; the drawings show the larva attaching in grid squares 18 and 53). The grid (dotted lines) was repositioned at the start of each new burst after the larva had inched forward, using the boundary between the fifth and the sixth visible body segments for reference. The attachments are concentrated in front of the larva and at the rear, near the sides of its body. For higher levels of analysis, the spinning area was divided into zones I–VI on the basis of this distribution.

ments was highly regular, the larva’s head often slowed as it neared an attachment, and movements following attachments were usually rapid and in directions very different from those immediately preceding them. The lines themselves were seldom visible in the images however, so attachments of lines at given sites could not be distinguished from brief pauses at such sites that did not result in attachments (if such occur).

Behavior was analyzed at the following arbitrary levels of organization: *attachment sites*—sites on the grid where attachments occurred; *movements*—movements from one area of the grid to another between attachments; *sequences*—sequences of up to four movements; *successions*—successions or pairs of sequences; *bursts*—entire trains of spinning movements from the end

of exploratory behavior until the next movement forward; and *records*—the entire set of bursts of behavior in a given taping session.

In each case the patterns found at one level were used as units in the search for patterns at the next higher level. Those details of behavior which showed clumped distributions when different bursts were compared (and hence suggested lack of direct external stimulus control; see Variation and Its Possible Causes and Discussion) were analyzed in special detail. Most analyses involved only first-order transitions because bursts were not long enough to permit useful analyses of higher-order sequences (see Douglas and Tweed, 1979).

Use of statistical tests was complicated by the tendency for behavior to be correlated from one burst to the next (see Tables II and V). Possible differences between behavior in different conditions were thus tested conservatively, using data derived from each encounter with a given condition as a single observation.

RESULTS

General Patterns

Attachment Sites

Attachments were concentrated along the larva's sides and to the sides of the area far in front of it (Fig. 2). This pattern occurred in records from both larvae [and probably also occurs in *L. subscaeruliosus* or *L. bifasciatus*; see Eberhard (1970)]. Spinning behavior was thus analyzed in terms of the six zones indicated in Fig. 2. This gross level of classification undoubtedly underestimates the variability in higher levels of analysis.

Movements from One Attachment Site to the Next

Some movements between attachment zones were much more common than others; the six most common movements (A-F in Fig. 3) of the total 32 different movements observed (Fig. 4) accounted for between 61 and 83% of all the movements in five different records by the two larvae on open glass.

Sequences

Some sequences of movements were much more frequent than others (Fig. 5). There were four particularly common sequences: C-B, D-A, E-A, and F-B. Some possible sequences (e.g., V-HH, Q-R, M-Y) never occurred, and others (e.g., K-Y, Z-B, U-W) were rare. Six sequences (DA, AC, CB, BD, EA, and FB) were most common in all records and accounted for from 48 to 71% of all sequences seen in four records totaling 322 bursts on open glass (Table II).

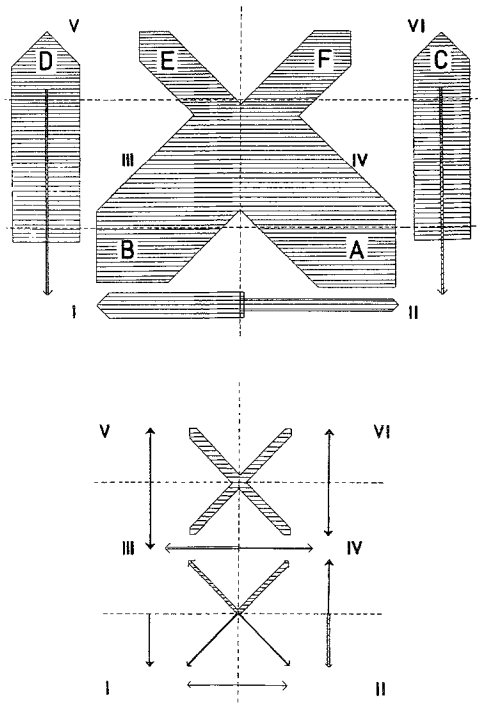


Fig. 3. Movements between successive points of attachment in different zones (I-IV) in Record 3 (2062 movements) (width of arrow denotes frequency; dashed lines are boundaries between attachment zones). Six movements (A-F) were the most common, accounting for 83% of all those observed.

Successions

Some sequences were often followed by other sequences (Table I). The most common successions were CB-DA and DA-CB (these symmetrical alternatives are referred to collectively as "DACB" in what follows except where right-left asymmetries are being discussed), while the next most common were EA-EA and FB-FB. DACB successions nearly always occurred at the beginning of a burst (Fig. 6). Once this succession was interrupted by another sequence (e.g., EA or FB), it usually did not reappear.

Bursts

Bursts or trains of spinning behavior by a larva were highly variable. For instance, in the entire record No. 3 of 112 bursts which were performed by

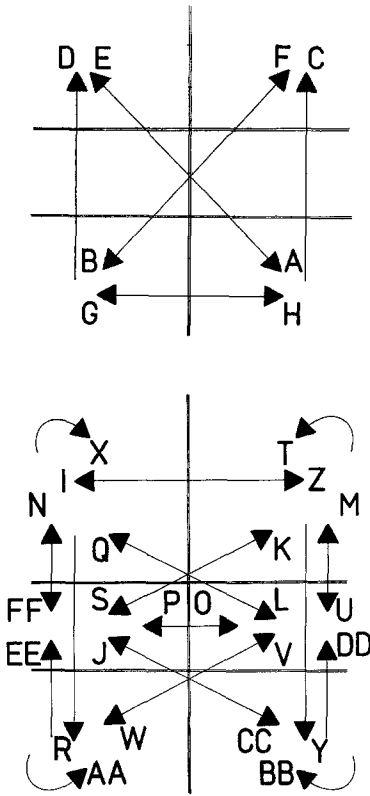


Fig. 4. Labels of all movements observed (the most common movements are in the upper drawing) (double lines are boundaries between attachment zones).

larva B as it moved forward across a fresh glass plate (part of this record is shown in Fig. 6), 104 were unique, and 4 were repeated once. In a second record (No. 5) of 158 bursts on a glass plate by the same larva, no two bursts were identical. These two records did not have a single burst in common.

Records

Differences between bursts did not average out over longer periods of time. Four records (of between 52 and 158 bursts) from the same individual larva on clean glass differed substantially in the frequencies of different movements and different sequences (Table II). Statistical comparisons are given comparing records 5a and 5b, assuming independent distributions of variables. The significant deviations from predictions suggest that many aspects of behavior were clumped in time at the level of records.

Records also showed clumping of higher-order patterns. For instance, the

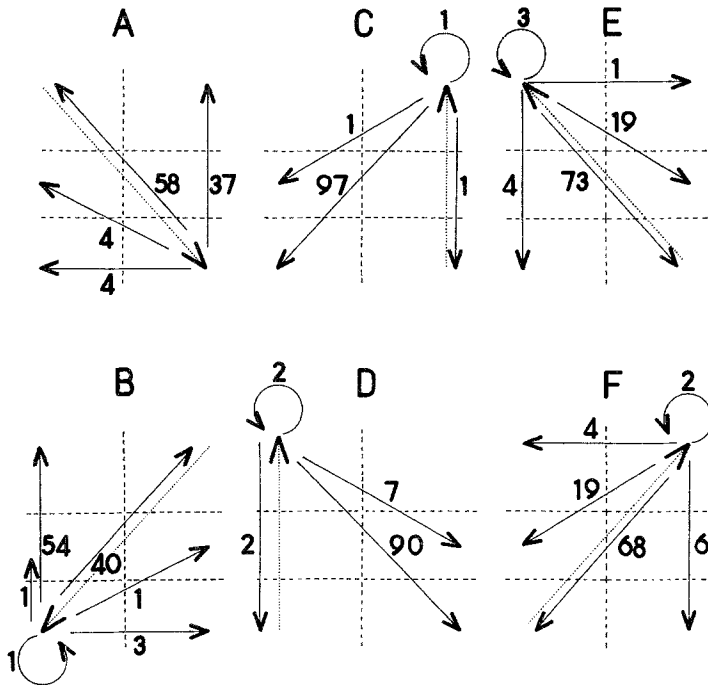


Fig. 5. Common sequences of movements. Numbers represent percentages of movements (solid lines) that followed each of the six most common movements A-F (dotted lines with arrows). Data are from larva B spinning on clean glass (Record 2); sample sizes for A, B, C, . . . , are, respectively, 237, 178, 97, 116, 149, and 94.

Table I. Frequencies (%) with Which Common Sequences or Movements Followed Each Other in Record 2 of Larva B, Showing that Some Transitions Were Much More Common than Others^a

First sequence or movement	Second sequence or movement								N
	DA	CB	FB	EA	H	G	Others	End	
DA	—	53.2	—	38.7	—	1.4	5.9	1.0	222
CB	64.0	—	31.5	—	0.5	—	3.0	1.0	203
EA	—	17.3	—	53.8	—	9.5	12.4	7.1	283
FB	32.8	—	34.4	—	16.1	—	10.0	6.7	180
H	—	5.9	—	73.5	—	0	8.8	11.8	34
G	6.3	—	75.0	—	3.1	—	6.3	9.4	32

^a“Others” includes all sequences and movements not listed at the top; “end” means the burst ended one movement later; “—” means the transition was not possible.

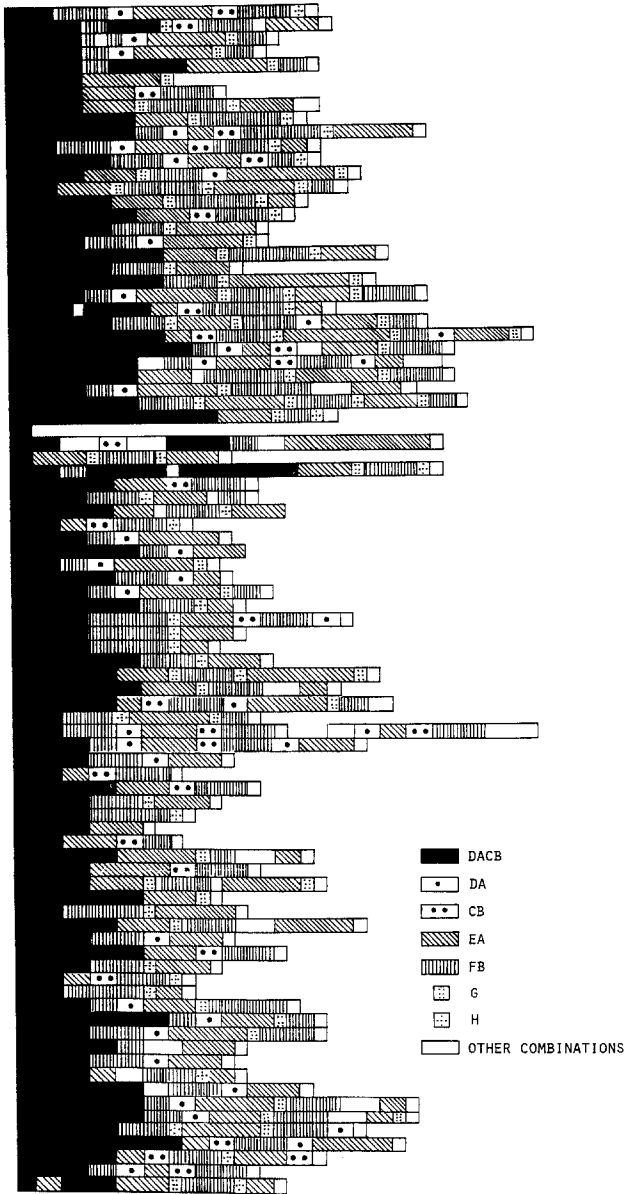


Fig. 6. Bursts of movements performed during 4 min and 35 s by larva B on a clean glass plate. Each horizontal row of boxes, read from left to right, represents a single burst of spinning. The order of bursts reads from the top moving down. The larva turned back on itself after a short burst about one-third of the way through. There is great variety in both the combinations of movements in a burst and the lengths of bursts, even though this representation underestimates the variation. Movements L and S resulting in attachments in grid squares in row 4 are classed as A and B, movements M and FF moving away from these squares are classed with C and D, and movements W and O moving away from this row are classed with G and H; see Figs. 2 and 4.

tendency to follow E movements with A movements was lower in 5b than in 5a ($P < 0.001$ with chi-square test); the fraction of a burst dedicated to DACB. . . was lower in record 2 than in any other ($P < 0.01$ with t test on log-transformed data); and the number of movements per burst was significantly smaller in record 3 than in any other ($P < 0.001$ with t test on log-transformed data). Differences between larva A and larva B (compare record No. 1 with others) were, in general no greater than those between different records of larva B. In summary, records differed in frequencies of movements, sequences, and other details of higher-order patterns.

Reduction in Variation After Contacting Large Objects

Wall of the Petri Dish. Behavior at several levels of organization (attachment sites, movements, sequences, and successions) was compared between bursts immediately preceding and immediately following exploratory swings in which the larva first contacted a wall of the petri dish after performing a long series of bursts (> 15) on open glass ($N = 11$). The larva's own behavior thus served as a control for effects of contact with the wall.

Contact was followed by reduction of behavioral variability at several levels of organization. Although the number of attachments per burst rose slightly (insignificantly) following contact (average 42.7 ± 27.7 for the burst immediately before versus 53.5 ± 17.2 for the burst immediately after), variation in attachment sites in the forward sectors (V and VI in Fig. 2) decreased. The percentages of attachments in each burst which occurred in each grid square within zones V and VI (Fig. 2) were calculated for the burst before and the burst after contact. Only 2 of 11 bursts before contact had $> 30\%$ of the attachments concentrated in a single grid square, as compared with 8 of 11 afterward ($P < 0.01$, $\chi^2 = 6.6$, $df = 1$).

A similar reduction in variety occurred with respect to the kinds of movements. When the percentages of total movements corresponding to each of the more common movements (A–H) were compared (Table III), very low and very high values were overrepresented in bursts after contact ($P < 0.001$, $\chi^2 = 30.7$, $df = 3$). In other words, the larvae performed a lower diversity of the common movements after contacting the wall. The same pattern occurred in the other, rarer movements ($N = 23$). In these same pairs of bursts, rare movements were more common before contact than after (comparing 0% versus $> 0\%$, $P = 0.025$, $\chi^2 = 5.04$, $df = 1$); and when they did occur they tended to be more evenly distributed before than after (very high and very low values were overrepresented after contact (Table III) ($P = 0.026$, $\chi^2 = 7.30$, $df = 2$).

Additional patterns emerged when sequential combinations (categorized as in Fig. 6) were compared. Sequences EA and FB were consistently rarer in bursts after contact (10 of 11 cases, $\chi^2 = 9.31$, $df = 1$, $P < 0.001$) and were, in fact, nearly absent (combining movements in different bursts, they accounted

Table II. Frequencies (% of Totals) of the Movements and Sequences Which Were Most Common^a

	Movement												
	A	B	C	D	E	F	G	H	J	K	L	M	O
Larva A on glass plate													
Record 1 (1982 movements)	20.7	10.2	10.6	13.1	7.7	9.4	4.8	2.1	2.1	0.2	0.7	0.2	1.9
Larva B on glass plate													
Record 2 (2062 movements)	22.9	17.4	9.7	10.8	10.9	8.0	0.8	0.6	1.4	0.6	2.4	0.5	1.6
Record 3 (2655 movements)	18.8	18.3	10.5	9.9	13.4	12.3	0.4	0.7	0.4	0.3	2.9	0.7	2.0
Record 5a (1365 movements)	19.9	21.2 ***	9.7 *	10.0	11.8	6.5	1.3	0.7	0.7 **	0.5 ***	3.0 ***	0.7 **	1.2
Record 5b (2466 movements)	15.6	12.2	7.2	8.7	10.6	6.9	0.9	0.9	1.7	1.9	6.7	2.0	1.4
Larva B on sheet on log													
Record 4	12.0	12.4	6.9	7.9	7.4	6.0	0.06	0.2	0.7	4.2	7.4	2.9	2.5

for only 2.7% of 583 movements after contact, as compared to 34.6% of 468 before) (Fig. 7). In addition, the asymmetrical sequences DAG and CBH were much more common after contact (10 of 11 cases, $P < 0.001$) (0.6% of 468 movements before versus 32.9% of 583 movements after) and correlated with the side on which contact was made. In all 10 postcontact bursts in which one of these two sequences occurred, the point where the larva had contacted the wall was on its right side (seen from below) when CB-H was employed and on its left when DA-G was employed. In sum, the balance of different types of sequences was altered in relatively consistent ways after contact.

Analysis at the level of successions of sequences showed still another trend toward reduction in variation: sequences (again categorized as in Fig. 6) were more likely to repeat themselves following contact. In 8 of 11 cases the percentage of repeats was higher after contact than before (average = 70.2% versus 45.12%; $P = 0.027$ with Mann-Whitney U test). Of 183 transitions from one sequence to the next that occurred in the 11 bursts before contact, 45% were repeats; the corresponding value for 167 transitions after contact was 68% ($P \ll 0.001$, $\chi^2 = 19.5$, $df = 1$). Thus there was a lower diversity of sequences on short time scales within bursts.

Summing up, contact with the wall of the petri dish during exploratory behavior reduced behavioral variation with respect to attachment sites, types of movements, and successions of sequences within bursts. The balance between different types of sequences was also altered substantially, and some asymmetries occurred which were related to the side of the larva on which contact had been made.

Cotton Thread. Only one encounter with a thread was analyzed, so statis-

Table II. Continued

Movement							Av. number of movements/ burst	Fraction of total movements			Av. no frames between	
Q	R	S	W	Y	CC	DD		DACB	FB	EA	Successive attachments	End of burst- inch body forward
0.3	0.3	0.9	1.8	0.3	0.2	0.3	43.0 ± 8.5	0.34	0.196	0.172	3.64 ± 0.57	21.7 ± 2.3
0.9	0.6	1.2	2.3	0.8	1.9	1.6	42.3 ± 13.2	0.27	0.0557	0.0949	2.93 ± 0.14	13.7 ± 1.2
0.7	0.8	2.2	2.1	0.8	0.4	0.3	23.8 ± 7.5	0.35	0.1582	0.0868	2.76 ± 0.13	10.9 ± 1.6
1.2 ***	0.9	2.3	1.8	0.8 ***	1.6 ***	1.0 ***	40.6 ± 13.4	0.35	0.0403	0.0901	3.10 ± 0.22 ***	15.8 ± 3.1
3.2	1.5	3.1	2.0	2.5	3.0	3.3	37.8 ± 11.0	0.37	0.0373	0.0632	2.98 ± 0.17	14.1 ± 2.1
3.9	0.7	6.5	1.3	0.2	1.6	1.9	48.7 ± 15.1	0.34	0.117	0.152	3.22 ± 0.31	13.2 ± 2.2

^aAlso given are average times between successive attachments, and between the last attachment of a burst and the extension forward (in numbers of frames of videotape; time between frames was 0.033 s). The larva rested immobile for 5–10 min between Record 5a and Record 5b; other records were separated by at least 5 h. The statistical significance of the differences between 5a and 5b are indicated; the binomial test was used except for number of movements per burst (*t* test), fractions of total movements (*t* test on log-transformed data), and numbers of FB and EA (chi-square test). Although Records 5a and 5b were indistinguishable with respect to both the number of movements per burst and the fraction of the burst dedicated to the succession DACB . . . , 10 of the 21 most common movements showed significant differences. Inspection shows that these and other movements also differed significantly in other pairs of records for this larva on glass.

tical tests cannot be employed (see Methods), but the changes from previous behavior were similar in several ways to those after contact with the wall of a petri dish. When larva B crawled alongside a cotton thread (about one-fifth the maximum diameter of the larva; Fig. 8), attachments were shifted forward on

Table III. Distribution of Percentages of Different Types of Movements in Each of the 11 Bursts Immediately Preceding Contact with the Petri Dish Wall and the 11 Bursts Immediately Following Such Contact^a

Common movements (A–H)					
	0%	1–11%	12–23%	≥ 24%	Total
Before	10	36	35	7	88
After	30	18	17	23	88
“Rare” movements (all others)					
	0%	1–2%	3–8%	≥ 9%	Total
Before	211	15	26	1	253
After	229	12	8	4	253

^aOverrepresentation of very high and very low values after contact reflects reduced variability in behavior.



Fig. 7. Eleven groups of bursts when the larva contacted a petri dish wall during exploratory behavior after it had moved across an open glass plate for at least 15 bursts. Each group consists of the three bursts immediately preceding contact, and the burst immediately following contact (marked with an asterisk). Conventions as in Fig. 6.

the thread side, and laterally on the other side (Fig. 8). These differences manifested themselves from the beginning of each burst, suggesting that the swinging behavior prior to spinning rather than spinning itself served an exploratory function.

As in the cases when the larva contacted the wall of the petri dish, the diversity of movements was reduced. Of the common movements (A–H), nearly all (96% of 254) of those after contact were A, B, C, or D (the corresponding figure for the 9 bursts with 339 movements which preceded contact with the thread was 78% of 256) (Fig. 9). Among the 23 less common movements (comparing the two sets of 9 bursts), only 8 of 23 were represented after contact, as opposed to 17 of 23 before.

Transitions between successions were also more diverse before contact: only 34% of 131 transitions before were repeats of the preceding succession, while 82% of 79 after were repeats. Also, as occurred after contact with the petri dish, the frequencies of EA and FB were reduced after contact (40.7% before versus 1.8% after).

Increase in Variation After Turning Back

On seven occasions larva B interrupted spinning by turning 180° and crawling back on itself ($N = 5$) or by sliding backward a body length or more before beginning to spin again. Unusual movements and sequences predominated in spinning behavior just after these maneuvers. In all seven cases the frequency of the most common movements (A–H) in the burst after a turnback was lower

than that in the burst just before ($P < 0.01$ with binomial test); averages of these frequencies were $32 \pm 18\%$ after and $78 \pm 16\%$ before (frequencies differed significantly, $P = 0.0033$ with Mann-Whitney U test). Increased variation was also suggested by the fact that greater numbers of different types of "rare" movements were used in bursts following turnbacks ($X = 6.4/\text{burst}$ before, $10.6/\text{burst}$ after). The totals were significantly different ($P = 0.0012$, $\chi^2 = 10.5$, $df = 1$), but the implication of greater variation is uncertain since this difference may be due to the smaller number of rare movements before turnbacks.

Sequences were also altered. The common DACB sequence and its derivatives (see Fig. 6) were less frequent after in six of seven cases (average $14 \pm 14\%$ of the movements in the first burst after, compared to $40 \pm 15\%$ of the burst just preceding) ($P = 0.021$ with Mann-Whitney U test). The portion of the burst which did not include any of the common sequences (DACB, CB, DA, EA, FB, G, H) averaged $30 \pm 18\%$ in the burst before and $73 \pm 18\%$ in the first burst after ($P = 0.008$ with Mann-Whitney U test). The increase in sequence diversity was not simply a result of the lower frequency of common movements, since even when the less common movements in derivatives of common sequences (see Fig. 6) were included, the frequency of the common sequences and their derivatives decreased in six of seven cases (the average declined from 81 ± 14 to $54 \pm 23\%$; $P = 0.035$ with Mann-Whitney U test). The fraction of the burst consisting of the DACB... succession gradually increased after turnbacks and withdrawals: averages for the three bursts immediately following were 0.14, 0.23, and 0.38. Thus patterns in both movements and successions which were typical of long, uninterrupted series of bursts became rarer immediately after the larva turned back, and they only slowly returned to their original values.

Behavior on an Intact Sheet on a Fungus

In order to determine whether the behavior of *Leptomorphus* sp. on a glass plate is highly unnatural, a record containing 48 bursts of spinning by larva B on its own sheet on a fungus was analyzed. In 37 of these bursts the larva had eaten a hole in the sheet just prior to spinning. Despite the larva being above rather than below the sheet (see Methods), its behavior on the log showed several patterns similar to those displayed under a glass plate. Behavior on the log is compared below with behavior on clean glass (Record 2) which had a similar number of bursts (52).

The pattern of attachments showed anterior and posterior concentrations on both sides of the body (Fig. 10), although there were more attachments in the intermediate zone (compare with Fig. 2). DACB... successions were also common ($34 \pm 18\%$ of the movements, versus $27 \pm 9\%$ for Record 2; see

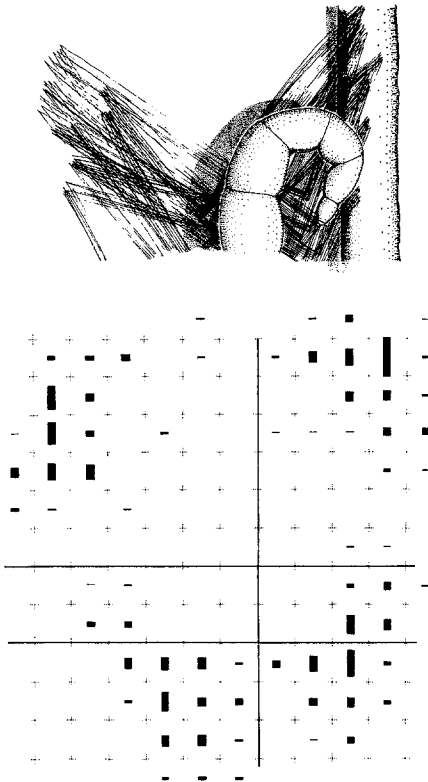


Fig. 8. Effect on distribution of attachment sites in nine successive bursts (number of attachments = 357) when a cotton thread about one-fifth of the maximum diameter of the larva ran alongside a spinning larva in columns 6 and 7 of the grid (shown diagrammatically at the top).

Table II) and nearly always were the first of the common sequences (top, Fig. 4) to appear in the burst (in 47 of 48 bursts; Fig. 11). As on glass, interruption of DACB. . . by EA or FB sequences was seldom followed by more DACB. . . (in only 9 of 48 bursts; see Successions for other records). Frequencies of G

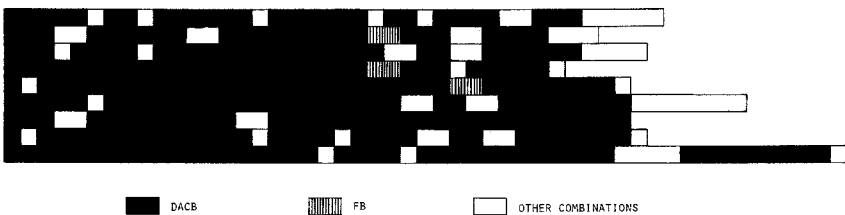


Fig. 9. Movements during nine bursts of spinning when a cotton thread ran alongside larva B (see Fig. 8). Nearly all sequences were DACB. . . (black), in contrast to behavior on open glass (Fig. 5). Many of the "other" sequences (white) were related to D, A, C, and B (e.g., FF, L, M, S), and the transverse sequences (EA, FB) common on open glass were nearly absent.

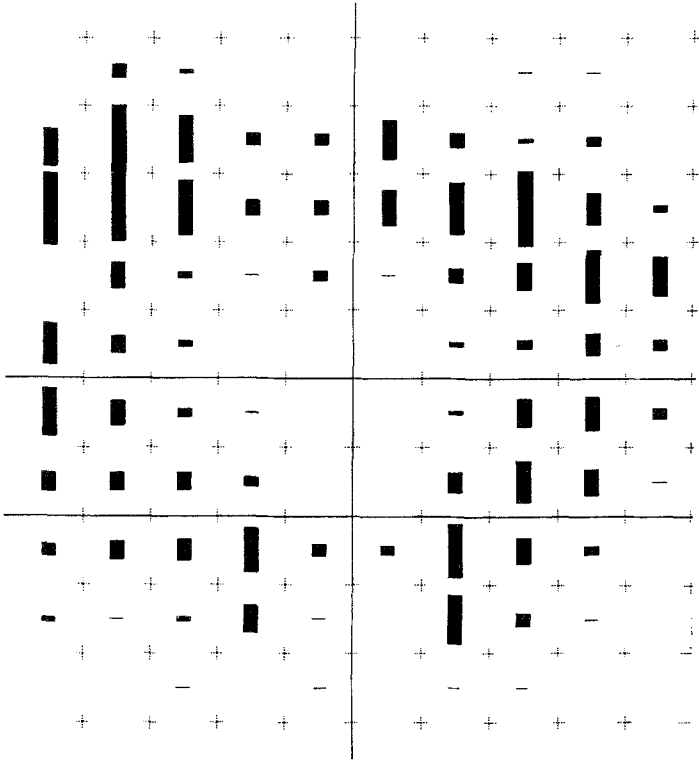


Fig. 10. Distribution of 1136 attachments during spinning by larva B while it was on its own silk sheet over a fungal fruiting structure.

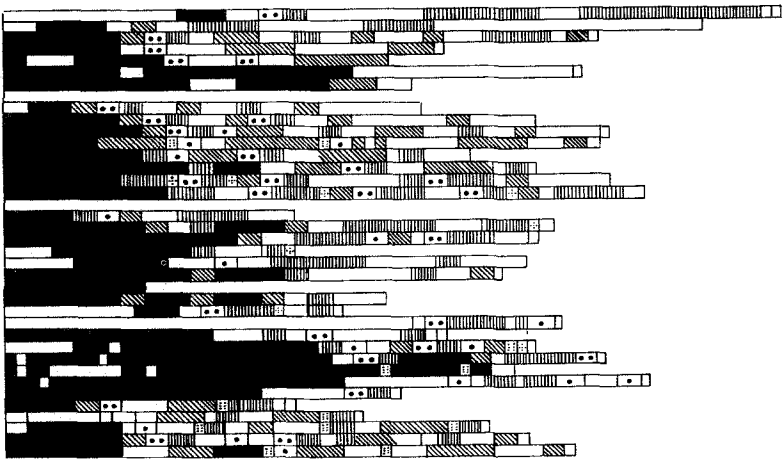


Fig. 11. Movements performed during 36 bursts of spinning while larva B was on its own silk sheet over a fungal fruiting structure (movements classified as in Fig. 6).

and H (and similar) movements were close to those in other records (0.9 and 0.7% versus, e.g., 0.8 and 0.6%, respectively, in Record 2). As with other records (see below), longer bursts were clumped ($P < 0.01$ with runs test), and bursts containing G- and H-like movements were also clumped in time ($P < 0.02$ and $P < 0.05$, respectively, with runs test).

The most dramatic difference was the decrease in the frequencies of the most common movements (A–F) on glass (52.6% of the moves on the log versus 61.2–83.2% in other records of the same larva on glass). Side-to-side movements between zone III and zone IV and between V and VI were more frequent. For instance, I and Z accounted for 6.5 and 7.0% of the movements on the log but $< 1\%$ in all other records.

In sum, even though the larva was observed in an unnatural position, when on its own sheet on a log it displayed many of the basic patterns seen on glass plates. Several of the detailed aspects of its behavior which are analyzed below also showed similar patterns in the two situations. Thus the patterns seen on glass plates are probably not unnatural artifacts.

Variation and Its Possible Causes

Despite the existence of the many patterns just documented, there was substantial variation in attachment sites (Fig. 2), movements (Fig. 3), sequences (Fig. 5), successions (Table I), bursts (Fig. 6), and records (Table II). Nearly every burst of spinning behavior performed by a single individual differed from all other bursts. What caused this variation? Was it the result of adjustments made by the larva to stimuli received from the “clean” but undoubtedly not absolutely homogeneous surface of the glass? Or was it “irrelevant” variation that resulted from imprecision in the larva’s behavior? In addition to theoretical reasons which suggest that such adjustments did not occur (see Discussion), three different lines of evidence suggest that imprecision was at least partially responsible: there were clear responses only to large, and not to small, objects encountered during the search behavior immediately preceding each burst of spinning; variations were clumped in time in a way that stimuli were not likely to be; and simple continuous variables such as turning and distance traveled did not correlate (at least in any simple way) with variations. These points are documented in the next sections.

Silk Already Present on the Glass

During Record 5 larva B encountered trails it had spun previously on several occasions. The discontinuities in the surface of the glass resulting from these trails are small in relation to objects such as the cotton thread (above) but are large compared to those likely to remain after the glass was washed and dried prior to being used in videotaping. The larva showed no clear response

to the trails; this lack of response suggests that the much smaller discontinuities in the glass itself were not responsible for variations documented above.

Six successive bursts (465 movements) were performed while a previous trail was in the left part of the larva's spinning field but not the right, and two groups of six successive bursts each (total 460 movements) were performed while a previous trail was on its right but not its left. Comparisons among these sets of bursts failed to show that the presence of previously laid lines had effects on either the sites of attachment (Fig. 12) or the sequences of movements (Table IV). In general, the two groups of bursts with lines on the right differed at least as much among themselves as with the bursts with lines on the left. Previously laid lines did not have large and dramatic effects, suggesting that smaller discontinuities in the substrate were not important in determining the larva's spinning behavior.

Patterns in Time of the Variations on Clean Glass

If microscopic discontinuities in glass surface were responsible for variations in behavior, then it seems unlikely that a larva moving forward from one burst to the next would encounter the same type of discontinuity in the same sectors of the areas covered by the successive bursts. Assuming that a given stimulus causes a behavioral response during the same burst of behavior in which the stimulus was perceived, the distribution of a given variation in different bursts in a given record should tend to be random. This was far from true. Instead, variations in numbers of different attachment sites, movements and sequences, left-right asymmetries, timing of movements, and other details were frequently grouped within records (Table V), suggesting that such stimuli were not responsible for the variations. Values in the runs tests in Table V were nearly always negative (110 of 116; 54 of 57 statistically significant differences are negative), indicating a widespread tendency for variations to clump. As noted above, the many differences in comparisons of entire records on clean glass (Table II) indicate that variations also clumped at the level of records.

Variations in the ordering of discrete behavior patterns such as the movements analyzed here might conceivably result from the effects of only a few continuous variables such as the tendency to turn or the rate of forward movement. It appears, however, that at least several and perhaps most of the details are not strongly influenced by either of these factors.

Turning

Larva B's tendency to turn right or left was estimated in Records 3 and 5 (112 and 158 bursts, respectively) in two ways. Asymmetry in attachment sites used in zones V and VI during the original DACB. . . succession was evaluated

Table IV. Effects of Previously Laid Trails that Were on One Side of the Larva on the Frequencies (%) of Symmetrical Pairs of Some of the Common Movements and Sequences (N = Number of Movements)

	Movement or sequence				DACB . . . ends with FB
	G	H	CB	DA	
Trail on left ($N = 298$ in 6 bursts)	0.7	1.3	2.0	2.3	0/6
Trail on right					
1st group of 6 bursts ($N = 187$)	9.6	4.8	1.1	3.7	0/6
2nd group of 6 bursts ($N = 218$)	1.4	1.4	0.9	2.3	5/6

(51 bursts) with strong right (52 bursts), there was no significant difference with respect to the balance of symmetrical pairs: the sequence (EA or FB) that terminated the original DACB. . . succession or the number of CB versus DA sequences that followed the original DACB. . . succession did not differ ($P > 0.05$ and $P > 0.1$, respectively, with chi-square test). There was a significant trend to have more G relative to H movements in strong right bursts ($P > 0.001$) but no trend to have more H in strong left bursts ($P > 0.1$) (both chi-square test). In sum, the symmetry of several details of sequences and successions was not clearly affected by turning tendencies. This lack of difference is especially notable since turning tendencies were clumped in time just as were many aspects of spinning (Table V).

Distances Moved Forward

The distance the larva moved forward in Records 3 and 5 correlated negatively both with the total number of spinning movements in the burst immediately preceding the movement and with the average time between attachments in that burst ($P < 0.01$ and $P < 0.05$, respectively, with Spearman rank correlation test). There was no correlation, however, in either record with the numbers of any of the common sequences (DA, CB, DACB, EA, FB, or G and H) or with the number of movements not included in these sequences. Again, the tendency for distances moved to clump, combined with clumping in numbers of these sequences (Table V), makes the lack of correlation especially significant.

Summary of Results

There were many general patterns in the spinning behavior of *Leptomorphus* sp. larvae, including clear preferences for some sites of attachment, some movements between attachments, some sequences of movements, and some successions of sequences. Variability in several aspects of spinning behavior was reduced in bursts performed immediately after the larva contacted large

Table V. Values of Runs Tests on Distributions of Various Behavioral Details Between Different Bursts of Spinning^a

	Record No.				
	1	2	3	4	5
A. Length of time between activities					
End of burst until extended to move forward	-0.67	-2.69**	-5.38***	—	-3.88***
Average time between movements for each burst	—	—	-2.00*	—	-2.67**
B. Numbers of movements					
Entire burst (total)	-2.17*	-2.93**	-3.01**	-2.94**	-2.13*
DACB	-1.14	-3.65***	-1.95	-2.04*	-0.84
Total other than DACB	-2.17*	-1.52	-2.06*	—	-1.09
FB	-0.58	-0.61	-2.30**	—	-0.93
EA	-1.42	-1.42	-2.46**	—	-1.77
G and H	-3.42	-1.36	-1.33	—	-0.75
Less common sequences	-1.66	-2.93**	-3.01**	—	—
C. Left-right asymmetries					
Start with C	+4.75***	+2.47*	+0.16	-2.08*	-0.14
End DACB . . . with FB	-1.42	-2.44*	-2.18	-2.35	+0.01
G	-0.37	-1.30	-2.85**	-2.40*	-0.58
H	-0.40	-1.52	-2.49**	-2.11*	-0.58
CB after DACB	-0.19	-0.42	-2.37**	+0.35	-0.09
DA after DACB	-2.47**	-1.02	-1.89	+0.72	-1.93
End burst with E	-0.60	+2.11	-0.16	+0.77	-1.03
D. Sites of attachments					
Zones III and IV during DACB . . .	—	—	—	-3.11**	-1.69
Rows 1 and 2 during DACB . . .	—	—	—	—	-2.84
E. Others					
DACB resumes after interrupted by FB or EA	-1.88	-5.00***	-5.51***	+0.19	-2.59**
N	50	52	112	48	84
					74
					158

^aNegative values indicate a tendency to clump (i.e., if the behavior occurred in one burst, the probability was greater than random that it would occur in the next); positive values indicate overdispersion. Behaviors are grouped according to the aspect of spinning to which they relate. Record 1 was from larva A; the rest were from larva B. In Record 4 the larva crawled on its own sheet of silk on a log; in all others the larva crawled on a clean glass plate. The larva rested immobile for 5-10 min between Records 5a and Record 5b, and Record 5 gives the composite results. N = number of bursts in the record; — indicates lack of sufficient variation to analyze or lack of analysis.

objects such as the petri dish wall or a cotton thread during exploratory behavior. On the other hand, interruption of spinning by turning back or withdrawing temporarily “disrupted” spinning in that the most common sequences were less frequent in bursts immediately following a turnback. Many of the patterns in spinning behavior seen on a clean glass plate also occur when the larva moves on its own sheet, eating holes in the sheet and spinning new lines across them.

Superimposed on these general patterns is a great deal of variation. Larvae almost never repeated bursts of spinning, and differences did not average out when larger blocks of behavior (5- to 10-min “records”) were compared. Small irregularities in the glass surface are unlikely to be responsible for the variations because larger irregularities (trails of silk laid previously on the glass) did not evoke clear responses. In addition, many variations were clumped in time, a pattern unlikely to result from irregularities in the surface. Larvae often moved in curving paths rather than straight forward, but turning was not clearly correlated with left–right asymmetries in spinning behavior. Variation in the distance moved forward from one burst to the next was also not correlated with numbers of any of the common sequences of movements.

DISCUSSION

Behavior of *Leptomorphus* Sp.

Larval spinning behavior in a simple, relatively uniform environment is surprisingly variable. Even when variation was underestimated by classifying attachment sites in only six regions, the number of different sequences of attachments that a single individual made in different bursts was several hundred. Judging by the very low frequency of repeats observed, the total repertoire of an individual must be at least in the thousands.

I have argued that some variations in *Leptomorphus* sp. spinning behavior are due to imprecision in the animals’ behavior rather than adaptive responses to environmental stimuli associated with spinning. One might object that the effects of all possible stimuli were not taken into account (perhaps the larvae were responding to humidity or light, for instance, or to variations in contents of different silk glands or occasional failures to attach lines from different spigots). It is also possible that there are undetected subtle patterns in the data and that what I have called “variants” are really part of these patterns.

These are difficult criticisms to refute because, in a sense, I am arguing a null case which can never be completely proven. There are, however, reasons to reject them: (1) larvae showed few clear responses to potential variations in stimuli of the same magnitude or somewhat larger than those they are likely to have encountered on “clean” glass plates; (2) many kinds of variation were clumped in time despite the low likelihood that any appropriate stimuli were

similarly clumped; (3) larvae could facultatively decrease the amount of variation; and (4) there is no clear advantage to having such an extremely wide range of variation in behavior under relatively uniform conditions. The last argument may be the most compelling since, if anything, greater variability is probably slightly *disadvantageous* due to the inefficiency that it entails in terms of energy and material expended (Barlow, 1968).

It might be argued that variability per se in spinning movements may be selectively advantageous because it would serve an exploratory function, increasing the likelihood that the larva would encounter different parts of its immediate environment and utilize the most advantageous attachment sites. An exploratory function for spinning movements seems unlikely, however: spinning was always immediately preceded by clear, wide-ranging exploratory behavior which covered nearly the same area as that covered by the following spinning movements; and adjustments of spinning behavior to uneven distributions of attachment points (e.g., Fig. 8) were immediate rather than gradual as would be expected if the spinning movements themselves were exploratory.

If the imprecision interpretation is correct, then one might expect the larva's behavior to become less variable when it needed to cope with special environmental contingencies. This appears to be what happened when larvae contacted large objects such as the walls of the petri dish and a cotton thread: the variability or diversity of subsequent spinning behavior was significantly reduced at several levels of organization.

Although the emphasis in this paper has been on higher-level variations (successions, bursts, records), there was also substantial variability in lower levels such as sites of attachment. This lower-level variability was at least partially independent of the higher-level patterns. For instance, on two occasions following periods of inactivity, larva B executed a series of bursts in which the scope of the movements of its head was much smaller than usual (Fig. 13), and few attachments occurred in the posterior zones (I and II). Nevertheless, these bursts contained sequences that clearly corresponded to the usual initial sequence (DACB. . .) (Fig. 13).

Although data exist in the literature on the variability in "modal action patterns" (MAPs) of other organisms (summary given by Barlow, 1977), comparisons with the results presented here are not straightforward. The "movements" of *Leptomorphus* sp. are probably best compared to the "acts" which make up MAPs (Barlow, 1977). But comparisons of common sequences of movements (EA, CB, etc.), successions of sequences (EA-CB-FB. . .), or entire bursts of spinning behavior with MAPs are probably not justified (G. Barlow, personal communication); similar problems occur in analyzing the grooming behavior of mice (Barlow, 1977) and flies (Dawkins and Dawkins, 1976). In the absence of clear criteria, detailed comparisons are not informative.

Clumping of variations in time was used to argue against the importance

of external stimuli as causes of variation in the behavior, but the pattern itself merits attention. Similar clumping, called "short-term motor habits," has been observed in mouse cleaning behavior (Golani and Fentress, 1985) and may occur in the songs of birds such as the chaffinch *Fringilla coelebs* which have never heard other birds sing; their songs drift slowly from one form to the next during a single song rather than varying randomly (Slater, 1989). It resembles the "inertia" associated with activating and deactivating both what ethologists have termed "motivations" (Fentress, 1983) and other behavioral processes (Blest, 1960). Presumably these patterns result from a tendency for the activity of a set of neurons producing a given variant (say interrupt and then resume DACB. . .) to persist from one bout of behavior to the next. Short-term persistent activation of a command neuron or a group of such neurons (Camhi, 1984) could produce a clumping pattern. This clumped type of "noise" occurs in many types of *Leptomorphus* sp. behavior (Table IV), suggesting a common underlying mechanism. A second pattern—the reduction in usual behavior patterns which immediately followed turnbacks and withdrawals—may be causally related: when spinning is interrupted, the larva may temporarily lose some short-term habits and need several bursts to reestablish them.

The Imprecision Hypothesis

The question of whether or not behavioral imprecision is common in other animals cannot be answered yet for lack of appropriate studies. Imprecision seems to occur in a variety of aspects of *Leptomorphus* sp. spinning behavior. Similar variability which is apparently unrelated to external stimuli may occur in the paternal retrieval behavior of the fish *Badis badis* at the time when fry are leaving the nest (Barlow, 1964), in rats' responses to gustatory stimuli (Berridge and Fentress, 1986), and in chick drinking behavior (Dawkins and Dawkins, 1973) (in this case, however, the authors stress the possible existence of causal factors too complex to readily disentangle), and in at least one stage of orb construction by the spider *Leucauge mariana* (Eberhard, in preparation).

Imprecision in behavior could be an evolutionarily important source of variation. If the degree of imprecision in a behavior is influenced genetically (as seems probable), then behavioral evolution may often consist of changes in differential suppression of variants. A possible example is the evolution of orb web construction in spiders (Kaston, 1964; Kullmann, 1972). Starting from an ancestor in which the orientations of lines laid in webs were highly irregular and unpredictable, certain behavior patterns leading to placement of lines in particular orientations have become established, while others were lost. Selective pruning of variant behavior could have produced orb webs, where lines are laid in a limited number of orientations (e.g., radial or nearly circular).

This view of the evolution of genetic influences on behavior contrasts with previous ideas which hold that new behavior patterns first arise due to the pres-

ence of new alleles (e.g., Brown, 1975) or imprecision in morphogenesis resulting in errors in the connections between command neurons (Kennedy, 1971). The behavioral imprecision hypothesis presumes that new behavior patterns are constantly being generated within the nervous system itself, and emphasis is placed on the subsequent action of genetic differences which result in selective inhibition or suppression of such patterns. This emphasis on what amounts to canalization of behavior is analogous to that placed by some evolutionary biologists on regulatory rather than structural genes as determining the evolution of physical characteristics.

Selection favoring behavioral consistency could thus act both to favor increased precision in translation of genetic information to neural networks (Dumont and Robertson, 1986) [just as it does on other morphological characters (e.g., Alexander *et al.*, 1984)] and to favor neural systems with feedback or filtering mechanisms which reduce variability in the behavior they generate.

If the hypothesis is correct, less variable (simpler) behavior may sometimes (often?) be the result of more complex rather than simpler neuronal networks. Just as additional gene products are needed to produce the negative feedback that canalizes developmental processes, additional neuronal complexity may be necessary to generate the negative feedback needed to shield a given network from irrelevant stimulation arriving from other parts of the nervous system and/or to suppress imprecision arising from the network's own activities. The apparent increase in the variability of the behavior of individuals of some hybrid birds (Barlow, 1981) hints that such selective suppression does occur. Neuronal complexity stemming from such behavioral canalization, along with complexity resulting from only partial elimination of connections associated with abandoned ancestral behavior (Dumont and Robertson, 1986), may help explain why it has been difficult to understand the details of neuronal circuitry strictly in terms of basic organizational principles (Dumont and Robertson, 1987).

ACKNOWLEDGMENTS

I thank R. Gagné for identifying the fly, M. Spivak for help with data analysis, and G. W. Barlow, J. C. Fentress, B. Hughes, A. S. Rand, E. A. Seyfarth, M. Spivak, F. G. Stiles, M. J. West-Eberhard, W. Wcislo, D. Zeh, J. Zeh, and two anonymous reviewers for constructive comments and help with references. The Vicerrectoría de Investigación of the Universidad de Costa Rica provided financial support.

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