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HIERARCHICAL ORGANIZATION AND POSTURAL FACILITATION: RULES FOR GROOMING IN FLIES

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Abstract. This paper is about rules governing grooming sequences in blowflies. Time was divided exhaustively into eight grooming and two non-grooming states. Using a keyboard connected to a computer, the times of all transitions between states during 1 hr were recorded for each of six flies. There is a strong tendency for certain acts to alternate with others. A model of alternating choice 'slots' and determined slots is presented. Grooming acts fall into discrete bouts, each involving either the prothoracic legs or the metathoracic legs, but not both. A great majority of bouts contain an odd number of acts. The beginning and ending of a bout constitute a characteristic structure regardless of the length of the intervening middle period. Unconvincing evidence for hierarchical organization of grooming decisions is presented. Convincing evidence is presented that postural facilitation is involved in the control of grooming.

If you watch a housefly or blowfly for a few moments, you will almost certainly see it rub one of its legs against another part of its body. We say it is 'grooming' that part. Neurophysiology is not yet ready to tell us what happens when, for example, a fly suddenly stops grooming its abdomen and changes to its left wing instead. Perhaps we can contribute to the eventual solution of problems of this kind by carefully recording the exact order in which animals do things, and when they do them, and by trying to discern rules, in the sense of empirical laws or patterns. Then we shall have to explain only the rules, rather than the much more numerous behavioural changes themselves.

Of course, it is not just grooming which is of interest. The same approach to the same kind of question can be made for any behaviour. But self-grooming sequences do have one feature of special interest: the external stimulus situation remains relatively constant, even when the animal walks around. Thus a fly can rub its back legs against its abdomen wherever it is, and whichever way it is facing, because its back legs and its abdomen necessarily go around together. Changes from one type of self-grooming to another are therefore quite likely to be internally triggered.

Some very successful ethological analyses of motivation have used grooming behaviour (Andrew 1956; Van Iersel & Bol 1958; Rowell 1961; Fentress 1972). These studies were all done on vertebrates. Complex behaviour where it occurs in invertebrates is especially worth studying because it is the product of a relatively simple nervous system. Grooming is one of the most complex things that many insects do (Szymanski 1918; Heinz 1949; Jander 1966; Szebenyi 1969; Farish 1972; Seibt 1972). We chose to look for rules governing grooming in the easily available blowfly, *Calliphora erythrocephala.*

Description of Grooming Movements

We recognized eight categories of grooming. Naturally this was an arbitrary decision: lumping into fewer or splitting into more categories would have been no less natural in our state of ignorance at the start of the study. We are not here concerned with the interesting question of the justification of dividing the continuous stream of behaviour into a determined number of discrete states (Dawkins & Dawkins 1973, 1974). We are making the same kind of arbitrary classification as has been made before, with all its weaknesses. Although the descriptions do not emphasize it explicitly, even parts of the body which are not actively moving during a particular behaviour pattern are probably involved in some way, for example in supporting the weight of the body. Information about the state of non-moving parts of the body is used in the 'postural facilitation' analysis.

All grooming movements involve rubbing some part of the body with a prothoracic leg (or legs) or a metathoracic leg (or legs). We shall normally speak in the active voice of the legs as grooming other parts of the body rather than being groomed by other parts of the body. This is for convenience only. The movements recognized were as follows:

(1) Front leg grooming (FR). The prothoracic legs are held up in front of the animal and rubbed against each other, while the fly stands on the other four legs.

(2) Tongue grooming (TG). The proboscis is rubbed between the two front legs.

(3) Head grooming (HD). The two front legs are together moved rapidly backwards and then forwards over the head.

(4) Middle leg groomed by front legs (FM). The prothoracic legs rub against each other in an action which is similar to FR, and at the same time they rub against the mesothoracic leg on one side of the body.

(5) Middle leg groomed by back legs (BM). Similar to FM, but performed by the metathoracic legs. These rub against each other and also against the mesothoracic leg on one side of the body.

(6) Back leg grooming (BF). Similar to FR, but performed by the metathoracic legs, which are held out behind the animal and rubbed against each other.

(7) Abdomen grooming (AB). One or both of the metathoracic legs are rubbed over the abdomen.

(8) Wing grooming (WG). One or both of the metathoracic legs are rubbed over the top or the underside of the wing(s).

Provided that the fly is on level ground with its dorsal side up, the following generalization can be made about these eight grooming movements. During those involving the front pair of legs (i.e. 1 to 4), the tibiae of the middle legs point forwards, whereas during grooming movements involving the back pair of legs (i.e. 5 to 8), the tibiae point backwards. This was a seemingly invariant rule for all flies observed, and is presumably related to the need to balance on two pairs of legs, illustrating the point that even stationary parts of the body contribute to a behaviour pattern. From now on, behaviour patterns 1 to 4 will be referred to as anterior grooming acts and 5 to 8 as posterior grooming acts.

In addition to these eight movements, we also recorded:

(9) Moving (MV): walking etc.

(10) Stationary (NO): fly stationary and not grooming.

This list of ten behaviour states is exhaustive for our testing situation: at any moment a fly had to be doing one of them and only one.

Keyboard Recording Method

Single flies were watched with the naked eye in a watch glass 47 mm diameter and 15 mm deep. A keyboard with one key denoting each of the acts listed above was connected to a small digital computer (PDP 8 L) equipped with a digital clock. The computer was programmed to punch out a paper tape encoding the times at which each key was depressed and released. Individual movements ('rubs') in an unbroken sequence of a named behaviour were not distinguished. The appropriate key was held down for the duration of the sequence. Each complete depression and release of one key designates what we call one 'act'.

The times were given by the apparatus to the nearest $\frac{1}{10}$ s which is obviously much more accurate than the human operator. The tape was later read back into the computer, and data such as the duration of grooming acts and their sequential order extracted. Six flies from a laboratory stock were used. Each was observed for 1 hr. The total number of grooming acts recorded was about 7000.

Results and Discussion

Do Behavioural Events Allow Us to Predict Other Behavioural Events in the Immediate Future More Accurately than Events in the More Distant Future?

Many authors have implicitly asked this question when they have attempted to analyse behaviour as a Markov chain (e.g. Nelson 1964). The answer is pretty certain to be 'yes' if we interpret 'immediate' and 'distant' in their extreme senses. In other words we can expect the curve of predictability (Dawkins & Dawkins 1973) to decay overall as we look further into the future, but it is less obvious what the actual time course of that curve might be. The purpose of this section is to see if there are any temporary

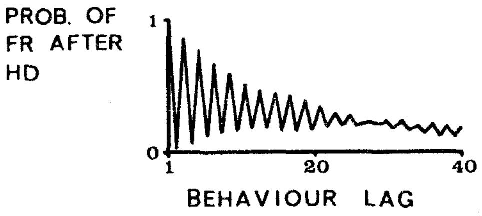

Fig. 1. Probability from 0 to 1 (ordinate) that the *i*th behaviour after head grooming (HD) will be front leg grooming (FR). *i* runs from 1 to 40 (abscissa). Data from one fly. All other flies very similar.

reversals or sharp kinks in the decay. For this, we have used two different sorts of 'time' unit; firstly, 'behavioural event time' measured in numbers of recorded behavioural acts, regardless of their duration; and secondly 'real time' measured in tenths of seconds regardless of numbers of acts recorded.

Figure 1 presents results from one pair of grooming acts only, HD and FR, for one fly. The horizontal axis represents time lag measured in 'behavioural event time' units, running from 1 to 40. The vertical axis represents probability that an occurrence of HD at 'time' 0 will be followed by FR at each of the various 'time' lags. For example, the peak at lag 1 indicates that HD is quite likely to be followed by FR as the immeditately next act; the trough at lag 2 shows that FR is very unlikely to occur as the next but one act after HD and so on. Each act in turn was considered as defining 'time 0'.

The most striking feature of the graph is the pronounced zig-zag pattern: the probability of HD being followed by FR does not decay smoothly into the future; rather it is high at odd-numbered lags and low at even-numbered lags. The amplitude of the zig-zags does not remain high but decays. A line joining the peaks would decay downwards and a line joining the troughs rise upwards toward the same asymptote. This asymptote has meaning: it is the overall probability that a behaviour will be FR, given that nothing is known of past behaviour.

Figure 1 is for one pair of acts only. A similar graph can be drawn for all 10 × 10 pair combinations of the acts distinguished. These graphs summed for all six flies are brought together in Fig. 2. The whole picture may be regarded as equivalent to forty superimposed tables of transition probabilities, one table for each of forty lags. Ignoring the bottom row for the moment, the remaining 100 cells are each equivalent to Fig. 1 but for a different combination of two acts. The preceding acts are designated by the column titles, and the following acts by the row titles. Figure 2 is thus analogous to the kind of 'cross-correlation' picture presented by Delius (1969). The left-to-right ascending diagonal contains the 'autocorrelations', the graphs of probability that each behaviour type will be followed by itself after various lags. All the autocorrelations necessarily start at 0, since, by definition, an act cannot follow itself.

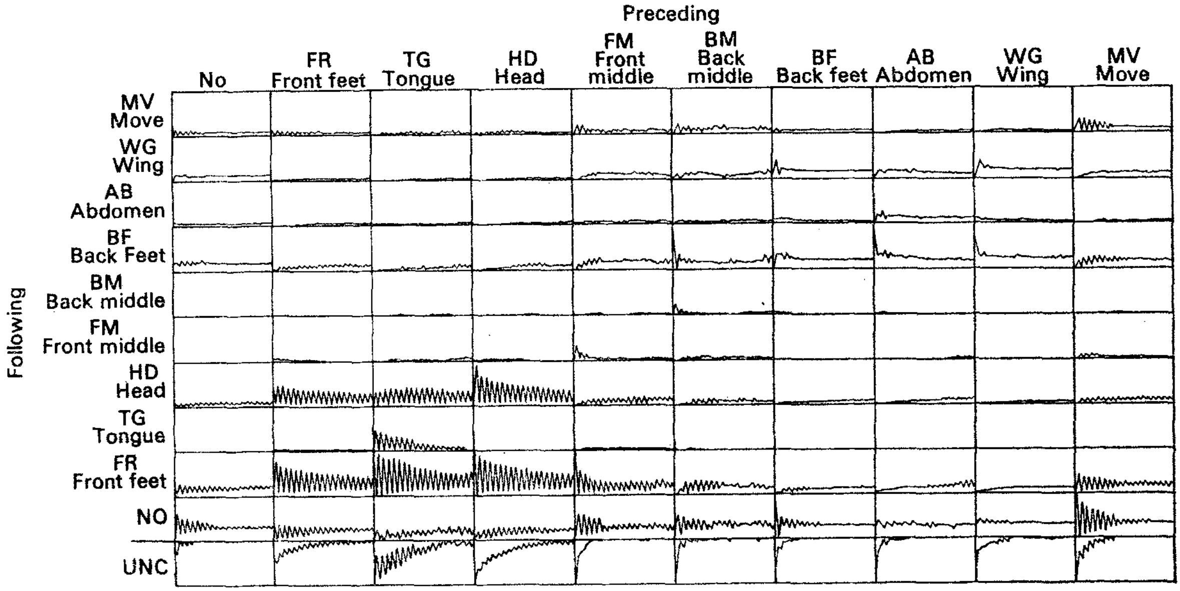

Fig. 2. As Fig. 1, but a separate graph for each combination of preceding and following acts. Bottom row (UNC) plots uncertainty of outcome of preceding behaviour (see text). All flies similar, this figure plots summed data from all.

Interpreting each little graph in the same way as Fig. 1 we see that the same sort of zig-zag pattern with an overall decay is characteristic of many of them. However, the peaks and troughs do not occur in the same places. For example, in the FR-to-FR graph the peaks occur at even-numbered lags and the troughs at odd-numbered lags, exactly the opposite way round from the FR to HD case. These results reflect the fact, obvious to the casual observer, that FR and HD show a pronounced tendency to alternate. Similarly, FR alternates with TG, and FR alternates with FM. Not all pairs of acts show such mutual interactions; for example the cell of the table showing relations between WG and TG is empty. Looking at the table as a whole, the eye seems to detect clusters of mutual interaction at lower left and upper right. What this might mean will be taken up later in the section on hierarchical organization.

The question posed at the head of this section can thus be answered for particular pair combinations of preceding and following acts by reference to the main part of Fig. 2. The bottom row of the figure attempts to give a more general answer. There is one little graph in this row for each preceding behaviour. As in the rest of the figure, this behaviour, designated by the column title, is regarded as occurring at 'time 0' of the horizontal axis which again runs from 1 to 40 'behavioural event units'. The vertical axis, however, is different. It shows the average uncertainty of outcome of the 'time 0' behaviour, for each of the various lags. The average uncertainty, H, is computed in bits using the formula

$$H = -\sum_{i=0}^{9} p_i \log_2 p_i$$

(Shannon & Weaver 1949). H is calculated separately for each lag, where p_i is the observed probability that the behaviour which occurs at that lag will be behaviour i. For each lag therefore, H is calculated as a form of weighted average from the ten probabilities immediately above it in the graphs of the main part of the figure. For reasons of convenience in scaling, H is not actually plotted in bits, but as a proportion of $H_{\max}$. A constant for all columns, $H_{\max}$ is the uncertainty of an observer who knows nothing about preceding behaviour, but knows only the overall frequencies of the various acts, i.e. p_i is here taken to be total number of occurrences of the ith behaviour, divided by the total number of behavioural events recorded.

It can be seen that the uncertainty graphs start low for short lags, and climb towards $H_{\max}$ for long ones as would be expected. However, in many cases there are temporary reversals of the trend, and, in particular, pronounced zig-zag patterns appear. For example the immediate successor to HD is highly determined: the uncertainty at lag 1 is almost zero. The lag 2 uncertainty on the other hand is relatively high, the lag 3 uncertainty is lower and so on. A glance at the main part of the figure tells us that the reason for the low uncertainty at odd numbered lags is the very high probability that FR will occur. The higher uncertainty at even numbered lags reflects the fact that at these times the fly has a choice between HD, TG and FM.

Figure 3 summarizes this idea of highly determined 'FR slots' alternating with 'choice slots' into which any of the other three anterior grooming movements is inserted. A similar though less rigid diagram could be drawn for posterior grooming movements, with BF filling the FR role. BF is likely to be followed by AB or BM or WG, but not by any of the anterior grooming movements. AB, BM and WG are all likely to be followed by BF.

Figure 3 implies by its simplicity that each 'choice slot' is independent of the previous one, i.e. that although the choice made after FR is confined to HD, TG and FM and is influenced for example by the overall greater rarity of TG, it is nevertheless independent of whether the previous choice slot was filled by HD, TG or FM. Table I shows this implication to be false. There is rather a strong tendency for the choice made in one choice slot to be the same as that in the previous one. Therefore, the picture drawn in Fig. 3 of alternating choice and determinism is oversimplified.

So far all discussion has been in terms of 'behavioural event time' which is related to real time only on a crude ordinal scale. Figure 4 is equivalent to Fig. 2 but with time lags measured in real time units. The horizontal axis of

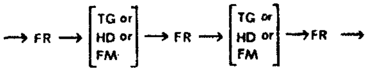

Fig. 3. Diagrammatic representation of typical anterior grooming sequence showing alternation between front-leg grooming (FR) and a 'choice slot' in which one of three acts is performed.

Table I. Frequency of Occurrence of Various Triplets of Grooming Movements, for Those Cases where an FR Occurred Between Two Other Acts. Making Allowances for Overall Frequencies, the Act which Precedes FR is Also Most Likely to Follow It (Matthews Test (1966), Type III). Data from all Six Flies Combined

First act of triplet	Second act of triplet	Third act of triplet	Frequency of triplet
TG	FR	TG	37
TG	FR	HD	23
TG	FR	FM	1
HD	FR	TG	7
HD	FR	HD	572
HD	FR	FM	11
FM	FR	TG	2
FM	FR	HD	6
FM	FR	FM	50

TG = Tongue
HD = Head
FM = Middle leg with front leg
FR = Front legs

each little graph runs from 0 to 4 s with a resolution of $\frac{1}{10}$ s. As before, the bottom row of graphs measures uncertainty of outcome. When allowance is made for time scale, these graphs are similar in overall shape to those of Fig. 2, except that the zig-zag patterns are absent. This is because the actual durations of grooming movements are sufficiently variable for the alternation tendency to be smothered in the averages. In one or two cases this covering up seems incomplete and in some graphs, for instance HD to HD, there is a suggestion of a zig-zag.

In qualifying the question which heads this section we said that, overall, a decay of certainty into the future was to be expected. The results, especially the real time graphs, bear this out. We said that of more interest would be temporary reversals and sharp discontinuities in the decay curve. Temporary reversals we have now seen in the zig-zag alternation patterns of Fig. 2. Other types of sharp discontinuities would not be shown up by the type of averaged time-lagged graphs we have so far plotted, and we must turn to a different type of analysis to reveal them, namely bout analysis.

Bout Analysis

Casual observation suggests that grooming is divided into discrete bouts interspersed with periods of locomotion or of stillness. Bouts seem to have sudden beginnings and endings and seem never to mix front and rear end

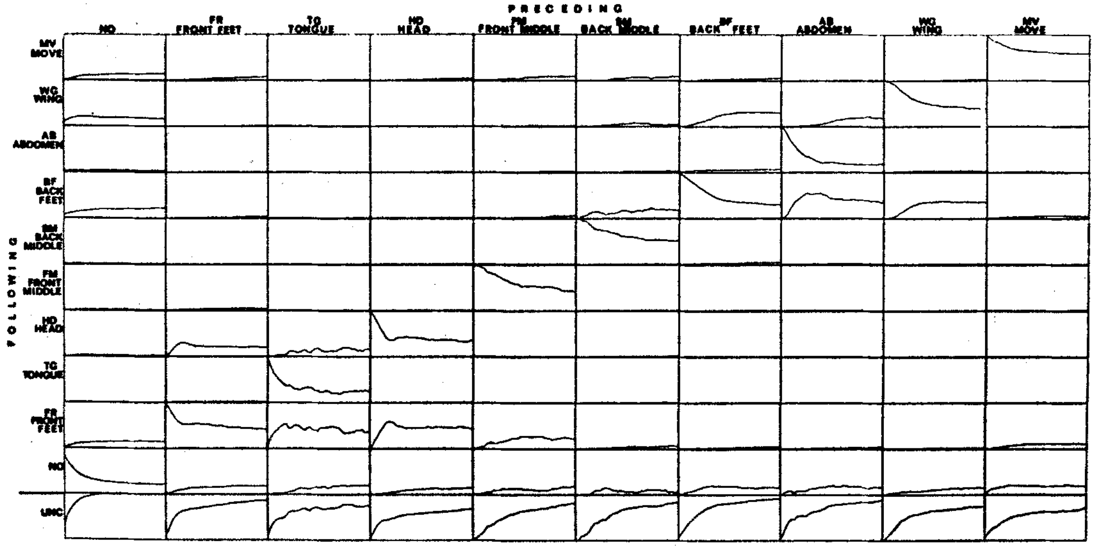

Fig. 4. As Fig. 2 except abscissa represents real time lag measured in tenths of a second from 0 to 40, i.e. a form of time-lagged cross-correlation with ordinate of each little graph measuring probability from 0 to 1 that the behaviour named in the row title will occur at various time lags after the behaviour named in the column title. All flies similar; this figure plots summed data from all.

movements. If it turned out that bouts have a characteristic structure, for instance with a beginning, a middle and an end, this would go against the idea of smooth decay of predictability from past to future behaviour which served as a form of null hypothesis for the previous section.

First we need a strict working definition of a bout, for example in terms of a criterion gap between grooming movements. Isaac & Marler (1963) studying mistle thrush song solved this problem by plotting the distribution of gap lengths and finding it to be discontinuous. Figure 5 is a similar gap-interval histogram for fly grooming, a gap being defined as a period containing no grooming movements. The time class width is $\frac{1}{10}$ s which is certainly as small as considerations of recording accuracy allow. It is possible that film analysis methods might reveal discontinuities at smaller intervals but, at time scales measurable by manual recording, the histogram is smoothly continuous and unimodal. This method of defining a bout criterion is thus not available to us.

There is, however, another way. As we have already shown, there is a very strong tendency for (HD, TG or FM) to be followed by FR and for FR to be followed by (HD or TG or FM). But if grooming movements are segregated into discrete bouts we need not expect this alternation rule to bridge the gap between bouts. If there were a criterion gap such that for all gaps longer than criterion the alternation rule were broken, and for all gaps shorter than criterion the alternation rule were upheld, this would constitute another way of defining a bout of grooming. Table II shows for anterior grooming movements that $\frac{1}{5}$ s appears to constitute such a criterion. Acts separated by a gap of less than $\frac{1}{5}$ s (in practice this usually meant no gap at all) uphold the normal alternation rule. Acts separated by a gap greater than (or equal to) $\frac{1}{5}$ s break the alternation rule: indeed they tend toward the exact opposite of alternation, for a reason to be discussed below. This suggests that a satisfactory definition of a bout is any sequence of grooming acts separated from the preceding and following bouts by a gap of $\frac{1}{5}$ s or more. From now on, this is the definition we use. Table III uses the definition to confirm the subjective observation made above that flies do not mix anterior and posterior grooming movements within bouts.

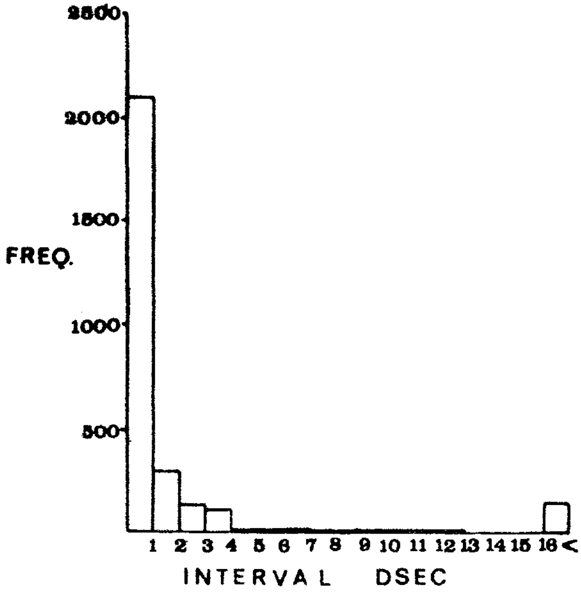

Fig. 5. Frequency distribution of intervals between grooming movements, i.e. of durations of periods containing no grooming. Data summed from all flies.

If bouts have a definite structure, one elementary way in which it might show itself is in a tendency for beginnings and endings of bouts to occur at particular phases of the alternation cycle of Fig. 3. For example a bout of anterior alternations might always begin and end with FR. That some such pattern exists is suggested by the great preponderance of anterior grooming

Table II. The Number of Anterior Grooming Transitions in which the Alternation of FR with One of (TG or HD or FM) was Preserved or Broken According to the Time Interval Separating Them

Fly	Intervals (s)	Alternation preserved	Alternation broken
1	< 0·2	233	0
	> = 0·2	7	22
2	< 0·2	438	0
	> = 0·2	0	41
3	< 0·2	470	2
	> = 0·2	29	71
4	< 0·2	188	0
	> = 0·2	4	41
5	< 0·2	199	1
	> = 0·2	5	31
6	< 0·2	131	1
	> = 0·2	0	28

Table III. The Number of Grooming Bouts Containing Only Anterior Grooming Movements, Bouts Containing Only Posterior Grooming and Bouts Containing Both Sorts of Grooming

Fly	No. of bouts containing only acts 1–4 (anterior grooming)	No. of bouts containing only acts 5–8 (posterior grooming)	No. of bouts containing mixtures of anterior and posterior grooming
1	51	103	0
2	70	69	1
3	147	50	0
4	114	191	2
5	79	272	0
6	67	90	0

bouts with an odd number of movements (Table IV). This indicates either that bouts start and finish with FR, or that they start and finish with a 'choice slot'. The former suggestion is the correct one, as we shall see. This accounts for the fact, noted above, that acts separated by more than the criterion interval not only break the alternation rule, but actually tend in the opposite direction from that rule.

Figure 6(a) gives the observed probability that particular positions or 'behaviour slots', counting from the start of all anterior bouts, will be filled by each of the possible grooming movements. Thus the first act in an anterior bout is almost certain to be FR, the second is unlikely to be FR, but might be either HD, TG or FM, the third is likely to be FR again and so on. Head (HD), tongue (not shown on the graph in the interests of clarity) and middle leg grooming (FM) occupy even-numbered 'slots', although there does not seem to be any tendency for them to occupy specific even-numbered positions: for example, HD does not seem to occur consistently later or sooner in a bout than, say, FM.

Table IV. The Number of Anterior Grooming Bouts Containing Odd and Even Numbers of Acts

Fly	Odd-numbers of acts	Even-numbers of acts
1	43	8
2	69	1
3	114	33
4	104	10
5	68	11
6	65	2

Posterior grooming bouts, on the other hand, do not consistently begin with a particular behaviour (Fig. 6(b)), but they do tend to end with back leg grooming (BF) (Fig. 7(b)). It is a rather striking phenomenon that bouts of

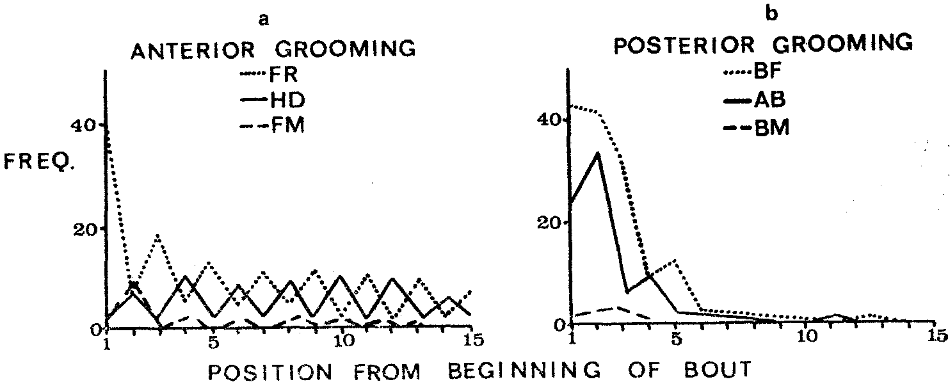

Fig. 6. Frequency (ordinate) of occurrence of various grooming movements in particular positions or 'slots' in a bout of grooming, counting the first behaviour of a bout as slot 1. Anterior and posterior grooming acts are plotted separately, only three of each in the interests of clarity of the graphs. For the same reason lines are drawn rather than histograms. Data from one fly, all others similar.

posterior grooming show more structure and organization if the end of a bout is considered as the reference point rather than the beginning (compare Figs 6(b) and 7(b)). Looking at the behaviour slots backwards from the end of a bout, posterior grooming is shown to exhibit strong alternation: back leg grooming (BF) alternates with either abdomen (AB), wing (not shown in the figure) or middle leg grooming (BM). The sequence leading up to the end of a bout of posterior grooming is thus rather fixed with respect to the end-point, somewhat in the same way that the landing drill of an aircraft might be timed backwards from the moment of touch-down (this is, of course, intended purely as a descriptive analogy, not as an explanatory model). Anterior grooming counted backwards from the end of a bout also shows typically highly patterned structure (Fig. 7(a)).

If instead of looking at behaviour 'slots' within a bout, we consider real time, we see a somewhat similar picture (Figs 8 and 9). Flies spend the time at the beginning and end of anterior grooming bouts in performing FR

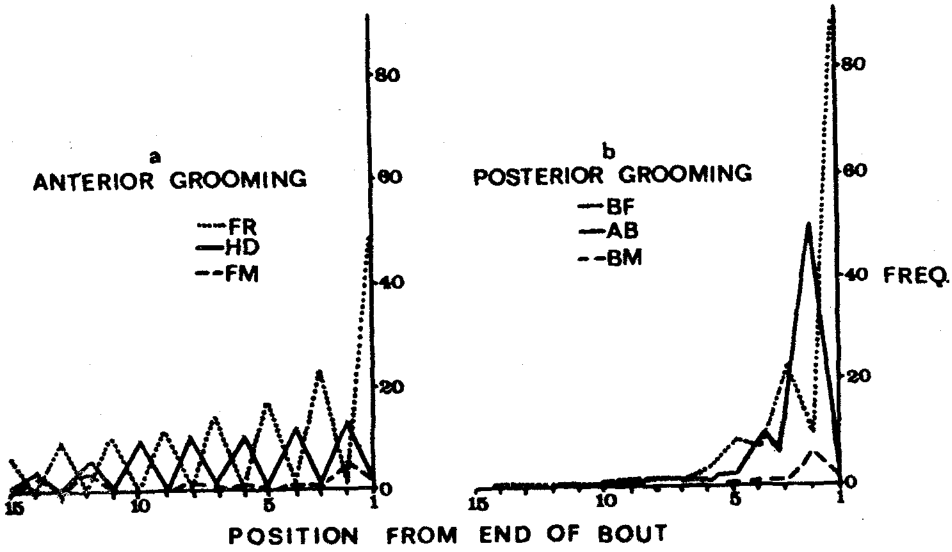

Fig. 7. As Fig. 6, but 'slots' are counted backwards from the end of each bout.

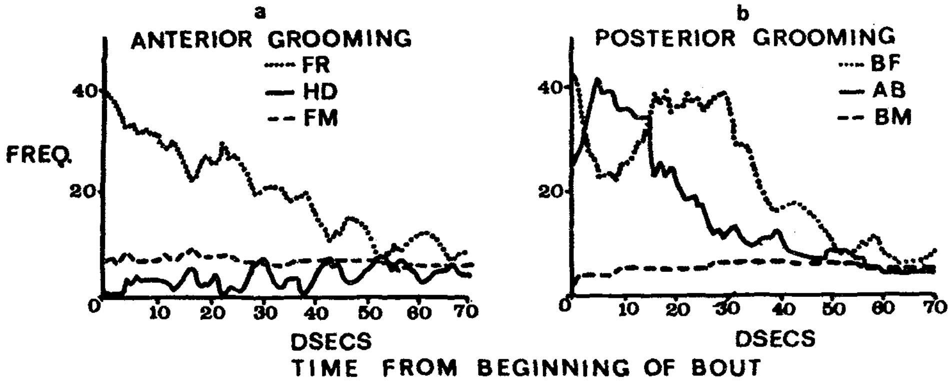

Fig. 8. As Fig. 6, but abscissa represents real time from start of bout, measured in tenths of a second rather than counted 'slots'.

(Figs 8(a), 9(a)) and alternation is again suggested in the out of phase relationship between the time of doing FR and the times of doing either HD, TG or FM. Posterior grooming bouts are ended with a period of back-leg grooming (BF), with the peaks of the other acts occurring earlier.

To conclude these first two sections and lead into the next, we may say that although, overall, the immediate future is more predictable than the more distant future, there are discontinuities in the time-course of this predictability. Figures 1, 2 and 3 for instance showed that in some cases the present act enables us to predict the next but one act with more certainty than we can predict the immediately next one. The bout analysis carries us further in the same direction. In the case of bouts of posterior grooming the most predictable part of a bout is its end (Figs 7(b) and 9(b)). The moment at which the 'decision' (in the sense of Dawkins & Dawkins 1973, 1974) is taken, that the end routine shall be executed, is the moment at which the bout of posterior grooming begins, since that is the moment at which its occurrence becomes suddenly highly probable. But the actual course and duration of the bout of posterior grooming before its stereotyped end is relatively unpredictable. This is then another example of behaviour leading to better prediction of the distant future than of the near future. But in this case 'indeterminate' might be a better word than 'distant', because the intervening period of uncertainty is itself uncertain in duration. From Fig. 2 we could say 'the performance of FR implies, regardless of the immediately next behaviour, that the next but one act will be FR'. After the posterior grooming bout analysis we have to say, less simply: 'the performance of any posterior grooming movement tells us little about the succeeding acts for an indefinite period, but it does tell us that the last act before posterior grooming ceases will probably be BF'.

This is rather suggestive of the type of hierarchic grammatical model of behavioural organization put forward by Marshall (see Dawkins 1976) and by Kalmus (1969). To discuss this fully here would take us too far afield: for the present we turn to one particular interpretation of the idea of hierarchical organization.

Is Grooming Hierarchically Organized?

Of the many meanings that 'hierarchical' can take in ethology (Dawkins 1976), the one which we are using here is based on the concept of decision (Dawkins & Dawkins 1973).

We define the organization of grooming decisions as hierarchical if it is possible to

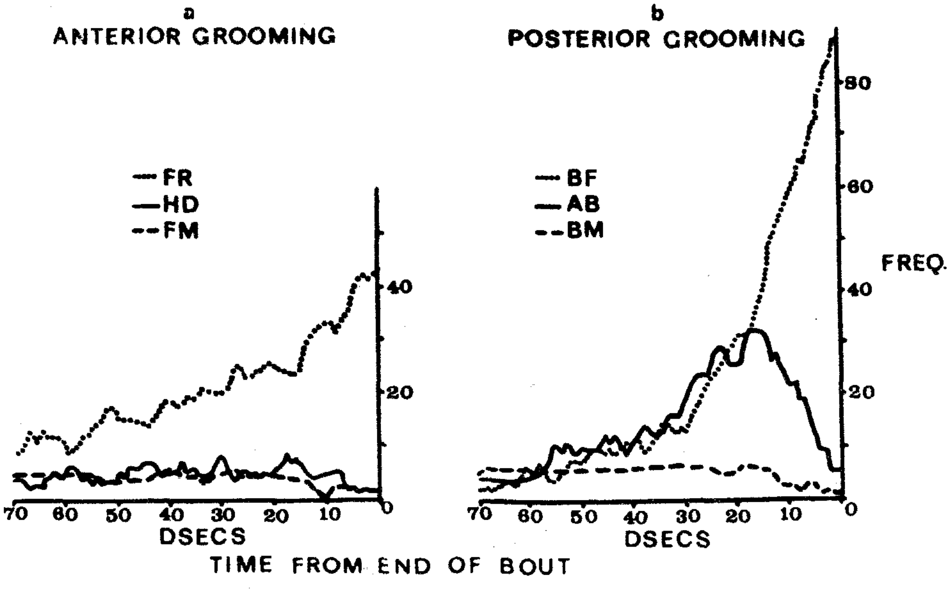

Fig. 9. As Fig. 8, but time in tenths of a second is counted backwards from the end of each bout.

group the various acts into clusters such that:

(1) For each cluster there exists a state of the fly being certain to do one element of the cluster, but still uncertain which. Thus behaviours *A*, *B* and *C* form a cluster if the fly is capable of entering a state in which it is definitely about to do (*A* or *B* or *C*) and nothing else, but this state still leaves open which of the three will be done.

(2) The elements within a cluster between which a choice is made may be sub-clusters defined in the same kind of way, or they may be grooming acts themselves. For example, the fly might also be capable of entering a state of being certain to do (*A* or *B* or *C* or *D* or *E*) but not anything else; at other times the fly enters a state of being certain to do (*D* or *E*) but not anything else, but it never enters a state of being certain to do, say, (*A* or *D*) but not anything else. A state of being about to do *A* or *D* must imply the possibility of being about to do *B* or *C* or *E*, because *A* and *D* belong to different clusters at the same level. Thus the cluster of five hypothetical acts can be presented as two sub-clusters ((*A* or *B* or *C*) or (*D* or *E*)).

(3) We make the additional strong and testable assumption that choices may be influenced by previous choices only within clusters not between clusters, and only by previous choices during the current entry of the current cluster. Thus if a transition is observed between *A* and *D* this implies that the fly must have left cluster 1 (*A* or *B* or *C*) and entered cluster 2 (*D* or *E*). By rule 3, the choice of which member of the new cluster is performed is uninfluenced by which members of the old cluster had been chosen. Thus the transition *A* → *D* has a probbility which is equal to the probability of the transition cluster 1 → cluster 2, with appropriate correction for the overall rarity or commonness of *A* and *D*. On the other hand, the transition *A* → *B* may, according to the model, be especially probable (or improbable) when compared with *A* → *C* and when allowing for the overall commonness of the acts This is because *A*, *B* and *C* belong in the same clusters, and so obey local transition rules. Rule 3 implies that there is not just one set of transition rules governing all acts, which can be expressed in a single transition matrix. Rather it postulates nested sets of transition rules, each set of rules holding sway only within a circumscribed cluster of elements (Fentress & Stilwell 1973). Transitions between elements which belong in different clusters at any particular level, are entirely predictable from the more global rules of transition between their respective clusters.

Of course this model could easily be wrong, which is why it is worth putting it forward. The easiest way to disprove it would be to show that there are no global transition rules with local mutually insulated transition rules nested within them, but one single set of rules describing the transitions between each behaviour and each other behaviour. That is, all acts belong in the same big cluster, and the 'hierarchy' is one-levelled and therefore trivial.

Can we arrive at testable predictions of this type of hierarchical model? Ideally it would be desirable to find a general prediction which followed from all multi-levelled as opposed to single-levelled systems, regardless of the details about which particular acts are assumed to be clustered with which. This we have failed to do, and we do not know whether any mathematician would consider it a worthwhile challenge. We have had to resort instead to guessing what might be the particular clustering of fly grooming acts, and testing predictions of this particular model.

It would be desirable to use an objective cluster analysis (Everitt 1974) to aid us in guessing what this natural clustering of fly grooming acts might be. However, it is important to realize that ordinary methods of cluster analysis which begin with a similarity matrix and then use a 'single-linkage' or comparable algorithm to draw a hierarchical tree, are not suitable. This is because no obvious measure of 'similarity', such as temporal proximity, is compatible with the decision model described above. That model is not saying that members of the same cluster necessarily tend to occur close to each other in time. Rather, the model is saying that members of the same cluster resemble each other in their sequential relations with other behaviour patterns which are not in the same cluster. If HD and TG are closely clustered together, according to the present model this does not mean they necessarily occur together in time. It means they are mutually replaceable in a sequence involving other acts (as in Fig. 3). To follow Kalmus's (1969) analogy of a menu, two sorts of fish are mutually replaceable as second-course dishes in formal dinners: for this very reason, a person would be unlikely to eat two fish dishes in succession. HD and TG are alternative contenders for the 'choice slot' in a front-end grooming sequence, just as trout and whitebait are alternative contenders for the 'fish slot' in a menu.

If we are to use cluster analysis, therefore, it must be a special sort of cluster analysis, based on *mutual replaceability*, rather than temporal proximity or the like. Such an analysis is applied to the fly grooming data in Fig. 10. The method is described fully elsewhere (Dawkins 1976). Briefly, the procedure is as follows. A table of frequencies of transition between the acts is scanned. Each pair of acts is considered in turn, and an index of mutual replaceability for that pair computed. This index, based on the Spearman Rank Correlation Coefficient, expresses the similarity between the two acts with respect to the distribution of the acts which precede and follow them. When all pairs of acts have been examined, that pair with the highest index of mutual replaceability is designated the lowest 'sub-cluster' of the tree. For example (Fig. 10), for the fly 'April', (TG and HD) were the first pair to be clustered together. The transition table is then collapsed, in that the data for the pair of acts just united are lumped together, as though they were one 'act'. The procedure is then repeated recursively on the collapsed table. In the case of April, the next pair to be clustered was (FM and (TG + HD)), followed by (FR and (FM + (TG + HD))). The process continues until there are only two elements left in the table, or until the maximum index of mutual replaceability fails to attain an arbitrary criterion value.

The hierarchical trees for the six flies are not identical (Fig. 10). The flies 'May 31' and 'Jun 4' did very little TG grooming. In them HD and FM come out closely clustered together. In all the rest, TG and HD cluster most closely of the front-end acts, and FM clusters most closely with them. Finally, FR 'joins in'. This is compatible with our subjective impression summarized in Figure 3, although there we had TG, HD and FM as a mutually replaceable triplet: something which the present cluster analysis is not capable of producing.

The clustering of rear-end grooming acts is more variable, as we should expect from earlier results. However, the tree diagram based on the sum totals from all flies shows a neat symmetry between front and rear end. TG and HD cluster first at the front; AB and WG first at the back. Then FM joins (TG + HD), and BM joins (AB + WG). This is satisfactory, since FM and BM are 'mirror-image' movements at their respective ends of the body. Finally, FR joins the front-end cluster, and BF joins the rear-end cluster. FR and BF are also mirror-images in form, and we have already suggested that they play similar roles in the temporal structure of grooming bouts at their respective ends. Under the heading 'Patterns of Pattern', the possible significance of behavioural symmetry of this kind is discussed speculatively elsewhere (Dawkins 1976). Briefly, it would be economical for the nervous system to adapt the same 'subroutine' to control more than one complex behaviour sequence, in this case to control both front-end and rear-end grooming.

Alluring though this apparent symmetry may be, it is seen only in the results summed from all six flies. In individual flies, rear-end grooming is too variable for clear generalizations to emerge. All that seems certain is that rear-end grooming acts cluster with each other before they cluster with front-end acts. This, together with results reported earlier in this paper, suggests that it is reasonable to guess that fly grooming movements fall into two main clusters, one containing anterior, and the other posterior grooming movements. This was also the conclusion of Seibt (1972) for Diopsid flies. It seems additionally plausible because the two groups of movements presumably involve primitively different thoracic ganglia, and each ganglion might be expected to be capable of some autonomous decision-making. Returning to the model with which this section began, we have used this guess, that front-end and rear-end movements constitute the two main clusters, in a direct test of assumption 3 of the model. This was the assumption that the details of within-cluster decisions are not influenced by prior decisions in a different cluster. To disprove the prediction would not disprove the whole hierarchical decision-making model. It might simply mean our initial guess as to exactly how the acts are clustered is wrong.

We have chosen to work with transitions between bouts rather than transitions between individually recorded acts. (A bout is defined, as above, in terms of the $\frac{1}{5}$-s criterion gap.) For example, we have counted the number of times a bout consisting of FR and TG is followed by a bout consisting of BF and AB. The reason for working with bouts is that for this analysis we are focussing on those rare transitions between front-end and rear-end acts, i.e. between members of different clusters. For instance, on those occasions when a front-to-rear transition is made, does the detailed choice of

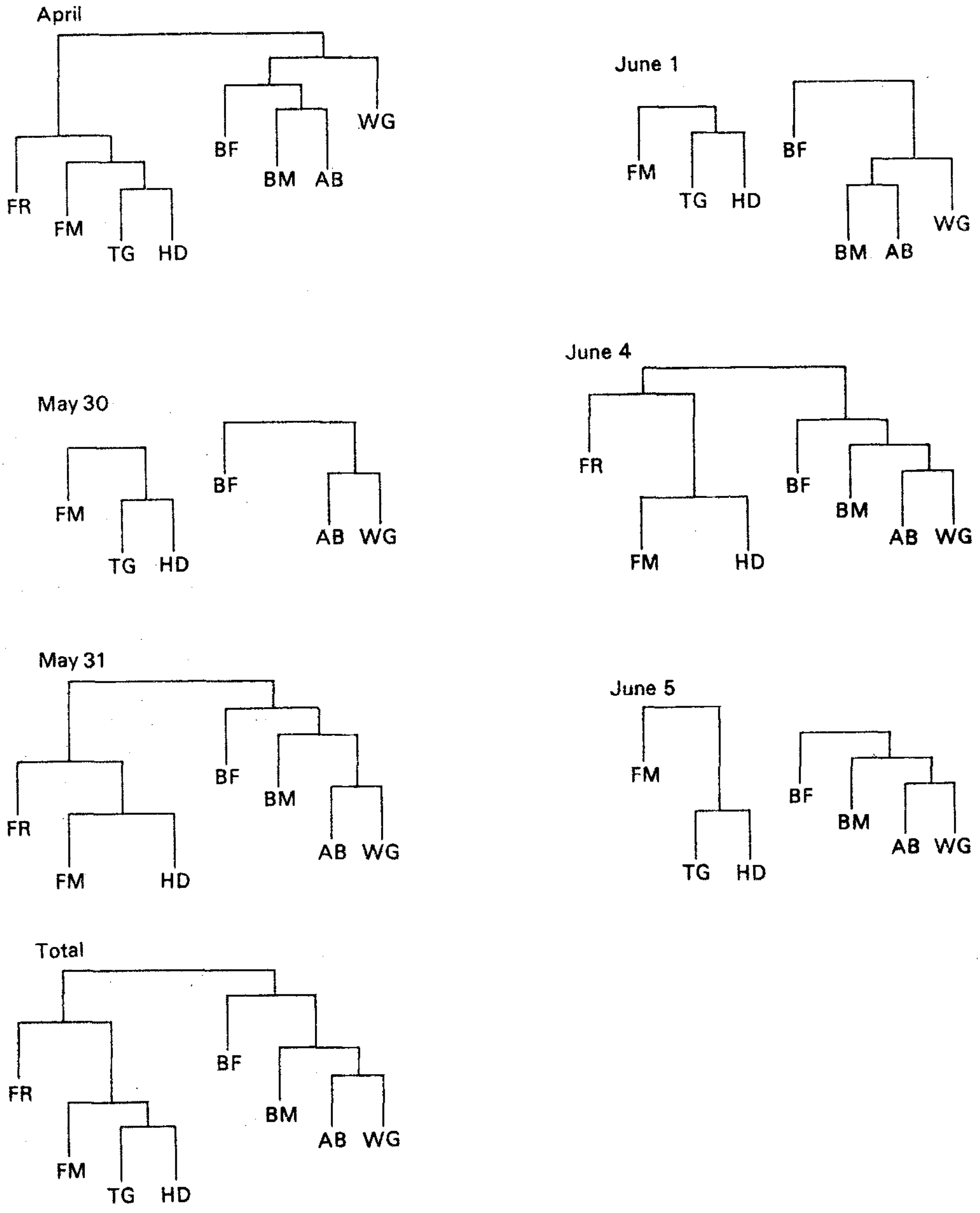

Fig. 10. Mutual replaceability cluster analysis for the six flies separately and for the totals summed from all six flies. Acts (or already formed clusters of acts) which cluster closely together are mutually replaceable in behaviour sequences. The index of mutual replaceability is based on the Spearman Rank Correlation Coefficent (further details in Dawkins 1976). The clustering is achieved progressively. For eech fly, the first cluster to be formed is lowest down the page. The last cluster formed is highest on the page. In the case of APRIL and TOTAL, all grooming acts were finally clustered together. In the other cases it was not possible to cluster some of the acts. The two non-grooming acts were omitted from the cluster diagrams, but were included in the sequence analysis used to form the cluster diagrams. Further details in text. On this figure the six flies are named by their date of testing. 'Flies 1 to 6' in the Tables correspond in chronological order.

rear-end act depend on whether the last front-end act was TG or HD, etc.? Since, as we have already seen, essentially all front-end bouts end with FR and most rear-end bouts begin with BF, transitions such as TG to AB are too rare to count. FR, and very likely BF as well, intervenes between them. We have therefore taken for granted the occurrence of FR in front-end bouts, and BF in rear-end bouts. We have defined ten bout-types in terms of the other acts which they contain (Table V). These are not the only ten bout types which could have been defined, but they are reasonable in the light of the results so far reported. For example, type 1 contains FR only, type 2 contains TG (+ FR), type 3 contains HD (+ FR), type 4 contains FM (+ FR). Type 5 embraces all more complex mixtures of front-end movements, such as HD + TG (+ FR). Types 6 to 9 are analogously defined for the rear end, and type 10 (very rare) contains any mixture of front- and rear-end movements.

The number of bouts is of course much smaller than the number of recorded acts and, in order to get enough data, it is unfortunately necessary to lump all six flies. This makes the results rather suspect, but we present them to illustrate the method, which may be of interest. Table VI shows the total frequencies of transition between each of the bout types and each other one. The table is divided into four quadrants corresponding to the four types of transition represented in Table VII.

If there really are 'within-cluster' rules separate from 'between-cluster' rules, the prediction is that the transitions in the 'homogeneous' quadrants will depart significantly from the random expectations based on overall frequencies of the acts concerned, while transitions in the two 'heterogeneous' quadrants will not.

Table V. Definitions of Ten Different Sorts of Grooming Bouts

Type	Contents
Anterior grooming bouts (hypothetical cluster 1)	
1	FR only
2	TG with or without FR
3	HD with or without FR
4	FM with or without FR
5	Any mixture of TG, HD and FM with or without FR ('anterior mixture')
Posterior grooming bouts (hypothetical cluster 2)	
6	BF only
7	AB with or without BF
8	WG with or without BF
9	BM with or without BF
10	Any mixture of AB, WG and BM with or without BF ('posterior mixture')

Each of the four quadrants was subjected to an N by N χ^2 analysis. For each cell an expected frequency was computed simply from the row and column totals as described in several papers (e.g. Nelson 1964). For each of the four quadrants χ^2 for sixteen degrees of freedom was calculated as the sum of

$$\frac{(\text{Observed}—\text{Expected})^2}{\text{Expected}}$$

for all 25 cells in the quadrant. Table VII gives this χ^2 value for each of the four cells. There seems to be substantially greater evidence of within-cluster interaction than of between-cluster interaction (Table VII). The prediction thus appears to be approximately fulfilled. However, if contingency coefficients are calculated, the predicted effect disappears, suggesting that it may be an artifact of the larger numbers of within- than between-cluster transitions.

A more convincing test of the prediction using data from the published literature is given in Dawkins (1976).

Is Grooming Behaviour Influenced by 'Postura Facilitation'?

A largely overlooked feature of behaviour is that it involves the concerted action of many different parts of an animal's body, and the simultaneous inaction of other parts. We have to understand not just how individual limbs are moved, but, in addition, how co-ordination between the different parts is achieved. Patterns of behaviour are brought about by the contraction of a select fraction of the muscles of an animal's body in precise relation to one another in time and space, but, as Roeder (1967) points out: 'An equally active and significant part of the behaviour pattern is the non-contraction or relaxation of the rest'. When a fly grooms its head, it may be only the head and prothoracic legs that actually move, but the other pairs of legs, although immobile, nevertheless have an important role in supporting the body. The second pair of legs adjust their position for this support function during anterior grooming (page 740) and if the back legs tried to start grooming movements of their own at the same time, the fly would fall over. The wings remain immobile. In giving causal explanations of grooming behaviour, it is consequently

Table VI. Transition Frequencies Between the Bout Types Defined in Table V. Data Summed from All Six Flies

	Following bout type											
Preceding bout type	1 FR only	2 TG	3 HD	4 FM	5 Ant. mix	6 BF only	7 AB	8 WG	9 BM	10 post. mix.	Ant. and Post. mix.	Sum
1 FR only	78	5	21	33	8	42	9	28	7	8	1	240
2 TG (+ FR)	2	9	3	0	4	0	1	0	0	0	0	19
3 HD (+ FR)	32	2	70	11	4	7	1	6	1	2	1	137
4 FM (+ FR)	29	1	8	21	3	10	7	10	0	3	1	93
5 Ant. mix.	7	1	10	5	3	2	1	3	0	1	0	33
6 BF only	35	0	3	9	3	7	24	60	6	10	0	157
7 AB (+ BF)	7	1	4	4	2	32	41	31	10	11	0	143
8 WG (+ BF)	30	0	10	1	3	49	36	170	13	30	0	342
9 BM (+ BF)	16	0	4	2	1	1	9	7	3	1	0	46
10 Post. mix.	3	0	4	5	3	5	13	27	5	19	0	84
Ant. and post. mix.	0	0	0	1	0	1	0	1	0	0	0	3
Sum	239	19	137	92	34	155	142	343	45	85	3	1294

Table VIII. Possible States of the Various Body Components

Left front leg	Right front leg	Tongue	Head	Left middle leg	Right middle leg	Left back leg	Right back leg	Left wing	Right wing	Abdomen
A: Rubs right front leg	A: Rubs left front leg	A: In	A: Still	A: Rubs front legs	A: Rubs front legs	A: Rubs right back leg	A: Rubs left-back leg	A:Rest	A: Rest	A: Rest
		B: Out	B: Moved down	B: Rubs back legs	B: Rubs back legs	B: Rubs abdomen	B: Rubs abdomen	B: Raised	B: Raised	B: Lowered
B: Rubs head	B: Rubs head			C: Stands pointing forwards	C: Stands pointing forwards	C: Rubs over left wing	C: Rubs over right wing			
C: Stands	C: Stands			D: Stands pointing backwards	D: Stands pointing backwards	D: Rubs under left wing	D: Rubs under right wing			
D: Walks	D: Walks			E: Walks	E: Walks	E: Stands F: Walks	E: Stands F: Walks			

necessary to explain not merely the mechanisms responsible for the movements of active parts of the body, but to include as well an account of why other parts of the body, which have the capability of moving, are not in fact moving at particular times. For this reason it would seem fruitful to try describing behaviour in terms of the state of all of the body, even those parts which are immobile.

It will be shown in this section that, if this is done, certain relationships between acts become apparent. The commonest transitions are shown to be between acts which involve a small number of changes in body component position: that is, an act is most likely to be followed by another act which shares with it many of the same body component positions. This could be taken as evidence for the phenomenon known as 'postural facilitation' (Cullen, unpublished; Lind 1959).

The body of the fly was divided for descriptive purposes into the following components: head, tongue, each of the six legs, each of the two wings, and abdomen. Each of these components can exist in various states which are listed in Table VIII. No signficance should be attached to the actual alphabetical labels given to the components. For example 'A' for the tongue means that it is in, and 'A' for the left middle leg means that it rubs against the front legs, but this does not imply any similarity between the two acts.

Using the scheme drawn up in Table VIII, it is possible to describe each major act such as front-leg grooming, in terms of the constituent states of all the body components (Table IX). Front-leg grooming is 'left front leg rubbing right front leg, tongue in, head still, left and right middle legs pointing forwards, back legs resting on ground, wings not raised, abdomen in rest position' and so on. The point is that each act is described in terms of the states of all body components.

Table VII. χ^2 for 16 *df* for Each of the Four Main Quadrants of Table VI. Contingency Coefficients $C = \sqrt{\{\chi^2/(N + \chi^2)\}}$ are Also Given

With in cluster 1 (homogeneous transitions) $\chi^2 = 177{\cdot}9$ $C = 0{\cdot}57$	Cluster 1 to cluster 2 (heterogeneous transitions) $\chi^2 = 15{\cdot}5$ $C = 0{\cdot}31$
Cluster 2 to cluster 1 (heterogeneous transitions) $\chi^2 = 35{\cdot}9$ $C = 0{\cdot}44$	Within cluster 2 (homogeneous transitions) $\chi^2 = 90{\cdot}2$ $C = 0{\cdot}36$

Consider now a transition between two acts, say, FR to TG. In order to turn FR into TG only one change in body component state is needed: the tongue is extruded but all other body components remain the same. In Table X, which may be called a difference matrix, all first-order behaviour transitions are similarly described as the number of body components that would have to change their state in order for the fly to change from one act to another. When this table of differences is compared to the observed first-order transition frequencies, relationships between the two emerge. The commonest transitions occur between acts with a small number of body component differences between them (Fig. 11). It should be pointed out that this is not to say that whenever acts share many body components they will always be very likely to occur after each other. For example TG to FM would involve only two changes, but it is a rare transition. However, it is true that if there is a common transition, it will almost certainly be between acts sharing a large number of component states. This postural facilitation may be regarded as functionally sensible, since it tends to minimize expenditure of energy and time.

Conclusions

We have discussed fly grooming in terms of *candidate principles* such as hierarchical organization and postural facilitation, but these are not mutually exclusive. The behaviour could be organized according to hierarchical decisions; and the decisions taken at all levels of the hierarchy could be influenced by postural facilitation. This theme is developed in a speculative way in Dawkins (1976) under the heading 'Patterns of Pattern'. There are other plausible candidate principles which we have not tested. For example, grooming might be added to the growing list of behaviour patterns which insect neurophysiologists are suggesting as coupled to one or a few central oscillators (M. Burrows, personal communication; Kutsch 1969).

Another candidate principle which has been used before to explain behaviour switching in a Dipteran (Bastock & Manning 1955) is that of thresholds interacting with a single variable, but this is difficult to test in practice (Dawkins & Dawkins 1974). It does, however, make subjective sense to an observer watching bouts

Table IX. The State of Various Parts of the Body During Different Acts. The Letters Refer to the States Shown in Table VIII

	Front legs		Tongue	Head	Middle legs		Back legs		Wings		Abdomen
	L	R			L	R	L	R	L	R	
NO	C	C	A	A	C or D	C or D	E	E	A	A	A
FR	A	A	A	A	C	C	E	E	A	A	A
TG	A	A	B	A	C	C	E	E	A	A	A
HD	B	B	A	B	C	C	E	E	A	A	A
FM	A	A	A	A	(A and C) or (C and A)		E	E	A	A	A
BM	C	C	A	A	(B and D) or (D and B)		A	A	A	A	A
BF	C	C	A	A	D	D	A	A	A	A	A
AB	C	C	A	A	D	D	(B and B) or (B and E) or (E and B)		A	A	B
WG	C	C	A	A	D	D	(C and C and A and A) or (C and E and A and A) or (E and C and A and A) or (D and D and B and B) or (D and E and B and A) or (E and D and A and B)				A
MV	D	D	A	A	E	E	F	F	A	A	A

FR = Front legs
TG = Tongue
HD = Head
FM = Front middle
BM = Back middle

BF = Back feet
AB = Abdomen
WG = Wing
MV = Move

Table X. The Number of Body Components which would Have to Change Their State if One Behaviour were to be Followed by Any of the Other Behaviours. The Figures Shown in This Table are Derived Directly from Table IX. Where a Behaviour Pattern may be Performed in More than One Way (see Table IX) a Range of Values is Given

	NO	FR	TG	HD	FM	BM	BF	AB	WP	MV
NO	0									
FR	2–4	0								
TG	3–5	1	0							
HD	3–5	3	4	0						
FM	3–5	1	2	4	0					
BM	3–5	6	7	7	6	0				
BF	2–4	6	7	7	6	1	0			
AB	2–5	6–7	7–8	7–8	6–7	4	3	0		
WG	1–6	5–8	6–9	6–9	5–8	3–5	2–4	2–5	0	
MV	6	6	7	7	6	6	6	6	6–8	0

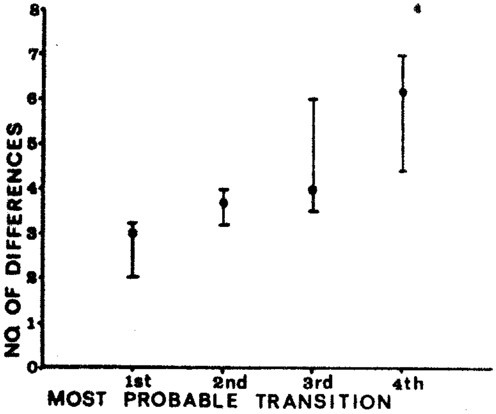

Fig. 11. The number of 'body state differences' (see text) that exist between acts most likely to follow each other, and 2nd, 3rd and 4th most likely to follow each other. Each point represents the median value, the vertical bars indicating inter-quartile range. The graph shows that the most probable transitions are those between acts with the smallest number of body state differences between them.

of anterior grooming (Figs 6 to 9). So too does yet another candidate principle, clearly enunciated as 'time-sharing' by McFarland (1974), but implicit in earlier ideas in the literature on grooming (e.g. Andrew 1956).

This study in itself is too brief to have yielded more than preliminary conclusions about the way sequences of behaviour are organized. But it has confirmed our original impression that grooming in flies is a promising subject with which to study the question.

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