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Self-organization and the evolution of division of labor

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Abstract – Division of labor is one of the most fascinating phenomena found in social insects and is probably responsible for their tremendous ecological success. We show how major features of this division of labor may represent self-organized properties of a complex system where individuals share an information data base (a stimulus environment), make independent decisions about how to respond to the current condition of that data base (stimulus environment), and alter the data base by their actions. We argue that division of labor can emerge from such systems even without a history of natural selection, that in fact such ordered behavior is an inescapable property of group living. We then show how natural selection can operate on self-organized complex systems (social organization) and result in adaptation of division of labor. © Inra/DIB/AGIB/Elsevier, Paris

self organization / division of labor / evolution / insect societies / *Apis mellifera*

1. INTRODUCTION

The main features of insect societies that are believed to be responsible for their tremendous ecological success are (Oster and Wilson, 1978; Wilson, 1985a, b): ‘division of labor’ – between reproductives and workers, and a further division among workers that is often, perhaps usually, based on age and/or anatomical differences; ‘specialization’ – some individuals perform some tasks with a significantly greater frequency than do other individuals; ‘homeostasis’ – colonies regulate internal conditions, such as food stores, temperature, humidity, etc.; ‘plasticity’ and ‘resiliency’ – colonies are able to change the numbers of workers engaged in different tasks in response to changing internal and external colony environments;

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and ‘mass action responses’ – colonies are able to mobilize large numbers of workers for specific emergency needs.

Much of the classical and contemporary research in insect sociobiology has been dedicated to studying these phenomena with the assumption that they represent colony-level functional adaptations. To identify a given trait as an adaptation is to imply that it has evolved by means of natural selection on available variants (Williams, 1966; Lewontin, 1978; Gould, and Vrba, 1982; Sober, 1984; Mitchell, 1987; Harvey and Pagel, 1991). For example, if division of labor and specialization are adaptations, then we assume a prior competition between colonies, some with a heritable division of labor and specialization, some without, and a colony-level selection process acting to preserve those traits through differential colony reproduction. However, if all groups of insects demonstrated these colony-level phenomena as a consequence of group living, then these characteristics are not themselves adaptations, even though their specific features may be. For instance, as we argue below, task specialization may be an inescapable property of groups of individuals that tolerate each other and share a nest, but having specific caste ratios may be adaptations to specific environments (Oster and Wilson, 1978).

The historical definition of adaptation we, and most biologists and philosophers, use has recently been criticized generally, and our arguments about division of labor specifically (Page and Mitchell, 1991), by Reeve and Sherman (1993). They promote instead a nonhistorical account of adaptation as “a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment”. The major, and we believe, devastating drawback of their definition is the complete disconnection between adaptation and evolution entailed by it. For a trait to be an adaptation on their account, says nothing at all about its relation to traits in past or future populations. This is in contrast to Darwin’s notion of natural selection acting on variation as the mechanism for evolutionary change producing, and hence explaining, the adaptation of traits to their environment. Our 1991 argument that division of labor could have arisen by self-organization implied that there would have been no variance between protosocial groups for the fundamental aspects of division of labor and hence no natural selection for those features. This view was criticized by Reeve and Sherman (1993). They mistakenly alleged that we see self-organization and selection as alternative, rather than complementary explanations [as do Bourke and Franks (1995); see also Mitchell (1998)]. This reading of our paper is difficult to understand because we elaborated in that paper, and again below, the ways in which once a crude division of labor has emerged, natural selection can then operate on the variations in features of this colony phenotype to preserve those variations that are more fit.

Here, using a boolean network modeling approach (Gelfand and Walker, 1984; Kauffman, 1984, 1993; Page and Mitchell, 1991) we demonstrate how extremely ordered group behavior can emerge from random aggregations of individuals. Our models only require that individuals have response thresholds associated with stimuli that result in behavior that in turn affects the current levels of stimuli. These are the very mechanisms believed to result in functional behavior of all animals, solitary and social. However, when living in groups, the actions of some individuals in response to common stimuli change the stimulus environment of others and, in turn, influence the behavior of other group mates [see also Bonabeau et al. (1996) and Page (1997)]. As a consequence, some features of insect societies are inescapable outcomes of interactions of individuals. We suggest how colony-level selection may change the organizational structure of colonies by acting on characters that affect system-level parameters.

2. THE MODEL

The model we construct here is analogous to a proto-society of insects. We later use honey bees as the exemplar organism because we make a transition from the simple organizational patterns of our models into exploring how more complex social organization may evolve. We assume that solitary insects suddenly become tolerant of each other and share a nest. However, there is no reason to assume that nontolerance is the ancestoral condition because many insects develop together in common nests then disperse after becoming adults. We simply want the initial conditions to assume that there is no prior history of group living that could have shaped specific patterns of social interactions.

Assume that individuals are analogous to elements (or nodes) of a binary switching network (Gelfand and Walker, 1984; see *figure 1*). Individual elements (insects) can be either *on* (1) or *off* (0) with respect to their likelihood of performing a particular behavioral act. Also assume that the number of elements in the network, **N**, represents all individuals that belong to a particular behavioral state that are behaviorally competent to perform that task. **K**, the connectance (Gelfand and Walker, 1984) of individual network elements, is large, close to or equal to **N**, with elements receiving directed inputs from and sending outputs to all other elements. In other words, all **N** – 1 elements (workers) receive information about themselves and the state status of all **N** – 1 other elements in the network. Individual input lines to elements are *on* or *off* according to the state of the element that initiates it. Each element is assigned a switching function (a decision rule) that determines whether the element is in an *on* or *off* state according to the numbers of *on* and *off* inputs coming to it from all other elements. Thus, each element has a threshold of response.

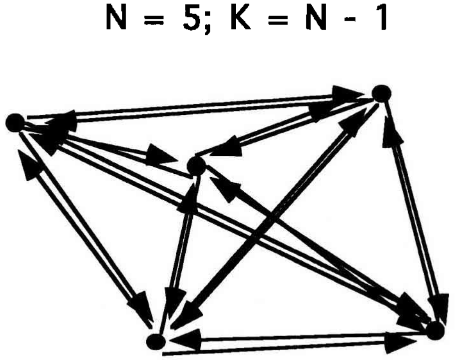


Figure 1. A directed arrow graph for the case **K** = **N** – 1. Each element (node) has an input arrow from all other **N** – 1 elements and an output arrow to all **N** – 1 elements. Each arrow carries an *on* (1) or *off* (0) value to the element at the arrow's head. The value carried by the arrow is the current value (*on* or *off*) of the element that initiates it (located at the tail). Each element is *on* or *off* as a consequence of the number of *on* or *off* inputs to it. For the **K** = **N** models presented, each element has an arrow to itself.

Individual threshold functions, $\mathbf{f}_i$, are assigned randomly to elements from the set {**F'**} which is a subset of the set of all boolean switching functions, {**F**}, that has as its members all and only those functions that switch the element *on* or *off* when the number of *on* or *off* inputs exceeds some specific value *(table I)*. During simulations of the model, network elements check the values on each of their inputs, evaluate, then respond by turning *on* or *off*. Assume for this model that individual elements are switched *off* when the number of *on* inputs is equal to or exceeds some given threshold value, and switched *on* when the number of *on* inputs falls below that threshold. Individual elements can check their inputs and respond by switching *on* or *off* either: 1) 'simultaneously' where all individuals check their inputs at the same time and respond together; 2) 'sequentially' as if they are queued up at a turnstile and check their inputs and respond individually in a repeated, sequential order; or 3) 'randomly' where each element is sampled individually and randomly, checks its inputs, and responds.

2.1. Simulation events

Assume that all individuals are initially *off* and the stimulus level, **S**, is initially set equal to **N**. **S** is a constant value that is decremented by the activities of individuals that are *on*. The order of events for the simulation is as follows:

1) All individuals of the network (model insects) are assigned a threshold of response $\mathbf{f}_i$ randomly drawn from a discrete uniform distribution represented by the set of threshold functions $\mathbf{F}' = \{\mathbf{f}_i, \mathbf{f}_j, \ldots \mathbf{f}_n\}$.

2) Individuals are selected using one of the three methods mentioned above: simultaneous, sequential, or random.

3) Each sampled individual is checked to determine if it is currently *on*. If it is *on*, it is turned *off* and the residual stimulus is incremented one unit. (The residual is the stimulus level 'perceived'. It is the initial stimulus level minus the number of individuals currently *on* because we assume that each individual decrements the stimulus one unit while she performs the task. We assume that an individual is not performing a given task while it is collecting and assessing stimulus information.) If the individual is currently *off*, the residual stimulus is not changed.

4) The threshold value for that individual (or each individual in the case of the simultaneous model) is then compared with the current residual stimulus level. If the residual stimulus level exceeds the

Table I. All $2^{2^k} = 16$ boolean functions for binary elements with **K** = 2 inputs[a].

Inputs		Boolean functions															
X_1	X_2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
0	0	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1
0	1	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	1
1	0	0	0	0	1	0	0	1	0	1	0	1	1	1	0	1	1
1	1	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	1

[a] The number of boolean functions increases exponentially with **K**, therefore, we present the set of boolean functions for the simple case of **K** = 2. Individuals realizing function 1 ($\mathbf{f}_1$) are *off* regardless of the values on their inputs, X_1 and X_2 while those with $\mathbf{f}_{16}$ are always *on*. $\mathbf{f}_2$ is a threshold function that returns a 1 (*on*) only for the case where all inputs, **t**, are *off*. $\mathbf{f}_5$ is *on* for $\mathbf{t} > 1$, $\mathbf{F}_{12}$ for $\mathbf{t} < 2$, and $\mathbf{f}_{15}$ for $t > 0$.

randomly assigned threshold value, then the individual is turned *on* and the residual stimulus level is decremented one unit. The individual is then recorded as being *on* or *off* for that sampling event.

2.2. The model and honey bees

An example of how this model may represent a honey bee society is to assume that individual workers (elements) receive information of the state (*on* or *off*) status of other workers via a common perceived stimulus, rather than by direct, individual inputs (*figure 2*). Each *on* individual performs a task and by doing so decrements the stimulus level associated with that task by one stimulus unit (negative feedback). When an individual switches *off*, she stops performing the task and the stimulus level is incremented one stimulus unit. An example of such a negative feedback system in a honey bee colony may be the number of empty food storage cells that stimulate individuals to forage. If colonies consume food from the storage cells, then there is some stimulus level that is a function of the rate of consumption and the rate at which foragers replenish the cells with food. The perceived stimulus levels change as a consequence of negative feedback. Storage cells fill up as more individuals forage and, with a constant food consumption rate, the number of empty or full cells provides a record of foraging activities of all foragers. Another example of this might be thermoregulation by honey bees. There is some constant ambient temperature and each individual that responds to the temperature stimulus by fanning her wings decrements the internal nest temperature one thermal unit while she fans but the temperature increases one unit as soon as she stops fanning.

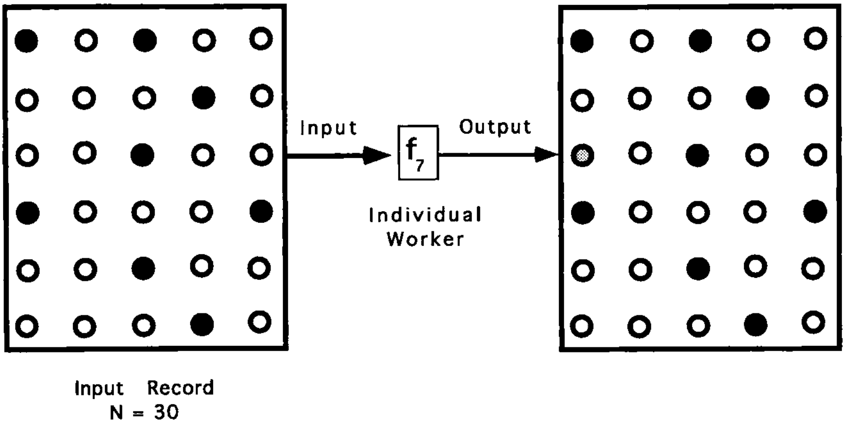


Figure 2. A diagram illustrating how a switching network can be transformed to represented a network of honey bees sharing information through cues provided by the amount of food, say pollen, stored in a comb. The left box represents a section of comb with 30 cells. The 22 open circles are empty while the 8 closed circles are full. An individual worker assesses the number of empty cells and compares it with its threshold function, f_7. Because the number of empty cells exceeds the threshold value of 7, the worker forages and fills the stippled cell represented in the right-hand box. The record now changes as a consequence of the behaviour of the worker.

3. RESULTS

3.1. Case 1: variable data sampling, N = 100, K = N, F' = $\{f_1, f_2, ..., f_N\}$, S = N

3.1.1. Simultaneous sampling

We investigated dynamical behavior of model systems over 100 simultaneous sampling events *(figure 3)*. Simultaneous sampling leads to highly ordered dynamical behavior with great instability. At time **t**, all **N** individuals are *off* and the residual stimulus level exceeds the thresholds of all individuals except those that have thresholds of 100 (individuals randomly assigned threshold values of 100 are never *on*). All individuals turn *on* simultaneously and drive the stimulus level toward zero at time **t + 1**. Now the stimulus level is below all thresholds so individuals turn *off*, subsequently driving the stimulus level back up to 100 at **t + 2**. The system oscillates between nearly all individuals *on* and all individuals *off*.

3.1.2. Sequential sampling

For sequential sampling, individuals are assigned numbers from 1 to **N** *(figure 3)*. Each individual is sampled in turn and the order of events described above are followed. A total of 2 000 samples were taken, 20 for each individual. Extremely ordered stable behavior emerges with this system. An initial negative feedback phase occurs that draws the residual stimulus level down near an equilibrium. This occurs as a consequence of individuals turning *on* so an increase in the proportion of the individuals *on* is observed. However, the system overshoots the equilibrium point and oscillates around it until it hits a steady state attractor. At this time all individuals are either frozen *on* or *off*, showing an extreme division of labor and specialization. In a real insect society *off* individuals may engage in different tasks.

3.1.3. Random sampling

It is difficult to imagine how a group of insects could coordinate turnstile-type sequential data access. It seems more likely that some kind of random sampling by individuals will occur by default. For this model system we assume that only one individual samples and changes the residual data base stimulus at a time. In this case, connectivity of the network can be asymmetrical, those that are sampled more frequently, due to chance, have more inputs than those that are sampled less often. Results of 2 000 sample events, an expected value of 20 per individual, are similar to the sequential sampling model. Again, there is an initial negative feedback phase followed by a search for an attractor, however, the search is random rather than oscillatory *(figure 3)*. It seems that search time to find the attractor may be longer for the random model than for the sequential model but, overall, the system stays closer to equilibrium while it searches.

The sequential sampling model always shows the same system behavior for a given ordered set of individual elements because the sampling order is always fixed. However, the random model behaves differently each time it is run but ultimately ends up at the same steady state value with respect to the proportion of individuals turned *on* (density). Steady state densities in these highly connected systems represent average, typical properties of the networks, the modes of response thresholds among elements. However, the activities (how many samples an element is *on* or *off*) of individual elements are not closely correlated with their response thresholds because they become fixed on or off.

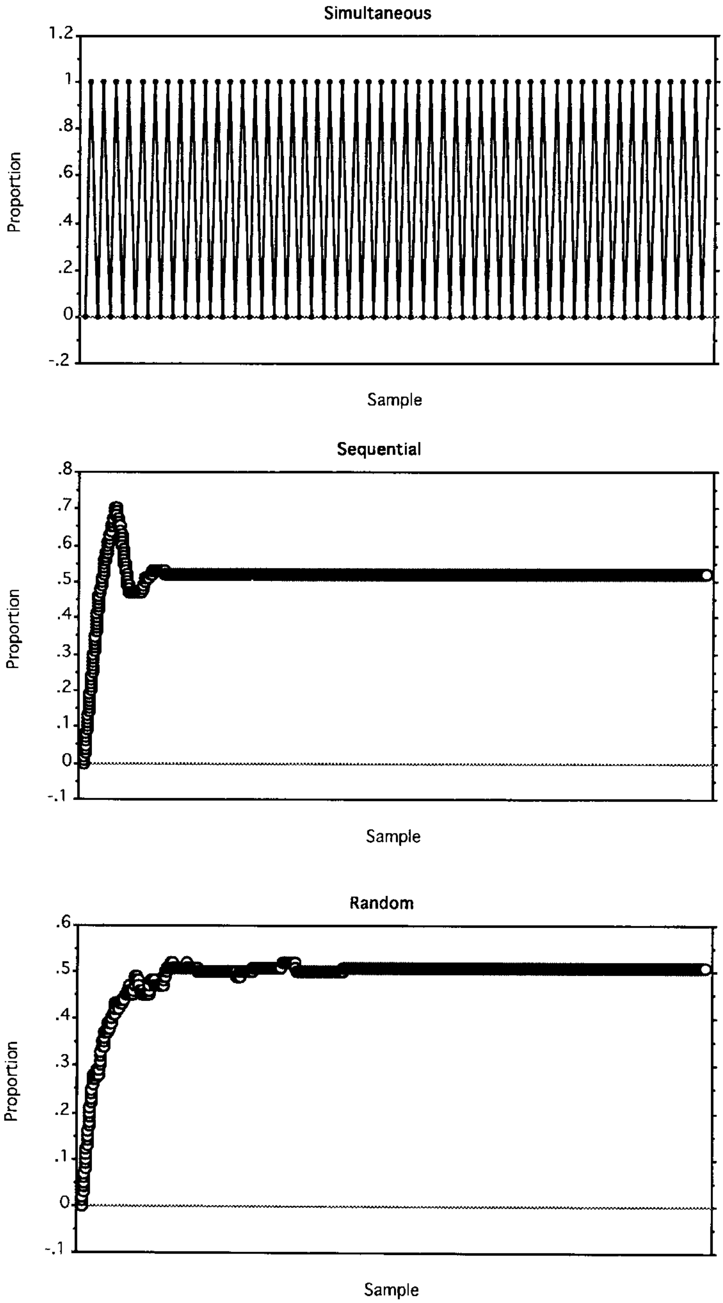


Figure 3. A comparison of the results of simulations using simultaneous (upper), sequential (middle), and random (lower) data access sampling of individual network elements. The proportion of individuals that are *on* is shown for each of 100 simultaneous sampling events and for each of 2 000 for the sequential and random sampling models.

3.2. Case 2: variable sampling, $N = 1\ 000, F' = \{f_1, f_2, ..., f_N\}$, $S = N$

The dynamical behavior of sequential and random sampling models with N = 1 000 was similar to the case of N = 100. The sequential sampling systems conduct oscillating searches for attractors while the random sampling systems search stochastically.

3.3. Case 3: variable threshold distributions, random sampling, $N = 100, S = N$

Threshold distributions used for random assignment of individual elements can vary with respect to their mean values and their variances.

3.3.1. Variable mean thresholds

Dynamical behavior of networks with thresholds drawn randomly from discrete uniform distributions with ranges 1–50, and 51–100 showed the characteristic negative feedback phase followed by random searching near an equilibrium point then each locked into a steady state attractor. Systems with higher mean thresholds, however, ended up in states with lower densities – in other words, fewer individuals worked.

3.3.2. Variable threshold variances

Changing the variance in thresholds around a given mean affects both the rate at which the system locates a steady state attractor and the stability of the system to external perturbation – homeostasis. The time (number of samples) that it takes for a network to arrive at a steady state was determined for discrete, uniform distributions of threshold functions of ranges f_i to f_n and for two point distributions of f_i and f_n. Thresholds were drawn randomly from these distributions and assigned to each of the 100 elements of the model networks. The interval beween f_i and f_n varied around a constant mean value of 50.5. After each sample event, the simulation checked to see if the density (proportion of individuals *on*) had changed since the last sample. It was determined that the system had located a steady state attractor after all individuals had been sampled at least once without effecting any change in density. The sample that resulted in the last change in density was considered to be the one that resulted in the system entering a steady state. We ran simulations of 100 random networks for each of 11 intervals for each distribution and determined the average number of samples required to acheive steady state conditions.

Systems with no variance in thresholds locate their steady state attractors quickly and avoid most of the search phase. This is the case with the least number of samples required ($\overline{X}$ = 69.3). However, as soon as variance in thresholds is introduced among elements, the time to locate an attractor increases dramatically *(figure 4)*. In fact, the systems with the least nonzero variance take the longest time to locate an attractor. Increasing the variance then leads to a decrease in attractor time. Two-point networks locate their attractors faster than networks with elements drawn from uniform distributions with the same range of values.

3.4. Case 4: variable stimulus level, variable threshold distribution, random sampling, $S = N$

The variance in thresholds among elements of our model systems profoundly affects dynamical behavior resulting from external perturbations to the stimulus level. Networks of N = 100 with thresholds drawn at random from a discrete uniform

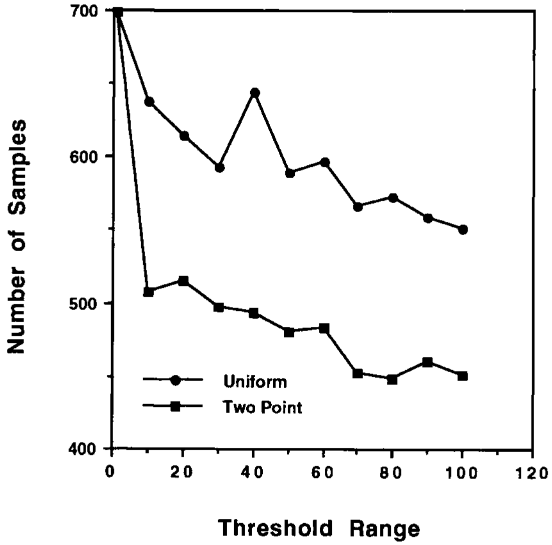


Figure 4. The average number of samples, based on 100 simulations each, required for networks to acheive steady states for uniform and two point threshold distributions with different ranges. The mean threshold for all simulations was 50.5. The case for threshold range = 1 was common for both sets of distributions. The case of threshold range = 0 had a mean value of 69.3 and is not represented.

distribution with range 1–100 were compared with networks where all elements had fixed thresholds of 50.5. The initial constant stimulus input, S, was equal to N, then it was increased by 20 units after every 500 random individual samples. The residual stimulus (the difference between the constant stimulus input and the number of individuals *on*) was measured at each of 2 500 sample events.

Networks with no variance in thresholds show strong homeostatic properties, they return the residual stimulus to predisturbance levels following each increment of stimulus until all individuals are *on (figure 5)*. Networks with variable thresholds do not regulate the stimulus level as well but do regulate the number of individuals turned *on* or *off* in response to each increase or decrease in stimulus *(figure 5)*. They buffer individuals from changing stimulus levels and provide a more integrated system response to external changes in conditions.

3.5. Case 5: two tasks, two thresholds, two stimuli

The complexity of our model dynamical systems were increased, possibly making them more realistic (but they are no longer boolean), by assuming that each individual element could be *off*, or *on* in more than one state. This may be equivalent to an individual worker honey bee having the capability of being *on* to task 1 or task 2, or *off*. Individuals that are *off* could be *on* for task 3, or may develop into a different behavioral state (age caste) and become members of different net-

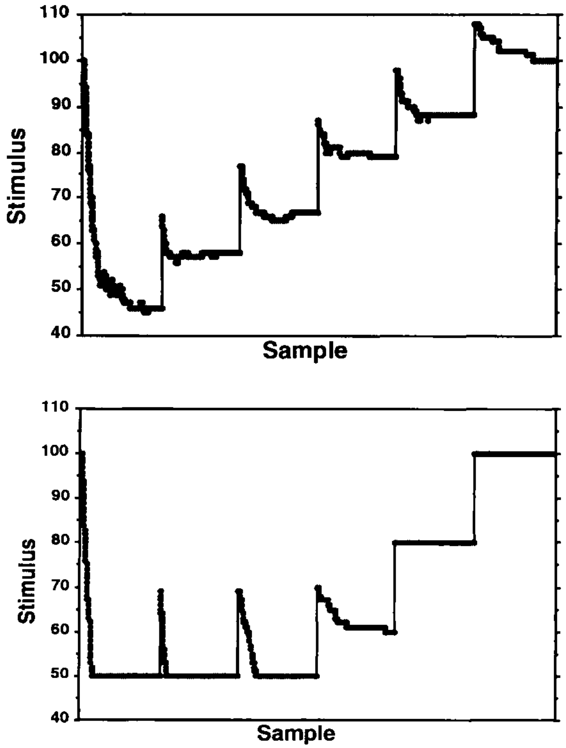
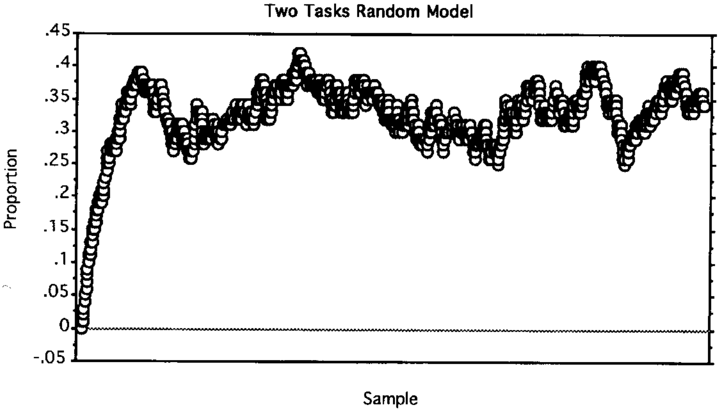


Figure 5. Regulation of stimulus level by model networks containing N = 100 elements with thresholds drawn at random from a uniform distribution with integer values of 1 to 100 (upper graph) and fixed threshold values of 50.5 (lower graph).

works. For these models, N = 100, and two thresholds were drawn randomly from a discrete uniform distribution with a range 1–100 and assigned to each element. Each threshold was uniquely associated with one of two stimuli that were initially set at 100 and individual elements were sampled at random, as before. Task threshold 1 or 2 for the sampled individual was then drawn at random from a distribution with equal probability and the stimulus level associated with that threshold compared. The individual then responded based on the stimulus–threshold differential. These model dynamical systems again demonstrate the negative feedback and stochastic search phases around an equilibrium value related to the mean of the threshold distribution but appear to lack easily located steady states *(figure 6)*. Simulations of 100 000 samples have failed to find steady state attractors, therefore, individuals demonstrated inherently less specialization than did individuals of the single threshold models.

3.5.1. Sample both stimuli

Highly ordered behavior and steady state attractors that result in extreme specialization do emerge from these two-threshold systems *(figure 6)* when individual elements check both of their individual thresholds against both residual stimuli and then



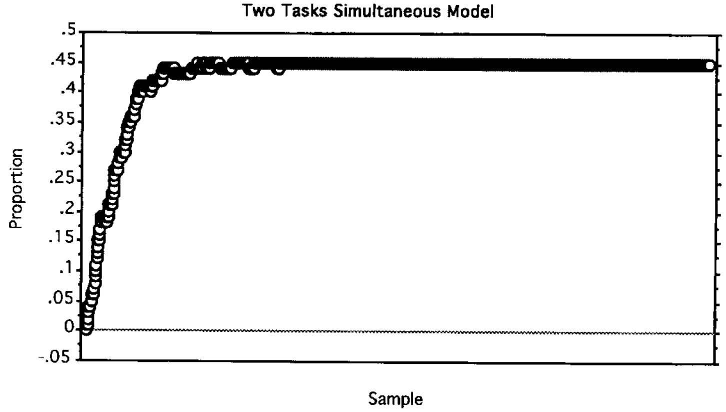


Figure 6. Results of simulations of model networks for the case of two thresholds and three possible states for each element (see text). The upper figure is the result when only one stimulus is sampled at a time while the lower figure shows the dynamical behavior when both stimuli are sampled simultaneously.

respond according to the following decision rule: turn *on* to task [i] **if**

stimulus [i] – threshold [i] > stimulus [j] – threshold [j]

and stimulus[i] – threshold [i] > 0

3.5.2. Thresholds dependent

Thresholds can be assigned randomly or they can be dependent on each other. We randomly assigned threshold 1, as in the model above, then assigned threshold 2 to individuals on the basis of the following algorithm:

threshold 2 = 101 – threshold 1

This resulted in a reciprocal integrative relationship between the thresholds of an individual with all thresholds of all individuals summing to 100. Integrating thresholds resulted in a greater proportion of individuals *on* for either task at the steady state phase *(figure 7).*

4. DISCUSSION

It is apparent that highly ordered dynamical behavior can emerge from these model networks of individual elements. Even in the simplest systems we see the kinds of behavior long marvelled in insect societies: 1) 'homeostasis' resulting from negative feedback reducing residual stimuli to near an equilibrium determined by the mean of the threshold distribution; 2) 'mass action responses' when all elements turn *on* then *off* when simultaneous sampling is employed; 3) system 'plasticity' and 'resiliency' in response to increases and decreases in external stimuli; 4) 'division of labor' and 'specialization' demonstrated most dramatically by steady state attractors where some individuals are frozen *on* and others are frozen *off*. Even in cases where we have failed to find steady state attractors, many individual elements with low thresholds remain *on* while those with high thresholds remain *off* and those with intermediate thresholds fluctuate *on* and *off*.

Our models suggest that division of labor with task specialization should emerge among individuals whenever they share a nest (Page, 1997). Spontaneous division of labor may have complemented the evolution of social behavior from the initial inception of group living but itself may not have been a direct product of natural selection acting on groups because it may be impossible to have groups that do not have a division of labor. This is a result of the stimulus–response–threshold relationship of behavior and because individuals change the levels of stimuli when they respond to them. The number of nest-

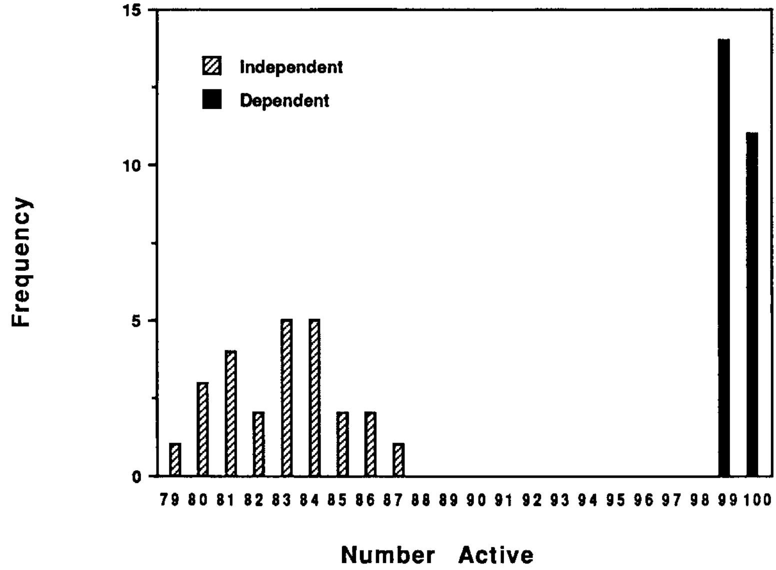


Figure 7. The distribution of the number of individuals active (*on* for either of the two tasks) for the two models, independent and dependent assignment of thresholds, from case 5 (see text). The figure shows the frequency distribution for 25 separate simulations.

mates, the distribution of response thresholds among nestmates, and the way in which they sample relevant stimuli shape the dynamics of division of labor. Natural selection may continue to modify and fine tune social organization by operating on the self-organizing features of the complex social system.

4.1. Natural selection operates on parameters of complex dynamical systems

In this section we show how natural selection can shape colony organization by acting on heritable variation for queen and worker traits that affect complex system parameters. Natural selection cannot act individually on behavioral components of workers but instead 'sees' the dynamical system properties of colonies. Therefore, natural selection for colony organization may operate on the dynamical system parameters **N**, **K**, and **{F'}**. Individual colony members may have behavioral and developmental properties that are indirectly selectable and affect these parameters.

4.1.1. Selection on N

For any given distribution of threshold functions, **{F'}**, and a residual stimulus level greater than 0, increasing or decreasing **N**, the number of individuals competent to perform a given task, will increase or decrease the number of individuals *on* or *off* for that task. Colonies with greater numbers of workers are expected to have greater **N** for a given age caste given a constant rate of behavioral development, therefore, selection for colony size will affect **N**. Colony size can be affected by both queen fecundity – a trait that may be controlled by workers – and worker length of life, both of which have been shown to have heritable variation (Page et al., 1995; Guzmán-Novoa et al., 1994).

An increase in **N** for a specific age caste may also be achieved by altering behavioral development rates so that individuals belong to a given age caste for a longer or shorter period of time [see Robinson (1992) for review]. Genetic variability for rates of development associated with age polyethism have been demonstrated repeatedly (Winston and Katz, 1982; Calderone and Page, 1988, 1991; Giray and Robinson, 1994; Guzmán-Novoa et al., 1994; Calderone and Page, 1996). **N** can also be affected by the sensitivity of individuals to environmental stimuli that results in changes in rates of behavioral development into different age castes. Individual workers in colonies that lack foraging age bees undergo an increased rate of behavioral development until there is a population of workers that forage at a precocious age (Huang and Robinson, 1992, 1996). Recent studies have shown genetic variability, hence the potential selectability, for the likelihood that an individual will undergo accelerated behavioral development (Robinson et al., 1989; Page et al., 1992; Giray and Robinson, 1994, 1996).

4.1.2. Selection on K

K can be altered by adjusting the cues and/or signals used as stimuli and by changing the data flow operations, e.g. the way individuals sample the stimulus environment. Tasks that require mass action – all or nothing – responses should employ simultaneous sampling. Highly volatile chemical signals (pheromones) that are released by individuals as soon as anyone is exposed to those released by other individuals may approximate this data flow structure. This is true for the alarm system of honey bees where a single disturbed individual may release a highly volatile compound that results in the release of pheromone and behavioral responses by all other behaviorally competent individuals that perceive it (Wilson, 1971). After individuals release their pheromone and respond, they turn themselves *off* and the colony returns to its original state. With this system, the *on* signals rapidly propagate, but are not instantaneous.

Cues such as the amount of empty or full storage comb in a honey bee nest may provide reliable information about colony needs and the foraging activities of other individuals. The use of these cues should be selected over highly transmissible chemical or mechanical, individual signals when ordered stable behavior is more appropriate. Increasing quantities of brood present in the nest results in more pollen foragers and larger loads of pollen (Eckert et al., 1995) while the presence of more stored pollen results in fewer pollen foragers and smaller pollen loads (Fewell and Winston, 1992). The interplay of these stimuli result in the regulation of the foraging population and the pollen intake of the colony (Fewell and Page, 1993). Camazine (1993) suggested that nurse bees serve as stimulus intermediaries providing inhibitory cues to foragers that relate to levels of stored pollen and brood. In any case, the specific mechanism, whether direct perception of stimuli by foragers, or indirect correlation of brood and pollen through nurse bee activities does not alter the interpretation of the models.

K can also be adjusted spatially by creating a structural modularity (Page and Robinson, 1991). Individuals located close to each other are more likely to share information – have greater connectivity – than those located in different parts of the nest, thus suggesting a nonuniform assignment of **K** to the **N** nodes. The spatial organization of tasks with respect to where they are performed in the nest may be selectable (Seeley, 1982). Calderone and Page (1988, 1991) demonstrated a nonrandom spatial distribution of nestmate workers derived from different genetic sources. Bees that forage on the same plant resources associate with one another in the nest (Lindauer, 1961). Oldroyd et al. (1991) suggest that honey bee workers that have the same father (super sisters) are more likely to attend each other's recruitment dances than those of their half sisters.

4.1.3. Selection on {F'}

Selection on threshold functions may occur by selecting for higher or lower mean thresholds or by selection to increase or decrease the variance in thresholds within colonies. Changes in mean thresholds result in changes in the likelihood that individuals belonging to specific behavioral castes will perform specific tasks, resulting in concomitant changes in the numbers of individuals engaged in those tasks. Genetic variability for the likelihood that individuals perform specific tasks has been demonstrated in honey bees for pollen and nectar collecting (Calderone and Page, 1988, 1991; Robinson and Page, 1989; Calderone et al., 1989; Rothenbuhler and Page, 1989; Guzman-Novoa and Gary, 1993; Guzman-Novoa et al., 1994; Dreller et al., 1995; Hunt et al., 1995; Page et al., 1995; Calderone and Page, 1996), grooming behavior (Frumhoff and Baker, 1988), guarding and corpse removal (Robinson and Page, 1988; Robinson and Page, 1995), hygienic behavior (Rothenbuhler and Page, 1989), defending the nest (Breed et al., 1990; Guzman-Novoa and Page, 1994), caring for queen versus worker larvae (Page et al., 1989; Robinson et al., 1994a), scouting for new nest sites (Robinson and Page, 1989b), and other activities performed within the nest (Calderone and Page, 1989, 1991).

Pollen and nectar foraging behavior have been examined in detail. Using the methods of Hellmich et al. (1985), Page and Fondrk (1995) produced artificially selected strains of bees for the amounts of pollen they stored. After three generations, two way selection produced high and low strains that differed by more than five fold in quantities of stored pollen. High strain colonies had significantly more pollen foragers and high strain workers individually were much more likely to forage for pollen than were low strain workers, even when raised in a common colony environment (Page et al., 1995).

Hunt et al. (1995) constructed a genomic linkage map of major quantitative trait loci (QTLs) responsible for observed differences in quantities of stored pollen between the the high and low pollen hoarding strains of Page and Fondrk (1995). They identified two genomic regions, designated *pln1* and *pln2*, that were likely to contain genes that jointly explained about 59 % of the total observed phenotypic variance. These two genetic regions also affected the likelihood that an individual would forage for pollen. These results suggest that colony level selection affected **{F'}** by fixing different alleles of *pln1* and *pln2* in the high and low strains.

Page et al. (1998) showed that nectar and pollen foragers from colonies unrelated to the high and low pollen hoarding strains differed in their response thresholds to varying aqeuous solutions of sucrose as measured by a simple proboscis extension reflex test. Workers from the high and low pollen hoarding strains varied predictably in their responses to different sucrose concentrations: high strain workers responded like pollen foragers of unselected colonies while low strain workers responded like nectar foragers. In addition, high and low strain nectar foragers differed in the sugar concentrations of nectar that they found suitable to collect, as predicted by their differences in sucrose response thresholds. They further showed that nectar foragers that inherited from their mother different alleles for QTL *pln2* varied in the sugar concentrations of the nectar they collected in the field, suggesting that *pln2* is directly affecting sucrose response thresholds.

Selection on the variance in thresholds may affect the colony's response to changing environments. Narrow variance may be advantageous when the stimulus itself is being regulated by workers, as in thermoregulation of the nest. Wide variances may provide a better regulation of work force when it is more important to regulate and integrate the proportion of workers engaged in different tasks rather than regulate the stimulus itself. Large variances also result in more rapid approaches to colony steady state conditions. Selection on the variance may occur by selecting for mechanisms that increase or decrease genetic variability within colonies such as the number of times queens mate, the number of reproductive queens in a colony, selection favoring heterozygous or homozygous queens (and kings in the case of termites), or the number of genetically variable loci associated with specific tasks.

Variance in response thresholds within colonies does not need to be generated by genetic variation. Response thresholds may change stochastically among individuals as a consequence of chance individual differences in experience. Behavioral modification through learning may also affect the variance. Individuals may alter their thresholds on the basis of prior experience. For example an individual's threshold may decrement on the basis of performing a specific task making it more likely that she will perform that task again the next time she encounters the stimulus. This kind of feedback system would increase the variance in thresholds and serve to functionally wall off those individuals with lower initial thresholds from the other members of the network.

Networks may also be coupled, or n-ary as opposed to binary, as we show in our two-threshold model. Individuals may have multiple states with respect to which tasks of a set they perform while they belong to a given age caste. These states may be determined by multiple stimulus–threshold complexes with various decision rules. Natural selection may determine the organization of these complexes forming specific task sets associated with specific developmental stages. Genetic covariance resulting in dependent thresholds of response may increase the overall activity level of individual workers of a given age caste. For example, dependent thresholds may lead to a greater likelihood that all individuals of the foraging age caste are foraging for something.

For other task sets associated with other age castes, fewer individuals may be needed to perform all the requisite activities and inactive individuals may undergo behavioral development into the next age caste in the sequence, or revert to a previous behavioral state. In this case, independent thresholds of response may serve to provide a pool of relatively inactive reserve bees that have high thresholds of response to most or all task-inducing stimuli and are capable of undergoing behavioral modification through development (Fergusson and Winston, 1985; Robinson and Page, 1989b, Robinson et al., 1994b).

5. CONCLUSIONS

The set of models presented here is by no means exhaustive. Additional models can be constructed using different methods of sampling individuals, exchanging information among individuals, coupling tasks, stimuli and thresholds of response, and different sets of decision rules. The additional complexity that can be built into the models may make them correspond more closely to real insect societies and may even suggest optimal design features of network systems that may lead to novel empirical investigations. For instance, negative or positive feedback on thresholds of response based on prior experience can easily be incorporated into the models. Individual workers can have different activity levels and subsample the activities of other workers rather than having complete information of the activities of all **N** subcaste mates. However, it is important to point out that highly ordered system behavior emerged from our model networks that were constructed with minimal lower level order. It would not be surprising to find more high level order with increasing amounts of order at lower levels.

The models presented in this paper provide transformational processes for building interactive, homeostatic social systems from collections of individuals. These processes are: 1) the stimulus–response–threshold relationship of performing a behavioral act, and 2) the correlation between performing a behavioral act and the stimulus environment. The recognition of self organization as a potentially important process in the organization of biological systems (Camazine and Sned, 1991; Page and Mitchell, 1991; Bonabeau et al., 1996; Gordon, 1996) provides evolutionary biologists with a new approach to understanding the evolution of complex biological design.

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Résumé – Auto-organisation et évolution de la division du travail. La division du travail et les phénomènes qui lui sont liés ont été considérés comme des exemples frappants de l'adaptation par la sélection naturelle au niveau de la colonie. Nous présentons des modèles *(figures 3* et *4)* qui montrent comment la division du travail peut survenir spontanément parmi des groupes d'individus mutuellement tolérants. Nous proposons de considérer les modèles d'organisation de base de la division du travail chez les insectes sociaux comme des résultats typiques de l'auto-organisation de systèmes complexes, tels qu'on peut s'attendre à les trouver dans des groupes d'insectes qui cohabitent. C'est le résultat de la relation stimulus–réponse–seuil dans le comportement de l'insecte et de la relation entre l'accomplissement d'un acte comportemental et le stimulus qui provoque la réponse. Lorsque le stimulus qui déclenche un comportement dépasse le seuil de réponse d'un individu, l'individu réagit. Lorsque l'individu réagit, il change le niveau du stimulus et, en conséquence, modifie la probabilité que d'autres individus accomplissent aussi cet acte comportemental *(figure 2)* ; il s'ensuit une division du travail.

Nous proposons en outre de considérer ces aspects grossiers de l'organisation sociale des insectes comme inéluctables et ne nécessitant pas l'intervention d'une histoire évolutive. Le rôle de la sélection naturelle dans l'adaptation de l'organisation sociale consisterait alors à agir sur les composantes sélectionnables du comportement des membres d'un groupe, composantes qui influent sur la façon dont les membres interagissent. Nous montrons comment la sélection peut modifier les quantités de pollen stockées par les colonies d'abeilles, par son action sur les paramètres **N**, **K** et {**F'**} des systèmes complexes, où **N** est le nombre de butineuses dans la colonie, **K** la façon dont elles partagent l'information et {**F'**} l'ensemble des seuils de réponse dans le groupe des butineuses aux stimuli qui déclenchent le comportement de récolte du pollen.

***Apis mellifera* / auto-organisation / division travail / évolution / société insectes**

Zusammenfassung – Selbstorganisation und die Evolution der Arbeitsteilung. Die Arbeitsteilung und ihre Begleiterscheinungen wurde als besonders hervorstechendes Beispiel für durch natürliche Selektion entstandene Anpassungen auf der Kolonieebene angesehen. Die von uns hier vorgestellten Modelle (siehe *Abb. 3* und *4*) zeigen, wie Arbeitsteilung zwischen Gruppen von untereinander verträglichen Individuen spontan auftreten könnte. Wir schlagen vor, daß die grundlegenden Organisationsmuster der Arbeitsteilung bei Insekten eine typische Folge der Selbstorganisation von komplexen Systemen darstellen, wie diese innerhalb von in Gruppen zusammenlebenden Insekten zu erwarten sind. Diese Organisationsmuster sind das Ergebnis der Beziehung zwischen Reiz und Reizantwort im Verhalten der Insekten, sowie der Beziehung zwischen der Ausführung einer Verhaltensweise und dem Reiz, der diese ausgelöst hatte. Das einzelne Tier reagiert auf einen verhaltensauslösenden Reiz, sobald dieser seine Antwortschwelle überschreitet. Sobald es aber reagiert, verändert es hierdurch den auslösenden Reiz. Hierbei ändert es gleichzeitig die Wahrscheinlichkeit, mit denen andere Tiere ebenfalls diese Verhaltensweise ausführen *(Abb. 2).* Das Resultat ist eine Arbeitsteilung.

Weiterhin schlagen wir vor, daß diese groben Aspekte der sozialen Organisation von Insekten unvermeidbar sind und ihr Auftreten keine evolutionsgeschichtlichen Entwicklungsverläufe benötigt. Die Rolle der natürlichen Selektion in der Anpassung sozialer Organisation könnte dann aber sein, daß sie auf diejenigen der selektierbaren Verhaltenselemente individueller Gruppenmitglieder einwirkt, die auf die Art der Interaktionen der Tiere Einfluß nehmen. Wir zeigen, wie die Selektion die Menge eingelagerten Pollens in Honigbienenvölkern dadurch beeinflussen könnte, daß sie auf die komplexen Systemparameter **N**, **K**, und **{F'}** einwirkt. Hierbei bezeichnet **N** die Anzahl Sammlerinnen im Bienenvolk, **K** die Art ihres Informationsaustauschs, und **{F'}** die Zusammensetzung der Ansprechschwellen in der Sammlerinnengruppe für die das Pollensammeln auslösenden Reize.

Selbstorganisation / Arbeitsteilung / Evolution / Insektenstaaten / *Apis mellifera*

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