The most obvious possibility is that the anomalous axons belong to the class of efferent neurons that normally issue a minor projection to the contralateral caudate nucleus. As proposed for other systems (*1, 2*) these cortico-striatal neurons may expand their terminal fields to occupy vacated synaptic space on the caudate neurons that were deprived of their normal input from the ipsilateral cortex. Another possibility is that the anomalous axons belong to callosal neurons, which, in the absence of their homotopic target cells, are attracted to and invade the caudate nucleus subjacent to the lesion to join with the normally meager complement of crossed cortico-caudate fibers. Still another possible explanation for the anomalous projection is that cortico-caudate projections may be bilateral at embryonic stages and become primarily ipsilateral by selective elimination of a large proportion of crossed projections during development. If so, many contralateral fibers may fail to retract in the absence of competition from the resected ipsilateral cortico-striatal system. Such a mechanism has been hypothesized for the unequal widths of ocular dominance stripes in the visual cortex of monkeys subjected to eye enucleation or monocular deprivation during critical stages of development (*9*). Obviously, overlapping of the prefronto-caudate pathway across the midline would involve a more drastic reorganization during development than that which occurs between adjacent cortical areas within a single hemisphere in the visual system.

The rearrangement of connections in the monkey is comparable to that described in nonprimate mammals (*1, 2*). It is probably important that this high degree of plasticity can be obtained in a primate when a lesion is made before birth. Major developmental events such as neuron genesis, cell migration, and elaboration of basic connections, which in rodents continue to a considerable extent after birth, occur largely prenatally in the monkey (*10*). Neuronal rewiring has been described in mature animals of several nonprimate species (*2*); definition of age limits for the neuroplastic phenomenon reported here requires further investigation.

The dramatic structural rearrangement is relevant to the evidence for sparing or recovery of function after brain damage incurred during early stages of development, particularly for lesions sustained unilaterally. The finding in a primate that neurons from an intact neocortex of one hemisphere can expand their terminal distribution to structures of a damaged hemisphere may provide a long awaited clue to a possible neural mechanism for sparing of associative and linguistic competence after early unilateral brain damage or hemispherectomy in humans.

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Caste in a Primitive Ant: Absence of Age Polyethism in *Amblyopone*

Abstract. *Polyethism, the divison of labor among members of a colony, is based on worker age and size in ants. In the ponerine species* Amblyopone pallipes *worker behavior is independent of age, therefore temporal castes, or groups of age-related task specialists, do not exist. This primitive caste system, previously unknown in ants, appears to be correlated with the peculiar characteristics of the life history and ecology of* Amblyopone.

Caste structures are nearly universal in the social insects. Although the most fundamental difference is between the reproductive queen and the sterile worker caste, within the latter category morphological and temporal subgroups often coexist and provide a finely tuned division of labor within a colony. These two common phenomena, physical polymorphism and age polyethism, are well documented in ants (*1*). In age polyethism, workers change roles in a predictable fashion, and the sequence of worker behavior shifts progressively from nursing to foraging with increasing age. Although this pattern of age-dependent behavior is consistent among the higher subfamilies of ants, age castes in primitive species have remained uninvestigated (*2*). I report here on the apparent lack of temporal division of labor in the ponerine ant *Amblyopone pallipes*, which appears to have the most primitive caste system yet documented in ants.

The genus *Amblyopone* contains the most diverse and widely distributed array of species in the ponerine tribe Amblyoponini (*3*). This assemblage, together with the genera *Myrmecia* and *Nothomyrmecia* contains, on behavioral and morphological grounds, the most primitive ants and represents the closest living approximation to ancestral forms. *Amblyopone pallipes* ranges throughout the northeastern United States and Canada, and populations are dense and local in distribution (*3*). The population structure is unicolonial; colony subunits typically consist of one or more queens and 9 to 16 workers (*4*). The behavior of *Amblyopone* contrasts sharply with the scavenging and homoptera tending habits of most ant species. These ants are exclusively hypogaeic and carnivorous, their predaceous habits being restricted to live linear arthropods with soft cuticles, such as centipedes and beetle larvae, which solitary huntresses paralyze by stinging and then drag to the nest. Both adults and larvae feed directly on the prey; regurgitation is totally absent. The life-cycle data of 28 colonies show that a single brood per year is reared to maturity, from which both sexuals and workers eclose in early August. Callow workers escape from their cocoons unassisted and behave precociously from the time of their eclosion.

The behavior of callows is not directed solely toward queen attendance or egg and larval grooming, as might be expected from comparative studies of other ants, and ethogram studies reveal a distinct, novel pattern for workers of this age. Callows differ from older workers in pigmentation only in a lighter coloration

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of the legs, meso- and metathorax, and gaster, and are behaviorally equivalent to fully sclerotized adults. Only 5 days after eclosion they leave the nest to forage and are capable of subduing large prey. These observations suggested that workers of *A. pallipes* do not follow the normal pattern of polyethism in ants, but the possibility of another mechanism that would result in task specialization among workers could not be ruled out. For the analysis of the organization of the division of labor, all workers in a colony (1 queen, 17 workers, 34 pupae, 5 larvae, 48 eggs) were marked with enamel to permit individual recognition, and ethogram data were compiled over a 2-week period. The worker profiles (Fig. 1) establish that there is little specialization within the colony. The relative frequencies of the eight behavioral categories are approximately equal, indicating an even contribution by most workers to the performance of each task. These results are consistent with data collected from other colonies. The individual ethograms composed of the frequencies of each category relative to the total number of acts in a worker's repertory (Fig. 2) are extremely interesting because they indicate that the behavior of 70 percent of the workers is directed principally toward pupal care. At any point in the life cycle of *A. pallipes* one stage of brood is dominant, except in August when a second group of eggs is laid. At this time, when the above study occurred, workers were occupied with grooming and transporting pupae, activities necessary to the maintenance of proper developmental conditions. After eclosion, callows do not attend to egg care, but assist their older sisters with pupal care, again illustrating the temporal abnormality of their behavior.

Two additional aspects require emphasis. First, there is no spatial association of tasks, as is illustrated by the behavior of a worker that displayed a high frequency of egg care and foraging (Fig. 1d). This is contrary to the temporal caste systems of most ants. Second, and more striking, is the absence of distinct roles, the linkage of two acts by a high transition probability. No acts were found to be significantly correlated (*5*).

There are anomalies in the behavioral profiles of workers (Figs. 1 and 2) since some workers consistently performed acts other than pupal care (see workers c, d, f, l, p, and q). Explanations other than age polyethism must be invoked to account for these differences in activity. Elitism, the variability in the readiness to work between workers of some ant species, is one possible reason (*6*), and these individual peculiarities could result in a finely graded division of labor whose basis remains unclear. A second possibility is the concept of task fixation (*7*), which is essentially a feedback-based behavioral stabilizing mechanism. Those individuals that are successful at a task, for example at foraging or nest repair, continue to perform the act at an amplified frequency as long as the worker receives positive feedback and the task remains unattended.

The lack of temporal castes represents a very generalized social system that has had little prospect of change due to the constraints of the life cycle and ecology of *A. pallipes*. The age structure within a colony is multimodal; a single cohort ecloses nearly simultaneously. Any age differences in a colony would not provide a large enough pool of age ensembles to function as specialized subgroups. Also, because the larvae feed directly, brood care is associated with foraging and not only proximate inner nest tasks. Therefore, workers are programmed to respond to a large number of different contingencies as they arise, continually "tracking" colony needs. The small colony size and extended brood development reinforce the necessity of worker flexibility; if a forager is lost another worker must become a functional replacement. But the lengthened period of pupal development also permits workers to be physically capable of performing a wide variety of behaviors. It appears that ant species with a temporal caste system have been able to "take advantage" of the potential labor force of unsclerotized adults that efficiently accomplish tasks

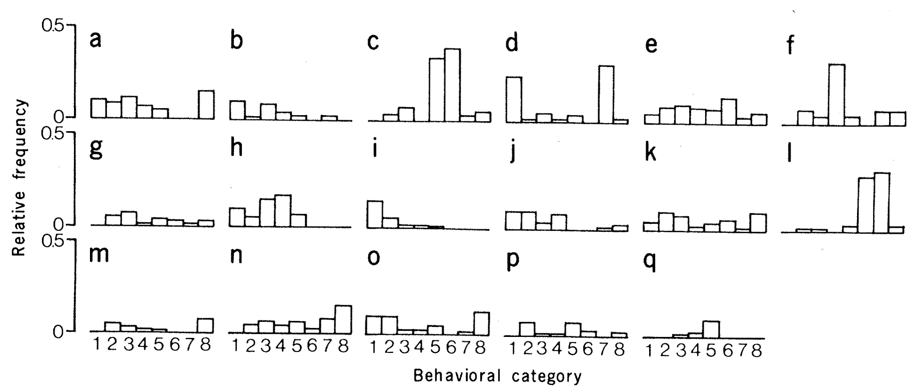

Fig. 1. Frequencies of eight behavioral categories relative to the total number of acts in a category summed over all individuals in a colony of 17 workers (a to q); 1, egg care; 2, larval care; 3, pupal care; 4, allogrooming; 5, nest maintenance; 6, guarding; 7, foraging; 8, prey handling.

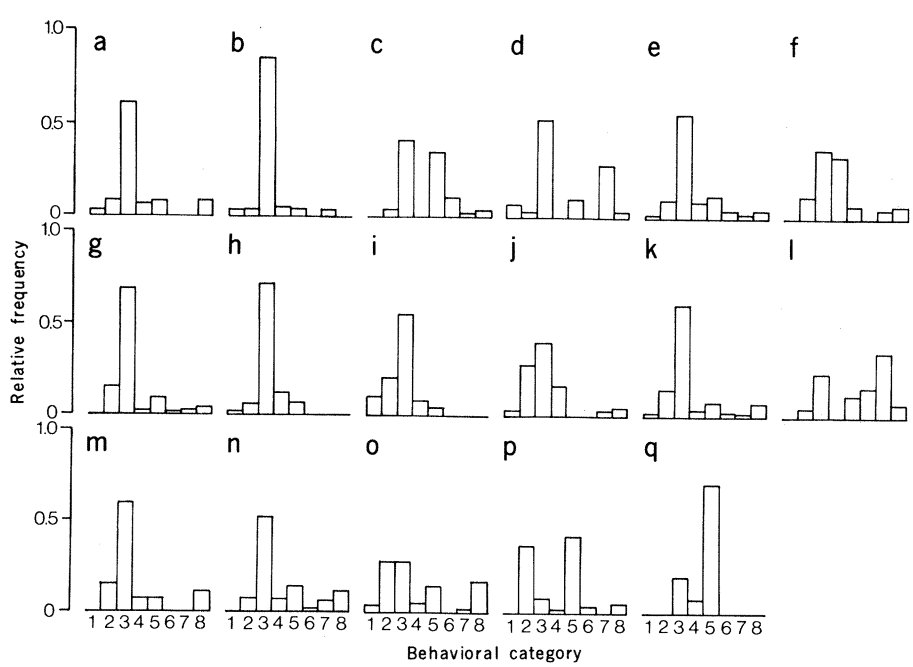

Fig. 2. Individual ethograms of workers. Frequencies are relative to the total number of acts of a given worker. See Fig. 1 for details.

related to queen attendance and brood care.

In addition to its prevalence in the ants, temporal polyethism has evolved in other social insect groups and is most elaborate in the honey bee, where the development of glands involved in certain tasks accompanies the sequence of worker activity. However, in the semisocial and primitively eusocial bees, and in the wasps, age polyethism is far less rigorous and patterns of age-related activity are variable (*8, 9*). The imprecise division of labor in *Amblyopone* and other primitively social species suggests that the elaboration of temporal activity patterns complemented the development of advanced social behavior.

Temporal caste systems are marked by a reduction in the repertory size of each age group (*6*), but in *Amblyopone* no such reduction has occurred and workers show a remarkable degree of behavioral plasticity. This lack of a well-defined division of labor in *Amblyopone* appears to be an extremely primitive character and may provide insight into the basic theme of sociality in ancestral ants. However, the biology of *A. pallipes* is a curious, ambiguous blend of primitive and advanced social traits, and it is difficult to accurately distinguish whether these characters are truly conservative or secondarily derived.

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Prolonged Inhibition in Burst Firing Neurons: Synaptic Inactivation of the Slow Regenerative Inward Current

Abstract. *By using voltage clamping and microiontophoretic techniques, it has been found that the prolonged cholinergic and dopaminergic inhibition seen in* Aplysia *burst firing neurons occludes the inward current on which slow oscillations depend. It also mimics the temperature and ionic sensitivity of that inward current. This prolonged inhibition, which cannot be inverted and is insensitive to extracellular potassium changes, thus appears to result from a synaptically produced inactivation of the regenerative slow inward current underlying bursting.*

In some situations a postsynaptic effect far outlasts the presynaptic firing burst that initiated it. A particularly well documented example of this is the prolonged inhibition produced in burst firing neurons L_2 to L_6 of the left upper quadrant of the abdominal ganglion of *Aplysia californica* (*1, 2*). These cells each receive a monosynaptic inhibitory connection from the cholinergic cell L_{10}.

In most of the follower cells of L_{10} the unitary postsynaptic potential (PSP) is relatively brief (100 to 200 msec), but in the burst firing neurons of the left upper quadrant the L_{10}-mediated inhibitory postsynaptic potential (IPSP) often has an additional phase lasting several seconds. Previous studies have shown that the short phase of the these IPSP's is easily inverted by hyperpolarization and represents an increase in the membrane conductance to chloride (*3*). On the other hand, Pinsker and Kandel (*2*) reported that the long IPSP was not reversible by hyperpolarization and that it was insensitive to changes in chloride and potassium equilibrium potentials. The inability of the long IPSP to invert, together with its high sensitivity to temperature and to ouabain, led Pinsker and Kandel (*2*) to suggest that it resulted from a synaptically mediated increase in the activity of an electrogenic pump. This was disputed by Kehoe and Ascher (*4*) and by Kunze and Brown (*5*), who showed that iontophoretic application of acetylcholine (ACh) to the neuronal soma produced long responses that were inverted at membrane potentials beyond the potassium equilibrium potential. They concluded that the long IPSP in these cells was due largely to an increase in potassium conductance occurring in a "remote area" of the neuron (*4*).

To examine whether the long IPSP in the left upper quadrant cells represents a remote increase in potassium conductance, as well as to explore alternative explanations, we combined voltage clamp and iontophoretic techniques. As a part of this study we also examined a similar prolonged inhibitory response to dopamine exhibited by burst firing neuron R_{15}. Ganglia were bathed in artificial seawater at pH 8.0. Voltage clamping was carried out with either single (*6*) or dual microelectrodes placed in the soma. Acetylcholine or dopamine was iontophoresed from the tip of a microelectrode, using a constant-current circuit (*1–4*). For ion substitution experiments potassium was added or removed without compensation, whereas sodium was replaced by sucrose.

Figure 1A illustrates the results of a voltage clamp experiment designed to measure the short and long inhibitory postsynaptic current (IPSC) components. Cell L_6 was voltage clamped and interneuron L_{10} was fired by passing current through an intracellular microelectrode. The postsynaptic current is composed of a short phase of outward current (approximately 100 msec) and a long outward current lasting at least 5 seconds (Fig. $1A_1$). The cell was next clamped to a more negative potential and L_{10} was fired more rapidly. Here the short IPSC's are inverted (inward) but the long IPSC continues to be an outward current (Fig. $1A_2$).

We have explored the voltage sensitivity of the long and short IPSC's by clamping follower cells to various potentials ranging from -30 to -120 mV and measuring the size of both components at each potential. We found that the short IPSC inverted slightly below -50 mV, but the long IPSC approached zero asymptotically and never inverted despite prolonged, high-frequency firing of L_{10}. Similar results were obtained in more than 50 cells clamped at potentials up to -150 mV. We have never seen the long IPSC invert. [Details of these experiments will be reported elsewhere (*7*).]

This unusual voltage sensitivity suggested to us that the long IPSP in bursting cells might result from some mechanism other than the simple increase in potassium conductance (*4*). Since these long IPSP's are capable of modifying the slow oscillatory rhythms of the burst firing neurons (*8*), we explored the possibility that they result from a mechanism that is intimately related to the slow oscillation generator.

Using voltage clamp techniques, it

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