[Communicative & Integrative Biology 2:2, 151-154; March/April 2009]; ©2009 Landes Bioscience

Mini-Review

Learning, specialization, efficiency and task allocation in social insects

Lars Chittka* and Helene Muller

Queen Mary University of London; Research Centre for Psychology; School of Biological and Chemical Sciences; London, UK

Key words: ants, bees, cerapachys, cognition, interference, themnothorax, transfer

One of the most spectacular features of social insect colonies is their division of labor. Although individuals are often totipotent in terms of the labor they might perform, they might persistently work as scouts, fighters, nurses, foragers, undertakers or cleaners with a repetitiveness that might resemble an assembly line worker in a factory. Perhaps because of this apparent analogy, researchers have often assumed a priori that such labor division must be efficient, but empirical proof is scarce. New work on *Themnothorax* ants shows that there might be no link between an individual's propensity to perform a task, and their efficiency at that task, nor are task specialists more efficient than generalists. Here we argue that learning psychology might provide the missing link between social insect task specialization and efficiency: just like in human societies, efficiency at a job specialty is only partially a result of "talent", or innate tendency to engage in a job: it is much more a result of perfecting skills with experience, and the extent to which experience can be carried over from one task to the next (transfer), or whether experience at one task might actually impair performance at another (interference). Indeed there is extensive circumstantial evidence that learning is involved in almost any task performed by social insect workers, including food type recognition and handling techniques, but also such seemingly basic tasks as nest building and climate control. New findings on *Cerapachys* ants indicate that early experience of success at a task might to some extent determine the "profession" an insect worker chooses in later life.

"*…The improvement of the dexterity of the workman necessarily increases the quantity of the work he can perform, and the division of labor, by reducing every man's business to some one simple operation, and making this operation the sole employment of his life, necessarily increases very much the dexterity of the work man.*"

"*…A man commonly saunters a little in turning his hand from one sort of employment to another. When he first begins his new work… for some time he rather trifles than applies to good purpose.*"

—Adam Smith (1723–1790), In: "An Inquiry into the Nature and Causes of the Wealth of Nations (1776)".[1]

*Correspondence to: Lars Chittka; Director, Research Centre for Psychology; Professor in Sensory and Behavioural Ecology; School of Biological & Chemical Sciences; Queen Mary College; University of London; Mile End Road; London E1 4NS UK; Email: l.chittka@qmul.ac.uk

Submitted: 12/09/08; Accepted: 12/09/08

Previously published online as a *Communicative & Integrative Biology* E-publication: http://www.landesbioscience.com/journals/cib/article/7600

You might sometimes question whether your job is right for you—but chances are that you are better at the current one than you might be in many alternative professions, and that you're also better at doing your job than most other people would be. This is, in part, because you've undergone years of training to obtain the necessary skills. With some probability, you've chosen this particular career path because there were early indicators that you would succeed at it. Even if you have reason to believe that you might be good at an altogether different profession, this might require extensive retraining with substantial costs and a somewhat unpredictable outcome. However, this will depend on the similarity of the tasks: because of transferable skills, it might be feasible to switch from being an actor to a politician, but not as easily from being a scientist to a concert violinist. Indeed, Adam Smith, the father of modern economics, considered skill learning, labor division and minimization of switching costs to be key components of improved efficiency of individuals and, as a by-product, society as a whole.

Specialization = Efficiency?

These considerations should apply to any animal society, not just *Homo sapiens*.[2] The insect societies, e.g., ants, bees and termites, arguably rule the planet, and their success, too, has been attributed to labor division, specialization, and the resulting efficiency.[3] Individuals of many insect colonies are indeed often highly specialized, so that animals will predominantly engage in colony defense, nursing larvae, removing debris, or foraging only for particular commodities but not other available ones.[4-7] With the exception of rigid castes, such as egg-laying "queens" or termite "soldiers", specialists are often not distinct in morphology, and indeed largely totipotent in terms of the tasks they can potentially perform. Indeed, even though social insect specialists might perform the same routine over and over for extended periods, with the same repetitiveness as assembly line workers, they can typically switch to other activities should these become necessary. Surprisingly, there is relatively little quantitative research into the question of how specialization contributes to colony efficiency (see refs. 2, 8 and 9). The proverb that the "Jack-of-all-trades is an ace of none" is perhaps so intuitively appealing that many scientists have not deemed empirical proof necessary. Past controversies from ecology[10] and psychology,[11,12] however, indicate that the advantages of specialization can not be assumed a priori, and might depend fundamentally on the tasks involved, and their context.

Generalists on a par with Specialists in an Ant

In what is perhaps the most comprehensive exploration of this question to date, Dornhaus[13] heroically marked 1142 *Temnothorax*

Figure 1. A laboratory colony of *Temnothorax albipennis* ants. While workers are not morphologically specialized for the various tasks required by the colony, individual paint marks reveal that many workers are specialists (repeatedly performing only certain activities) while others are generalists, often sequentially performing multiple tasks. This side-by-side existence of individuals that vary in their level of specialization makes it feasible to test whether specialists are more efficient than generalists. Photo by Anna Dornhaus, with permission.

albipennis ants from 11 colonies with paint dots (Fig. 1), so that she could identify individuals and measure their performance in four different tasks that became necessary as a result of various emergencies that required immediate attention. In the first treatment, the roof of the colony was removed, so forcing the entire colony to migrate to a new nest, and carrying the helpless brood along in the process. In the second treatment, ants were offered diluted honey and dead flies a small distance away from the colony after a period of starvation. Finally, the front wall of the ants' dwelling was removed, so that they had to scramble to obtain building material (small stones; Fig. 2).

For each individual ant, performance was quantified by averaging the duration of the first two successive trips. Performance was evaluated as a function of that individual's degree of specialization (its propensity to focus activity on only one task, or two or more). Unexpectedly, specialists did not outperform generalists for any of the tasks. Also, an individual's readiness to engage in a task (as quantified by the time taken to first embark on it after the start of the experiment) did not consistently predict its performance.

These results are provocative, and a healthy reminder that we should not assume that biological complexity is automatically adaptive in any situation. However, the specialization of workers in social insects must surely be adaptive in some situations, and our hope is that studies as comprehensive as the one by Dornhaus will be performed to identify these conditions. Perhaps the emergency situations that were in force in this study meant that as many individuals as possible (independently of previous specialization, experience and efficiency) needed to engage, resulting in recruitment of many suboptimal performers into a task they would not otherwise perform. It might also be informative to test colonies in emergency-free situations, where they are given a choice between multiple activities that can be performed concurrently.

Much research on social insect specialization has been concerned with the stimuli by which workers identify the need for a task to be performed, and the sensory thresholds at which individuals respond to these stimuli.[4,5,14,15] Ideally, the readiness with which an individual engages in a task should correspond to its innate ability (or "talent") at performing the task.[8] Although such a correlation has been found in some tasks,[8] the results of Dornhaus' study show that it should not be assumed to be general. However, a correlation between response thresholds and efficiency might be generated over an individual's lifetime, since the thresholds themselves might become gradually lower with experience,[16] but also because, as a result of a lower threshold, an animal might perform the task more often, allowing it to polish its skills over time.

Learning, Transfer and Interference in Social Insect Work

Indeed, our introductory remarks about labor division in humans indicate that the most decisive factor that generates advantages of task specialization might relate to learning and memory, task transfer and interference. In Dornhaus' study, "all hands on deck" were needed; thus individuals might have had little chance to familiarize themselves with a task and improve performance over time. In more day-to-day situations, experience might often be the single best predictor of performance. Learning has been shown to play a fundamental role in efficiency of many everyday tasks in social insects' lives, including food handling techniques[17,18] (where performance can improve with experience by an order of magnitude[12]), information about the locations and identification of food sources,[19-23] nest repair,[24] nestmate recognition,[25,26] comb building,[27] strategies in handling prey[28] and nest climate control[16] (but not, for example, in corpse removal in honeybee colonies[8]). For complex tasks such as natural foraging at long distances from the nest, efficiency can increase with experience over a substantial portion of an insect's lifetime.[29,30]

Just like in human laborers, there can be substantial interference if insects switch from one task to another[12,31]—in one study on butterflies, feeding on a new plant species resulted in almost complete forgetting of the handling procedures for a previously visited flower species.[32] In other studies, individuals seemed comfortable in juggling two tasks.[33] If interference occurs, then the very mechanisms that make it preferable for an individual to work efficiently may lead to a certain inertia in switching tasks.[6] In some cases, the transition from one task to another may be orchestrated by fundamental alterations in brain structure, neuronal wiring pattern and protein synthesis, in

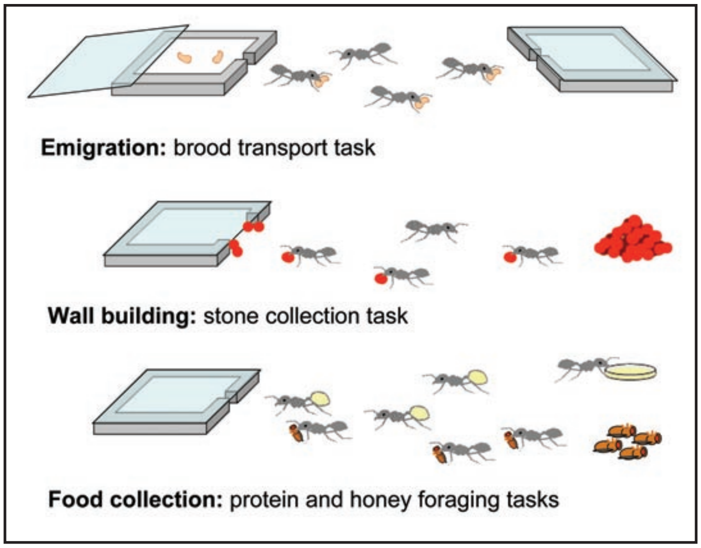

Figure 2. Are multi-taskers less efficient than specialist ant workers? In a recent study testing the adaptiveness of task specialization in *Temnothorax albipennis* ants,[13] each colony was subjected to three treatments. (A) The glass cover of the artificial nest was removed, exposing the ants and brood. At the same time, another nest with glass cover was placed 10 cm away from the original nest. The workers had to move the brood from the unsuitable, uncovered, nest toward the new, covered, nest. (B) The front wall of the nest was removed and a pile of small stones was left at the ants' disposal in the foraging area. The workers could carry the stones to their nest entrance so as to build a wall with a smaller opening. (C) The colonies were starved for two weeks and then provided with diluted honey solution and dead Drosophila flies in the foraging area. There was no significant difference in performance between specialists (performing only one task) and generalists (performing two, three or even all four tasks), for any of the tasks tested.

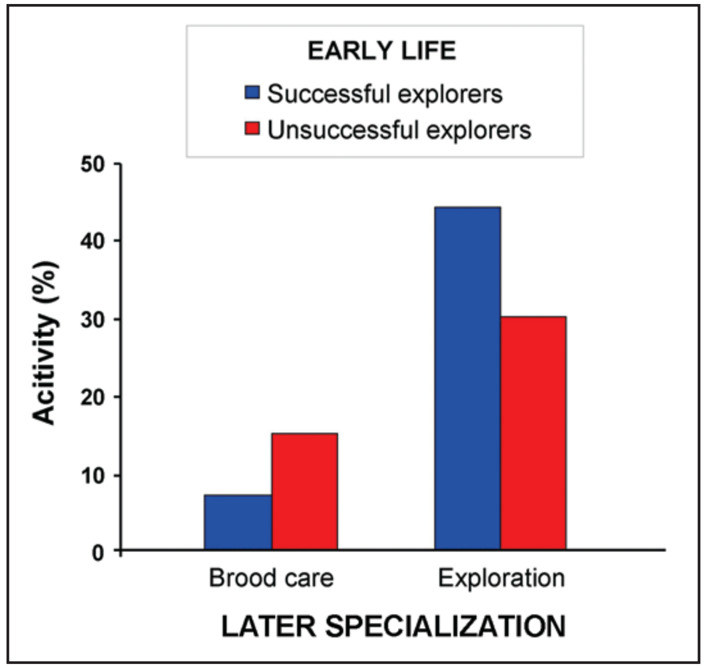

Figure 3. Early success or failure determines task specialization in *Cerapachys biroi* ants.[41] Age matched cohorts of ants with very low genetic diversity were subdivided into two groups that differed in terms of their foraging success in early adult life. One group was regularly rewarded when exploring the nest's surrounding, whereas the other never found any food. Weeks later, individuals that had been successful explorers in early life showed a much higher propensity to continue exploring, whereas their unsuccessful sisters showed a stronger tendency to care for brood inside the nest. Data approximate; redrawn from ref. 41.

part to generate the hardware to facilitate learning activities that come with the new tasks, but the changes can also be directly induced by new experience.[34-37] These changes have been examined primarily in the mushroom bodies of honeybees at the major transition from within-nest activities to foraging, and there might be less pronounced alterations of circuitry when switching between activities does not involve a near-complete change of life-style. Nonetheless, this research suggests that costs of task switching can extend substantially beyond those of temporal inefficiency at a new task.

Transfer is likewise important—in some cases, there might be similarities in two tasks that facilitate performance on a new job.[12,31] For example, in Dornhaus' study,[13] all tasks involved locomotion, orientation within the (presumably familiar) surroundings of the nest, and three of four tasks involved carrying items with the mandibles—thus skills at these tasks would have been largely transferable, whereas more specialized activities (such as wall-building[38]) or handling live prey[28] might involve learning (because the precise nature of the substrate is not predictable on an evolutionary scale), but skills obtained at either of these activities might not be transferable to the respective other one.

The extent to which transfer and interference exist for many of the within-nest tasks of social insect colonies remains to be shown on a case-by-case basis, but they could be more important in determining an individual's efficiency at any given task than the response threshold that causes it to engage with the task in the first place. The reason is that almost any motor task, however simple, will require some fine-tuning, i.e., adjusting actions to desired outcomes, even if it is based on genetically pre-programmed templates.[17,39] Even in basic locomotion, "robotic", fully hard wired motor routines would fail when load is redistributed along the body (such as when a prey item is carried) or when alterations occur to body structure (such as in insect flight when asymmetric wing wear occurs with ageing[40]).

Conclusion

Over a social insect's lifetime, it might come into contact with a large variety of tasks, and have a go at several of them. What are the feedback loops that ensure that individuals perform the tasks that they are good at? In humans, there is self-assessment (as well as feedback from others) of talent and the steepness of the learning curve: for example, it was clear fairly early on to these authors that they would never succeed as professional footballers, even with many years of training. In insects, there is likely no feedback from others ("*Hey Jane, you're* ***rubbish*** *at pollen foraging!*"), but there might be a role of individual experience in deciding which task an individual specializes on in the first place. In a fascinating recent report,[41] previously naïve *Cerapachys biroi* ants repeatedly explored their environment for food—only for some individuals, the experimenters had made sure they never found any. Such ants gradually decreased their efforts, and in the end, stayed mostly in the confines of the nest and became specialist brood carers, whereas their more successful relatives happily continued to forage in the outside world (Fig. 3). In this case, the experience of success and failure determined specialization. We therefore suspect that the biggest missing piece of the puzzle in our understanding of labor division in animal societies relates to extent that individual experience, transfer and interference contribute to efficiency, just as Adam Smith pointed out at the dawn of the industrial revolution for human labor division.

References

1. Smith A. An Inquiry into the Nature and Causes of the Wealth of Nations; reprinted 1976. Oxford: Clarendon Press 1776.
2. Jeanson R, Clark RM, Holbrook CT, Bertram SM, Fewell JH, Kukuk PF. Division of labor and socially induced changes in response thresholds in associations of solitary halictine bees. Anim Behav 2008; 7:593-602.
3. Hölldobler B, Wilson EO. The Ants. Berlin: Springer 1990.
4. Gordon DM. The organization of work in social insect colonies. Nature 1996; 380:121-4.
5. Beshers SN, Fewell JH. Models of division of labor in social insects. Ann Rev Entomol 2001; 46:413-40.
6. Chittka L, Thomson JD, Waser NM. Flower constancy, insect psychology and plant evolution. Naturwissenschaften 1999; 86:361-77.
7. Tofts C, Franks NR. Doing the right thing: Ants, honeybees and naked mole-rats. Trends Ecol Evol 1992; 7:346-9.
8. Trumbo ST, Robinson GE. Learning and task interference by corpse-removal specialists in honey bee colonies. Ethology 1997; 103:966-75.
9. Langridge EA, Sendova-Franks AB, Franks NR. How experienced individuals contribute to an improvement in collective performance in ants. Behav Ecol Sociobiol 2008; 62:447-56.
10. Waser NM, Chittka L, Price MV, Williams N, Ollerton J. Generalization in pollination systems, and why it matters. Ecology 1996; 77:1043-60.
11. Allport DA. Attention and performance. In: Claxton G, ed. Cognitive Psychology—new directions. London: Routledge & Kegan Paul 1980; 112-53.
12. Chittka L, Thomson JD. Sensori-motor learning and its relevance for task specialization in bumble bees. Behav Ecol Sociobiol 1997; 41:385-98.
13. Dornhaus A. Specialization does not predict individual efficiency in an ant. PLoS Biology 2008; 6:285 doi:10.1371/journal.pbio.0060285.
14. Spaethe J, Brockmann A, Halbig C, Tautz J. Size determines antennal sensitivity and behavioral thereshold to odors in bumblebee workers. Naturwissenschaften 2007; 94:733-9.
15. Waibel M, Floreano D, Magnenat S, Keller L. Division of labour and colony efficiency in social insects: effects of interactions between genetic architecture, colony kin structure and rate of perturbations. Proc R Soc B 2006; 273:1815-23.
16. Weidenmüller A. The control of nest climate in bumblebee (*Bombus terrestris*) colonies: interindividual variability and self reinforcement in fanning response. Behav Ecol 2004; 15:120-8.
17. Laverty TM, Plowright RC. Acquisition of handling skills on a complex flower: behavioural differences between specialist and generalist bumble bee species. Anim Behav 1988; 1-20.
18. Raine NE, Chittka L. Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*). Naturwissenschaften 2007; 94:459-64.
19. Srinivasan MV. Honeybee vision: in good shape for shape recognition. Curr Biol 2006; 16:58-60.
20. Collett TS, Zeil J. The selection and use of landmarks by insects. In: Lehrer M, ed. Orientation and communication in arthropods. Basel: Birkhäuser Verlag 1997; 41-65.
21. Saleh N, Chittka L. Traplining in bumblebees (*Bombus impatiens*): a foraging strategy's ontogeny and the importance of spatial reference memory in short-range foraging. Oecologia 2007; 151:719-30.
22. Menzel R, Giurfa M. Cognitive architecture of a mini-brain: the honeybee. Trends Cogn Sci 2001; 5:62-71.
23. Chittka L, Raine NE. Recognition of flowers by pollinators. Curr Opin Plant Biol 2006; 9:428-35.
24. Downing HA. Hole repair and the influence of learning on nest repair in the paper wasp, *Polistes fuscatus* (Hymenoptera, Vespidae). J Insect Behav 1992; 5:459-68.
25. Sheehan MJ, Tibbetts EA. Robust long-term social memories in a paper wasp. Curr Biol 2008; 18:851-2.
26. Chaline N, Sandoz J-C, Martin SJ, Ratnieks FLW, Jones GR. Learning and discrimination of individual cuticular hydrocarbons by honeybees (*Apis mellifera*). Chem Sens 2005; 30:327-35.
27. Oelsen Gv, Rademacher E. Untersuchungen zum Bauverhalten der Honigbiene (*Apis mellifera*). Apidologie 1979; 10:175-209.
28. Corbara B, Dejean A. Adaptive behavioral flexibility of the ant Pachycondyla analis (*Megaponera foetens*) (Formicidae: Ponerinae) during prey capture. Sociobiol 2000; 36:465-83.
29. Dukas R, Visscher PK. Lifetime learning by foraging honey bees. Anim Behav 1994; 48:1007-12.
30. Peat J, Goulson D. Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris*. Behav Ecol Sociobiol 2005; 58:152-6.
31. Dukas R. Transfer and interference in bumblebee learning. Anim Behav 1995; 49:1481-90.
32. Lewis AC. Memory constraints and flower choice in *Pieris rapae*. Science 1986; 232:863-5.
33. Weiss MR, Papaj D. Colour learning in two behavioural contexts: how much can a butterfly keep in mind? Anim Behav 2003; 65:425-34.
34. Gronenberg W, Heeren S, Holldobler B. Age-dependent and task-related morphological changes in the brain and the mushroom bodies of the ant *Camponotus floridanus*. J Exp Biol 1996; 199:2011-9.
35. Fahrbach SE, Farris SM, Sullivan JP, Robinson GE. Limits on volume changes in the mushroom bodies of the honey bee brain. J Neurobiol 2003; 57:141-51.
36. Robinson GE, Fernald RD, Clayton DF. Genes and Social Behavior. Science 2008; 322:896-900.
37. Krofczik S, Khojasteh U, de Ibarra NH, Menzel R. Adaptation of microglomerular complexes in the honeybee mushroom body lip to manipulations of behavioral maturation and sensory experience. Dev Neurobiol 2008; 68:1007-17.
38. Aleksiev AS, Sendova-Franks AB, Franks NR. Nest 'moulting' in the ant *Temnothorax albipennis*. Anim Behav 2007; 74:567-75.
39. Wolf R, Voss A, Hein S, Heisenberg M. Can a fly ride a bicycle? Phil Trans R Soc Lond B 1992; 337:261-9.
40. Higginson AD, Barnard CJ. Accumulating wing damage affects foraging decisions in honeybees (*Apis mellifera* L.). Ecol Entomol 2004; 29:52-9.
41. Ravary F, Lecoutey E, Kaminski G, Chaline N, Jaisson P. Individual experience alone can generate lasting division labor in ants. Curr Biol 2007; 17:1-5.