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COMMENTARY

Division of labor is not a process or a misleading concept

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Abstract Deborah Gordon (Behav Ecol Sociobiol. doi:10.1007/s00265-015-2045-3, 2016) advocates abandoning the term "division of labor" (DOL) on the grounds that it implies a process by which individual colony members become persistent specialists by virtue of their "essential internal attributes." She claims that there is little evidence for such links, and that continued use of the term distracts us from focusing on how distributed processing leads to task allocation (TA) in the colony, which she considers to be sufficient explanation of how colonies organize work. I argue instead that the term DOL as understood by most social insect researchers today is descriptive, useful, and carries no such implications of process or links to internal attributes. I suggest that the confusion can be addressed by recognizing the distinction between the ontogenetic causes of DOL, which set individuals' response thresholds (RT) during their development, and the behavioral and physiological mechanisms that act in the moment to determine TA via distributed processing. I further suggest that the term "specialization" as applied to social insects should be understood to mean simply "to concentrate on," without requiring that it be accompanied by increased performance efficiency.

Deborah Gordon (2016) argues that the term "division of labor" (DOL) should be abandoned because it "refers to the notion that individuals are specialized to perform particular tasks" by virtue of "essential internal attributes" and thus embodies an explanation for specialization that is based on these attributes. She also refers to DOL as a "process." Gordon further claims that "there is little evidence for persistent individual specialization in task," claiming that DOL is something "that isn't there." Her inference seems to be that all members of the colony are equally likely to respond to a demand for a particular task. Finally, she asserts that the phrase is a "misleading way to describe the organization of tasks in social insect colonies" because it improperly focuses attention on the behavioral correlates of fixed differences among individuals, and thereby "distracts from the main questions of interest in current research," by which she means how interactions among workers result in task allocation (TA) and give rise to the collective behavior of the colony. Gordon thus appears to deny any role for DOL and claims that distributed processing is a sufficient explanation of how colonies organize work.

I respectfully disagree with these views. I argue below that Gordon's claims don't hold up and conclude that the concept of DOL occupies a central place in our understanding of the organization of work in the social insects and should not be abandoned. I bring to this discussion a perspective somewhat different from hers, gained from several decades of research on the social wasps (Vespidae), a group in which morphological and size differences among workers are absent and even queen-worker dimorphism is rare.

Does the term DOL link specialization among colony members to their internal attributes, as Gordon contends? Social insect researchers in recent decades have largely adhered to a strictly descriptive definition of DOL, defining the concept variously as "any behavioral pattern that results in some individuals in a colony performing different functions

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from others, even if only temporarily" (Michener 1974:119); "a stable pattern of variation among workers within a colony in the tasks they perform…" in which "…(a) each worker specializes on a subset of the complete repertoire of tasks performed by the colony, and (b) this subset varies across individual workers in the colony" (Beshers and Fewell 2001:415); DOL implies "that each task is performed by a particular subset of the workers" (Dornhaus 2008); and "a statistical pattern in which different individuals perform different functions" (Holbrook et al. 2011:960). These definitions can be distilled down to the following: *division of labor is non-random variation among the members of a social group in the tasks they perform*. That is, there is some degree of specialization, or polyethism, among group members. The specialization can be temporary or permanent and can take a variety of forms, including reproductive division of labor (a defining trait of eusociality), and division of labor among workers, including but not limited to morphological, size, and age-related subcastes. Although it is sometimes difficult to unambiguously assign colony members to one or another category, this does not negate the value of defining such categories in the first place. Even such seemingly discrete concepts as "male" and "female" often lack clear boundaries.

It is important that the terms we use in science to name biological phenomena and concepts not include any assumed explanatory process, mechanism, or function. DOL as defined above and in wide current use meets this criterion. Thus, there is little evidence in the literature of the past 40 years that the term has assimilated the baggage Gordon loads onto it, and she provides no documentation that this has happened. By claiming that the concept of DOL links behavior rigidly to morphology or other "internal attributes," Gordon sets up a straw man, which she proceeds to knock down to support her argument that interactions are sufficient to explain why workers perform the tasks they do. Because the definition of DOL is silent on mechanism, it leaves us free to investigate all the possible causes of the phenomenon without bias. DOL concisely refers to a pattern that is a key component of the colony phenotype of all social insects; it is useful and should not be abandoned.

Gordon further claims that there is little evidence for the persistent individual specialization or "essential internal" differences among colony members that she says are implied by the term DOL. Her implication is that all colony members are equally likely to respond to a need, and that whether an individual responds or not is entirely a function of the distributed processes behind TA, mediated through interactions with nestmates and the environment. I believe that this notion arises from a failure to recognize the distinction between DOL and TA.

To explore this distinction, it helps to frame it in terms of the four levels of analysis of causation in biology (Mayr 1961; Tinbergen 1963; Alcock and Sherman 1994). Analyses at the level of "ultimate causes" seek answers to questions about the phylogenetic history of a trait, and also about the trait's origin and maintenance through natural selection, i.e., its adaptive value. These causes act at the population level over evolutionary time. In contrast, "proximate causes" act within the lifespan of the individual. The two levels of proximate cause are both critical to understanding social behavior. "Ontogenetic causes" include the genetic and environmental sources of input during development that affect subsequent behavior. "Physiological causes" are the immediate mechanisms behind the performance of a particular behavioral act at a given moment.

In seeking to understand ontogenetic causes of DOL, we ask such questions as "What sets an individual's likelihood of performing a given role or task within the colony?" and "How do behavioral differences among individuals arise?" Of the numerous models of DOL that have been proposed (reviewed by Beshers and Fewell 2001), the most widely accepted is the response-threshold model (Robinson and Page 1989). It hypothesizes that workers differ in their response thresholds (RT) for each task; that is, they vary in their probabilities of performing a given task. RTs in turn are set by genetics and by environmental inputs experienced during larval development (e.g., nutrition, pheromones, temperature) (Jeanson and Weidenmüller 2014). Each individual enters its adult stage with a unique set of RTs for performing each of the tasks in the colony's repertoire; the sets of RTs may vary with caste. These thresholds do not remain fixed, but are modulated within limits during adult life by such factors as social context, age, nutritional state, exposure to primer pheromones, experience, and learning (Theraulaz et al. 1998; Jeanson and Weidenmüller 2014). Thus, the causes behind the interindividual variation in RTs include everything in the history of the individual, from its genotype through its larval development to its experience 3 min ago as an adult. These are the "internal attributes" that Gordon wants us to dismiss as irrelevant to understanding how a colony organizes work. In contrast to Gordon's view, the array of RTs across the colony's members can be seen as the underlying causes that give rise to division of labor. These ontogenetic inputs, through their setting of RTs, in effect "prime" colony members to respond (or not) to the cues and/or signals that can trigger a given behavioral response.

The second level of analysis of proximate causes is "mechanism," sometimes referred to as the physiology of behavior, or "causation" in the narrow sense (Tinbergen 1963). In contrast to ontogenetic causes, which act over the individual's developmental history, physiological causes act in the present. Causation of behavior at this level includes the properties of the external signals and cues that trigger a behavioral response (i.e., that cause a change in the individual's behavior) as well as all aspects of the sensory-integrative-motor pathways involved in the initiation and performance of the behavior.

Gordon's interindividual interactions fall into this category. Environmental conditions that do not directly trigger a response may also be important in determining whether a response will occur. For example, the rate of nest construction behavior in tropical social wasps is positively correlated with relative humidity (Loope and Jeanne 2008). Social context is also important: single, isolated worker honey bees, for example, will not respond to alarm pheromone (Robinson 1987), and in social wasps, the RTs for defensive behavior decrease as the colony's investment in brood increases (London and Jeanne 2003).

The two levels of proximate causation—ontogeny and physiology—are logically as discrete as past and present. In arguing that "'(t)ask allocation' extends 'division of labor' to explain what each worker is doing at a given moment as a response to social interactions and external stimuli, as well as the consequence of internal characteristics of the worker," Gordon at best blurs this distinction, and at worst seems not to recognize or accept that ontogenetic causation plays any role at all in determining which individuals perform what tasks.

Gordon goes on to claim that the phrase DOL is misleading because it distracts us from the main questions of interest in current research—the interactions among individual colony members that give rise to TA through distributed processes. First, this fails to acknowledge all the active investigation going on into ontogenetic causes of DOL. Second, even if we explained everything we could by analyzing worker-worker interactions, we would still be left with such questions as "What causes some ant workers to remain near the nest entrance where they may respond to interactions with nestmates by beginning to forage, whereas others reside deeper in the nest and out of range of those interactions?" For answers, we have to go back to investigating their developmental history, as described above, to understand the causes of differences in RTs. RTs influence task allocation through interactions. The interplay of RTs with nestmate interactions and other sources of sensory input manifests itself as division of labor. To put all the focus on interactions cannot provide a complete understanding of the organization of work in the colony.

Turning to ultimate causes, in her Section 2 ("Division of labor and distributed processes") Gordon expresses skepticism regarding the evidence in support of the fitness benefits of specialization. Citing Wilson's (1980) finding that leaf-cutter (*Atta sexdens*) workers with head widths of ~2.2 mm are more efficient at cutting hard leaf tissues than are larger or smaller nest- mates, she challenges his conclusion that this specialization is adaptive at the colony level on the ground that Wilson did not directly test its effects on colony fitness. She goes on to assert that the enhanced efficiency of morphological specialists cannot explain the evolution of such specialization because most ant species lack strong polymorphism. Such an argument is akin to claiming that the evolution of eye spots on the wings of some moth species cannot be explained by their advantage in defense because most moth species lack eye spots. This is hardly the way to advance the field. If Gordon has an alternative, testable hypothesis for the selective advantage of worker polymorphism, she should propose it. Meanwhile, numerous other studies have demonstrated task-performance efficiency gains associated with worker size and morphological subcastes (e.g., Porter and Tschinkel 1985; Kay and Rissing 2005; Tschinkel 2006; Mertl and Traniello 2009).

Division of labor entails specialization, a term that may itself carry some baggage. To require that the specialist be more efficient or more reliable at a task than a non-specialist is unnecessarily limiting. Again, we are better off if we define terms so as not to ascribe to them any such restrictive quality. To "specialize" should simply mean to concentrate on, without requiring that the concentration be permanent, linked with a particular morphology, or come with a higher task-performance efficiency (Oster and Wilson 1978; Fewell et al. 2009). Such a general, descriptive definition leaves a path open to hypothesizing all the possible ways that concentrating on a limited set of tasks might be adaptive. Benefits to the colony accrue in ways other than via enhanced individual performance efficiency, such as by increasing overall efficiency through task partitioning (Jeanne 1986a, b; Ratnieks and Anderson 1999). A human analogy that is more realistic for social insects than Gordon's permanently specialized candlemakers and shoemakers is two people engaged in repairing the chimney of a house. Their first task is to get the bricks to the roof. The non-specialized method for accomplishing this is for each person to repeatedly carry loads of bricks up the ladder, which requires each to expend the energy to ascend and descend the ladder carrying the bricks as well as his own weight, not to mention dealing with the bottleneck when they meet at the ladder. The alternative is to specialize via task partitioning: one person remains on ground and hands or tosses bricks to the other on the roof. This approach reduces the overall cost of the operation in both time and energy. An important point is that the benefit does not require that each person is able to do one task better than the other, or that they specialize permanently; they could switch jobs halfway through without losing the ergonomic advantage of this way of organizing the task. An example of this kind of specialization among social insects is "bucket brigading," known for a few species of ants and termites (Hubbell et al. 1980; Anderson et al. 2002). Another way specialization increases overall efficiency without increases in individual task-performance efficiency is via the demographic advantage of age polyethism. Allocating the riskiest tasks (typically foraging) to last in the age-polyethic sequence maximizes worker longevity (Jeanne 1986a; Tofilski 2002, 2006). These examples show that division of labor can lead to efficiency gains at the colony level, even in the absence of the specialists' being "better at" the task they specialize on.

So what is division of labor? It is a descriptive name we give to a defining colony-level phenotype of social insects. According to how most researchers use the term, it carries none of the implications of process or mechanism that Gordon wishes to burden it with. By adopting an extreme and unfounded interpretation of what DOL is, Gordon tries to argue it out of existence, then sends distributed processing and task allocation in to take its place. Instead, distributed processing/TA acts on the range of RTs among colony members to give rise to the DOL that we can observe and measure in a colony. Rather than being fixed attributes, RTs are probabilities of response that are roughly set during development, but are modifiable in the adult by age and experience. Task allocation, in contrast, acts in the moment, at the physiological level of causation. It is a mechanism through which cues, signals, and social interactions elicit responses by workers to contingencies facing the colony. A worker's response in a particular situation becomes the most recent addition to its ontogeny and has the potential to modulate its RTs, however slightly. Far from distracting us from a focus on how individuals interact with one other and with the environment, DOL and its underlying causes are essential parts of a complete understanding of how social insect colonies function.

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