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Implications of iterative communication for biological system performance

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ABSTRACT

The performance of integrated biological systems can often be described by the behavior of component subunits: the proportion of subunits performing an activity, and the rate of recruitment to the activity, can be relevant to system performance. We develop a model for activation of subunits (receivers) to a task when activation requires repeated signals (iterative communication). The model predicts how system performance will be affected by the parameters of iterative communication. Receiver activation is influenced by the frequency of stimulation, by forgetting about past interactions, and by the number of stimuli needed to activate the receivers. These parameters, along with the probability of activated receivers returning to a de-activated state, modulate the system-wide time course of activation and the steady-state proportion of activated receivers. Parameters can interact to affect system-wide activation, and multiple parameter combinations can yield similar patterns of activation. Group performance is less variable at higher stimulation frequencies and in systems with greater numbers of receivers. Biological constraints on iterative communication, such as time and energy costs, may limit the parameter values that are feasible for a given system. Iterative communication parameters may be subject to natural selection at the system (group) level because they affect system performance.

1. Introduction

The behavior and function of integrated biological systems – i.e., systems comprising autonomous subunits from a lower level of organization – often depends on the activities of the component subunits. We consider the common case where the behavioral or functional state of a system is described by the proportion of subunits that are activated to perform a task, and by the rate of their activation. Examples include the proportion of neurons firing action potentials in a brain region (Salinas and Thier, 2000; Pi et al., 2013), the number of females choosing mates in a lek mating aggregation (Widemo and Owensi, 1995; Borgia and Keagy, 2015), the number of insect colony foragers recruited to a food source (Grueter and Leadbeater, 2014; Czaczkes et al., 2015), and the number of consumers in a human population choosing to buy a particular product (Smith and Swinyard, 1988; Moore et al., 1995).

We present a model for predicting how key parameters of the process of activating subunits (henceforth, receivers) affects behavior at the system level. We model the case where repeated exposures to a stimulus are needed to induce behavioral responses in receivers (Hawkins et al., 1990). Stimuli are remembered and the effects of repeated stimuli are cognitively summed by receivers. Exposure to a sufficient number of stimuli induces a behavioral change in the receivers (Mowles and Ord, 2012; Baker and Carlson, 2014; Bell, 2015) or maintains receivers in a new behavioral state (Cao et al., 2009). We will refer to such information transfer systems as iterative communication.

Natural examples from diverse integrated biological systems exhibit the properties of iterative communication. Group-member activation can be relevant to organized systems that have been subject to system- or group-level selection, as well as to non-organized assemblages. *Networked cells:* Neurons are generally induced to fire action potentials via synaptic input from multiple upstream neurons; excitatory and inhibitory neurotransmitter inputs from the upstream neurons are summed both spatially and temporally on the membrane of the receiver neuron. Excitatory neurotransmitter inputs can sum to initiate an action potential (Toth and Marsalek, 2015). *Insect societies recruitment of workers to perform a new task:* In several species of ants, repeated contacts with nest mates are necessary to stimulate the onset of task performance, such as foraging for food, in workers (Detrain and Deneuborg, 2009). In harvester ants, workers are induced to perform new tasks simply by repeatedly contacting certain types of nest mates, and workers will shift to a new task if enough en-

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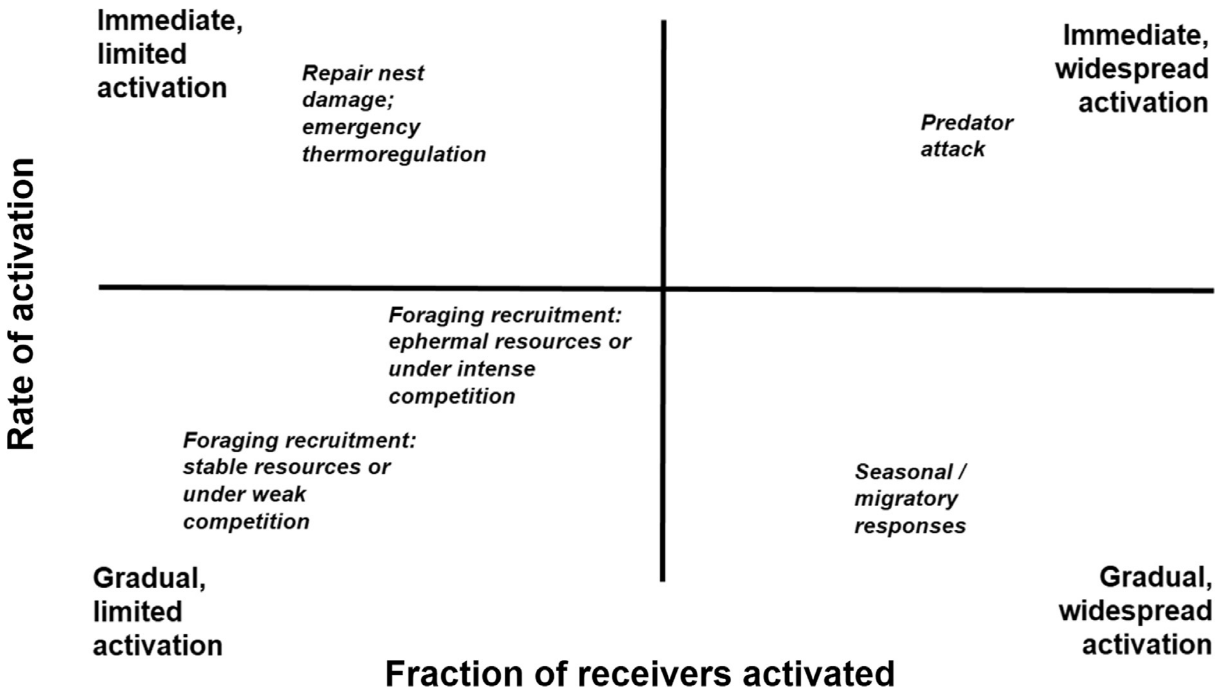

Fig. 1. Diagram illustrating relative expected adaptive positions of different behaviors or social group demands (listed in italics) along axes representing independent variation in rate of receiver activation (y-axis) and proportion of receivers activated (x-axis).

counters happen in an appropriate time window (Greene and Gordon, 2007). Repeated biting interactions can induce foraging behavior in wasp workers (O'Donnell, 2001, 2006). *Alarm calls in social and mixed-species groups:* In social or mixed-species groups, repeated encounters with predators can affect the probability and intensity of anti-predator responses (Tilgar and Moks, 2015). The alarm calls given in response to predators are themselves repetitive in many social and mixed-species groups, and the rate and frequency of alarm calls can modulate the responses of receivers (Weary and Kramer, 1995; Shah et al., 2015).

Iterative communication can provide two important advantages to biological systems. First, the magnitude of system responses can be graded, in other words, the proportion of receivers activated can be modulated. Second, the rate of activation of receivers can vary. Fig. 1 uses natural examples to illustrate cases where varying combinations of low- to high-proportions of receivers activated, and slow- to rapid-activation rates, can be adaptive in different systems or different contexts. Our model explores whether and how the rate and the magnitude of activation may vary independently. We show how the properties of iterative communication can shape patterns of receiver activation. Steady-state levels of receiver activation are attainable under biologically plausible conditions and the proportion of receivers activated is readily modified. Parameters of iterative communication, and interactions among these parameters, can therefore constrain system-level performance. In the special case when natural selection acts on organismal or social group performance, some major features of iterative communication are likely to evolve via system-level selection (Smith and Szathmary, 1997).

2. The model

2.1. Model rationale

Our model explores the process of changing the behavioral states of a set of receivers, or *activation*. The receivers represent component units in an integrated biological system. An earlier analysis of receiver activation used agent-based simulation models (O'Donnell and Bulova, 2007a,b); we show that system-wide processes of receiver activation can be represented more generally as transition matrices. The matrix model identifies key parameters of iterative communication that can affect the system-level dynamics of activation.

In our model we made three simplifying, but biologically plausible, assumptions. I. Stimuli are probabilistic and not targeted; all receivers have the same probability of being stimulated. II. Stimuli have quantitative and equal effects on receivers. III. Stimulus effects on receivers are strictly additive. Although many natural systems likely involve some degree of receiver targeting, and variation in stimulus strength and/or stimulus additivity, we expect our model to capture and predict fundamental features of iterative communication systems.

We modeled the process of receivers moving from one behavioral state (e.g., inactive at a given task) to another state (e.g., active at the task). In our time-discretized model, individual receivers experienced stimulatory interactions with a set probability (P) during each time step. The process of stimulation and eventual behavioral activation of an individual receiver can be treated as a ladder of discretized stimulation states (Fig. 2). A successful stimulation event brought a receiver one step closer to the number of accumulated stimuli needed to activate the behavioral change. At each time step, one of four outcomes was possible for each receiver. *I. Stasis (default).* If no stimulation (or forgetting, below) occurred, the receiver remained at its current stimulation level (Fig. 2). *II. Stimulation.* The receiver could be stimulated one step closer to activation with constant probability (P) (Fig. 2). *III. Forgetting.* If not stimulated in a given step, the receiver could lose a single stimulation level probabilistically by 'forgetting' . As with stimulation, the *forgetting probability* (F) was constant. Thus, individual receivers could move randomly up and down the stimulation ladder at rates dictated by the probabilistic model parameters (P, F). The minimum number of stimulations to activate a receiver was a third model parameter, the *activation threshold* (Θ; Fig. 2). We investigated both smaller ($\Theta = 2$ or 5) and larger ($\Theta = 15$ or 25)