Trends in Cognitive Sciences

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Special Issue: Time in the Brain

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Synchronization: The Key to Effective Communication in Animal Collectives

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From the rapidly expanding spiral waves exhibited by colonies of giant honeybees to the ripples of light that cross a turning school of fish, synchrony proves essential to the lives of group-living organisms. Here I consider what we know about the mechanisms and adaptive value of synchronization among animals, as well as outlining open questions that, if answered, could advance our understanding of the functional complexity of animal collectives.

In the early 1990s, two ant researchers, Nigel Franks in the UK [1] and Blaine Cole in the USA [2], made a near-simultaneous observation during their studies of small, cavity-dwelling ants. While the individuals in these colonies (which number only a few tens of to a few hundred individuals) tended to spend approximately 70% of their time inactive, sometimes a large proportion of the colony was seen to be active simultaneously. Employing early-developed computer vision tools, these researchers discovered that colony activity levels followed a clear rhythm, increasing and decreasing with a periodicity of approximately 20 min [1,2]. Reminiscent of the waves of neural activity exhibited in the brain, the question arose of whether, and if so how, synchronization may enhance the efficiency and/or the collective computational capabilities of colonies.

Mechanistically, it was demonstrated that local interactions among the ants are sufficient to explain the emergence of this oscillatory activity [3]. Inactive ants, on spontaneously ‘waking’ and becoming active, move within the nest, contacting and (probabilistically) activating others who are inactive. They in turn, if activated, may activate other ants and so on. This effect, combined with a propensity for ants to become inactive (especially those who have a low frequency of contacts) and the natural relatively restricted motion of ants to individual-specific ‘spatial fidelity zones’ in the nest, can account for the waves of activity seen spreading outwards from the nest center. However, a key mystery remains: we still do not have a decisive answer as to why these ants exhibit such clear rhythmical activity.

In South and Southeast Asia, colonies of the giant honeybee also exhibit synchronized activity, but here the waves are much faster and more complex. These large bees nest on a single, open comb, with the workers densely populating the comb surface. This open nest presents an opportunity for predatory wasps. In response to such threats, the bees exhibit a remarkable collective response; they create ‘shimmering’ waves, which form when a typical subset of individuals (which tends to initiate waves) rapidly raise and lower their abdomens, inducing those near them to do similarly (in ‘Mexican wave’ fashion). Unlike the ants, but much like neurons and other ‘excitable’ cells [4], individual bees appear to exhibit a ‘refractory’ period whereby once an individual has raised and lowered its abdomen there is a short period in which it appears insensitive to its neighbors. The resulting waves are rapid and highly visible and propagate across the colony surface as a series of expanding rings or spirals in a fraction of a second (Figure 1A), startling and repelling preying wasps [5].

Such collective properties are not unique; patterns of synchronous activity have been found in almost every animal group studied, from the simplest multicellular animals (Placozoa) to humans. Synchrony plays a role (over a wide range of timescales) in almost every aspect of group behavior. For example, to maintain the benefits of group living, organisms on the move must synchronize their decisions about when, and where, to move to find food and appropriate habitats and to avoid threats (Figure 1B,C). The speed at which waves of turning can propagate across bird flocks (e.g., in the dramatic ‘murmuration’ of starlings; see Figure I in Box 1 [6]) led to the belief in the early 20th century that synchrony must be facilitated by telepathy, or the ability of the brain to detect directly synchronized muscle activity in others. While much remains a mystery, in recent years advanced imaging techniques that allow automated tracking of individuals within groups, both in the laboratory and in the wild [7], are beginning to reveal some key principles.

For example, studies of the propagation of behavior in fish, birds, and humans have demonstrated that despite the vast differences among these organisms, there is a fundamental commonality in the mechanism by which behavior spreads. Unlike the spreading of disease (where a single source can be sufficient for transmission and spreading occurs via independent exposures to infected individuals), for behavior to spread individuals require reinforcement from multiple individuals. Reinforcement tends to depend not on the absolute number of other individuals exhibiting a behavior but on the fraction of perceived individuals exhibiting a certain behavior [8,9]. In addition, there is evidence from both fish and humans that the influence individuals have also depends on the structure of social networks. In Facebook, for example, reinforcement (the probability of joining or engaging with others on the social network) tends to be stronger if the reinforcing individuals are perceived as belonging to different social cliques (and thus may

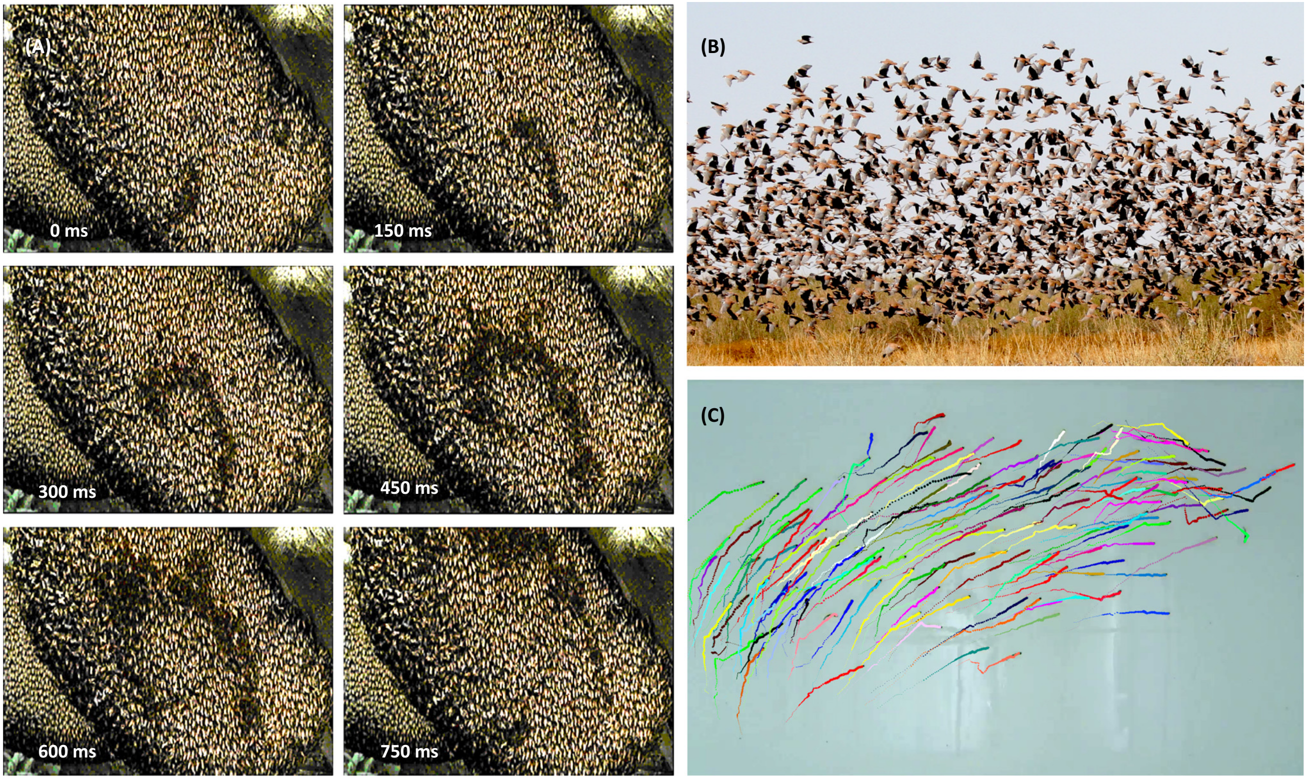

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Figure 1. Examples of Synchronized Behavior in Animal Collectives. (A) An image sequence, with intervals of 150 ms, showing the propagation of a spiral wave in a colony of giant honeybees (*Apis dorsata*) (filmed by Gerald Kastberger) [5]. (B) A flock of bronzewing pigeons (*Phaps histrionica*) taking flight together in inner Australia. Photograph courtesy of Damien Farine. (C) Visualization of the trajectories of 150 schooling golden shiner fish (*Notemigonus crysoleucas*) demonstrating the synchrony of their movements (by Vivek Sridhar and Matt Grobis).

provide more independent, less-correlated information) [10]. In schooling fish, analysis of the evolved network of social influence reveals that it is structured to reduce the probability that individuals obtain correlated (redundant) information from others [11]. In both scenarios this can benefit individuals since the utility of obtaining information from multiple others (the 'wisdom of crowds') is eroded if that information is correlated.

Explaining the remarkable speed at which information propagates in some animal groups, such as starlings and silverside fish, however, remains a key challenge. One proposal is that the importance of collective information transfer (e.g., regarding predators) is so profound that such systems have evolved to be in a special 'critical' regime (Box 1; [6]). Another, not mutually exclusive, hypothesis is that, much like when humans play the 'mirror game' in which participants are instructed to mirror the motion of others [12], individuals may reduce the time delays of communication, and thus enhance synchrony with others, by interacting not with the current state of the system (e.g., the current positions and velocities of others) but rather with a projected 'future state' (the projected future positions and/or velocities of neighbors). Biologically such a mechanism is plausible for nonhuman animals; archer fish, for example, have been shown to be able to predict complex 3D target motion. It would be fascinating to determine whether organisms in groups are similarly responding to a projected future state of the world, and if so whether this enhances the speed of behavioral synchronization.

The study of animal groups offers great potential to reveal more clearly the role that synchronization plays in information processing. Many groups are highly amenable to manipulative experimentation: they can be taken apart and put back together again to reveal how, and why, the components influence one another. Considerable scope exists to explore new questions, such as the interplay between behavioral and physiological synchronization, about which we know very little. We must strive to develop such an integrative perspective, as doing so will contribute enormously to our understanding of collective phenomena.

Box 1. Synchrony and 'Criticality' in Animal Groups

The extremely high speed at which behavioral change (e.g., turning) or density propagates across flocks of birds (Figure 1B and Figure I) or schools of fish (Figure 1C), along with certain statistical properties observed in such groups (e.g., the presence of long-range correlations in individuals' velocity despite the presence of highly local interactions), has caused some researchers to speculate that such animal groups, as has previously been suggested for the brain, are 'poised near criticality' [6]. Taken from statistical mechanics, the theory of critical phenomena demonstrates that certain generic properties appear in a collective system, be it of physical particles, neurons, or birds, when local interactions are tuned in a certain way. Near the critical point, remarkable properties emerge spontaneously, such as individuals' behavior becoming correlated irrespective of the distance between them (which is mathematically equivalent to information being able to propagate almost without loss over the entire structure). Biological systems may benefit from being close to a critical state in a variety of contexts since they must often satisfy two, seemingly opposing survival conditions: to respond quickly to changing environmental conditions, such as the appearance of a predator, and to remain robust and organized in the face of noise (e.g., in the case of fish or birds, eddies or gusts of wind, respectively). While still controversial, criticality provides a fascinating, plausible, and increasingly testable hypothesis for effective information processing in large collectives.

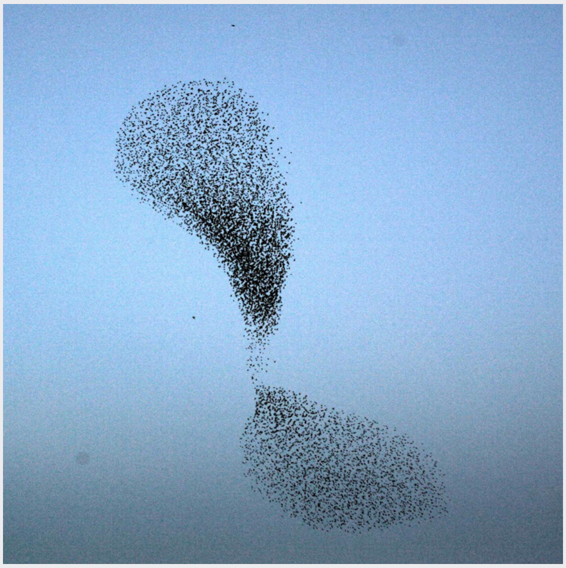

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Figure I. A 'Murmuration' of Starlings (*Sternus vulgaris*). Here the flock is being attacked by a peregrine falcon (*Falco peregrinus*) just to the left of the center of the flock. Photograph courtesy of the COBBS Laboratory, Institute for Complex Systems, National Research Council, Rome, Italy.

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Stuck in the Present? Constraints on Children's Episodic Prospection

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The examination of children's ability to simulate their future has gained increased attention, and recent discoveries highlight limitations in this ability that extend into adolescence. We propose an account for this protracted developmental trajectory, which encompasses consideration of retrieval flexibility across timescales and self-knowledge. We also identify avenues for future research.

We spend considerable time imagining what our future might bring, savoring a desired turn of events or dreading the opposite. The mental simulation of a future event sometimes includes so much