Journal of Multiscale Neuroscience

Perspective

All intelligence is collective intelligence

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DOI: https://doi.org/10.56280/1564736810

Received 2 December 2022; Accepted 23 February 2023; Published 28 April

Abstract

Collective intelligence, broadly conceived, refers to the adaptive behavior achieved by groups through the interactions of their members, often involving phenomena such as consensus building, cooperation, and competition. The standard view of collective intelligence is that it is a distinct phenomenon from supposed individual intelligence. In this position piece, we argue that a more parsimonious stance is to consider all intelligent adaptive behavior as being driven by similar abstract principles of collective dynamics. To illustrate this point, we highlight how similar principles are at work in the intelligent behavior of groups of non-human animals, multicellular organisms, brains, small groups of humans, cultures, and even evolution itself. If intelligent behavior in all of these systems is best understood as the emergent result of collective interactions, we ask what is left to be called "individual intelligence"? We believe that viewing all intelligence as collective intelligence offers greater explanatory power and generality, and may promote fruitful cross-disciplinary exchange in the study of intelligent adaptive behavior.

Keywords*:* Collective intelligence, self-organization, multicellularity, neural Darwinism, behavioral coordination, cultural evolution

1. Introduction

Collective intelligence, broadly conceived, refers to the adaptive behavior achieved by groups through the interactions of their members, often involving phenomena such as consensus building, cooperation, and competition. Within the last two decades, collective intelligence has exploded as a topic of interest within the cognitive sciences. Consider that from the year 2000 to 2019, there was a more than 5-fold increase in the appearance of the term "collective intelligence" in Google's Ngram corpus; there are now more than 100,000 articles or books published with "collective intelligence" in the title; there are at least two annual scientific conferences dedicated to the topic; and 2022 saw the inauguration of a new journal called *Collective Intelligence*. In spite of this massive increase of interest in the topic, the present authors admit to harboring some doubts about whether *collective* intelligence is really a distinct phenomenon from the good ol' fashioned intelligence cognitive scientists have long studied. Instead, individual intelligence and collective intelligence may be expressions of the same phenomena playing out on different spatiotemporal scales. As such, we suggest that individual-intelligence researchers may have much to gain by drawing insights from collective intelligence research, while collective-intelligence researchers could begin to apply their lens to more systems that are typically not viewed as collectives.

In their recent Handbook of Collective Intelligence, Malone & Bernstein (2022) write, "This book takes the perspective that intelligence is not *just* something that arises inside individual brains–it *also* arises in groups of individuals" (emphasis ours). Their perspective, which we take to be the standard view, presents individual intelligence as the norm, and collective intelligence as something different and perhaps special (let us ignore for a moment the fact that the notion of "intelligence" itself has evaded any attempts to reach an agreed-upon definition, and suppose that "we know it when we see it"). But this perspective becomes problematic once one recognizes that individuality is also not so simple to define. A growing number of biologists have begun to raise problems with the ubiquitous assumption that organisms are individuals separated by clear physical boundaries (Clarke, 2010). In many cases, upon closer inspection, we find that such boundaries are fuzzy and/or change over time. As Krakauer et. al., (2020) recently argued, individuality may be both a matter of degree and dependent upon the spatiotemporal scale of analysis—or, we would add, the theoretical and ontological perspectives taken. For example, a behavior that psychologists may describe as an expression of intelligence in an individual person, neuroscientists may attribute to the interactions between several specialized brain regions, each of which may be subdivided into the interactions of several millions or billions of neurons. Similarly, in light of the growing recognition of the importance of the human microbiome to our cognitive operations (Sarkar et al., 2018; Davidson et al., 2018), are we to include these trillions of microorganisms (our *holobiont;* Margulis, 1990) as a part of our body in order to preserve the notion of the organismal individual? Or are we to conclude that a single human is actually more like an ambulatory ecosystem? Without a clear definition of an individual, it is also unclear how intelligence is to be instantiated by one.

We argue that it is more effective to understand intelligence as being collective "all the way down," so to speak. That is, for any apparent individual, closer inspection may reveal its intelligence to be instantiated by collective dynamics on a lower (and sometimes higher) scale of analysis. We propose several advantages of this approach: First, understanding intelligence as primarily a process enacted by groups places the study of intelligence on firmer ground for empirical research, basing the phenomenon in observable mechanisms, including networks of interactions, competition and cooperation dynamics, and consensus building. We argue that any mechanistic explanation of individual intelligence must ultimately fall back on such phenomena, and therefore it is unclear what is to be gained by separating individual and collective intelligence into distinct categories. Second, our perspective leaves an opening for a truly general theory of intelligence, without making prior assumptions about the type of system by which intelligence may be exhibited. Third, our perspective permits an evolutionary consideration of intelligence, focused on how the mechanisms of collective intelligence may be honed over generations to make groups smarter and more coherent. Fourth, this perspective may ultimately help to shed light on the very concept of individuality, which we suggest may be in part a reflection of the intelligence embodied in group dynamics. That is, groups that have honed the mechanisms of collective intelligence over evolutionary time may become highly entangled and interdependent, thereby appearing to observers as a coherent individual. In sum, we view intelligence as a *process* enacted by many interacting parts, rather than a property, and view the individual/collective distinction as a continuum, rather than a binary, determined by the relative interdependence of interacting parts.

In what follows, we begin by considering more-or-less canonical examples of collective intelligence by a standard view, as exhibited in groups of non-human animals. Here we emphasize the continuity of forms of collective intelligence, which lays the groundwork for viewing collective intelligence as a spectrum (likely, a multi-dimensional spectrum). Next, we move on to a type of system that is not typically understood as an example of collective intelligence–a multicellular organism–and emphasize the evolution of these apparent individual intelligences from collective roots. Then, we proceed roughly "upwards" in spatio-temporal scale, touching upon the intelligence of brains and individual humans, dyads and small groups of humans, cultures or societies, and finally entire species, explaining how each level of analysis may be understood through the same general mechanisms of collective intelligence. In each section, we offer arguments and examples that push against the standard intuition that intelligence is typically a property of singular things, and thereby that collective intelligence is something else. In particular, we focus on the fuzzy edges and transitional periods wherein systems blur the line between being a collection of parts and acting as a unit. These examples suggest, on the one hand, that researchers of so-called individual intelligences may benefit from grappling with the fuzziness of individuality, towards which many insights can be found in the literature on collective intelligence. On the other hand, these examples also suggest that collective intelligence researchers may benefit from recognizing that their typical phenomena of interest are not necessarily distinct from phenomena that are typically attributed to individuals.

Our approach here is a form of argument-by-elimination: If it can be seen that mechanisms of intelligence at every level of analysis are best understood as collective behaviors, what is left to qualify as individual intelligence? Ultimately, we suggest that human brains occupy one end of a gradient in which a collective has become exceptionally interdependent, but that nonetheless operates according to mechanisms of collective intelligence that are present across species and scales of analysis. We hope that these considerations may help students of *individual* intelligence to recognize the value of seeing their phenomena of interest as emerging from collective dynamics, while simultaneously encouraging students of *collective* intelligence to recognize how collectives may come to act as individuals.

2. Collective intelligence in non-human organisms

The mind, and by extension intelligence, has traditionally been thought of as something possessed by individuals. However, eusocial insect colonies challenge the idea of intelligence as exclusively a property of an individual (Theiner, 2014). Colonies of ants, bees, and termites clearly display vastly greater and sometimes qualitatively distinct abilities compared to the individuals that they are composed of (Sumpter, 2006). Moreover, the intelligence of these collective units cannot simply be characterized as the sum of the intelligences of its constituents. The collective cognition and decision-making of the colony is determined by the interactions between the individuals, resembling mobile neural networks, and the algorithms that determine their output (Couzin, 2009). Thus, one approach to reconcile the intelligence of these colonies with individual intelligence may be by considering colonies as superorganisms (Wheeler, 1920) that parallel the intelligence and cohesive unity of a multicellular organism.

A common argument in favor of comparing a eusocial insect colony to a multicellular organism has been the high genetic relatedness among the components of the system – cells of an organism and individual members of a colony. High relatedness of individuals enabled by haplodiploidy among hymenopterans such as ants and bees was originally thought to be an important constraint for the evolution of eusociality (Hamilton, 1964; Trivers & Hare, 1976). However, some eusocial animals such as termites and naked mole rats do not have a haplodiploid genetic system (Thorne, 1997; Anderson, 1984) and some eusocial wasps and bees may not even have high relatedness (Brand & Chapuisat, 2016; Landi et al., 2003). Hence, resembling an organism in terms of genetic identity of constituent elements does not appear to be critical to the cohesive functionality of a colony.

Some species of animals can also switch between forming cohesive groups and existing as independently foraging individuals. For instance, cellular slime molds exhibit both a solitary phase where they exist and reproduce as individual cells and a social phase where unrelated cells collect together and appear to transform into a multicellular organism where many of them forfeit reproduction (Sussman, 1956). Similarly, many grasshopper species live as individuals where they avoid other conspecifics and forage alone, but under certain conditions, undergo behavioral and morphological change to become gregarious locusts that migrate over large distances, foraging as a group (Pener & Simpson, 2009). These changes to collectives are typically associated with high densities and patchiness of resources, where coming together allows individuals to disperse across larger distances and forage more efficiently (Nauta et al., 2022). This is suggestive of evolution favoring the switch between individual and collective intelligence based on the ecological context, allowing species to persist in different conditions.

The distinction between collective groups and solitary individuals is also not a clear binary. The extent of sociality exhibited by animal groups exhibits continuous variation between obligate eusocial colonies where some individuals forfeit reproduction to temporary associations of animals that come together for performing a task. This includes fission-fusion groups of fish and birds that may forage independently but roost together or converge under predation threat (Smith, 1995; Cote et al., 2013). However, facultatively social groups can also display collective intelligence in tasks ranging from spatial navigation to light-gradient sensing (Sasaki & Biro, 2017; Puckett et al., 2018). Indeed, even groups of birds and fish with population turnover across generations can learn important tasks such as foraging puzzles and maintain traditions of mating sites (Chimento et al., 2021; Warner, 1988), reminiscent of human cultures (discussed in a later section). This goes against the idea that only temporally cohesive units may display intelligence.

Furthermore, groups are not always formed by individuals of the same species (Sridhar & Guttal, 2018) and some such interspecific groups can cooperate to hunt together, thereby increasing their predation success (Bshary et al., 2006; Diamant & Shpigel, 1985). Thus, the wide variety of animal collectives found in nature that can operate intelligently contradicts the notion that intelligence is an aspect or trait of a spatiotemporally cohesive unit composed of relatively identical subunits.

Finally, while most of the examples reviewed above concern instances of cooperation between individuals, in some cases competitive dynamics both external and internal to a group can also lead to collective intelligence. For example, collective motion in schools of fish is often attributed to individual predator-escape movements combined with intragroup influence in heading direction (Lopez et al., 2012).

However, in some mass-migrating insects like locusts, cannibalism may drive intragroup pursuit and escape behavior that leads to collective motion (Romanczuk et al., 2009). Nonetheless, in both cases collective motion may lead to adaptive behaviors at the group-level (e.g. successful predator avoidance in the case of fish; migration to better resource patches in the case of locusts) that would be unachievable by individuals.

To summarize this section, collective intelligence in non-human animals is a highly diverse phenomenon, displayed by groups with many different types of individuals, in many different ecological contexts, driven by many different types of interactions between individuals, and encompassing many different types of intelligent behaviors (e.g. migration, search, and foraging; predator avoidance; niche construction; memory; decision making). In some cases, intelligent collectives are composed of closely genetically-related individuals, in others by more distantly related individuals, and sometimes even among individuals of entirely different species. In some cases, obeisance to a collective is universal in a species, while in other cases, individuals may switch between foraging alone and participating in a collective. Sometimes, collective intelligence appears driven by cooperative behaviors, other times by relatively selfish behaviors (e.g. individual predator avoidance) combined with social influence, and still others by entirely competitive behaviors (e.g. cannibalism). Thus, the system requirements for collective intelligence can only be stated at a quite abstract level: (1) a group of individuals, (2) a mechanism of interaction between them, that (3) leads to self-organization of the group towards (4) behaviors that are adaptive for the group (echoing a characterization of "complex systems" from Ottino, 2004). Given that natural selection is not picky about the micro-level details that instantiate these requirements, it should come as little surprise that similar dynamics occur at many different scales of analysis, as we will describe in the next sections.

3. Multicellular collective intelligence

The paradigm example of biological individuality is a metazoan animal. Despite increasing difficulties, related, for example, to the concept of holobiont mentioned in the introduction—the ecological unit formed by symbiosis between a host organism and the many microorganisms that live in and around it (Margulis, 1990)—the dominant assumption is that we want our theories of individuality to regard humans, frogs, sharks and cnidaria as individuals. However, at a sufficiently fine-grained level, there is no doubt that they do constitute highly integrated collectives of small living organisms – cells, of an astounding variety of types. Hence, the standard approach in the research on the evolution of multicellularity in the history of life on Earth, has been to ask how groups of (unicellular) organisms become (multicellular) individuals. The question has been put forward this way for decades, in fact reiterated at multiple levels: the seminal work of (Smith & Szathmáry 1997) discusses evolutionary "major transitions", asking about the subsequent evolution of chromosomes from individually replicating nucleic acids, of eukaryotes from independently living cells that developed into mitochondria and chloroplasts, of multicellulars from single-celled organisms and eventually of social groups, most importantly insect colonies, which transmit genes only together. This multiscale framing of the question places the point of the switch from unicellular mode of life into obligatory multicellularity in a doubly important position: as it can both offer insight into the emergence of sociality and become enlightened by the studies of collectivity in multicellular organisms. One way to disentangle this co-dependence is to approach the problem of the emergence of obligatory multicellularity through the lens of the concept of collective intelligence, as introduced above in previous sections of this paper.

Michael Levin and Daniel Dennett have proposed the phrase "cognition all the way down" (Levin & Dennett, 2020) to frame this approach. They propose to model individual cells in the multicellular collective as intelligent agents on their own, that coordinate (likely via bioelectrical communication, see: Levin, 2019, p. 17; this hypothesis is supported by the fact that bacterial biofilms use equivalents of neural ion channels to communicate, see: Prindle et al., 2015) to form a "compound" intelligence. In doing so, Levin puts forward a quite general definition of intelligence as the degree of competence in navigating spaces (Fields & Levin, 2022): both physical 3D space, as well as less standard kinds of spaces, such as morphospaces (space of possible morphologies, explored in morphogenesis), transcriptional spaces (explored by mRNA), and physiological spaces (explored by ion channels).

This agentive characterization of cells in a multicellular system has been concurrently proposed by Arnellos & Moreno (2015) who specifically investigate the shift from agency of individual cells into the agency of the collective they constitute. Levin uses the concept of "computational boundary", referring to the spatiotemporal limits of information processing of a system to describe the change that occurs during this shift: he proposes to view compound intelligences (e.g. collectives of cells forming a multicellular organism, but also insects forming a colony) as expanding individual organisms' computational boundary, allowing them to process information referring to more distant events, both in time and space. Fields & Levin (2019) have suggested that this might be in fact what has driven the evolution of somatic multicellularity: organisms in which non-reproductive cells "protect" their parents capable of reproduction might profit from the extended computational boundary and be able to protect themselves from a wider range of environmental threats. This view of collective behavior as expanding the computational boundary of organisms allows one to notice many similarities across scales and species involved in collective behavior. For example, work by Cavagna et al. (2010) suggests that collective motion in starling flocks provides "each animal with an effective perception range much larger than the direct interindividual interaction range, thus enhancing global response to perturbations."

Morphogenesis, the processes of development of shape in living organisms, is a model example of the collective agency and information processing of multicellular systems. All living organisms undergo this process during development, but it takes its most complex form in multicellular organisms, where individual cells must orchestrate the process together and physical forces such as tension or nuclear forces have a less direct impact. Furthermore, some organisms are capable of re-initializing morphogenesis to restore their body shape after injury, regrowing entire limbs (Choi et al, 2017) or even non-skeletal elements including, in the case of the flatworm, the entire head and brain (Gentile et al., 2011). To achieve this goal, cells need to solve a plethora of distinct problems: they need to migrate to specific places in a developing organism, initiate processes of cytodifferentiation in appropriate ways depending on their location, and finally they need to stop differentiation and division at a suitable moment, when the target morphology has been achieved–a moment that none of the cells have direct information about.

As research shows, this process is incredibly versatile and robust: consider studies conducted by the Levin lab in which scientists modified tadpoles of African frog *Xenopus laevis*, a model organism in developmental biology, by scrambling the positions of their facial organs (Vandenberg et. al., 2012). Astonishingly, over the course of the development into an adult organism, the morphogenetic "program" was adaptively modified: the organs moved in novel ways to ultimately achieve morphology in line with the standard adult morphology. In another experiment, tadpoles were surgically implanted with an additional eye located ectopically on the tail, transplanted from another frog (Blackiston & Levin, 2013). In a significant portion of those animals, an optic nerve has developed from donor tissue connecting to host locations: either towards the stomach or through the trunk and towards the spinal cord. A few of those cases had the nerve terminating at the spinal cord. In those cases, the transplanted eye allowed the animal to see, as researchers have shown through an associative learning task (Blackiston & Levin, 2013). This shows that morphogenesis is not a simple implementation of a pre-set recipe (of a form 'move cell X distance Y in the direction Z'), but rather that cells react to their environment in a way that is appropriate, even if the circumstances widely differ from normal.

The forms of obligatory multicellularity, recapitulated above, have been more difficult to understand for bioresearchers, as they require an apparently non-adaptive behavior from cells that develop into somatic cells, voiding the evolutionary imperative of transmitting genes to future generations. They become unable to continue a life independent of the group that they now form. While the metazoan animal is the most obvious example, other forms of this type of collectives exist as well: for example, some genera of the volvocine algae (*Volvox carteri* is a standard example, as a model organism with a fully sequenced genome) form colonies comprised of about 2000 somatic cells, creating a spherical monolayer, and about 16 germ cells which lie just below this sphere (Kirk, 2005). The colonies are motile, with an anterior-posterior axis, and with hollow interiors hosting the embryogenetic processes of the next generation. *V. carteri* offers a unique glimpse into evolution of multicellularity, with just two cell types and a much shorter history of multicellular lifestyle than eukaryotic groups (about 30-70 million years compared to 1 billion; Kirk, 2005). In the lineage of its closest unicellular ancestors, *Chlamydomonas reinhardtii*, there are four other extant volvocine genera, traditionally arranged in a conceptual series along their increasing cell number, size, and the tendency to develop sterile somatic cells. Some of its close relatives (e.g., various species of *Gonium*), while they do have a multicellular lifestyle, retain the reproductive abilities in all cells. More distant organisms, however, have more complicated lifestyles in which they switch between uni- and multicellular stages. This is the case for many multicellular slime molds (e.g., *Dictyostelium discoideum*, already mentioned in the previous section) where individual cells forage and reproduce normally if food is available, and when the supply is exhausted, they switch into a multicellular mode, where they assemble into a pseudoplasmodium, a slug-like structure which has an anterior-posterior axis, responds to light and temperature gradients, and can migrate (e.g., Kitami, 1982). Interestingly, the non-obligatory type of multicellularity is possible to replicate in the lab by inducing specific selection pressures (Bozdag et al., 2021; Ratcliff et al., 2012).

Hence, the variety of multicellular systems is connected primarily by fact that they exhibit the joint action and information processing as a single, complex system—rather than by factors which likely appear only as the forms of multicellularity increase in complexity, such as the cell type division of labor. The benefits of the framework like the one offered by Levin, which takes individual cells to exhibit some levels of intelligence and the emerging multicellular system to exhibit a "collective" or "compound" intelligence is clear in the case of morphogenesis. Furthermore, we can use this approach to help clarify some of the extant debates in cognitive science and philosophy of mind, such as the dispute between proponents of a computational theory of mind and of embodied accounts of cognition. This is possible through the concept of "morphological computation" (see Rorot, 2022) which offers a bridge between the two theories by focusing on the forms of computation and intelligence exhibited by bodies, from the level of individual cells all the way up to highly complex human brains, as we highlight in the following sections.

4. Brains as intelligent collectives

If our reader were to do a quick image-search for the word "intelligence," what you will see are human brains; lots and lots of brains. The brain is, of course, our archetype of intelligence. But what makes brains intelligent? For many cognitive scientists and laypeople alike, brains are intelligent because they are like computers, with neural circuits implementing logical operations over stored representations or symbols, served up to a "central executive." In this vein, evolutionary psychologists describe the evolution of human intelligence as the evolution of computational "modules" selected to solve specific problems for the individual organism. From this perspective, the brain evolved as a coherent whole, adding functions one at a time.

But such a view belies the complex evolution of the nervous system. Before the existence of a central nervous system as found in modern mammals, there were nerve nets of the kind found in jellyfish and octopuses—diffuse, homogenous networks of interconnected neurons that extend throughout the entire body with no central controller (Arendt et al., 2015). Prior to the nerve net, there was the emergence of synaptic signaling in colonial single-celled eukaryotes, such as Obelia (sea fur; Dunlap et al., 1987). Prior even to the existence of synaptic communication, there was the emergence of coordinated behavior of multicellular organisms through purely mechanical means. For example, recent research from (Prakash et al., 2021) on *Trichoplax* has revealed that the local mechanical interactions of millions of cilia produce coordinated "walking" behavior and even thermotaxis, with mechanical signals propagating much like electrical signals do in nervous systems. And finally, prior to coordinated behavior of obligatorily-multicellular organisms like *Trichoplax,* there was the emergence of temporary coordinated collectives, such as the way that single-celled *Choanoflagellates* cluster together under conditions of stress, forming cup-shaped colonies that can rapidly flip inside out to move as a unit (Brunet et al, 2019). From our perspective, the evolution of brains is not primarily a story of a coherent "computer" that incrementally adds specialized modules. Instead, it is a story of increasingly coordinated collective behavior, driven by the emergence of more efficient forms of intercellular communication, increasing differentiation and specialization of cell types, increasing interdependence, and progressive refinement of organization. At each stage, the benefits achieved through cooperation must have outweighed the costs of increased competition for resources that comes with sharing territory. Thus, we view brains as one end of a continuum of collective behavior wherein the collective has become especially coordinated and complex in organization.

At this point, a skeptic of our view might suggest that the evolution of brains along such a trajectory has, at some point, crossed a threshold or exhibited a phase-transition of some kind, whereby it is now more useful to understand a brain as a coherent unit driven by logical operations, rather than collective dynamics. We present three arguments against such a conclusion. First, consider that despite being an incredibly coordinated system, competitive dynamics remain a key aspect of the success of brains. For example, early development of humans is characterized by a period of synaptogenesis in which neurons are overproduced, followed by a period of neural pruning, driven by competition for input. Neural structure is not hard-coded into the genes—indeed, there couldn't possibly be enough information in the human genome to encode neural structure (Zador, 2019)—but instead is robustly reproduced time and again through these competitive dynamics. Malfunction of these processes (i.e., overproduction of neurons or lack of pruning) is associated with a number of brain disorders. Along these lines, proponents of "Neural Darwinism" (Edelman, 1993) and related views suggest that brain development, and intelligence more generally, can be understood as analogous to the evolution of a species through variation and selection.

Competitive dynamics are also important at the level of behavior and decision-making. Consider that, in connectionist models of cognitive functions, the competition (i.e. mutual inhibition) of localist representations is a crucial mechanism for determining an output, which may represent an interpretation of a stimulus or a choice between two or more mutually-exclusive response options. Neuroimaging studies on bi-stable perceptions of ambiguous figures, such as the duck/rabbit figure, have established analogous processes of competition between distinct populations of neurons (Seely & Chow, 2011). In sum, competitive dynamics are crucial both in brain development and in "online" cognition and behavior. We suggest that it is the precise parameterization of such competition dynamics that contributes to the intelligence of the brain. As such, we believe these mechanisms are best understood as a form of collective decision-making.

Second, despite the complex, heterogeneous structure of the brain into distinct regions, research in the past several decades has begun to reveal that the brain is far less functionally-modular than previously thought. That is, the brain is characterized by a high-degree of "interactivity"—constant cross-talk between regions traditionally associated with specific functions such as vision, language, action, emotion, and more (Falandays et al., 2020). Neuroscientists are increasingly abandoning the goal of localizing brain functions, instead moving towards network-based approaches (Pessoa, 2022). Each region of the brain is now thought to be involved in a multitude of processes, and coordinates with different partners depending upon the context, forming temporary "functional networks"—what Anderson (2014) refers to as TALoNS: "transiently active local neuronal subsystems". Functional networks are known to form and dissipate rapidly—on the order of milliseconds in visual processing (Wu & Sabel, 2021), or on the timescale of minutes in skill acquisition (Bassett et al., 2011)—in a process that is often called "soft-assembly" (Kello & Van Orden, 2009). This process is best understood as a form of self-organization, in that the best functional network for a task or context comes online through distributed interactions, rather than by virtue of a central executive that assembles the best neural partners after assessing a situation. Indeed, it would be nonsensical to suggest that such a task could be accomplished by a central executive, in that it would assume that the central executive somehow knows the nature of the task to be accomplished; in other words, it would require a homunculus. We suggest that the dynamic reorganization of functional subnetworks in the brain and the massive interactivity of the brain is best understood through the lens of collective intelligence, akin to a crowd that efficiently forms an effective committee for each task on the fly.

Third, consider that, in the dominant view of the brain as a computer, neurons (or populations thereof) are subordinated to the role of carriers of "representations." If this view of neural activity were accurate, it would be understandable to see the brain as an example of individual intelligence, in that the lower-level parts (neurons) exist just to serve up representations to a central executive, and the activity of neurons should track the mental operations of that central executive. Leaving aside the philosophical arguments against such an interpretation of brain activity (Dennett, 1978; Bickhard, 1996; Brette, 2019), there are also empirical reasons to reject the premise of neurons as vehicles of representation. Consider the phenomenon of "representational drift," wherein the correspondences between neural activity and stimulus properties may change dramatically over the period of days or weeks (Rule et al., 2019; Schoonover et al., 2021; Deitch et al., 2020). For example, a study by Driscoll et al. (2017) found that the responsiveness of cells in the posterior parietal cortex (associated with spatial navigation) of rats navigating a T-maze changed dramatically across testing days, despite the rats exhibiting continuous mastery of the maze. Results such as this suggest that, if neural activity were to effectively encode or represent features of the world, the brain would also need to accurately track continuous changes in its encoding scheme—today, a population firing may mean "red," tomorrow it may mean "green." Such an inefficient encoding mechanism strikes us as highly implausible.

But the instability of neuronal activity in response to stimuli becomes much less problematic if one abandons the view of neural activity as representational, instead focusing on the brain as primarily a controller for action. There are many neural pathways that may produce the same outcome, and therefore the brain need not worry about reproducing stable response patterns so long as the overall outcome is the same. Furthermore, as each action results in a change to sensory information, and as the brain continually reorganizes in response to its own activity, it may in fact be necessary to change firing patterns in order to achieve stable outcomes. That is, given a different state of the neuronal milieu at two points in time, distinct patterns of activity will be needed to achieve an identical outcome in behavior. Like the ship of Theseus, the brain is capable of maintaining higher-order stability despite continuous exchange of its constituent parts. We contend that such dynamics are representative of collective intelligence, rather than of centralized intelligence as exemplified in the computer metaphor of mind.

Some recent empirical work exploring the learning capabilities of homogenous cultures of brain cells may speak to self-organizing capacities of neural systems described above. Kagan et al., (2022) grew cultures of rodent and human cortical cells on high-density microelectrode arrays and embedded these cultures into a feedback loop for the classic arcade game "Pong." One arbitrary subset of the network was designated as sensory neurons, and provided stimulation dependent upon the position of the pong ball, while another subset was designated as output neurons, and used to control the position of the two paddles. The authors found that such networks were able to self-organize based on this feedback loop, improving performance with as little as five minutes of training. A similar, earlier paper from Masumori et al., (2015) showed that cortical cultures could also be used to control a moving robot that learned to avoid walls. Work such as this suggests that the intelligence of brains is due not to precisely designed neural circuits that implement specific computations, but instead due to an intrinsic capacity for collections of neurons to spontaneously organize in service of survival of the group.

Importantly, self-organization of neural cultures can emerge from purely "selfish" neurons, acting only in the interest of individual survival. A recent artificial neural network model from Falandays et al., (2021) illustrates one possible mechanism by which this could occur. Their model is composed of allostatic nodes, which seek to keep their own activation level near some variable "target" level, which has a minimum. That is, each node needs some input in order to survive, but can adjust internal parameters in order to handle greater amounts of input if necessary, just as real neurons can modify synaptic receptors or membrane potentials to adapt to local resource availability. However, sudden over-stimulation is also a threat to survival, so nodes have a strategy available to dissipate energy rapidly when needed: they may spike, spreading some of their energy to connected neighbors. While spiking behavior is therefore a kind of "emergency" survival mechanism for each individual, opportunistic neighboring nodes may learn to depend upon these spikes to accumulate resources for their own survival.

Falandays et al. (2021) fed this network inputs generated by a probabilistic grammar, with only a subset of the network, designated as "sensory nodes," receiving external stimulation from each "word" in the grammar. Thus, in order to keep activity near their target level, non-sensory nodes need to recruit input from externally-stimulated neighbors. However, even sensory nodes won't be stimulated on every timestep, so all nodes need to form coalitions with their neighbors such that they will receive excitatory input when their own activity is low, and inhibitory input when their own activity is high. With only local learning rules that allow each node to adjust weights with neighbors and their own activity-targets, the network rapidly reaches an equilibrium in which most nodes are successfully keeping activity levels stable over time, despite a dynamic input signal.

Examination of the activity of the network at this point reveals that each node, acting in the interest of its own survival, results in apparently intelligent behavior at the global level. For example, correlating the activity of the network in response to the input signal reveals pseudo-population codes that capture features of the input including the exact word, the grammatical class, and the position of the word in a sentence. The dynamics of the network even appear to *predict* the input signal: when input is suddenly shut off, the network endogenously produces a pattern of activity that resembles the population-code for the most-likely next input. Note, however, that the authors call these *pseudo*-population-codes because any correspondences between network activity and stimulus features were found to drift around in the network over time, such that stable correlations could only be found in short time-windows of observation, akin to the phenomenon of representational drift mentioned above. The authors take this to suggest that the anticipatory behaviors of the network arise *without* the formation of stable internal representations of the kind that would be expected under a computational view of brain activity.

Furthermore, the collective intelligence of these nodes appears able to generalize to very different tasks. In more recent work, Falandays, Yoshimi, Warren, and Spivey (*under review*) have embedded this network into the action-perception loop of a simple agent presented with a moving visual stimulus. They found that the same local, allostatic learning rules produce spontaneous object-tracking behavior, with the agent moving so as to keep a stimulus stable in its visual field, as well as wall-avoidance behavior (akin to the findings of Masumori et al., 2015) and Pong-playing abilities (akin to the work of Kagan et al., 2022), despite having no explicit incentive to engage in these behaviors. That is, these behaviors emerge naturally from the local drive for homeostasis in the context of a network.

The foregoing discussion illustrates how apparent intelligent behavior, such as language processing or visual object-tracking, may emerge from collective dynamics of cooperation and competition, with each neuron interested only in its own survival. Although the brain has evolved into a highly complex, specialized, differentiated organ, we suggest that these features were selected primarily due to their role in facilitating mechanisms of collective intelligence. In other words, the structure and development of the brain is characterized by highly efficient and robust mechanisms of competition, cooperation, consensus building, and dynamic reconfiguration of neural coalitions. When all goes well, these mechanisms may be so effective that we may be tempted to think of brains as akin to a man-made computer, performing logical operations over internal representations or symbols. In some cases, the collective dynamics of brains may in fact approximate what would be done by a man-made computer on a similar problem. Nonetheless, we suggest that thinking of the brain as a computer obscures the actual mechanisms by which it solves problems. In contrast, viewing the brain as an intelligent collective may offer more both in the way of explanatory mechanisms of individual human cognition, and towards understanding general principles of intelligence across species or scales of analysis. Humans may have much to learn from neurons about constructing harmonious societies.

5. Collective intelligence in dyads/small groups

For readers familiar with the literature on collective intelligence, it may have seemed odd for us to begin our discussion with examples of intelligent behavior in groups of non-human animals, cells, and brains—after all, the term is most often applied to one system in particular: groups of humans. This tendency towards anthropocentrism in collective intelligence research is driven, in part, by the reasonable fact that human researchers prioritize solving human problems: how to make society or government better, fairer, or more harmonious, how to make teams more efficient, and the like. On the other hand, anthropocentrism may also be driven by a bias towards thinking that we humans, individually, are the only *really* intelligent creatures on the planet, and thus the only true form of collective intelligence is among us already-intelligent humans. But as we turn now towards consideration of human collective intelligence, we hope that having the foregoing discussion in mind will help persuade the reader that the dynamics of collective intelligence in humans share deep commonalities with those other systems. We emphasize that collective intelligence in humans actually has *little* to do with how intelligent we are as individuals, and instead to the extent to which we are evolutionarily prepared for spontaneous interpersonal coordination. As we saw in the last section that our brains—themselves intelligent collectives—adaptively resonate to patterns of stimuli in the environment, consider that sometimes that environment contains other humans. Thus, when multiple humans observe and interact with one another, they may become intertwined in a sensorimotor feedback loop, leading the group to exhibit complex, coordinative patterns, without requiring any individual to do anything all that intelligent in a traditional sense (e.g. planning, reasoning, storing information).

Over the last two decades, a large body of literature has amassed demonstrating that individuals engaged in conversations or joint tasks tend to spontaneously align their linguistic behaviors and synchronize many rhythms of the body. For example, it has been found that, over the course of some types of interactions, individuals entrain their neural oscillations (Montague et al., 2002; Konvalinka & Roepstorff, 2012), their postural sway (Shockley et al., 2003) and other movements (Richardson et al., 2007; Schmidt & O'Brien, 1997). Individuals also align their speech patterns at the level of pronunciation (phonetic convergence; Pardo, 2006), word choice (lexical alignment; Branigan et al. 2011), grammatical structure (syntactic alignment; Branigan et al., 2007), and speaking rate (Manson et al. 2013), as well as coordinate the position of their gaze (Richardson & Dale, 2005). Furthermore, human individuals may imitate each other's facial expressions (McIntosh, 2006), postures, gestures, etc. (Chartrand & Van Baaren, 2009). In some cases, patterns of synchrony emerge in groups even when individuals are not directly interacting. For example, Konvalinka et al. (2011) found that, during fire-walking rituals, the heart rates of fire-walkers and spectators become synchronized. In some cases, these effects may simply be the result of multiple individuals with similar perceptual systems entraining to the same signal in a shared environment. Nonetheless, these effects may still have functional relevance for human behavior, such as increasing social cohesion (Konvalinka et al., 2011). In line with this idea, a study on real-life dating interactions by Prochazkova et al. (2022) found that attraction between dating partners was best predicted by synchrony in heart rate and skin conductance—bodily reflexes that are covert, unconscious and difficult to regulate consciously.

In some cases, the rhythmic patterns that emerge across individuals are more complex than simple alignment or synchrony, and are better described as "synergy"—these are cases when rhythms across individuals are coordinated in a meaningful way, compensating for and complementing one another, but are not identical. Even patterns of this kind may emerge spontaneously (i.e. self-organize) without the conscious awareness of the individuals involved (Dale et al., 2013). For example, Patil et al. (2020) reported the results of a dyadic shepherding task in which two human participants each control a virtual "shepherd" in a 2D space in order to wrangle virtual "sheep," which are repelled by the shepherds, into a target location. Even in the absence of visual or linguistic communication between humans, dyads can spontaneously fall into a pattern of coordinated movements that optimizes performance on the task.

In all of these cases, small groups of humans engaged in joint tasks begin to perform as if they are one mind extended across multiple individuals. For example, while a common theory of language use is that individuals attempt to minimize communicative effort for themselves, recent work from Rasenberg et al., (2022) found that dyads engaged in conversation during a joint task actually minimize the *joint* cost of multimodal communication. Or consider results from the joint Simon task. The standard Simon task is a measure of conflict resolution in which one individual responds by pressing a button on the left for one stimulus (e.g. a red circle) and a button on the right for another stimulus (e.g. a blue circle). These stimuli may be presented on the left or right side of a screen in a way that is either congruent with the response (e.g. a red circle on the left side of the screen, requiring a left-button response) or incongruent (e.g. a blue circle on the left side of the screen, requiring a right-button response), and response times are slowed for incongruent trials. In the *joint* Simon task, each of two individuals is responsible for responding to only one stimulus type, and therefore one button, which might be expected to eliminate any congruency effect. Nonetheless, the same congruency effect emerges, which has been taken as evidence that each individual mentally represents the task requirements of their partner (Dolk et al., 2014; Sebanz et al., 2006). Results such as these suggest that small groups of humans engaged in joint activities actually begin to process information as if they are a single entity.

Perhaps one of the most complex scenarios in which collective intelligence may emerge in small groups of humans is that of joint musical improvisation. Improvisation is a medium that can express creativity, consciousness, and intuition (Pressing, 1994). Creativity, in particular, is often considered a consummate example of human intelligence, and is often viewed as a stage-like process taking place inside individual minds. However, joint improvisation reveals that, at least in some cases, creative activity is in many ways a collective effort that develops spontaneously through interpersonal coordination. Although creative improvisation from groups may seem methodically planned from an audience perspective, the output of the ensemble may be the result of perceptual and physical interactions from emergent coordination. In emergent coordination, individuals may act in a coordinated fashion, but this is not due to shared knowledge or a common pre-established goal. In support of these ideas, Seltzer et al. (2018) found that critical musical transitions during joint jazz improvisation (transitions between one texture or style and another) were preceded by a brief increase in entropy. This same signature has been shown to predict critical transitions in many other natural, distributed systems, such as ecosystems. These findings suggest that joint musical improvisation shares important properties with many other systems that self-organize into adaptive regimes, without the influence of any central controller.

Instead, emergent coordination is often due to a tendency to match the actions of individuals that are being observed, known as perception-action matching (Knoblich et al., 2008). Perception-action matching may also facilitate "action simulation," or the prediction and anticipation of upcoming actions of an observed individual (Knoblich et al., 2011). In the case of music improvisation, these two abilities allow accompanying musicians to anticipate the actions of the leading improvisor in order to compliment the solo (Sawyer, 2006).

When multiple individuals are coupled together by these matching and anticipatory processes, the end result is often a product that is something more than the sum of the individual contributions (Gorman et al., 2017). For example, there could be melodic and rhythmic ideas produced by the ensemble as a whole that would otherwise not be present without the ensemble's collective interaction. In line with this claim, studies on interpersonal coordination generally report that an individuals' joint behavior is distinct from the sum of behaviors produced by each individual alone. For example, when partners create spontaneous motion together, their personal signatures of movement (observed during individual performance) can no longer be recognized, and new signatures of movement emerge (Hart et al., 2014). This work suggests that emergent coordination between individuals forms unique signatures of improvisation that would not exist outside of that interaction. Similarly, interpersonal coordination at a much larger scale of culture leads to phenomena that could not exist in smaller interactions, as we will consider in the next section.

6. Culture as collective intelligence

Decades of research in cultural evolution, anthropology, and other social and ecological sciences have posited that the "secret of our success" as a species is our capacity to learn collectively (Henrich, 2015; Laland, 2018). The ways by which we engage in social learning and manipulate our ecological niche have bestowed us with capacities to comulatively "ratchet up" our cultural evolution—build innovations upon innovations—in what can be described as a thoroughly collective process (Tennie et al., 2009; Cazzolla Gatti et al., 2020).

We argue that human cultures' tendency to learn and develop socially implies that, in practice, all our knowledge and intelligence is at least to some degree collective. Research in behavioral ecology and cultural evolution tends to distinguish between "individual" and "social" learning (Hoppitt & Laland, 2013; Heyes, 1994). This is in many cases a useful distinction, especially when modeling social diffusion, innovation, evolutionary trade-offs, and so on. However, contemporary humans' lifeways are so thoroughly culturally embedded that few (if any) kinds of learning can truly be considered as entirely "individual".

Social learning is often defined in terms of learning that is "facilitated by observation of, or interaction with, another individual or its products" (Heyes 1994; Hoppitt & Laland, 2013). Given that today practically all human development occurs within cultural contexts, it is questionable whether any form of learning would fall entirely outside the scope of this definition. Humans develop in an environment that is a cultural product: we are the ultimate niche constructors (Laland, 2018; Laland et al., 2001), creating environments and institutions that facilitate both social learning (think: schools, universities, workshops) and individual trial-and-error learning. In such a world, even autodidactic learning is culturally mediated. For example, could you learn to play a guitar if an artisan had not crafted it, or if a cultural continuum of woodwork traditions (see Ennos, 2020) had not afforded the tools and methods for constructing the instrument? Research has shown how human cultures often organize the world in ways so that the next generation has increasing amounts of affordances for social and individual learning (Sterelny, 2012). Indeed, this is one driver for the exponential diversification of human technologies over time (Cazzolla Gatti et al., 2020).

In such a context, truly "individual" learning must be exceedingly rare. Accordingly, some have argued that most learning is "hybrid learning": human individuals acquire skills through socially mediated trial and error and culturally evolved practice (Sterelny, 2012). Of course, one could argue that humans still have innate predispositions to be adept individual learners (see, e.g., Heyes, 2018), although research in gene-culture coevolution suggests that even our individual-level cognitive mechanisms have likely been thoroughly shaped by our species' collective history as social animals (Schaik & Burkart, 2011; Thompson et al, 2016).

This collective intelligence of human cultures has recently been called the "collective brain" (Muthukrishna & Henrich, 2016). The notion of the collective brain or collective intelligence has put into question many persistent myths about innovation and ingenuity. For instance, research has illustrated how innovation is to a large degree recombination, involving the reuse of pre-existing components in novel contexts (Muthukrishna & Henrich, 2016; Arthur, 2009). Science, too, is much less a feat of "lone geniuses" than a collective search process which involves high degrees of fiduciary relations and reapplication of previously useful solutions (Polanyi, 1957; Wu et al., 2022).

Given that cumulative cultural evolution is a fundamentally collective process (Migliano & Vinicius, 2021), it should come as little surprise that cumulative cultural evolution has been shown to be driven by a number of demographic factors, which are largely independent of the qualities of individuals that make up the group. For example, larger groups often produce more innovation and cultural diversity (Kline & Boyd, 2010; Derex et al., 2013), but these effects are very sensitive to network structure (Kobayashi et al., 2016). Intermediate levels of clustering, for example, seem to maximize accumulation over time by balancing a trade-off between local innovation and global recombination (Derex et al., 2018): innovations in a cluster are protected from homogenization but can still recombine with information from neighboring clusters (Derex & Mesoudi, 2020). Population turnover also appears to drive cumulative culture, because naïve individuals are less conservative and more likely to discover efficient solutions (Chimento et al., 2021; Falandays & Smaldino, 2022). Finally, the types of cultural networks that emerge can be driven by the evolutionary pressures facing collectives, for example with selection for generalist learning favoring the evolution of sparser and modular networks (Smolla & Akçay, 2019).

Even if one accepts that human intelligence is largely attributable to experience within a collective, a skeptic might suggest that learning from others is still largely an individual process. In response to this, we would point out that social learning strategies—biases and heuristics that help us get the best information from others—have also tightly coevolved with collective structure. For example, conformity is a common strategy across a variety of domains (Youngblood, 2019) that allows us to quickly collect adaptive information (Aplin et al., 2017), but only under certain conditions. The strength and utility of conformity appears to increase with group size because there is more information to choose from (Muthukrishna et al., 2016). The utility of conformity tends to decrease with the proportion of strong conformists, because fewer innovations are able to spread (Kandler & Laland, 2013). Similarly, payoff bias (i.e., bias for information with highest payoff) is most effective when population size is high (Henrich, 2004; Hudson & Creanza, 2022), and negativity bias (bias for emotionally negative information) is stronger when networks are less dense (Fay et al., 2021).

A byproduct of this coevolution between learning strategies and demographic structure is that major changes in the latter can reduce the adaptiveness of social learning strategies. In global and interconnected online communities, tendencies to defer to prestige or attend to negative messages might enhance the spread of misinformation or conspiracy theories (Acerbi, 2016; Youngblood et al., 2021). In declining animal species with learned migration and foraging routes, tendencies to conform might reduce their ability to respond to human-induced environmental changes (Barrett et al., 2019). And in rapidly changing environments, such as those experienced in the Anthropocene, collectively evolved problem-solving strategies may become outdated and face cultural evolutionary mismatch (Morgan et al., 2022; Kaaronen et al., 2021). Generally, collectives with more diverse and flexible learning strategies are probably better at exploring and exploiting adaptive knowledge over time (Molleman et al., 2014; Kendal et al., 2018; Morgan et al., 2022). These findings suggest that we cannot fully understand the adaptiveness of strategies used by *individuals* to learn from others without considering how these mechanisms have been shaped by our evolutionary history within a collective, and the potential (mis)match to present contexts.

Other decision-making strategies, too, are culturally inherited products of collective intelligence. Rationality is stereotypically portrayed as being one of the most individualistic features of social and especially economic life. However, at closer inspection, even rational decision-making is suspect to collective influence. Firstly, even if humans were fully rational agents, our rational judgments would be based on sets of axioms that can’t be justified or derived from logic alone (Callebaut, 2007). Simon (1983) called this the Original Sin of reasoning: rationality and reason go to work only after they have been “supplied with a suitable set” of inputs or premises. Whatever preferences or premises a rational agent might have (what they choose to maximize, optimize, or prioritize) are largely cultural inputs. This is not only evident in culturally variable responses to economic games (e.g., Henrich et al., 2010), but also in everyday politics. For instance, economies around the world are currently struggling with whether we should optimize for environmental welfare or economic growth, with culturally variable responses that affect the lives of billions of individuals.

Second, by now it has been well accepted that humans do not have access to the cognitive capacities or environmental stabilities that would allow for completely rational decision-making (Simon, 1957; Todd & Gigerenzer, 2012; Gigerenzer & Selten, 2002). Rather, humans are boundedly rational, using various sets of culturally evolved heuristics and biases to solve problems and make decisions (Todd & Gigerenzer, 2012; Kaaronen et al., 2021; Jiménez & Mesoudi, 2019). In our everyday lives, we largely make decisions based on culturally inherited rulesets, heuristics, and “rules of thumb” (Kaaronen et al., 2021; Kaaronen, 2020). Because cumulative cultural evolution is collective, not everyone needs to know how or why these heuristics work for them to function. Indeed, many case studies exist of humans solving problems with heuristics without understanding the causal mechanisms underlying their success (Henrich, 2015; Kaaronen et al., 2021). In sum, as boundedly rational agents, we have a tendency of “offloading” our decision-making strategies to our cultural environment. Culturally inherited rulesets guide our problem-solving in various everyday domains, such as cooperation, technological evolution, food choice and mate selection (Henrich et al., 2001; Kaaronen et al., 2021).

7. Evolution as collective intelligence

Throughout this paper, we have emphasized how an evolutionary perspective on intelligence highlights the importance of collective dynamics. Interestingly, evolution *itself*, as a description of a general process of several systems, can also be described as a form of collective intelligence. While many may view the process of adaptation or similar fundamental evolutionary dynamics as processes affecting single units—e.g., in the framework of “selfish genes” or of individuals outcompeting other individuals—a primary question in nearly any evolutionary framework is how adaptations (or non-adaptations, when generally speaking of traits) can either be discovered or become fixed in a population (Dawkins, 1976; McCandlish & Stoltzfus, 2014). When explored via this group lens, it is easy to see how any question about adaptation on a population level becomes one of collective intelligence.

Indeed, one of the most popular analogies used to model collective intelligence, that of the fitness landscape, has its origins directly in biology. Conceived by Sewell Wright in the 1930s, fitness landscapes have come to find direct transfer in problems of optimization, of group behavior, and complex systems (Kauffman & Levin, 1987; Wright, 1932; Zou et al., 2022). Wright, who saw the discovery of novelty as the central problem of evolutionary biology, used the analogy of a landscape comprised of fitness "valleys" and "peaks" to think about both the distribution of different traits in a population of individuals and the potential distribution of traits a population could acquire (Wright, 1982). A central issue for the theory of natural selection in Wright's view was how it was that a population at any given sub-optimal peak could traverse fitness valleys, where populations would have to undergo fitness losses, to discover fitness peaks higher than the ones they are currently on. In other words, what are the mechanisms by which a population could increase its fitness in the long-term by shedding its current fitness gains and decreasing its fitness in the short term? The answer for Wright formed the basis of the now somewhat controversial Shifting Balance Theory (Wright, 1932, 1982). Wright's answer was that the ideal population on the fitness landscape was one in which the global population subdivides into subpopulations with limited gene flow between them. By sub-dividing in this manner, sub-populations would drift away from the global population's local optima where individual units could more efficiently explore the overall landscape, discover local adaptations, and, through migration, transfer these local adaptations to the global population.

Wright's exploration of this topic led to controversy between him and another founder of population genetics, R.A. Fisher (Fisher & Ford, 1950). Fisher saw the primary question of evolutionary theory that of gradual adaptations and refinement (Fisher, 1958a). His question was how is it that, with variation, the *global average* fitness of a population increases over time and how is it that adaptations *fixate* in a population? For Fisher, Wright's explanation would lead populations towards randomness, with random drift towards non-specified, hypothetical, and, for some populations, non-existent global optima leading to net fitness losses in populations (Fisher, 1958b). Yet in another lens, the useful applications of both the theoretical frameworks developed by Wright and Fisher may point to the observation that the nature of the argument they had with one another was not one of empirical processes, but one of *emphasis*. As noted by (Wade & Goodnight, 1998). Wright's central question was one of *discovery* of novelty and Fisher's central question was one of the *refinement* of existing adaptations. In the parlance of modern collective intelligence, the mechanism Wright proposed was one of exploration, while the mechanism Fisher proposed was one of exploitation (Toyowaka et al., 2014).

The generalizability of Wright's arguments to collective intelligence is not novel, as there is one evolutionary thinker whose similar conceptualization of Wright's framework have gained much prominence outside of biology in his own studies of cultural evolutionary and market-based processes: Friedrich Hayek. Similar to Wright, a central problem for Hayek was how information could be distributed and dispersed in a population in the absence of central control, what he referred to as the "economic calculation problem" (Hayek, 1935). In a formulation of the "local knowledge problem," Hayek argued that local, dispersed, and incomplete knowledge held by individuals within a market system allow for the rapid adaptation of the market to inputs and outputs in the economy (Hayek, 1945). Hayek saw the emergence of a central intelligence, in the form of the price system, as being one way in which distributed systems create the appearance of a central actor. As noted in his essay, *The Use of Knowledge in Society* (1945), *"The mere fact that there is one price for any commodity—or rather that local prices are connected in a manner determined by the cost of transport, etc.—brings about the solution which might have been arrived at by one single mind possessing all the information which is in fact dispersed among all the people involved in the process."* The similarity between the use of local knowledge at scale in both Hayek's frameworks and in Wright's should be noted (nor is it a sheer coincidence: Hayek and Wright overlapped with one another at the University of Chicago for a period of four years where they worked together on a seminar on evolution (Caldwell, 2008).

Central to Wright and Hayek's theories was one form of biological selection which placed the performance of a group at the center of the analytical framework now referred to as group selection (Hayek, 1973; Wright, 1982). Per Wright's formulation, the forces of selection act not only on the individual members of a group and their fitness outcomes, but on the preservation and survival of groups competing with one another. Consider a system in which competition between groups takes place. In one group, individuals within the group compete with one another for their limited resources, maximizing their individual gains. In another group, individuals forego some of the same benefits acquired by other groups in order to ensure group survival. In situations like these, the group in which individuals exchange some personal cost for group benefits will outcompete the other. In Hayek's crude view, the evolution of many forms of society which he deemed "the results of human action, but not of human design," were explained by invoking group selection (Hayek, 1967). Many of these behaviors, while both nonrational and incompatible with individual human moral intuitions, such as the institution of private property and the large-scale acceptance of inequality found in modern capitalist states, could only be posited as being evolved through a process of group selection. As stated in his address to the 33rd Meeting of Nobel Laureates at Lindau, “mankind was civilized by a process which is intensely disliked by being made to submit to rules which it neither could understand nor liked… the mechanism of selection was that those groups were selected, which thanks to the institution of private property were able to multiply faster than others” (Hayek, 1983).

Strict forms of group selection remain controversial in biology writ large (Okasha, 2001; Wilson, 1983). Despite these challenges, cases like kin selection, where genetically related individuals cooperate to allow for the perseverance of genes common in their relatives, and cultural evolution, where the units which allow group-selective behaviors to propagate are non-genetic, allow for the emergence of altruistic behaviors similar to those postulated by a theory of group selection without conforming to the traditional group selection paradigm (Hamilton, 1964; Maynard Smith, 1964; Richerson et al., 2016). Nevertheless, even in the absence of group selection as its mechanism of employment, one can see how the process of filtered change in the form of natural selection acting on *any* level leads to a collective intelligence that extends beyond the fitness and lifespan of any single individual.

8. Summary

In this position piece, we have presented examples of collective intelligence in a variety of systems, emphasizing that similar abstract principles of communication, cooperation, and competition underlie the emergence of intelligent behavior in groups of various species and at various spatio-temporal scales. Since we have covered a lot of ground, a brief summary is in order before we conclude. In Section 1, we began with canonical examples of collective intelligence in non-human animals, such as the flocking, swarming, or schooling behavior of birds, insects, and fish, and emphasized the diversity of systems in which collective intelligence may arise: collective intelligence can emerge in groups of closely genetically-related individuals of the same species, but also in groups of distantly-related individuals or even individuals of different species; collective behavior is sometimes obligatory, and other times systems may switch between collective and individualistic modes; and collective intelligence is sometimes driven by mechanisms of cooperation, but other times by competition. The overarching point we hope to establish here is that systems with many different parts and many different mechanisms of interaction have the potential to facilitate self-organization of groups of individuals into regimes that are capable of dealing with a variety of cognitive problems, including search, predator-avoidance, memory, and decision-making. These examples suggest that there is little reason to expect collective intelligence to be restricted to any particular species or spatio-temporal scale of activity.

In Section 2, we next considered systems that are not always thought of as examples of collective intelligence—multicellular organisms—but emphasized that similar mechanisms as observed in groups of non-human animals may facilitate the interaction of single cells to produce complex, adaptive behavior without a central controller, including morphogenesis (the formation of a body through development). We also briefly considered the evolution of obligatorily multicellular systems from single-celled organisms that sometimes switch into a multicellular mode. This evolutionary trajectory points to a role for group-level selection, wherein groups of cooperative individuals may propagate over groups of competitive individuals, despite potentially sacrificing individual reproductive success to some extent. We suggest that natural selection may act at the group-level in this way to hone mechanisms that facilitate collective behavior in any type of system, including groups of humans.

The discussion of multicellular collective intelligence sets the stage to begin considering the brain as an intelligent collective, in cooperation with a massive community of cells that constitutes an entire body. In Section 3, we argued against a view of the brain as a serial-processing machine with highly-localizable functions and representations, like a man-made computer. Instead, we emphasize that a brain is a collection of living cells struggling for survival. By virtue of mechanisms of competition, such as synaptogenesis/pruning and mutual inhibition, and mechanisms of cooperation, such as energy-sharing through spiking behavior, these collections of cells are able to rapidly self-organize into different patterns of functional connectivity that are adaptive at the group level with respect to a current task and context. For these reasons, we prefer to view the brain as one end-point of a continuum of collective behavior, in which the collective has become particularly inter-dependent and efficient. Nonetheless, we emphasize that the principles that make brains intelligent remain best-understood as principles of collective self-organization.

Next, in Section 4, we moved up to the spatio-temporal scale of dyads or small groups of humans engaged in joint-action and considered how the dynamics of collective behavior in individual brains and bodies may scale up to incorporate *multiple* brains and bodies. Here, we considered how multiple individual brains and bodies may intertwine their action-perception loops, developing particular phase-relationships in their neural signals and behaviors that facilitate group performance. Sometimes these phase-relationships are rather simple, such as synchrony or turn-taking, but in other cases they are more complex and dynamic. Joint musical improvisation provides an interesting example of the latter, in which two or more individuals may dynamically change between leading- and following-behavior and produce complex temporal patterns without explicit planning or organization. This example also serves to show how creativity, which is commonly thought of as an individual, high-level cognitive process, may emerge naturally from local perception-action couplings within a group.

In Section 5, we moved up yet another spatio-temporal scale to consider the collective dynamics of large groups constituting societies and/or cultures. Here, we emphasized that humans are a consummately cultural species, with almost every aspect of our learning, development, and behavior being influenced by social interaction. We described how cultural progress is dependent upon many demographic factors, such as population size, network structure, and population turnover. As such, examples of cumulative culture, such as the progress of science, can be understood as a collective search process, rather than simply the sum output of "lone geniuses." Even in contexts where individual learning appears important, we highlight how individual learning mechanisms have been shaped over evolutionary time by our history as a social species, and are influenced in the present by a socially-constructed niche of environments and institutions. This illustrates the important point that collective intelligence does not just scale "upwards" (i.e. from cells to brains to cultures), but may also act "downwards," with new scales of collective behavior constraining the continued development of lower spatio-temporal scales.

Finally, in Section 6, we considered how evolution as a whole may be thought of as a form of collective intelligence. Evolving populations may be thought of as traversing a dynamic "fitness landscape," with individual phenotypes occupying a point on this landscape. Wright's Shifting Balance Theory suggests that species may optimize the search process through this landscape by forming sub-populations with minimal genetic exchange, allowing phenotypes in these sub-groups to drift apart and thereby search more of the fitness landscape. This dynamic mirrors the discussion of collective search in cultures, where sparse networks of information exchange can prevent groups from settling into local optima. Additionally, in Section 6 we again emphasized the importance of group-level selection, whereby the fittest *groups* of organisms increase in frequency. This kind of mechanism may be a key reason why collective intelligence emerges in so many systems, at so many scales of analysis, even when it involves mechanisms whereby individual members of a group sacrifice reproductive success for the good of the group. However, we point out that even in the absence of group-level selection, other mechanisms such as kin-selection can facilitate the emergence of collective behavior.

8.1 The benefits of viewing all intelligence as collective intelligence

Our claim that "all intelligence is collective intelligence" is intended not as expressing a strong metaphysical stance, but instead a pragmatic one. We have no qualms with speaking of "individual intelligence" if or when such a stance is useful. However, there are two major reasons why we consider it generally more useful to understand intelligence as a *process* instantiated by groups, rather than as a *property* of individuals. First, we hope the foregoing discussion makes a strong case that clear examples of individual intelligence are likely few and far between. If intelligent behavior, from multicellular systems up to human culture, is driven primarily by the cooperation and competition of individuals with only local information, we ask what is left to be called "individual intelligence"? We believe that if mechanisms of collective behavior do most of the heavy lifting in explanations of intelligence, then viewing all intelligence as collective is the most parsimonious stance and confers the greatest explanatory power across domains.

Second, and perhaps more importantly, we suggest that this stance may benefit research into intelligent behavior by facilitating cross-disciplinary exchange. Given that similar abstract principles are present in systems as diverse as swarms of insects, temporary collections of single-celled organisms, brains, small groups of humans, and entire societies, researchers in each of these areas may have much to gain through collaboration and communication (after all, we have argued that science too is a collective endeavor!).

Research in cognitive science already has a long history of interdisciplinarity upon which to build in the study of collective intelligence. For example, models of population genetics originating in biology have been applied to cultural evolution (Liu & Stout, 2022), models originating in statistical mechanics, such as the Ising model, have been applied to collective behavior and brain dynamics (Kozhin, 2022), and models originating in classical mechanics, such as coupled-oscillator models, have been applied to the study of individual behavior, joint-action, and neural activity alike (Kelso, 2021). We suggest that an explicit recognition of the shared mechanisms of intelligence behavior across scales may facilitate discovery at all of the scales.

As one concrete example of the benefits that may be gained through such a perspective, consider the field of artificial intelligence (AI), which has deep historical ties to the concept of collective intelligence. AI as a discipline grew out of pioneering research on the behavior of social organizations: Herbert Simon and Allen Newell's Logic Theorist (Newell &Simon, 1956), one of the first AIs, was explicitly based on the bureaucracies that Simon had studied earlier in his career. Marvin Minsky (1988), who conducted pioneering work in neural network analysis (but also had a major role in discouraging further exploration for many years), imagined AI as a "society of mind" composed of many "mindless" interacting agents whose intelligence unfolded in complex patterns of emergent coordination much like cells in an organism or neurons in a brain.

Since the 1990s, we have seen a growing number of practical algorithms in AI that work by organizing the efforts of many agents to a collective end, from ensemble methods that combine the inputs of many classifiers to differentiable games that match machines against each other and against themselves. In recent years, research in machine learning has gravitated toward such techniques due to their spectacular performance in unsupervised image and natural language tasks. A crucial feature of these methods is the way in which agents interact, and the degree to which that interaction is tailored through the careful composition of loss functions. There are many examples of this: generative adversarial networks (GANs; Goodfellow et al., 2020), adversarial training (Goodfellow et al., 2014), intrinsic curiosity modules for reinforcement learning (Pathak et al., 2017), warped gradients for meta-learning (Flennerhag et al, 2019), hyperparameter optimization through implicit differentiation (Lorraine et al., 2020), and so on. Much like the Logic Theorist or Minsky's society of mind, many of these algorithms are reminiscent of extant institutional patterns in economics and the social sciences—there is clearly a pattern in which the intelligence of the whole is a product of the "intelligence" of the parts that is in some ways reminiscent of social choice theory (e.g. aggregation of experts in boosting and bagging) and in other ways more reminiscent of emergent collaboration in biological contexts (e.g., early subsumption architectures; Brooks, 1986). We take this work as an illustration of the scientific progress that may be gained through an explicit recognition that all intelligence is driven by collective dynamics.

Another beneficial side-effect of adopting our perspective may lie in helping to avoid the "homunculus problem" associated with the computer metaphor of mind—the fallacy that the intelligence of humans can be explained by recourse to an intelligent agent inside the head, who "reads" the activity of the brain. Views of cognition that entail the existence of a homunculus are not only logically problematic, but also may falsely imply a distinction between what goes on in human brains, and what goes on in intelligent collectives, which clearly lack a central executive. In Section 5, we described how collective interactions in the human brain can contribute to intelligent adaptive behavior, without requiring one to posit the existence of internal representations nor a homunculus who reads these representations. This work illustrates how viewing the brain as an intelligent collective can not only help to address issues in the study of individual human cognition, but can also put the study of human cognition into dialogue with the study of many other systems.

9. Conclusion

In conclusion, we believe that research in many areas—including animal behavior, multicellular intelligence, neuroscience, human cognition, joint-action, cultural evolution, biological evolution, and AI—may have much to gain by adopting the perspective that all intelligence is collective intelligence. Importantly, while we have emphasized the parallels between intelligent behavior in each of these domains, we are by no means suggesting that all of these systems are the same. To the contrary, our perspective may also help to clarify the dimensions that *differentiate* forms of intelligence across domains. Some relevant dimensions of difference that have emerged in our discussion include spatiotemporal scale, interdependence of elements, rate of information transfer, task diversity, network structure, transient diversity (i.e., the degree to which elements of a system resist consensus), and mechanisms of interaction (e.g., collaboration vs. competition). By elaborating how these and other potential dimensions influence the dynamics of collective intelligence, we may move towards a truly general theory of intelligence, furthering both our understanding of the natural world and our ability to design intelligent systems.

Acknowledgements

We are thankful to the Diverse Intelligences Summer Institute for facilitating this work of collective intelligence. WR wants to thank David Harrison and Urte Laukaityte for many discussions on the topics related to this paper. RK acknowledges the Academy of Finland for funding (grant no. 347305).

Author contribution statement:

VV wrote Section 1 ("Collective Intelligence in Non-human Animals"). WR wrote Section 2 ("Multicellular Collective Intelligence"). JBF wrote Section 3 ("Brains as Intelligent Collectives"). TW and JBF wrote Section 4 ("Collective Intelligence in Dyads/Small Groups"). ROK and MY wrote Section 5 ("Culture as Collective Intelligence"). CM wrote Section 6 ("Evolution as Collective Intelligence"). JT contributed the section on artificial intelligence to the conclusion. JBF wrote the introduction, summary, conclusion, and was the primary editor. All authors contributed to the major ideas presented in the introduction and conclusion. Save for the first author, authorship order was chosen alphabetically and does not reflect the significance of contributions.

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