Evolution and Development of the Brain

January 16, 2014

1 Introduction

The human and mouse genomes both consist of a little over 3 billion base pairs, which produce approximately 21 and 23 thousand genes, respectively. Interestingly enough, a rice plant has only one order of magnitude fewer base pairs but, in fact, 28 thousand genes. These numbers, huge in their own right, represent the tips of enormous icebergs, i.e. search spaces. Assuming that all combinations of base pairs are possible, though many are surely lethal, a sequence of length 3 billion is a point in a space of $4^{3,000,000,000}$ possibilities, which is approximately equivalent to 166 followed by 1.8 billion zeros. By comparison, the estimated age of the universe, in seconds, is 43 followed by 16 zeros.

How in the world (or universe) could evolution find the needles in the haystack that are (or have been) the DNA codes for viable phenotypes? Darwinism clearly explains how evolution selects good over bad genotypes, thereby filtering inferior designs; and modern genetics reveals how the good genes get passed from parents to children. But what about variability? How does nature generate this collection of thriving phenotypes when the odds of generating any one of them would appear to be so infinitesimal as to discourage even a repeat lottery winner from investing in nature’s grand-prize drawing?

The 3rd-order emergence of the brain (as best understood by evolutionary neuroscience) provides an intriguing account of gradual complexification, producing nervous systems capable of progressively more sophisticated behavior. This shows how evolutionary adaptation has achieved impressive cognition but no indication that it should: it gives no hints as to forces that might stack the deck in the brain’s favor. In short, Neo-Darwinism sheds little light on whether brains are evolutionarily inevitable or impressive conquests of intimidatingly long odds. If it is merely the latter, then AI has little to gain from a deep exploration of the evolutionary paper trail, since brains would be the contingent outcomes of the lengthy history of life on earth, a history that not even the most die-hard bio-inspired hacker would hope to recreate in simulation. However, if general principles (not just historical contingencies) underlie the brain’s evolutionary emergence, then these might prove invaluable for AI and the automated search for sophisticated machine intelligence.

Many of the more promising general principles involve tight interactions between evolution and development, as thoroughly reviewed in books such as Allman’s Evolving Brains [2], Striedter’s Principles of Brain Evolution [44], West-Eberhard’s Developmental Plasticity and Evolution[47], and Kirschner and Gerhart’s The Plausibility of Life [24]. This chapter investigates several of these phenomena in light of their relevance to AI.
1.1 The Neuromeric Model

Though different species follow different developmental pathways, they exhibit remarkable similarities at an intermediate point known as the phylotypic stage [48]. So the search for general principles of neural evolution and development might profitably begin there. In 1953, Bergquist and Kallen [7] noticed that all vertebrate embryos have a similar elongated, segmented hindbrain during the phylotypic stage, as shown in Figure 1. The ringed segments, termed neuromeres, are modular zones of high cell division (to form neurons) and radial migration (of neurons to their proper layer). Later, Puelles and Rubenstein [40] found that this pattern encompassed the midbrain and forebrain as well.

Figure 1 sketches the basic neuromeric structure of the vertebrate phylotype. The hindbrain neuromeres develop into brain regions such as the cerebellum and pons, which are tightly tied to sensory and motor systems, while the midbrain and forebrain segments become areas such as the basal ganglia, hippocampus and prefrontal cortex, all of which are involved in high-level cognitive processes. Hence, the Neuromeric Model provides the perfect developmental scaffolding for the brain’s emergent control heterarchy (Figure 2).

Figure 2: Depiction of control levels in the brain, which form more of a heterarchy than as strict hierarchy: interactions are too abundant to claim that any one region fully directs another, though higher level reasoning is known to involve the upper areas, while purely reactive behavior only requires the lower components.

Genetic evidence shows that homeobox (a.k.a. Hox) genes control brain segmentation, just as they control the subdivisions of the body’s central axis [40, 2, 44]. In fact, the vertebrate brain archetype, as sketched in Figure 3, looks remarkably similar to a body plan. The evolutionary complexification of the brain begins with the simple addition
of more modules, like extra scoops on top of an ice-cream cone. Folding these modules to fit them inside the skull complicates brain anatomy, particularly that of primates and other mammals, whose large cortices obscure the view of other regions. However, at the coarse level, the basic pattern of complexifying brain anatomy is one of simple linear addition along with differential growth of each segment. The relevance of this spatial patterning for AI is questionable: computational success often depends upon modularity, but proximity relationships among modules are normally more of a hardware than software issue.

The more useful principle involves the homeobox genes and the manner in which they support complexification. Classic work by Ohno [39] shows the prevalence of gene duplication in evolution, and work by several Nobel-laureate geneticists (summarized in [2]) illustrates the importance of duplication and differentiation of genetic material to the gradual emergence of complex phenotypes. A shown in Figure 4, a copied gene (or gene group) gives evolution the flexibility to experiment with new functionalities (by mutating the copy) while retaining the original functionality. This is a low-risk route to complexification that begins with the production of an evolutionarily-neutral copy that can eventually morph into a selectively advantageous trait.

The homeobox, a sequence of 180 DNA base pairs, provides a textbook example: it has duplicated and differentiated several times during evolution, with all mutated copies aligned in sequence along the chromosome. During development, only some of these Hox regions become activated in particular body or brain segments, but as shown in Figure 5, the activation sequence mirrors the segment topology: neighboring segments involve the activation of neighboring Hox regions. Each new Hox derivative provided by evolution yields new and varied segments along the phenotype [2].

Once again, the spatial aspects of Hox evolution and developmental expression may serve a limited utility in AI - in the automated design of physical structures [6] - but the general principle of duplication and differentiation supports a wide range of simulated evolutionary discoveries. For example, [27] employs this principle in genetic programming (GP): modules are copied then allowed to mutate in order to diversify phenotypic behavior. Similarly, [43] recognize its importance in artificial developmental systems, while [14] fully leverage duplication and differentiation in the evolution and development of artificial neural networks. More generally, the theory of neutral complexification [22] and its potential for improving search (particularly in rugged landscapes) has drawn considerable attention in the evolutionary computation community [50, 49].
Figure 4: Duplication and differentiation of genetic material. Gene A, which produces functionality F, duplicates, yielding a redundant source of F. Subsequent mutations to the copy produce A' (useless) and A* (useful), while maintaining F via the original A gene. Thus, the phenotype complexifies without risking the loss of F.

Figure 5: Hox groups are aligned on chromosomes in the same order as they are activated in different body and brain segments.
1.2 Neural Darwinism and Displacement Theory

For Bio-AI, the Neuromeric Model combined with duplication and differentiation constitute a promising scheme for evolving gradually-complexifying controllers composed of neural regions. Deacon’s [9] Displacement Theory (DT) complements this scheme by explaining the sizing and connectivity of these regions, and via a process that renders the coevolution of bodies, brains, and brain regions as a much less improbable accomplishment.

The basis of DT lies in Edelman’s [11, 12] Neural Darwinism, also known as The Theory of Neural Group Selection (TNGS). It is well known [41] that considerably more neurons are produced during development than survive into adulthood. Neural Darwinism essentially frames this as a survival-of-the-best-networkers competition. Neurons must first grow axons to physically search for target structures (e.g. neurons or other types of cells), some of which can only accept a small number of afferents. Then, the source and target must exhibit correlations in activity patterns to firm up the link. A neuron pair may initially fire randomly but eventually become entrained. Failure of either search process (for physical contact or behavioral coordination) can spell death for the source and/or target. Thus, the formation of active connections is paramount to survival.

DT expounds on TNGS by proposing that the networking competition during early development enables brains to scale to fit the body’s sensory and motor apparatus. In short, primary sensory and motor areas of the brain are sized according to their immediate inputs or outputs, respectively. Secondary region sizes derive from those of the primary regions, and deep cortical structures grow or shrink to fit their input and output sources. Figure 6 conveys the essence of TNGS and DT. Note a) the expansion of the 3 neuron groups along the path from the largest sensory input, S1, to the largest motor output, M2, and b) the decline of groups B and D, which lose the competition for C’s dendrites and C’s axons, respectively. As Deacon explains:

So although genetic tinkering may not go on in any significant degree at the connection-by-connection level, genetic biasing at the level of whole populations of cells can result in reliable shifts in connection patterns...relative increases in certain neuron populations will tend to translate into the more effective recruitment of afferent and efferent connections in the competition for axons and synapses. So, a genetic variation that increases or decreases the relative sizes of competing source populations of growing axons will tend to displace (my emphasis) or divert connections from the smaller to favor persistence of connections from the larger.

Developmental neuroscience clearly supports and employs the key tenets of DT. For example, Fuster [17] documents the earlier maturation of posterior brain regions (used in early sensory processing) and late maturation of frontal areas such as the prefrontal cortex (PFC). Striedter [44] combines DT with the work of Finlay and Darlington [15] to explain the trend of greater neocortical (and especially PFC) control of lower brain regions in higher organisms. First, Finlay and Darlington show that late equals large in neurogenesis: larger brain regions are those that mature later in development. Second, a key corollary of Deacon’s DT is that large equals well-connected: big brain regions send many axons to other regions and thereby exercise significant control over them. Together, these show how small changes in developmental timing (in higher mammals) have enabled the frontal regions to mature later, hence grow larger, and hence exhibit greater control over a wide variety of cortical areas. And greater frontal control correlates well with behavioral sophistication, as illustrated by Nakajima et al.’s [37] comparisons of manual dexterity vis-a-vis frontal control of motor areas in mammals such as cats, monkeys and humans.

Together, these theories paint neurogenesis as a process in which genetics determines the neuromeric structure, the basic properties of neurons in different layers of the neuromeres, and the maturation speed of neural regions; but the final sizes of these regions and their interconnectivity arise from self-organizing activity, wherein neural regions competitively search for targets: they compete for the opportunity to cooperate (i.e., fire in a coordinated fashion).

DT agrees with theories of concerted evolution of brain regions, which argue for the interdependence of developing neural modules, in contrast to mosaic theories, which champion independence [44]. In general, the notion of scaling
Figure 6: (Left) The Theory of Neural Group Selection (TNGS), wherein genes govern the production of neurons whose ultimate survival depends upon their ability to establish active efferent and afferent connections. Unconnected (and soon to perish) neurons are unfilled in the figure. (Right) Displacement Theory (DT), in which neuron groups with good networking possibilities expand, while others shrink. Sizes of sensory, motor, and neuron-group icons depict relative sizes of the corresponding neuron pools.

to fit reduces the long odds of brain-body coevolution; in DT, the body evolves and the brain grows and wires to accommodate it. This casts a large part of brain formation as an extensive, physical, search process, as explored further in the next section.

2 Facilitated Variation

Around the turn of the 21st century, two biologists, John Gerhart and Marc Kirschner published two key papers [23, 18] and a book [24] motivating and detailing their Theory of Facilitated Variation, the means by which variation has been enabled/facilitated by an evolutionarily emergent set of constraints.

The account begins with evolvability [23], which they characterize as the capacity to generate heritable, selectable phenotypic variation. It is one thing to produce variation, but quite another to yield variations that are viable, can be inherited, and offer natural selection something to grab onto and use to differentiate successes from failures (and thereby maintain evolutionary transition). Evolvability has two key prerequisites: robustness and adaptability. A robust system tolerates perturbation by, in effect, damping their internal consequences. Genetically, this means that mutations rarely have lethal consequences: genomes can buffer the effects of random changes to a few base pairs. Conversely, a system is adaptive if it can easily achieve internal modifications to combat external change. So the genetic version of adaptivity lies in the ability to achieve significant phenotypic change with minimal genotypic change: if the environment changes drastically (such that the available phenotypic plasticity cannot cope), then within a few generations, a genotypic modification will arise to produce a more viable phenotype.

Facilitated variation postulates several key mechanisms for achieving robustness and adaptability. In a nutshell, the theory states that structures and mechanisms that are modular, structurally connected via exploratory growth and functionally coupled via weak linkage, will produce species that are robust to both genetic and environmental change but can also adapt by easily transitioning to new phenotypes.

Nascent biological mechanisms that exhibit these key properties are termed core processes and are believed to have reached a stable evolutionarily status, such that the vast majority of phenotypic change (whether minor or extensive)
now involves modifications to the interaction topologies of these processes, but not to the mechanisms themselves. Thus, these core elements have an evolutionary analogous status to the major body plans that arose during the Cambrian explosion [19]. Some of the oldest core processes, whose origins date back 3 billion years, include energy metabolism, membrane formation, and DNA replication. Those aged closer to 2 billion years include meiosis, contractile activity and microfilament and microtubule formation, while one billion years have passed since the emergence of intercellular signalling pathways, cell adhesion and apical-basal cell polarization. Finally, anterior-posterior and dorsal-ventral axis formation, along with complex regulatory processes are a mere 550 million years old, having arisen 10 or 20 million years prior to the Cambrian explosion of body forms.

They are the building blocks of life, but unlike the building blocks championed by Holland [20] and the typical agents of complex systems, they do not map uniquely to specific phenotypic traits nor exhibit relative simplicity compared to the emergent complexity of the entire organism. Whereas Holland’s building blocks are compact regions of the chromosome, and thus not likely to be broken apart by crossover, the genetic basis of core processes may be spread throughout a genome that has gradually evolved to support and preserve these fundamental mechanisms.

Systems built upon core processes derive their complexity from both the intricacy of the primitive elements and their interaction networks. Facilitated variation involves complex regulatory networks among sophisticated components, but whose pairwise interactions are simple, a crucial prerequisite to the whole enterprise. Termed weak linkage, the principle that signals between core processes are simple compared to intra-process activity, this is arguably the theory’s strongest supporting pillar of robustness and adaptability.

![Figure 7: The combination of robustness and adaptability embodied in facilitated variation. Each of the phenotypic changes are assumed to arise from similar, small genotypic perturbations.](image)

Facilitated variation embodies several aspects of complex systems. First, robustness and adaptivity cover both ends of the classic edge-of-chaos, power-law distribution, as shown in Figure 7, where the x axis plots the degree to which a phenotype changes in response to a single, random, genetic mutation, and the y axis charts the frequency of each amount of phenotypic change. Evolvability entails a power-law distribution over this space, wherein most mutations lead to no significant phenotypic change (the high, left side of the power-law curve) but, occasionally, a single mutation can produce a major (useful) jump in design space (the curve’s non-zero tail on the right). Thus, the curve displays robustness on the left and adaptability on the right.

Second, exploratory growth, so vital to the emergence of coordinated interactions among a multitude of components (as elaborated below), is a textbook example of Mitchell’s [35] fourth principle of complex systems: parallel exploration and exploitation among the individual agents. Thus, search is fundamental to facilitated variation, not merely as an abstract perspective from which to interpret the emergence of a properly linked collection of components, but as visible
processes occurring within individual cells and regions, processes in which many trial structures arise but only a few persist.

2.1 Modularity

Basically, modular structures are those in which the intra-component activity is more extensive than its inter-component counterpart. Structurally, in, say, a neural network, the vast majority of synapses onto a neuron of module M would come from other neurons of M, with only a small minority arising outside of M. This is modularity at the phenotypic level. As summarized in Figure 8, many levels of modularity exist. On the chromosome, a modular gene is one whose component base pairs are co-located, and thus difficult to separate by the perturbing effect of crossover. A genotype-phenotype mapping can exhibit varying degrees of modularity, inversely proportional to the pleiotropic interactions among genes. For example, in a modular situation, gene A is only involved in the production of trait X, while in a less modular (more pleiotropic) scenario, it would also play a role in the production of traits Y and Z. In the former case, a mutation of A would only affect X, while the latter case would entail more widespread change. Finally, on the right of the figure, modular phenotypic structures (such as cortical columns, brain regions, or tightly interacting subsets of a neural network) can typically restrict a perturbation’s extent to the module itself.

Figure 8: Three examples of modularity in an evolutionary context: (Left) the locations of genes on the chromosome, (Middle) the genotype-phenotype mapping, and (Right) the structures constituting the phenotype. In each case, the lightning bolt indicates a perturbation that, amidst a modular system, should only cause local damage.

Modularity is a widely recognized factor in the emergence of sophisticated systems [20, 21, 42], whether via evolutionary or other adaptive means. Once structures or mechanisms are consolidated and isolated (to some degree) from external influences, their probability of disruption declines and their potential for self-modification without global repercussions increases: they enhance both robustness and adaptability.

2.2 Weak Linkage

The lack of strong inter-regional activity is not only a hallmark of modularity but also a prerequisite to facilitated variation. As shown in Figure 9, a key biological distinction exists between instructive and enabling signals. The former is characterized by core processes that require considerable external assistance for their normal operation: the prerequisite external signals are complicated, possibly housing large chunks of the complete process. Thus, the process itself exhibits less modularity due to the intricate external communication.
Conversely, an enabling signal is quite simple and merely serves as a tiny piece in the complete puzzle of the core process. A highly modular system only requires these low-complexity external interactions in order to function properly. Weak linkage entails a good deal of these enabling signals, originating either from simple individual messages or simple pieces of more complex messages. For example, with chemical messages, the active signal may be a single benzene ring which can be found on a wide variety of chemicals, any of which could thus serve as the messenger. Thus, enabling signals can be quite general.

![Diagram](image)

**Figure 9: The difference between a complex, instructive and a simple, enabling signal.**

Whereas the ability to produce a particular instructive signal may only arise a few times in nature, the simplicity of enabling signals makes them easier to generate. Hence, many other components may send them, an immediate boon to robustness and adaptability. For example, if the usual source of an enabling signals weakens or vanishes, an alternate source might already exist or easily arise, aiding robustness. Similarly, a network of interacting processes can more easily reconfigure (into a new phenotype) in the advent of a simplified signaling protocol, whereas complex communication would over-constrain the situation, giving few (if any) alternative arrangements.

In fact, Gerhart and Kirschner [18] consider most core components to house the entire interaction network plus an inhibitor: the enabling signal then blocks the inhibitor, thereby dis-inhibiting the core process. The signal is thus selectable only for its ability to block the inhibitor, not for its role in the actual core process. Hence, the core process can evolve without a corresponding change to the signal, and the long odds of coevolution are avoided such that viable variations can more readily evolve.

Weak signaling can produce situations in which the control of a core process can shift between internal and external sources, which would allow an environmentally-induced mechanism to become innate. As shown in Figure 10, an enabling signal might originally stem from an external source, but due to its simplicity could easily become internally produced via a simple genetic mutation. West-Eberhard [47] provides numerous examples of this phenomena, including sex-determination by temperature (instead of genes) in turtles and snakes, cricket wing-length controlled by either crowding conditions or genes, and foraging strategies in fruit flies determined either innately or by starvation/satiation levels.

Thus, a phenotypic change of a plastic nature could smoothly become innate, providing a selective advantage in environments where the particular change had become ubiquitously desirable. Furthermore, this internalization of a signal source helps explain how natural selection could favor weak linkage (and other aspects of facilitated variation). Assume that various species benefit from lifetime flexibility due to evolved weak linkage between the environment...
and core components. If simple mutations could easily internalize these linkages to the genome, then there would be a steady influx of weakly-linked, internal-signaling networks to the gene pool. In short, there would be no shortage of genomes that exhibited facilitated variation, and some would presumably have a selective advantage for individual organisms, particularly those living in unpredictable environments. Thus, many genotypic adaptations may indirectly arise from selective pressure favoring phenotypic flexibility.

![Figure 10: Shifting the control of a core process from environmental to internal via a simple mutation that allows the organism itself to produce the enabling signal.](image)

Neurons are classic examples of weak-signaling core components, since they all employ the same communication currency: action potentials. In addition, signal transmission across synapses involves neurotransmitters, of which there are only a few dozen, well-conserved varieties such as glutamate, GABA and acetylcholine. Furthermore, post-synaptic terminals often house receptors for several of the neurotransmitters, thus further increasing their communication possibilities. Essentially, if a new neuron type were to arise from the mutation of a contemporary variety, it would almost certainly sprout some of the same receptors and thus be immediately prepared to talk to the rest of the brain.

### 2.3 Exploratory Growth

Along with the ability to easily communicate with one another, the core components of facilitated variation can find each other (or important internal or external entities) using trial-and-error, exploratory search processes whose high energetic costs trade off (very favorably) with an amazing level of developmental flexibility. As explained by Gerhart and Kirschner [18]:

Examples include the formation of microtubule structures, the connecting of axons and target organs in development, synapse elimination, muscle patterning, vasculogenesis, vertebrate adaptive immunity, and even behavioral strategies like ant foraging. All are based on physiological variation and selection. In the variation step, the core process generates not just two output states, but an enormous number, often at random and at great energetic expense. In the selective step, separate agents stabilize one or a few outputs, and the rest disappear. Although that agent seems to signal the distant process to direct outputs to it, it actually only selects locally via weak linkage among the many outputs independently generated by
the process. Components of the variation and selection steps of the process are highly conserved. (page 8285)

In some cases, many such explorations coordinate to form biological structures. A most impressive example, as detailed in [23], involves the development of limbs. Hox genes determine the locations of cartilaginous points in the developing embryo; and exploration does the rest. Namely, bones form to join these points, muscles and tendons grow to link up the bones, motor neurons sprout axons to innervate the muscles, and blood vessels grow to feed them. Furthermore, within each neuron, selection occurs among the many axons, only a few (if any) of which manage to find a target dendritic tree; the rest wither away. As discussed earlier, Neural Darwinism and Displacement Theory explain the search processes wherein neural sub-populations attain sizes and connection patterns in a grow to fit manner.

In their seminal developmental biology text [48], Wolpert et. al. describe the use of filopodia - thin cytoplasmic extensions - to pull mesenchyme cells along during migration:

When filopodia make contact with, and adhere to, the blastocoel wall, they contract, drawing the cell body toward the point of contact. Because each cell extends several filopodia, some or all of which may contract on contact with the wall, there seems to be a competition (my italics) between the filopodia, the cell being drawn toward that region of the wall where the filopodia make the most stable contact. The movement of the primary mesenchyme cells therefore resembles a random search (my italics) for the stable attachment...(pp. 281-282)

The authors cite a similar behavior for neural crest cells, precursors to the entire peripheral nervous system (along with other parts of the body) and travelers of many long and diverse migratory routes. Kirschner and Gerhart [23] view neural crest cells as the epitome of an exploratory process, with a) variation stemming from the ability to follow many paths and differentiate into numerous cell types, and b) selection performed by the chemical signals in various compartments (defined by signaling-chemical portfolios, not necessarily physical barriers) during the early stages of development.

Crest cells originate from different rhombomeres of the developing brain, with each having a different characteristic set of active Hox genes [41], as discussed earlier. These give each migrating crest cell a general identity, which then determines the target region for its wandering search. Striedter [44] proposes a similar mechanism for the formation of laminae and topological maps in the brain.

Laminae are simply parallel layers of cells, classically illustrated by the 6-layered mammalian cortex. The key point is that neurons from one layer of a region will often target neurons of a particular lamina of another region. If each layer has a characteristic portfolio of chemical signals, then growing axons read that chemical signature and internalize it to the extent that it affects the target regions they seek.

A topological map is a connection pattern between two regions wherein nearby neurons in layer A have targets in layer B that are also neighbors. The general concept extends beyond the nervous system to sensory inputs and motor outputs. For example, nearby fragments of the visual field are normally handled by nearby neurons in retina, which, in turn, feed signals to neighboring neurons in the thalamus, which maintain these spatial correlations in sending signals to the visual cortex. As discussed earlier, similar sequences of maps exist in the auditory system, where the environment consists of sound frequencies; those that are similar are detected by nearby hairs in the cochlea, which maintain the topography through several consecutive neural regions [5]. Again, Striedter cites evidence of chemical signatures biasing axonal target selection to form the initial maps, with experience-based synaptic change fine-tuning them afterwards (See Sidebar)

Laminae and topographic maps are critical components of neural systems with several functional advantages, including modularity, wiring efficiency (since axons between these regions tend to run in parallel, exhibiting much less
criss-crossing than with random connections), and generalizability. The latter stems from inter-region correlations, which help insure that similar sensory situations promote similar neural firing patterns, which invoke similar motor responses. This allows organisms to handle novel situations with behaviors that were successful in similar contexts. Thus, exploratory growth produces efficient neuroanatomical structures that support adaptive behavior.

Figure 11 illustrates another contribution of exploration to robustness and adaptability in a neural context. The former occurs when the C neurons are abnormally displaced, but axons from the A neurons still find them: the perturbation is countered via exploration, enabling standard A-C connections to form. Similarly, adaptability occurs when a single mutation changes the affinity of A or C neurons such that B neurons become the dominant source of afferents to the C population, thus yielding a new neuronal topology, and potentially a new phenotype.

![Figure 11](image-url)

Figure 11: Exploratory axonal growth processes leading to the formation of neural topologies. Dashed lines are exploratory axons, while solid lines are those explorers that found targets.

In all of these examples, DNA only encodes the exploratory processes, not the resulting patterns of connectivity. Again, the genome encodes recipes, not blueprints.

Analogously, the evolutionary algorithm for finding Steiner Trees presented earlier uses a chromosome that, like the Hox genes, only indirectly encodes locations of special (Steiner) points. Kruskal’s algorithm determines the best way to connect them. To add more biological realism to that example, evolution would need to discover Kruskal’s, Prim’s or some similar connection-generating algorithm as a core process.

The practical implication of exploration and its facilitation of variation is an important take-home lesson: the production of novel phenotypes does not require concerted change to many parts of the genome, a very low-probability combination of events, but rather a single change to a factor affecting an early phase of development. The rest just grow to fit the altered context.

In short, nature has not endowed core processes with intelligence, but with persistence. A multitude of parallel explorations combined with weak linkage allow many core elements to eventually find connection points. From this, networks emerge, and with them, the possibilities for more patterned, predictable and intelligent behavior.

### 2.4 Sidebar: Emerging Topographic Maps

Figures 12 and 13 depict the emergence of topographic maps through development and learning. First, similar concentration gradients in the two regions will bias the searching axons to target corresponding neurons in the lower layer, though errors may abound. Despite the errant connections, experiences in the real world can easily fine-tune the map,
as shown in the scenarios of Figure 13. In each case, an abstract object activates the upper (presumably sensory) neurons, with can, in turn, team up to fire the lower-level neurons. For example, in scenario 1, the object activates A and B, which stimulate W.

Synaptic tuning occurs via standard Hebbian means:

1. The synapse strengthens when pre- and post-synaptic neurons fire simultaneously or with pre-synaptic activity slightly preceding post-synaptic.
2. The synapse weakens if one but not the other neuron fires or if post-synaptic firing precedes pre-synaptic firing by a small amount.

Thus, in scenario 1, the A-W and B-W links strengthen, while the D-W link weakens. Similarly, D-W weakens in scenario 2, as does C-Y. Only in scenario 3 does D-W strengthen, and this would seem to be a more atypical sensory situation (i.e., one that stimulates A and B but then hops over C but stimulates D) given the general continuity of the sensory world. Also note that D-W weakens in scenario 4, since A and B suffice to activate W, while D activates slightly later (since the object moves left-to-right). Thus, the pre-synaptic node (D) activates after the post-synaptic node (W), leading to further synaptic depression.

Note that a right-to-left movement of the same object would not have the complete opposite effect. D would activate before A and B, but D alone would not suffice to activate W, which probably could not activate until both A and B did. Thus, although the D-W link would strengthen (since D fires just before W), the A-W and B-W links would not weaken, but only get stronger. Thus, in the overall competition to activate W, A and B would not lose ground to D.

Switching to a more realistic, continuous scenario where lower-layer firing depends upon an integration of incoming signals over time, with significant leak of existing charge as well, then any strengthening of A-W and B-W relative to D-W can quickly set a positive feedback in motion: any co-occurrence of A and B could fire W almost immediately, so even if D fires a few milliseconds after A and B, it will be too late, thus compounding the depression of D-W.

In short, the regularity of the real world will, in all likelihood, provide an overwhelming number of stimuli that strengthen the connections shown in scenario 5, while weakening non-topographic links such as D-W, which only activate on very large or discontinuous stimuli. Hence, the combination of coarse, imperfect chemical gradients, Hebbian learning, and the continuity of the real world suffice to promote the emergence of the brain’s topographic maps.

Figure 12: The developmental emergence of a topographical mapping between the upper and lower layers, assuming that concentration gradients (shading in each rectangle) mirror one another (based on descriptions and diagrams in [44]). Note the biased, but imperfect topology, best illustrated by the errant link from D to W and the missing link from B to X.
Figure 13: Once formed by development, the topographic map is tuned by experience. Each black bar denotes stimulation in the sensory (i.e. visual) field corresponding to neurons A-D. Each of scenarios 1-4 results in some neurons activating, where it is assumed that lower-layer neurons require at least 2 upper-layer inputs (within a short time window) to activate. Synaptic tuning follows basic Hebbian learning and STDP principles. Scenario 5 depicts the network after many rounds of learning; two of the synapses (that many experiences would tend to weaken) have disappeared.
2.5  Deconstraining Evolution

The net effect of modular core processes, weak linkage and exploratory growth is a deconstraint of evolution. Now, many genotypic and phenotypic changes become viable because a) perturbations are constrained to remain within a modular area, but b) those with non-local consequences are non-lethal due to the flexibility inherent in weakly-linked interaction topologies and exploratory growth mechanisms. Just as it is easier to innovate with a group of open-minded individuals, all self-confident in their own abilities but willing and eager to interact with many others, in many constellations, so too can nature more readily produce novel phenotypes when its core components are stable, complex and competent, but easy to interface with others.

As a simple example of how constraints affect a search space, consider the boolean logical constraint in equation 1, where the goal is to find an assignment of truth values to the 4 boolean variables such that the entire expression is true. There are $2^4 = 16$ possible states in the search space, and as shown in Table 1, 9 of them satisfy this constraint.

\[(a \lor \neg b) \land (c \lor d)\]  \hspace{1cm} (1)

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Table 1: The 9 viable solutions to the constrained logical expression of equation 1 written in bold text. Binary vectors denote the truth values for a-d, where 1 is true, and 0 is false.

Notice what happens when the second disjunction is supplemented with a $b$ (equation 2). This makes the disjunction easier to satisfy, which in turn deconstrains the entire expression, allowing more points in the search space to satisfy it, as shown in Table 2.

\[(a \lor \neg b) \land (b \lor c \lor d) \equiv (a \lor c \lor d)\]  \hspace{1cm} (2)

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<td>1000 101 1010 1011</td>
</tr>
<tr>
<td>1100 111 1110 1111</td>
</tr>
</tbody>
</table>

Table 2: The 14 viable solutions to the deconstrained logical expression of equation 2 written in bold text.

This simple example has direct parallels with biological deconstraint. Anytime a core process is modified to accept an additional type of enabling signal, it effectively supplements its disjunction of salient signals, thereby allowing a wider variety of components to serve as afferents; and this increases the set of viable interaction topologies. When a design space has more feasible solutions, the probability that an emergent process can stumble onto one of them can only increase.

But if evolution has become deconstrained, then how has nature managed to navigate the ominous design space of living things? Though weak linkage and exploratory growth reduce constraint, the core processes, now well locked in for the past billion or so years, greatly increase it. In essence, the evolutionary emergence of the core has shifted nature’s evolutionary search to a small corner of the space of possibilities. Given the chemistry and physics of earth,
that corner may be a strong attractor, or it could be one of several viable regions. Either way, without very powerful intervention, life as we know it is basically stuck there. Weak linkage and exploratory growth then deconstrain that region of search space. Thus, in terms of search-space terrain, these features help nature make the most out of the corner into which the core processes have corralled life.

3 Representation and Search in Neural Evolution and Development

By now, the fact that Darwinian evolution is an impressive trial-and-error search process should need little elaboration: it finds amazing designs both in nature and in Bio-AI by, essentially, tossing options out there and letting selection filter them out. The role of search in development has traditionally received less attention. However, researchers such as Edelman, Deacon, Kirschner and Gerhart - though not discovering these mechanisms - have highlighted the importance of exploratory actions combined with selection during the growth of neural structures.

In order for AI to incorporate the essence of exploratory growth, a study of the representations underlying it could prove helpful. In nature, of course, that representation is DNA, which contributes to life’s robustness and adaptability in many ways. For our purposes, the essential facts about DNA are:

1. Triplets of DNA bases, called codons, constitute amino acids, which are the building blocks of proteins but also have other uses in the body.

2. A gene is a long continuous segment of DNA bases that code for compounds of functional significance in the organism, typically polypeptides or RNA chains.

3. Functional genes directly express functionally-significant compounds, while regulatory genes produce signaling compounds that promote or inhibit the expression of other genes, whether functional or regulatory. These signals serve an enabling (or, more often, inhibiting) role, but not an instructive role. As indicated earlier, many such signals can arise from the genome or the organism’s environment.

4. Junk DNA are segments not known to express anything of functional nor regulatory significance.

First, the coding scheme for amino acids houses many redundancies: only 2 of the 20 amino acids stem from unique codons, while all others have between 2 and 6 different codon sources. This enhances robustness, since many mutations may alter base pairs without changing the resulting amino acids (and proteins).

Another form of insurance against genetic change is junk DNA, which seems to provide buffer zones between expressed genes such that crossover during meiosis has less chance of splitting a coding gene in two: the crossover points often occur within the junk DNA.

In general, the exact positions of genes on the chromosome have little significance; interactions between genes (for example a regulatory gene R and a functional gene F) happen through an intermediary chemical signal, S, that R produces, not via direct contact between the R and F segments. So gene R may be close to or far from F on the chromosome. This supports gene duplication, since copied genes need not bump existing genes from important, pre-defined chromosomal locations. The modularity of genes combined with the lack of location specificity facilitates changes to the gene composition of a chromosome: additions and subtractions should not interfere with the other genetic interactions. Only when a gene differentiates can it alter functionality.

All told, these features of DNA and the general (and evolutionarily successful) arrangements of it (i.e., genotypes) lend ample support to both phylogenetic and ontogenetic search processes. For evolution, the robustness of nascent genotypes to genetic change allows nature to experiment with novel genotypes, many of which are neutral by producing
the same phenotypes (and or equally-fit phenotypes) as their predecessor chromosomes. Evolution can thus explore
design space with much lower risk than if every mutation yielded new phenotypes.

The combination of control and functional genes into a genetic regulatory network (GRN) forms a mill of novelty. Without regulation, every functional gene would presumably be ubiquitously expressed - otherwise its presence on the chromosome would seem entirely inefficient and have only a vestigial justification. New phenotypes would require the addition of new functional genes. The presence of regulatory genes provides an exponential number of possible phenotypes from the same set of functional genes, some of which may be on (expressed) and others off at any particular time in evolution, or any spatiotemporal point in development. In fact, cell types are largely differentiated by the subset of functional genes that they express.

This means that at any point in evolution or development, anything with a chromosome has myriad options, with regulatory signals (from both the environment and the cell itself) determining the outcome: the state of the GRN. From the evolutionary perspective, there are many GRNs in many different states that constitute an organism; in development, the focus is often on a particular cell and the status of its GRN. For example, Kirschner and Gerhart [24] discuss neural crest cells and their ability to migrate within the embryo and then eventually transform into their final cell type based on signals in the extracellular environment. In essence, these cells search for a fitting location and for the appropriate biochemical behavior from a long list of possibilities. The options exist all the time; they just require the proper signals to activate. Thus, the exploratory search underlying so much of development depends upon the flexibility of the GRN to read impending signals and react accordingly.

In fact, Kirschner and Gerhart have considerable evidence that functional genes (like core processes) have been conserved over millions of years, possibly all the way back to the Precambrian era and beyond. Variation has become the sole province of the regulatory genes, which, like the automatic steering of a car, can affect change with minimal effort (due to weak linkage).

GRNs take the direct-vs-indirect distinction to a higher level. Indirect representations require a complex translation process, but one that could just involve two stages: a) the formation of all products of the individual genes, followed by b) a complex of interactions between those products to produce the phenotype. GRNs add considerable variability to stage 1 by only expressing a subset of the genes, but possibly a different subset in a different context: a subset adapted to its surroundings. This changes the game completely; and while nature has mastered this innovation, Bio-AI researchers have only just begun to investigate.

### 3.1 The Bio-Inspiration

What biological inspiration should AI draw from the evolution and development of the brain? Clearly many of the core processes (such as energy metabolism, exploratory axonal growth, and anterior-posterior axis formation, etc.) demand a (computer) module or two in simulations designed to accurately mimic biology, but how many of them are vital to the emergent design of an artificial intelligence? Does a computational system need a metabolism, a procedure for gradually growing a connection between two hardware or software modules, or a means of differentiating top from bottom? These are clearly more relevant for an embodied AI system, but lower-level core processes such as cell adhesion and contractile activity may have few implications for AI.

Good AI systems are often flexible at the phenotypic level. They use sophisticated Machine-Learning algorithms to adapt. However, if, as argued earlier, AI wishes to take advantage of indirect encodings and the genotype-phenotype distinction in the search for intelligent systems, then genotypes may need enhancements to facilitate useful variation. Nature eventually found these enhancements in GRNs, but whether AI should employ bio-inspired abstractions of these representations (or pursue entirely different, engineering-based routes) remains unclear.

GRNs have been used in many ALife systems, often producing impressive low-level emergence, such as a single cell
Figure 14: Sketch of a basic genetic regulatory network (GRN) as implemented by several Bio-AI researchers. The evolutionary-computation chromosome encodes a group of operons, each of which takes several input substances and can produce one (or more, in some implementations) outputs. The relationships between inputs and outputs then form a network, with the cell serving as the repository for all substances, which are analogous to proteins in biology.

Figure 15: Cells can also exchange substances; and although they share the same GRN, cells can vary in substance concentrations. Different compositions reflect different cell types, as denoted by solid, dashed and dotted borders. Certain substances (e.g. stars) can initiate cell division.
that repeatedly divides to produce a multicellular clump that then performs a physical task, such as pushing a box [8],
or a similar seed cell that divides and differentiates into a spatial form that matches a target pattern, such as a French
or Norwegian flag [34, 14].

In these and many other Bio-AI systems, the GRNs resemble that of Figure 15, where an evolutionary-algorithm
chromosome encodes several modules known as operons, each of which works similar to an if-then rule: when its pre-
conditions are satisfied, the consequent is performed. For example, if the concentrations of all substances mentioned
in the precondition exceed particular thresholds, then a product substance is produced (whose amount and possible
location of production may also be specified by the operon). Unlike the if-then rules of classic GOFAI expert sys-
tems, the operons often run in parallel, not series, to continually update the concentrations of substances in the local
environment, i.e., the cell.

Systems employing GRNs normally consist of many cells, which may exchange substances either directly or via
an external milieu. The full portfolio of substance concentrations often determines a cell’s type, which then maps
to a functional component of the AI system. For instance, the cell may correspond to an artificial neuron, or a
body segment, or even an innervated body part. Special substances may also promote cell division or death, axonal
migration; or it may translate into receptors (on the cell membrane) for other substances. The general operon-based
model supports a wide range of applications, all of which empower the genome with considerably more flexibility
than in traditional evolutionary computation.

Instead of the artificial chemicals of GRNs, some Bio-AI systems employ grammars (i.e., sets of rewrite rules) as
the basis for simulated development [43, 16]. This exhibits less biological realism but often creates more life-like
structural facsimiles of both plants and animals, as best exemplified by L-systems [29] and their many applications
[16]. Both the GRN-driven (a.k.a. chemical based) and grammar-based developmental models have the advantages
of:

1. Scaling - small genotypes suffice to generate large phenotypes, and the reduced genotype defines a more man-
ageable search space.

2. Symmetry - large phenotypes produced from the repeated execution of small genotypes typically have recurring
structures, offering a selective advantage for many tasks, such as those involving locomotion.

3. Robustness - re-execution of the developmental procedure (later in the life of a system) can often repair a
damaged phenotype, or, in general, help to maintain it in a stable, functioning state.

Regardless of these advantages, artificial evolutionary developmental systems have yet to achieve convincing success
on anything beyond quite simple tasks - though simplicity in the eye of the observer often belies fascinating emergence
at the evolutionary and developmental levels. Finding effective developmental recipes for growing complex physical
structures and/or their control systems has proven to be an extremely daunting task, despite the help of artificial
evolution in exploring the genotype search space. Researchers always return to the same question: What aspects of
natural development can actually contribute to improving artificial design, as opposed to merely being scientifically
interesting to implement?

The most appropriate bio-to-tech transfer might be at a very high level of abstraction. For example, Bio-AI can benefit
from the general concept of conserved core processes, which evolutionary search employs as building blocks that, due
to weak linkage, can be combined in many ways. Specialists in the area of genetic programming (GP) understand
this well. Their evolutionary simulations begin with a set of primitive modules/functions that can be combined into
an exponential number of problem-solving systems. Search occurs within the space of these combinations, but the
primitives are hand-designed and fixed.

GP also incorporates weak linkage to varying degrees. Original versions of the concept [25] employed the closure
property (discussed earlier) to insure that the outputs of any module could be accepted as the inputs of any other
module. This allowed the full complement of module combinations to at least run (i.e., not crash the computer), though not necessarily produce useful results. Later versions [36, 26] introduced strongly-typed modules: they only accept certain types of arguments. This restricted GP search but in no way detracted from the creativity of GP design. The field exploited these and other constraints to make quantum leaps from toy problems to real problems to the automatic design of devices that rival or surpass those of modern engineers.

Perhaps no other AI researchers have embraced facilitated variation more than Michael Lones and Andy Tyrrell [31, 30], who employed weak linkage and classic GP modularity in their Enzyme Genetic Programming (EGP) system. In this work, the genome encodes modules but says nothing about their interaction topology - whereas standard GP employs genomes that fix the topology. Each module includes an interface whose syntax reflects the module’s computational semantics, in much the same way that an enzyme’s 3d shape (its interface) implicitly mirrors its functionality; the interface is not an arbitrary signal nor receptor. The complete topology then emerges from a search process in which modules attempt to find others with output interfaces compatible with their input interfaces.

EGP’s interfaces are sophisticated versions of the more general concept of tags, which have received more attention in the EA community. In fact, John Holland [21] includes tags in a short list of key elements of a complex adaptive system. A tag is simply a syntactic structure (typically a string of bits or other symbols) attached to a component that is visible to other components and typically determines the degree to which different components interact. Unlike EGP’s interfaces, tags generally do not reflect the behavioral semantics of the component, although they may eventually evolve to correlate in some way with the internal activity. Or, to achieve deception in situations where agents are best suited by avoiding interactions (e.g. with predators), tags may evolve to signal something totally different than the component’s actual behavior. Either way, tags influence interactions and allow interaction topologies to emerge during development, as opposed to being predetermined by the genome. This allows more natural topologies to form in which components have affinities for one another, and many such local compatibilities increase the odds of global coherence.

Depending upon the matching criteria, tagging can support weak linkage. For example, if one agent’s output tag must perfectly match another’s input tag, then this obviously restricts interaction. But if local compatibility requires only, say, a 50% match, then more relationships can form.

Matching criteria also have a strong effect upon the robustness of a tag-based representation. Figure 16 plots the matching probabilities of two binary tags (of length 200) as a function of the bit-wise mutation rate. The two tags are originally identical, but, naturally, as the mutation rate rises, matching declines. However, the algorithm for computing matches varies for the 3 plots, and each yields a different curve. The streak criterium seems to yield the most desirable behavior: it tolerates a good deal of mutation, though certain well-placed mutations (e.g., in the middle of the maximum equal or unequal streak) can perturb the match values between the strings, which may alter the emerging interaction topology.

Basically, tags allow good designs to fall into place once proper combinations of core elements and tags arise. In this case, the inspiration from facilitated variation entails hand-designing the core modules but allowing the search process to determine the quantities of each component along with their tags. The exploratory process is then embodied in the algorithm that components use while searching for neighbors in the emerging topology.

Another relevant, though often overlooked, aspect of contemporary evolutionary-developmental theory involves the bi-directional interactions between evolution, development and learning. Bio-AI researchers often implement each adaptive phase in lock step: first generate a new chromosome using genetic operators, then convert it into a phenotype using a developmental routine, and then run the phenotype in an environment and permit small behavioral tweaks based on experience. However, these mechanisms interact in many ways. For example, development often continues well into adolescence and even adulthood, thus overlapping with (and often blurring the distinction between itself and) learning. More importantly for our discussion, the effects of phenotypic and developmental change can affect evolution.
Figure 16: Varying degrees of robustness (to bit mutation) for different tag-matching algorithms, where the x-axis denotes the probability of bit mutation, while the y-axis records the matching probability of two tags that were originally identical. Matching probabilities are computed using three different algorithms based on Hamming distance (solid line), the integer value of the bit string (dotted line), and a special chemically-inspired, streak model (dashed line), wherein match degree stems from a) the longest contiguous segment of perfect bitwise equality, b) the longest segment of perfect bitwise inequality, c) and the comparative odds of each such streak.

The prevalence of equivalences of genetic and environmental factors in producing phenotypic traits (as discussed above) allows evolution to a) find GRNs that confer an immediate selective advantage (in an unstable environment), and then b) co-opt this phenotypic flexibility for evolutionary purposes by allowing gene products to (permanently) enable or disable various operons to stabilize phenotypes in more predictable environments. Thus, the evolutionary search for GRNs that equip phenotypes with effective lifelong search capabilities also enhance evolutionary search. This relationship is easily confused with Lamarckianism [28], a thoroughly disproven evolutionary theory that proposed the (relatively immediate) genetic transmission of phenotypic change. However, it is best exemplified by The Baldwin Effect [4, 46], a very plausible, indirect mechanism wherein a) the emergence of lifetime plasticity can have a selective advantage to a new (but predictable) environment, followed by b) genetic hard-wiring (via mutation) to handle these conditions, which offers a better solution in situations where lifetime plasticity has a significant cost to the organism.

This bi-directional relationship between evolution on the one hand and development and/or learning on the other has received considerable interest in Bio-AI [45, 3, 32, 10], as has the more general combination of a) a broad-scale search process (such as evolution) to find general strategies, and b) a focused process of adaptivity for tuning those strategies during the course of their deployment [13, 38, 33].

4 Appreciating Add-Hox Design

One glance at a diagram of brain anatomy, with its lobes, gyri, sulci and vesicles, is normally enough to convince an AI researcher to keep her day job at the keyboard. More detailed figures - of layered cortical columns and their mishmash of connections - only bolster the impression that, although a good deal of brain activity seems computational, the organ has evolved a form that is more historically contingent on the Precambrian era than the industrial revolution. Brains were designed for survival on a merciless planet, not for designing lightbulbs, steam engines and transistors. So it is, indeed, easy to write-off the engineering potential of many neuro-inspirations.
However, when viewed as multiple modular extensions of a segmented body by the duplication and differentiation of the same Hox complex that governs so much of development, brain anatomy appears less ominous and more generalizable to a wide range of problems requiring hierarchical control. When the *grow to fit* search processes forming our networks of muscles, vessels, axons and dendrites are fully exposed on the drawing board, the coevolution of controller and body seems more inevitable than enigmatic. This awareness - that evolution eventually crafted an omnipotent strategy that can, with only small tweaks, generate an exceptionally diverse menagerie of morphologies and regulators - is one of the most valuable sources of bio-inspiration that mammalian evolution has to offer. One search process, evolution, configured the primitives for another search process, development, which produces phenotypes capable of even more (mental and physical) search.

So aside from the Darwinian trilogy of inheritance, variation and selection (and their roles in design search), and the well-documented, machine-learning contributions of large networks of simple, neuron-like processors, the key motivation for AI researchers to study brains and their evolution is the general system properties that help produce useful variation: modularity, duplication and differentiation, weak linkage, exploratory growth and flexible genomes. The details of their realization may vary across application domains, but the general concepts deserve careful consideration when equipping a search algorithm with tools for discovering innovative forms of intelligence.

### 5 Sidebar: Finding Minimally-Independent Sets using Fruit-Fly Development

An interesting (and very bio-inspiring) example of search and emergence during development involves the sensory organ precursor (SOP) cells [41] of the Drosophila’s nervous system. SOP cells, which become sensory bristles, originally differentiate from a homogeneous population of proneural cells. Interestingly enough, this differentiation creates a population in which a) every non-SOP cell is adjacent to at least one SOP, and b) no SOP cells are adjacent. This pattern emerges from chemical signaling in which SOPs inhibit neighbor cells (from becoming SOPs) by emitting the protein Delta, which interacts with another protein, Notch, to prevent SOP formation. Although the details of these chemical processes are beyond the scope of this book, their essence has been abstracted into a very elegant, fully distributed solution to a vexing problem in computer networks [1].

The Minimal Independent Set (MIS) problem involves finding a set of *local leader* nodes in a network such that a) all non-leaders are adjacent to a leader, and b) no leaders are adjacent to one another. Computer scientists and mathematicians struggled with distributed algorithms for solving this problem for decades, before Afek et. al. [1] looked to the Drosophila for a solution. The resulting algorithm highlights the role of localized search (within each node) in leading to the global solution: the MIS.

The procedure/simulation begins with a network of N nodes, many connections between them, and two empty pools, one for leaders (L) and one for non-leaders (NL). D is the maximum number of neighbors for any node in the network. Each step of the simulation involves two signaling rounds for each node (n) that has not yet been assigned to either of the pools. These nodes presumably execute this procedure synchronously, with the same step being concurrently executed by all nodes.

1. \( p = \frac{1}{D} \)
2. if \( p \geq 1 \) exit
3. Repeat \( M \log_2 N \) times:
   (a) Round 1
      - With probability \( p \) do:
        - Broadcast message B to all neighbors(n)
state(n) ← 1

• If n receives B in round 1, then state(n) ← 0

(b) Round 2

• If state(n) = 1 (i.e., n broadcast B but did not receive B in round 1):
  – Add n to L
  – Broadcast B to all neighbors(n).
• If n receives B in round 2, then add n to NL.

4. p ← 2p
5. GOTO Step 2

The authors show that when $M \geq 34$, success of the algorithm is, for all intents and purposes, guaranteed. Figure 5 shows three sample networks with MIS’s found by this algorithm.

![Figure 17: Networks of varying sizes and topologies for which a minimally independent set (MIS - red circles) is easily found using the distributed algorithm of [1], inspired by fruitfly neural development.](image)

Notice that each unassigned node makes a simple stochastic decision on each pass through round 1: whether or not to broadcast B, which constitutes declaring its intention to become a leader node. These declarations, when met by similar messages from a neighbor, simply cancel one another: neither becomes a leader (on this pass). Initially, these declarations occur infrequently, but each round through the outer loop doubles p, leading to more declarations among the remaining uncommitted nodes. Thus, each node exhibits a probabilistic try-and-try-again behavior until either its eagerness is rewarded (thus gaining entrance to L) or its passivity is punished by an eager neighbor, thus relegating it to NL. The individual search behaviors are quite simple, but the end result is the emergent solution to a complex problem.

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