Investigating the Emergence of Multicellularity Using a Population of Neural Network Agents

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Abstract. This paper expands Mosaic World, an artificial life model, in order to directly test theories on the emergence of multicellular life. Five experiments are conducted and demonstrate that both the presence of predation and accidental aggregation are sufficient conditions for the transition to multicellularity. In addition, it is shown that division of labour is a major benefit for aggregation, and evolves even if aggregates 'pay' for abilities they do not use. Analysis of evolved results shows multiple parallels to natural systems, such as differentiation in constituent members of an aggregate, and life-like, complex ecosystems.

1 Introduction

Explaining the transition from single cells to multicellular organisms is one of the key challenges faced by evolutionary theory. A multicellular organism is comprised of more than one cell that are in physical contact; these cells are specialised (or differentiated) to perform specialised tasks - and their activities are coordinated, at least with regards to some key functions. Multicellular life, which is believed to have independently arisen multiple times in the different kingdoms [3], is evident even in the most ancient fossils dating some 3.5 billion years [18]. Multicellularity can be achieved in two ways: through aggregation and through cell division accompanied by adhesion.

Although it is accepted that for this transition to repeatedly take place it must offer some advantages, no one knows for certain the conditions that led to the original emergence of multicellularity, nor how it emerged. One view is that the transition to multicellularity occurred by accident, caused by a mutation that prevented offspring cells from separating [3], and that at first there were no advantages. In this scenario, the benefits came later, thus causing the selection of the organism. Another theory suggests that predation pressure was one of the causes leading to the emergence of multicellularity, as multicellular organisms would be more resistant to phagotrophy (ingestion of whole prey) [19]. This theory was tested by exposing a unicellular organism, Chlorela vylgas, to a predator. Within few generations the multicellular version of the organism, a rare mutant, evolved and was nearly immune to predation [5].

The possible advantages associated with multicellularity are numerous. One is the enhanced efficiency of dividing labour between cells [11]. This can provide advantages in feeding (e.g. efficient feeding through cooperation) and dispersion (e.g. a

larger fruiting body improves spore dispersion) [3]. The larger size may improve protection from environmental disturbances [1] and enable greater storage capacity of inorganic nutrients [9]. It also enables a greater division of labour – more cell types that offer greater specialisation [4]. Perhaps, most importantly, sheer size itself can be advantageous with regards to predation: the prey may be too large for the predators to eat and organisms may be able to move faster so could better catch prey or escape predation (e.g., in water environments [2]).
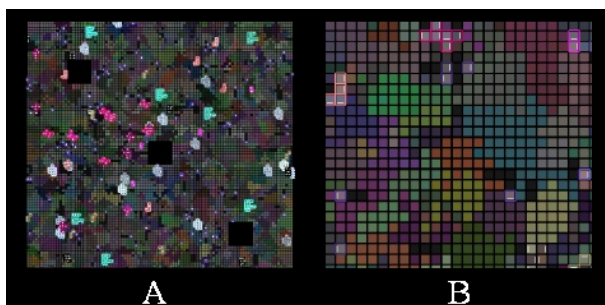

Fig. 1. (A) A screenshot of Mosaic World. (B) A close-up of Mosaic World.

It is important to emphasise that a group of individual cells (i.e. a colony) is not a multicellular organism. The first necessary step for this transition is that the individual cells stop competing and start cooperating; in other words, the individual cells start sacrificing their fitness for the fitness of the group [12]. Only then can cell differentiation begin and the organism becomes multicellular [10]. It is crucial that functions that limit internal conflict emerge [13]. According to some, successful complex multicellular organisms must be comprised of genetically identical members [20].

It is difficult to study events such as the emergence of multicellularity for obvious practical reasons. This is where artificial life models can greatly help. Indeed, several researchers have modelled aspects of the emergence of multicellular life: for example, Rothermich and Miller investigated the emergence of multicellularity by modelling cells using Cartesian genetic programming [15]. Bull used versions of the abstract NKC model to examine the conditions under which multicellularity is likely to occur [7]. Furusawa and Kaneko studied the origin of multicellularity using artificial chemistry [8]. Bryden modelled the macrocyst stage in slime mould in order to understand why an organism might decide to aggregate [6].

In this paper, we expand Mosaic World, a multi-agent system [16] [17]. Although originally created to understand the principles that underlie colour vision, its extensive model of evolutionary agents in a complex environment lends itself perfectly to gaining insights into the emergence of multicellularity. Specifically, we wish to explore the factors that may have provided an advantage for multicellular life when it first appeared in nature. Mosaic World is inhabited by a population of agents that sense their environment, consume food, reproduce and die. In this study, we have expanded their capabilities to include aggregation: they can now literally become multicellular organisms – reproduce as one, and divide tasks among members.

2 System

Mosaic World comprises a 2D grid of 'coloured' surfaces and is modelled after key characteristics of natural scenes. Its environment is inhabited by a population of virtual agents, 'critters', that try to survive. Survival requires consuming positive resources, and avoiding negative ones. Critters must also keep from falling from the world. There is no explicit fitness function in this model: by reproducing both sexually and asexually, the critters themselves maintain their population. Critters are instantiated with a given amount of health, and die if it drops below zero. If all critters die, a new population is generated where 80% are random critters and the rest are mutated clones of critters that showed general promising survival skills earlier in the run. By evolving the genome of the critter that determines all critter aspects and behaviour, the critter population becomes increasingly better at survival (for a more thorough discussion of Mosaic World and its critters see [16])

Critters can sense their environment through specialised sensors (called receptors), and must learn to generate behaviour accordingly. All critters are created with the ability to perform several actions, but must also learn how (and when) to perform them: moving, turning, sexual and asexual reproduction, resource consumption and predation. Each of these behaviours costs energy, so a critter must learn to balance its energy gain with its energy consumption. Additionally, every critter has a metabolism which determines the rate of energy it loses over time. The metabolic rate is determined according to the actions the critter has the capacity of performing. This attempts to model the notion that in nature, different types of cells have different energy costs (e.g. [14]) – although the costs used do not capture the mechanisms of biology in detail, the model does – in our view – present the critters with the same fundamental ecological challenges that is faced in the evolution of natural systems.

Even though at first all critters are created with the capacity to perform all actions except predation, by losing some of these capabilities (through evolution), the critters can decrease their metabolic rate – however, even a critter with no capacity to do anything still loses energy at a slow rate. Critters that lose the capacity to perform a certain action cannot perform it. The basic metabolic rate for a critter is 10 units per time step, reproduction adds 30 units, consumption adds 30 units, moving/turning adds 30 units, and predation adds 30 units. E.g. a critter that can only reproduce and move, but not eat, loses 70 energy units per time step, which is 70% of the rate of a critter that can also eat. There are two ways of gaining energy. The first is by consuming surfaces – a surface's value is determined from its colour (using a value function, see [16]). The second is by hunting for prey. However, an organism must be larger than its prey, and so, a standard critter cannot be anything other than an herbivore, and has no use for the capacity of predation.

Every critter has a brain, which is comprised of a control module (a gating network), and up to 8 secondary modules. The control module receives stimuli and determines which of the modules to activate at any given time step. Previously we have shown that this mechanism facilitates modular specialisation and increases critter performance [17]. Each of the modules is a modified 3D feed-forward neural network, and is comprised of multiple 2D layers. The visual layer, which corresponds to a standard input layer, contains receptors (input units with novel additions) which receive stimuli from the environment. Each of the secondary modules has three extra

receptors: a health monitor which receives the percentage of the critter's remaining health, an aggregate monitor which indicates whether the critter is a part of an aggregate, and if it is, the aggregate's size, and a neighbour indicator, which receives a positive signal if another critter is on the same surface as this critter. The hidden layer contains standard hidden units. The output layer contains output units, which determine the critter's behaviour: turning, speed of movement, reproduction (sexually or asexually), resource consumption, predation, join or split from an aggregate.

In terms of evolution, every aspect of the critter brain is evolvable: weight values, module topology (number of hidden units, connectivity, etc) and other attributes (e.g. critter colour), as well as the actual number of modules (for a full description, see [16]). In addition, the critter can evolve (or devolve) its capacity to perform all actions: the capacity to consume surfaces, the capacity to move/turn, the capacity to prey, and the capacity to reproduce; as mentioned, this affects its metabolic rate.

Crossover takes place during sexual reproduction. Several modules (randomly determined) are cloned from one parent, and the rest are cloned from the other. The control module is recombined by 'slicing' all layers of the modules of both parents at a random point, cloning a part from each and combining these to form the brain of the offspring. In addition, the resulting brain is mutated at this point.

Mutation takes place during both sexual and asexual reproduction. The last active secondary module (as determined by the control module) and the control module are subject to several types of mutations; (i) Mutation operators that change receptor attributes. (ii) Mutation operators that change module topology (iii) Mutation operators that change the weight values. Additionally, the brain has its set of mutations (add module, delete module, duplicate module), a mutation that changes the critter's colour and a mutation that change the critter's behavioural capacities (6% per action).

2.1 Aggregation in Mosaic World

In order to investigate the emergence of multicellularity, mechanisms for critter aggregation have been added. An aggregate can comprise up to 25 adjacent critters in any form within a 5x5 square, and is subject to all the costs and limitations that critters incur. Two goals were aimed for: first, the usage of neural networks and sensors within critters is intended as a functionally equivalent model of gene regulatory networks and cellular receptors. Also, by making the aggregation methods optional, we enable evolution to discover the utility (or not) of aggregation - there is no bias towards multicellularity or differentiation and no requirement for critters to aggregate.

Aggregates can use all abilities of their constituent members: if no members have the capacity to perform certain actions, the aggregate cannot perform them. Decisions for reproduction, preying on critters/smaller aggregates, and splitting are determined 'democratically'; an aggregate performs these only if at least half its members wish to. Members that have lost the capacity to perform an action do not participate in this decision process. When critters form an aggregate, their genomes merge (see fig. 2). The aggregate genome is the combined genomes of its members, with an additional gene indicating the member's position in the aggregate. The genome defines all the traits of the aggregate, and by definition, of its comprising critters.

Aggregates pool the energy of their constituent members; an aggregate's current and maximum health levels are the combined total of its members' current and

maximum health levels. Similarly, an aggregate's metabolism is the combined metabolic rates of its members. Aggregates enjoy the combined sensing capabilities of all their comprising members: every individual critter senses the environment, and can affect the behaviour of the aggregate. In addition, every member that has the capacity to consume can still decide whether to consume a surface or not, although it is still subject to the same limitations faced by critters (i.e. it cannot consume while moving, which depends on other members of the aggregate as well). The energy gained (or lost) is added to the aggregate's energy pool.

Location in aggregate [2,2]				Location in aggregate [2,3]			
Eating	Movement	Predation	Reproduction	Eating	Movement	Predation	Reproduction
true	false	true	false	false	true	false	true
-Begin control module Receptor (location [0,2], peak [430nm], tuning [0.25], on) Hidden (location [0,0]) Hidden (location [0,1]) * Weight (Rec[0,2], Hid[0,0], val[0.83], on)				-Begin control module Receptor (location [0,0], peak [400nm], tuning [0.003], on) Receptor (location [0,1], peak [470nm], tuning [0.01], on) Receptor (location [-1,0], peak [550nm], tuning [0.02], on) Receptor (location [0,-1], peak [630nm], tuning [0.09], on) Receptor (location [1,1], peak [690nm], tuning [0.5], on)			

Fig. 2. Sample aggregate (size 2) genome; most genes for critters are not shown (see [16])

An aggregate's movement is determined by its members, and is effectively their combined movements. Since aggregate members can turn inside an aggregate, an aggregate's overall movement depends on its members' individual orientations. Consequentially, the movement of an aggregate is difficult to coordinate. The movement and turning energy costs are identical to those of an ordinary critter – this models multicellular organisms using flagellates for swimming [2]. An aggregate does not fall from the world as long as its central member is still on it.

Aggregates can prey on critters and smaller aggregates. An aggregate must be larger than its prey to consume it, and must physically overlap at least 75% of it. Preying may not kill the target: only some of its energy is transferred to the aggregate (80% of full capacity). Preying also incurs an energy cost that depends on an aggregate's size.

Aggregates can only reproduce asexually. To reproduce, an aggregate must not move for a given number of time-steps and must also transfer a percentage (20%) of its maximum health to its offspring. All reproduction attempts incur an energy cost relative to the aggregate's size regardless of their success. When an aggregate reproduces, all its members are cloned and mutated (similarly to standard sexual reproduction). The members' spatial position is also copied, thus, cloning the aggregate's shape as well. There are three types of mutations, which may affect the metabolic rate of the offspring. The *clone element* mutation causes one of the offspring's members (randomly determined) to be cloned twice at a given probability (4%). The new member is attached randomly to an existing member. The *delete element* mutation (4%) causes an offspring's member (randomly selected) not to be copied. The picked member must not be the only connection between two parts of the aggregate (it cannot split the aggregate in two). The *shift element* mutation (4%) causes an offspring's member (randomly picked) to change position (altering the aggregate's shape).

There are two ways for critters to form an aggregate; each is used in different experiments. **Aggregation by choice** enables critters to aggregate with other willing

critters and aggregates that are in immediate contact with it. A critter may be in 'join' mode, where it adheres to any willing organism it is in contact with, 'neutral' mode where it does not initiate aggregation, but adheres to any other organism that attempts to adhere to it, and 'split' mode where it never aggregates. **Accidental aggregation** causes a percentage (4%) of every reproduction to result in a small (size 2) aggregate – this models an offspring that does not separate from its parents during reproduction. In this setting, aggregates cannot split or grow during their lifetime.

Aggregates cannot increase their size by joining other organisms; however, a critter attempting to join an aggregate succeeds and adds its energy to the aggregate (with a corresponding increase in its metabolic rate). Aggregates can also decide to split – this causes the aggregate to split to its individual members. When an aggregate splits, every critter receives the appropriate part of the full genome.

3   Experiments

Five experiments were run with the aims of: (i) obtaining data that will directly test existing theories for the emergence of multicellularity in nature; (ii) examining whether evolved aggregates share characteristics common to natural multicellular systems (i.e. differentiation); and (iii) analysing the evolved ecosystems and discerning whether there is any consistent correspondence between the structure of the aggregate and its ecosystem. In each experiment, the environmental conditions are set to emulate conditions suggested to have affected the emergence of multicellularity. The data collected measures the percentage of runs in which aggregation occurred. Additionally, a representative aggregate is taken from all runs (where applicable) and its genome analysed; this data, together with the population statistics is used to characterise the type of ecosystem that was evolved. Behavioural analysis of aggregates is done by presenting the selected aggregates 500 random surfaces at two levels of consumption ('full' and 'eaten') while recording their actions; this enables characterising the behaviour of members of the aggregate and understanding the task they perform.

All experiments require a random population of evolving individual critters to be placed in a test world, and end after 400,000 time steps. Once finished, the critter population is stored and analysed. Each experiment is repeated at least 10 times.

Hypothesis 1: predation is sufficient to cause the emergence of multicellularity.
Three experiments examine the hypothesis and attempt to discern what aspect influences multicellularity: the *ability to prey* or *the presence of predators.* In all runs, the aggregation mode is 'aggregation by choice'.
Experiment 1: 'predation' is disabled - aggregates must be herbivores.
Experiment 2: conditions identical to exp. 1, however, every 1000 time steps, 7 sterile predators are placed in the population. These predators cannot reproduce, split, or consume surfaces, and die unless they can catch prey. Furthermore, they are very small (size 2), and so can only eat critters but not other aggregates.
Experiment 3: 'predation' is enabled - evolved aggregates may prey on organisms.

Hypothesis 2: accidental aggregation is a sufficient condition to cause the emergence of multicellularity.
Experiment 4: the aggregation mode is set to 'accidental aggregation'. 'Predation' is disabled so it would not affect aggregation. This experiment explores whether

statistics alone - random occurrence of aggregation - is enough to initiate multicellularity without any guiding selection pressure.

Hypothesis 3: member differentiation is important to multicellular organisms.
Experiment 5: the ability of aggregates to evolve the capacities for different behaviours is turned off – in other words, the aggregates' differentiation is disabled – they are always capable of performing all actions. A secondary effect of this condition is that evolved aggregates have multiple redundancies of all behavioural capacities, consequentially, a very high metabolic rate. The aggregation mode is set to 'aggregation by choice', and 'predation' is enabled (to encourage multicellularity).

4   Results

Table 1 shows the percentage of runs that evolved aggregates for every experiment. As the data shows, preventing evolution of predators when critters 'choose' to aggregate results in no aggregates evolving (exp. 1). However, the presence of predators is enough to encourage some aggregate formation (exp. 2). When predators can be evolved, aggregates form very frequently (exp. 3). Furthermore, accidental aggregation is sufficient to cause aggregation quite frequently even when predators cannot evolve. Last, although differentiation is disabled, multicellularity still occurred according to exp. 5, albeit less than when differentiation is enabled (exp. 3).

Table 1. Percentage of runs that evolved aggregates for every experiment

#	Experiment	% with Aggregates
1	Aggregation by choice, predation disabled	0.00%
2	Aggregation by choice, predation disabled, sterile predators present	30.00%
3	Aggregation by choice, predation enabled	76.92%
4	Accidental aggregation, predation disabled	60.00%
5	Aggregation by choice, predation enabled, differentiation disabled	60.00%

During the analysis of the representative aggregates and ecosystems, it became apparent that there are recurring patterns. Three types of aggregates and four types of ecosystems that repeatedly emerged are summarised in fig. 3 with details of a run that exemplified them. Since the number of shapes and structures the aggregates evolved was large, 4 aggregates were picked for close analysis (fig. 3). Aggregates A,B,C were picked from exp. 1. Aggregate D was picked from exp. 5 (no differentiation).

Aggregate A: Critters in aggregation: 6. Classification: relatively unoptimised carnivore. Metabolic rate: 270 units. Critter tasks: critters (C2)(C4) Splitting. (C3) Eating, reproducing, moving/turning, splitting, preying. (C5) Eating, reproducing, preying. (C1)(C6) No task ('fat cell').

Aggregate B: Critters in aggregation: 6. Classification: optimised herbivore. Metabolic rate: 210. Critter tasks: critters (C3) Eating, moving/turning. (C5) Eating, splitting. (C6) Eating, reproducing, splitting. (C1)(C2)(C4) No task.

Aggregate C: Critters in aggregation: 3. Classification: 'coral' carnivore with complete division of labour. Metabolic rate: 90. Critter tasks: critters (C1) Reproducing. (C3) Preying. (C2) No task

Aggregate D: Critters in aggregation: 9. Classification: carnivore. Metabolic rate: 1170. According to genome, members can do all tasks. However, the behavioural test revealed that although every member can perform all tasks, effectively each only performs some tasks: critters (C1) Eating, preying, reproducing, turning. (C2)(C6) Eating, preying, reproducing. (C5) Eating, preying, reproducing, moving, turning, splitting. (C3)(C4)(C7)(C8)(C9) Eating, preying.

Types of aggregates:
Herbivore: an aggregate that consumes surfaces and cannot prey.
Carnivore: an aggregate that can only prey and cannot consume surfaces.
'Coral' Carnivore: a carnivore that cannot move and only eats prey that moves into its area.

Types of ecosystems:
Herbivorous Aggregates: this ecosystem is dominated by herbivorous aggregates - there are few or no unaggregated critters. E.g. exp. 1, run 5: total of 248 herbivorous aggregates, 16 critters.
Coexistence - Herbivorous Aggregates and Critters: this ecosystem contains stable amounts of herbivorous aggregates and unaggregated critters. E.g. exp. 4, run 4: total of 20 herbivorous aggregates, 227 critters.
Predator/Prey: this ecosystem contains stable amounts of carnivorous aggregates and unaggregated critters. E.g. exp 1, run 11: total of 45 carnivorous aggregates, 158 critters.
Predator ('Corals')/Prey: this ecosystem contains stable amounts of 'coral' carnivorous aggregates and unaggregated critters. E.g. exp 1, run 2: 280 'coral' carnivorous aggregates, 149 critters.

Fig. 3. Types of aggregates and ecosystems that were repeatedly evolved during experiments
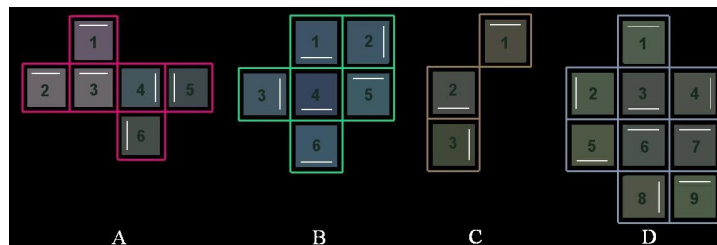

Fig. 4. Four representative aggregates. Note: every member has an orientation (the white line).

Table 2. Average size of aggregate per type of ecosystem (classified using fig. 3)

Type of Ecosystem	Ave. Size of Aggregate
Herbivorous Aggregates	2.22
Coexistence: Herbivorous Aggregates and Critters	3.04
Predator/Prey	5.64
Predator/Prey ('Corals')	2.06

Table 2 shows the average size of aggregates per type of ecosystem (using the definitions of fig. 3). It seems that the type of ecosystem greatly affects the size of the aggregate: carnivores are significantly larger than herbivores and 'coral' carnivores. In addition, herbivorous aggregates that coexist with critters are larger than herbivorous aggregates that dominate their ecosystem.

5 Discussion

Our results suggest several conclusions. First, it is clear that in our system, when there is no threat of predators and aggregation is 'by choice', there is not enough selection pressure for critters to form aggregates – individual critters are more adequate as they need less energy and can more easily reproduce. However, the threat of predation is enough to cause critter aggregation, primarily in order to gain protection from predation, but also to obtain a new energy source: prey. In addition, leaving aggregation to random chance by enabling accidental aggregation is sufficient to induce multicellularity: although at first aggregates are inefficient in comparison to critters, eventually evolution learns to exploit the benefits multicellularity offers. Last, in runs where the aggregates could not differentiate, the percentage of multicellularity was somewhat lower, supporting the notion that differentiation is important. More so, of particular interest is the fact that evolution found a way to implicitly differentiate: although the aggregate's members had the capacity to perform all behaviours, *and the aggregate 'paid' the metabolic rate cost for these capabilities,* most members still chose **not to** perform certain tasks (e.g., aggregate D in fig. 4). This result clearly supports the idea that differentiation is a major benefit for aggregation.

Even from only viewing the 4 representative aggregates, it is possible to state that many shapes and specialisations were evolved, ranging from complete redundancy to a complete division of labour. A common pattern was to evolve several 'eater' members (as each member eats independently), a single 'mover' member (to minimise coordination issues), and several prey/reproduce/split members (allows several critters to affect the overall behaviour of the aggregate - e.g. fig. 4, A, B). Also, members without any capabilities were often evolved and were apparently used as 'fat cells'; their only purpose was to grant the aggregate a larger maximum health capacity.

Of particular relevance is that there was a consistency in the different types of evolved ecosystems. Furthermore, different types of aggregates appear to require different structures (indicated by the consistency in average size). This is unsurprising: herbivores eat often while carnivores have to catch their prey so are not likely to eat as frequently, thus, require larger energy storage. Another explanation is the predation ability: larger predators can eat more types of organisms, and are harder to eat. The emergence of 'coral' carnivores was intriguing: in these ecosystems, there were enough critters that 'corals' would rarely starve and had no need to move. As 'corals' reproduced in the vicinity of their parent, reef-like structures consistently emerged.

Our system has investigated perhaps the earliest, most primitive form of multicellularity using the notions of aggregation for growth and fission for reproduction. This can be seen as analogous to the hypothesised symbiosis that resulted in mitochondria becoming incorporated into modern cells [11]. Multicellular organisms comprising more complex cells are capable of developmental growth via mitosis and differentiation, and reproduction via a specialised gamete cell, resulting in all cells sharing identical genes and thus all genes benefiting from the collaboration. This work can be seen as the first evolutionary step towards this ultimate form of multicellularity.

6 Conclusions

The results of our experiments support the theories examined in the paper: both the presence of predation and accidental aggregation are sufficient to initiate the transition to multicellularity. The model also shows that differentiation is indeed a major benefit for aggregates and it will evolve even if aggregates obtain it by not using capabilities they had 'paid for' with an expensive metabolism. Last, our evolved results shared many parallels with natural systems, from the emergence of a division of labour within an aggregate, to the life-like dynamics of the evolved ecosystems.

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