Current state of research - approx. 5 relevant publication. one page max

Description of questions - originality and significance to the field (approx. 2 pages)

Methods (clearly described) - two pages

Not required:

comprehensive bibliography

time plan

Research outline (five pages max)

* **The current state of research** should first be briefly described and underpinned by approximately five relevant publications from the research area. (one page max)
* The outline should focus on a clear **description of the questions** you intend to address in your research, their **originality and significance** for the advancement of the research field. (approx. two pages)
* Furthermore, the academic **methods** to be used to achieve these goals should be clearly described. (approx. two pages)
* A comprehensive bibliography and a detailed time plan are not required.
* The research outline should comprise approximately five pages in total. Should you significantly exceed this length, you may be asked to cut it down to approximately five pages.
* For the purposes of evaluation it must be clearly demonstrated that you yourself have drawn up the main contents independently and agreed them beforehand with your host. Any contents contributed by the host institute must be attributed accordingly.

From Christopher Harris’ blog:

Overall, fish and mammals have similar brain topologies. The fish forebrain pushes forward during development rather than wrapping itself around the lower brain regions as it does in mammals ('eversion' rather than 'evagination'). The fish pallium is nevertheless homologous to the mammalian cortex, with distinct sensory and motor regions, although in fish a disproportionate amount of visual processing takes place in the tectum, a homologue of the mammalian superior colliculus ([Salas et al., 2003](http://www.ncbi.nlm.nih.gov/pubmed/12937346)). Likewise, the subpallium of fish corresponds to the mammalian basal nuclei, including the striatum, the key recipient of dopaminergic reward in the mammalian brain. So far so good; most forebrain structures involved in reward processing appear to be conserved among vertebrates, and cognitive abilities previously thought of as exclusive to 'higher' animals (i.e. birds and mammals) are now being studied also in fish ([Salas et al., 2003](http://www.ncbi.nlm.nih.gov/pubmed/12937346)).

However, the fish dopamine supply is all over the place, quite literally. Dopamine neurons are found throughout the zebrafish brain, *except for* the midbrain, where almost all mammalian dopamine neurons are located. A few dopaminergic clusters in the hypothalamic region project to the subpallium/striatum and were previously thought to be homologous to the mammalian mesolimbic dopamine system, but more recent research has debunked this view ([Schweitzer et al., 2011](http://www.ncbi.nlm.nih.gov/pubmed/21567980); [Tay et al., 2011](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3105308/)). There simply is no mesencephalic dopamine system in the zebrafish brain. Nevertheless, fish *are* capable of both classical and operant reward conditionning ([Valente et al., 2011](http://rubenportugues.net/valente_et_al.pdf)), including dopamine-dependent place preference, and even intracranial self-stimulation ([Boyd & Gardner, 1962](http://www.ncbi.nlm.nih.gov/pubmed/13872148)), so what gives?

As far as I can tell, dopaminergic reward mechanisms remain remarkably poorly understood in the zebrafish, despite intense research in recent years on the neurobiology and genetics of this model system. Most of the dopamine in the zebrafish subpallium/striatum appears to originate in local dopaminergic projections from neurons whose cell bodies are distributed throughout the subpallium/striatum ([Tay et al., 2011](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3105308/)). These neurons look like plausible mediators of reward, but their input, physiology and function remains unknown(!). The function of the ascending dopaminergic fibres that project to the subpallium/striatum is also not known. Moreover, pretectal dopamine neurons arborize extensively in the tectum, suggesting a possible role in visually guided reward-seeking behaviour, such as hunting.   
  
Plenty of reward-related research to be done in other words, but what do we make of this? [Hills (2006)](http://csjarchive.cogsci.rpi.edu/2006v30/1/s15516709HCOG0000_50/s15516709HCOG0000_50.pdf) argues that the evolution from anamniotes (fish and amphibians) to amniotes (reptiles, birds and mammals) involved a number of changes regarding dopamine and reward-processing, including: 

* The number of cortical imputs to the striatum increased significantly
* The number of dopaminergic inputs to the striatum increased significantly
* The synaptic machinery that allows dopamine to modulate cortical input to the striatum expanded to include DARPP-32
* The dopaminergic signal transitioned from representing the presence of food to representing the expectation of reward more generally

As a consequence of these changes, Hills argues, amniotes were able to apply the neural mechanisms of foraging (e.g. 'area-restricted search', the ancestral function of dopamine, present even in worms and mollusks ([Barron et al., 2010](http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2967375/))) to search for *any* kind of information or goal, whether internal or external to the brain; a profoundly powerful adaptation. In addition to the four changes suggested by Hills I would add: 

* Dopaminergic cell clusters became centralized in the midbrain

This centralization, together with some specific adaptations, such as gap junctions connecting dopaminergic axons, allowed amniote brains to generate a single, scalar reward signal that adjusts dopamine concentrations homogenously throughout the forebrain.   
  
I think what I need to ask now is: how does the more ancient dopamine reward system of fish actually work; what forms of reward-processing is it capable of; and does its distributed anatomy offer any advantages to the animal or to attempts to understand the neural basis of reward-based cognition?

projects:

mimic presence of predators with optogenetic activation of ORNs

induced learning with closed-loop optogenetic activation of dopaminergic pathways

* first find dopaminergic reward neurons
* silence to find what is actually rewarding about collective behaviour
* activate to create fictive learning regimes

group-level decision making with modified VCRDM

* Goal 1: to demonstrate emergent intelligence of large animal groups by group-size dependent improvement in a challenging discrimination task.
  + Schadlen’s group uses the coherence of visual stimuli to precisely vary the difficulty of decisions, in order to observe the integration of conflicting information in neural networks in a drift-diffusion model.
  + We hypothesize that groups of schooling fish integrate conflicting information in an analogous process to neural integrators
  + Many fish species exhibit strong negative phototaxis, as demonstrated in Berdahl et al 2013
  + give a rotating stimulus, fish will follow
  + give conflicting ones, group should distinguish majority direction
    - first establish that groups perform more accurately than alone
    - with high res tracking, observe the formation of emergent decisions
* Goal 2: to use schooling fish as a model of complex information integration and observe the resolution of complex conflicts.
  + In goal 1, we will demonstrate the ability of this system to integrate complex information and establish a method for guiding fish behaviour
  + Using moving light patterns, steer fish schools into configurations that will cause conflicts.
  + The system should operate with dual-phase evolution. By steering fish with projections, we should be able to induce fragmented and connected states and observe the transitions between them.
  + Dual-phase evolution vs Self-organized criticality
* Goal 3: System memory (hysteresis)

1. Demonstrate that large groups can interpret global trends from locally-noisy stimuli through VCRDM
   * Establish the method of using visual stimuli to drive behaviour of schooling fist (cite Berdahl and pilot experiments).
   * Explore the relationship between group size and stimulus coherence to identify the efficacy of collective decision making.
   * Compare the relationship from (2) across species to demonstrate the importance of the “biological filter”. The parameters that vary between species will give some indication of the function of the filter.
   * Hysteresis
2. Characterize individual responses to stimuli to interpret “filter” functions of fish.
   * What specific sensory inputs lead to distinct and/or stereotyped behavioural responses in individuals and groups?
   * Explore the function of the network from one level up, interpeting how filtered information is processed.
   * Are there higher-level functions of collectives that are due to the processing of filtered information? In other words, what phenomena of collectives cannot be explained by purely physical interactions?
3. Use visual stimuli to create critical network environments.
   * Using knowledge of behavioural responses to visual stimuli, first establish configurations with high conflict, then observe the resolution back to low-conflict states.

Emergence:

Through mechanistic understanding of binary decision making by various collective systems, we will learn complementary concepts about emergent intelligence. Each system can provide a structured view of the solution, although some aspects of the solution are obscured due to experimental limitations.

Whether in swarms of animals, networks of neurons, or colliding molecules, emergent properties of “repeated systems” share commonalities across scales. Concepts of emergence, no matter from whence they are derived, are relevant to other collective systems.

Emergent properties can inform about the inherent properties of agents that are not easily observed or recognized at the individual level.

There are advantages to using biological systems over computer generated models.

Scaled examples of analogous phenomena:

* Water molecules flowing into a drain. Brownian motion, latent flow, and weak centripetal forces act on still water. Rotational flow emerges as the only non-random force (earth’s rotation) from the weakest forces applied billions of times. (Shapiro, A.H (1962). “Bath-tub Vortex”. Nature, 196(4859):1080-1081.)
* Neural processing of noisy signals (ex VCRDM). Local estimates are summed and integrated, and majority emerges.
* Milling fish.
* SEED-SCALE

Top-down feedback in emergent systems

can lead to scale-dependent properties (See, e.g., [*Korotayev, A.*](https://en.wikipedia.org/wiki/Andrey_Korotayev); Malkov, A.; Khaltourina, D. (2006),[*Introduction to Social Macrodynamics: Compact Macromodels of the World System Growth*](http://cliodynamics.ru/index.php?option=com_content&task=view&id=124&Itemid=70), Moscow: URSS,[*ISBN*](https://en.wikipedia.org/wiki/International_Standard_Book_Number) [*5-484-00414-4*](https://en.wikipedia.org/wiki/Special:BookSources/5-484-00414-4)

)

Current state of Research:

Five publications:

1. Something from Schadlen
2. Berdahl
3. Ioannou 2016

**Emergent information processing**

Throughout the natural world, we observe phenomena that result from the collection of many small entities to a larger, emergent entity. For example, the structural properties of water prescribe molecular interactions that ultimately give rise to the characteristic shape of snow flakes. In this case, the supervening properties of snowflakes emerge from the local interactions of water molecules on a micro scale, without information or supervision on a macro scale. These emergent properties are novel, and not observed in the water molecules themselves. Thus, decentralized processes that assemble entities into supervening entities form the basis of emergence.

Emergence is pervasive in living systems. Many animal species engage in sophisticated collective behaviours, such as swarms, flocks, or colonies, from which new functions emerge.

Intelligence:

Slime moulds solve mazes (Reid and Beekman 2013).

Animal groups engage in collective behaviours that often exhibit emergent properties. Although the motivation toward collective behaviour varies from one species to another, that supervene the capabilities of the individual animals themselves.

**Collective Intelligence in Fish Models**

The field of collective intelligence has been studied for over a century (REF Galton 1907 (foundin in Ionnou 2016)). Despite its longevity, a fundamental component of collective intelligence, the mechanism of improved cognitive performance, remains difficult to discern. Ioannou (2016) summarized this fault, and divided the mechanisms into four broad categories: individual-level, centralization, leadership, and swarm intelligence. Individual-level cognitive abilities derive from individuals' re-allocating cognitive processes in response to group size. Centralization and leadership both involve groups selectively processing or distributing information from selected individuals. Swarm intelligence, on the other hand, occurs when information flows throughout the group and no individuals are particularly influential. Ioannou argues that only swarm intelligence is a truly emergent property (\*\*\*DOUBLE CHECK THIS). Examples of swarm intelligence are prominent in some species, mostly social insects, but the existence of swarm intelligence remains a topic of debate for others, particularly schools of fish.

Studies of fish schooling have mainly focused on performance of a few ecologically relevant tasks, such as predation response or foraging. In these tasks, some animals receive strong cues, and others receive little to no information. This unequal distribution of information results in obligatory leader-follower relationships. It is therefore impossible to distinguish between models of centralization/leadership or distributed (aka “swarm”) intelligence. As a notable exception, Berdahl *et al* (201X, REF) demonstrated collective perception in fish schools by exposing the group to patterned light/shade gradients. In this study, the collective responses to local light intensity affected an emergent optimization response. Importantly, the information was distributed across the entire group; decentralized information was processed in a decentralized way to produce a meaningful response. Therefore, with the appropriate experimental design, the collective behaviour of fish can serve as a model of swarm intelligence.

QUESTIONS

Can

collective behaviour and collective intelligence

fish as a model system

analogy to neural processing

collective problem solving and/or processing

cyclones/vortices

slime moulds

“link individual interaction mechanisms to emergent collective patterns. “ (Reid and Latty, 2016)

Throughout the natural world, we observe emergent phenomena that derive from the collective activity of smaller entities. For example, snowflakes take their characteristic geometry due to millions of molecular interactions of water molecules. Emergence can be an extremely powerful mechanism for extracting weak signals from noisy systems. For example, despite turbulent air currents, rotating cyclones robustly report the direction of rotation of the Earth due to the Coriolis effect on the atmosphere. Perhaps the most fascinating emergent properties are observed in the collective behaviour of animal groups such as insect swarms, bird flocks, and fish schools. Some animal species, by congregating and coordinating their behaviour, avoid predation or forage more effectively than solitary animals, and perform tasks that would be impossible for individuals to accomplish alone.

Sophisticated tasks require cognitive functions at the group level, termed collective intelligence. A fundamental component of collective intelligence, the mechanism of improved cognitive performance, remains difficult to discern. Ioannou (2016) summarized this fault, and divided the mechanisms into four broad categories: individual-level, centralization, leadership, and swarm intelligence. Individual-level cognitive abilities derive from individuals' re-allocating cognitive processes in response to group size. Centralization and leadership both involve groups selectively processing or distributing information from selected individuals. Swarm intelligence, on the other hand, occurs when information flows throughout the group and no individuals are particularly influential. Ioannou argues that only swarm intelligence is a truly emergent property (\*\*\*DOUBLE CHECK THIS). Examples of swarm intelligence are prominent in some species, mostly social insects, but the existence of swarm intelligence remains a topic of debate for others, particularly schools of fish.

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Emergence is an extremely powerful mechanism for extracting weak signals from noisy systems. For example, cyclonic weather systems rotate in directions defined by the Coriolis effect, or the force of the Earth's rotation. The Coriolis effect is extremely weak relative to other air currents, but it is slightly imbalanced relative to other forces. Despite the turbulent atmosphere, rotating cyclones robustly report the rotation of the Earth through emergence.

Emergence is an extremely powerful mechanism for extracting weak signals from noisy systems. For example, despite turbulent air currents, rotating cyclones robustly report the direction of rotation of the Earth due to the Coriolis effect on the atmosphere.

Throughout the natural world, we observe large-scale phenomena that derive from the combined activity of smaller entities, termed “emergence”. Emergence can be an extremely powerful mechanism for extracting weak signals from noisy systems. For example, despite turbulent air currents, rotating cyclones robustly report the direction of rotation of the Earth, due to the Coriolis effect on the atmosphere. Perhaps the most fascinating emergent properties are observed in the collective behaviour of animal groups. Some animal species, by congregating and coordinating their behaviour, avoid predation or forage more effectively than solitary animals, and perform tasks that would be impossible for individuals to accomplish alone.

Sophisticated collective tasks require cognitive functions at the group level, or collective intelligence. The mechanism of improved cognitive performance is difficult to discern, particularly in schooling fish (Ioannou, 2016 REF). Studies of fish schooling have mainly focused on performance of a few ecologically relevant tasks, such as predation response or foraging. In these tasks, some animals receive strong cues, and others receive little or no information. This unequal distribution of information results in obligatory leader-follower relationships. It is therefore impossible to distinguish between models of centralization/leadership or distributed, collective intelligence. As a notable exception, Berdahl *et al* (201X, REF) demonstrated collective perception in fish schools by exposing the group to patterned light/shade gradients. The collective responses to local light intensity affected an emergent optimization response. Importantly, the information was distributed across the entire group; equally-distributed information was processed in a decentralized way to produce a meaningful response. Therefore, with the appropriate experimental design, the collective behaviour of fish can serve as a model of collective intelligence and cognition.

Collective cognition is a fascinating process by which individuals' movements and interactions effectively perform some calculation about the environment on the group level. In many respects, collective cognition resembles individual cognition, in which networks of neurons integrate noisy information to generate understanding of the environment of the individual. Neuronal cognition has been studied extensively, particularly with respect to decision making (REF Shadlen & Kiani, 2013). Insights from decision making studies may provide a framework of questions and concepts with which to explore collective cognition. A prominent tool in decision making studies is the use of Variable Coherence Random Dot Motion (VCRDM, Shadlen & Newsome, 1996) to vary the difficulty, noise, and variability of sensory information that contribute to a decision. Employing similar strategies in a group cognition task may provide unprecedented control of parameters that determine collective behaviour.

Research questions:

Previous studies of collective intelligence have focused on ecologically important areas, including predator avoidance and foraging. Most of these studies involve tasks that rely on the transfer of information between members of a group to generate a collective response. Still others have focused on the relationship between group sizes and the speed and accuracy of collective responses. However, the full essence and power of collective intelligence have not yet been demonstrated in biological systems. Here, I propose a novel method to study collective decision-making and conflict resolution. My general goal is not to describe the collective mechanisms by which animals achieve ecologically-important cognitive tasks. Rather, my aim is to demonstrate and characterize the extent to which collective animal groups can process information.

Objective 1: Demonstrate decision making in fish schools.

Decision-making studies in primates aim to resolve how networks of neurons integrate noisy information to make a decision. For this task, experimenters present primates with visual stimuli of moving dots that move either left or right with variable coherence (“Variable coherence random dot motion, or VCRDM”, Shadlen & Newsome, 1996). The primate's task is to determine whether the majority of motion is leftward or rightward. By varying the parameters of VCRDM stimuli and recording from specific brain regions, it has been possible to characterize information processing with tremendous specificity (REFS).

Large schools of fish at swim in circular arrangements, called milling. Typically, milling is interspersed with translational movements, and milling direction changes frequently. These directional changes are a result of hundreds or thousands of individual conflicts among individuals, and therefore milling direction serves as a binary readout of a collective decision.

Through recent pilot experiments, I have found that schools of fish (sunbleaks, sticklebacks, zebrafish) robustly follow moving dots projected onto the arena floor (outlined in methods; Bath & Couzin, unpublished data). With this method, it is possible to control milling direction by presenting clockwise or counter-clockwise rotating stimuli. By varying the coherence of rotation direction, it is possible to conduct experiments analogous to primate VCRDM, using large (1000 or more individuals) schools of fish.

With an experimental paradigm analogous to VCRDM in primates, it is possible to address questions of information processing in collective systems. Do larger groups perform better at discrimination tasks? To what extent do collective decisions resemble neural decisions, with respect to relationships among coherence, variability (etc) of VCRDM stimuli? To what extent do they differ? Addressing these questions will be crucial to determine the universality of decision-making theory. Assuming that some properties of decision-making processes are universal, collective decisions may provide a complementary paradigm to decision-making studies. In particular, with respect to connectivity. In neural decision-making networks, the precise connectivity of neurons is impossible to observe, and thereby precise interaction of information is unknown. In collective systems, the analogous component to neural connectivity is the local interactions of individuals. These interactions, through computer tracking, can be observed and resolved, providing a framework to observe information processing of the entire system.

There are of course many differences between neural processing of decision-making and the collective counterpart. Neural processing requires constant connectivity and is arranged in a hierarchical way, with motion sensitive layers, summating layers, confidence layers, etc. On the other hand, collective processing exhibits dynamic connectivity and non-hierarchical structure. Nonetheless, comparing and contrasting different solutions to similar problems will be generally informative to the problem of emergent information processing.

Objective 2: Determine filter properties of individual fish responses

Emergence in physical systems is common, but requires either extremely large systems or extremely low noise in order for supervening processes to emerge. For example, consider two circumstances in which the rotation of the Earth is detectable by the Coriolis effect. On a large scale, cyclones in the northern and southern hemispheres rotate in accordance with the unbalanced force of the Earth's rotation on the turbulent atmosphere. On a smaller scale, one can observe the Coriolis effect in the vortex created by a draining pool of water, but only if the water is very still (Shapiro, 1962).

Biological systems, on the other hand, make particularly good use of emergence to solve problems. Even in small, dynamic contexts, emergent properties reliably enable group-level functions. How do biological agents enhance the efficacy of emergence? Animals perform cognitive functions that form an additional layer of processing. Interaction of individuals serves to compare local estimates at this layer. Thus, the additional layer of processing in biological systems is likely the source of enhanced emergent properties in collective intelligence.

But what aspects of individual signal processing contribute to enhanced emergence? Presumably, there is a set of environmental stimuli that cause robust behavioural responses. Through individual closed-loop experiments (outlined in Methods), it should be possible to determine the relationship between visual stimuli and behavioural response, thus characterizing the individual-level processing of the system.

Understanding individual-level processing will provide important information for mathematical and analytical models of collective behaviour, and enhance the efficacy of external control of fish behaviour (relevant to Objective 3). Perhaps more importantly, understanding the relationship between individual processing and emergent behaviours may provide key insights relevant to information technology by distributed processes. Additionally, comparing and contrasting individual-level processing across animal species may provide insights into how specific individual processing parameters contribute to emergent behaviours at the group level.

Objective 3: Use fish schools to characterize distributed conflict resolution

Through objectives 1 and 2, I expect to refine experimental techniques for controlling the locomotion of captive fish. Given this level of control, it should be possible to create group scenarios that test specific hypotheses but that rarely occur in nature. For example, first generating two milling schools and bringing them together