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The effect of observing trained conspecifics on the rate of spatial learning, navigation strategy and motivation in goldfish, *Carassius auratus* 

> James Christopher Blane Supervisor: Prof Richard A. Holland Bangor University

Keyword: Carassius auratus, cognitive maps; spatial memory; social learning; cognition; fish;



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# THE EFFECT OF OBSERVING TRAINED CONSPECIFICS ON THE RATE OF SPATIAL LEARNING, NAVIGATION STRATEGY AND MOTIVATION IN GOLDFISH, CARASSIUS AURATUS

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### Abstract

Spatial and social cognition are two aspects of fish behaviour that have been subject to an increasing amount of research in recent years, but few have investigated potential behaviour where the two coincide. Testing the ability for an individual to socially learn a spatial task would bridge this gap in understanding. We made naïve goldfish, Carassius auratus, observe a trained conspecific navigate a T-shaped maze, and then recorded how many trials it took for them to learn the maze, as well as time taken per trial, motivation and acceptance of the food reward. We also conducted reverse trials to understand whether allocentric or egocentric navigation was being learnt. On average, it took significantly longer for the observer group to learn the maze than it did the control group. The observer group were more likely to navigate allocentrically, whereas the control group were more likely to navigate egocentrically. There was no difference between allocentric control and allocentric observer subjects, but the egocentric control learned the maze in significantly fewer trials than egocentric observers. Although the observer group took significantly more time per trial and were less motivated, they were significantly more likely to accept the food reward. Although social learning was taking place, which was apparent from their increased acceptance of the food reward, something about the social information was inhibiting the learning process, as well as influencing navigation strategy choice. In conclusion, the act of a goldfish observing a trained conspecific resulted in a slower rate of training and an increased chance that place learning is occurring. This study assists in developing our understanding of spatial memory in teleost fish, which further justifies the use of zebrafish and goldfish as model species in spatial memory experiments.

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# Literature Review – teleost fish spatial and social cognition capabilities

# Introduction

Fish cognition is a field of research which has been increasing in interest and focus (Bshary and Brown, 2014). The topics of the social and spatial cognition of fish are no exception, seeing sharp increases in studies since the 1960s (Brown et al. 2011). Social cognition is the interpersonal knowledge and perception of others and self (Beer and Ochsner, 2006), whereas Hart and Moore (1973) define spatial cognition as "the knowledge and internal or cognitive representation of the structure, entities, and relations of space". This literature review will be focusing on social learning and behaviours, spatial memory, and any overlap between the two topics. To understand the importance of these topics, it is important to understand the importance of learning in animals. The main advantage of learning is to adapt to ecological aspects that change too quickly for genetic adaptation (Johnston, 1982), such as a change in prey choice or food availability. The ways for an individual animal to learn may include observation (Zentall, 2003) and experience (Ranta and Nuutinen, 1986). The ability to socially learn, which is the ability to retrieve information through observation or interaction with another individual (Brown et al. 2006), can provide an advantage by allowing for another avenue to learn. Fish have been shown to be capable of operant and classical conditioning, habituation and associative learning (Guttridge et al. 2009). Certain species, like zebrafish, are being used as model species for behavioural neuroscience due to their ability for relational learning and episodic memory (Gerlai, 2017). This is particularly true if the experience required to gain certain information is dangerous, such as predator recognition. Some cases of sociality are acts of altruism, either in hopes to receive future benefits or to avoid costly consequences (Stevens and Hauser, 2004). Spatial memory in animals is a field that aims to investigate how animals retrieve, encode, store and present information about the external environment, typically the geography of the area surrounding their habitat (Bshary and Brown, 2014).

One reason for the increase of research in fish cognition is that fish make for optimal subject species for many cognitive experiments; they are easy to obtain, maintain and manipulate in a laboratory setting, whilst often varying in social behaviours and cognitive capabilities between species (Pouca and Brown, 2017). Furthermore, recent studies have revealed similarities in the brain structures and social behaviours between fish and amniotes (Bshary *et al.* 2014), meaning breakthroughs in the field of fish cognition could directly impact future breakthroughs in human cognition (Bshary and Brown, 2014) and social cognition (Weitekamp and Hofmann, 2014). As this literature review aims to expose, there is a lack of research investigating the potential overlap between social learning and spatial memory – especially within the fish discipline. Research into this untapped aspect of cognition may

lead to identifying more behaviours in fish, and therefore amniotes, as well as potential breakthroughs via a new perspective to old problems in social and spatial cognition. The experiment that this literature review precedes will investigate a potential overlap between social learning and spatial learning, in order to help fill this gap of knowledge. Although some studies do exist, there is a definitive gap in our knowledge of the capabilities of fish to socially learn spatial information; the little we do know does not hint at the magnitude, flexibility and ecological importance of such capabilities. This research is essential to investigate such factors, in order to go forward with more confidence and stronger foundations for future studies regarding fish cognition. Therefore, the targeted literature to be scrutinised will provide relevant topic information, and what should be taken into consideration when designing such an experiment.

This literature review is split into four sections. Firstly, it shall address the relevant research into fish brain anatomy and homogeneity to amniote brains, in order to provide a basis for the important aspects for spatial and social cognition. The second and third sections will highlight the spatial and social (respectively) capabilities of fish and other animals that may help in understanding of the behaviours that may impact the outcomes of the consequential experiment. The final section will review literature, or the lack thereof, regarding the overlap between social and spatial cognition.

## Themes

#### Brain research

The hippocampus in humans, *Homo sapiens*, is responsible for a large quantity of functions, which include cognition, memory, learning, emotion, and even some social behaviours (Anderson et al. 2006; Rubin et al. 2014), with particular importance to spatial cognition of amniotes (O'Keefe and Nadel, 1978). The amygdala plays a central role in emotional learning and memory (Balleine and Killcross, 2006), whereas the isocortex is an important mammalian part of the cerebral cortex, partly responsible for cognition and spatial reasoning in mammals (Palomero-Gallagher and Zilles, 2015). It is important to know the homologous functions between the brain parts of amniotes and fish, as egocentric and allocentric navigation are utilised in different parts of the brain (Salas et al. 2017). These all work together to process spatial information, both memory and learning in the mammalian brain. Initially, literature was conflicted about the extent of the homologous nature of fish brains and vertebrate brains. Salas et al. (1996) investigated the functions of the telencephalic hemispheres. Ablations to the telencephalic hemispheres was significantly detrimental to the performance of allocentrically-trained individuals (place). This hints that the fish telencephalon is important to complex place learning. López et al. (2000) reinforced this with a similar experiment, ablating bilateral telencephalon of mapping-strategy goldfish, Carassius auratus, finding reduced spatial capacity in the test subjects. Furthermore, Durán et al. (2000) found that bilateral lesions do not affect acquisition performance but reduces resistance of extinction. The argyrophilic nucleolar organizer region (AgNOR) in the goldfish telencephalon is also important in spatial memory. In a group of goldfish trained in a spatial task, the AgNOR areas of the dorsolateral telencephalic neurons increased greatly, suggesting increased protein synthesis when engaged in learning or memory (Vargas et al., 2000). Further homologous functions have been investigated in the spatial learning function of the telencephalon in fish, and its similarities to the mammalian hippocampus. Vargas et al. (2006) investigated the homogeneity of the pallia and the hippocampus, respectively. Goldfish either had their lateral pallia or medial pallia, ablated to then undergo geometric, feature and dissociation tests. Lateral pallia goldfish were found to have a greatly reduced ability to use geometric information, which emphasises their impaired ability to represent spatial information. This, including the fact that lateral pallia fish were more effective at being trained than medial pallia/sham individuals in featural tests, reflects an insensitivity to geometric spatial information rather than a visual/motor deficit. The lateral pallium is most homologous to the mammalian and avian hippocampus. Vargas et al. (2009) later came to a further conclusion through further experimentation, and literature, reviewing the function of the separate areas of a fish pallium. The role of the lateral pallium is spatial learning and temporal learning processes; the medial pallium is important in avoidance learning and dorsal pallia is the centre for short-term spatial and episodic memory. In addition to this, it is hypothesised that the common ancestor between mammals and fish had a more teleost fish-like brain, rather than a paleomammal brain. For these reasons, Vargas et al. (2009) suggests that the mammalian

hippocampus, amygdala and isocortex are derivatives from a primitive fish-like lateral, medial and dorsal pallia, respectively. Homogeneity of the brain structures are supported by Broglio *et al.* (2003), Broglio *et al.* (2010) and Rodríguez-Expositó *et al.* (2017).



*Figure 1. A graphic by Mueller (2012) portraying the distributions of the lateral pallia, dorsal pallia and medial pallia in a goldfish brain and a mouse brain, respectively.* 

With homologous structures and functions found in both amniotes and fish, it is possible information about the fish telencephalon may be interpolated from amniote studies. Similarly to Vargas et al (2006), it was found that lesioned pigeons, Columba livia, can learn spatial feature tasks faster than others, but were insensitive to geometric information (Vargas et al, 2004a). Sovrano et al. (2007) studied cue usage by redtail splitfins, Xenotoca eiseni, in spatial tasks leading to the theory that animals normally use metric properties of the environment in small spaces, and use landmark cues in large spaces. However, comparing to the results from chicks in an alternative study that fit this theory (Sovrano and Vallortigara, 2006), redtail splitfins prioritise geometric information more than chicks prioritise landmark information. This prioritisation of visual cues from chicks outlines a possible difference between the spatial processing of birds and fish. Reptiles, such as the red-eared slider, Trachemys scripta elegans, possess a medial cortex responsible for complex place learning and is homologous to the hippocampus (López et al. 2003a). Rodríguez et al. (2002) ran place and cue maze tasks on painted turtles, Chrysemys picta, with lesioned-medial cortexes and goldfish with lesionedlateral pallia. The turtles were unable to locate a goal when the startling location was changed, and the fish displayed impaired navigation in a place task. The reptilian medial cortex is homologous with the fish lateral pallia, and further proof for avian and mammalian hippocampus homogeneity. Likewise, reptilian medial cortex lesions result in reduced spatial functions, but not learning processes (López et al. 2003b).

Lateralisation generally refers to asymmetry in the brain in function (Rogers and Anson, 1979), a feature that was initially thought of as a human trait. Recent research has expanded our understanding on the presence of lateralisation in animals. Zebrafish, Danio rerio, have been used as a model for studies examining the role of lateralisation in vertebrates (Concha, 2004). Some other fish have laterality in sensory organs. Fish may use their right eye for novel objects (Miklóski et al. 1997), but their left eye to view social stimuli (Sovrano et al. 1999). Blind Mexican cave fish, Astyanax *fasciatus*, use the lateral line organ to detect water displacement interacting with obstacles (Hassan, 1985; Montgomery et al. 2001). An experiment conducted by De Perera and Braithwaite (2005) showed that in novel areas, blind Mexican cave fish prefer using the right sided lateral line organ. Lateralisation appears to vary between populations of fish of the same species, as variance may be a direct result of presence of predation (Brown et al. 2004). Branchraphis episcopi from areas of high and low predation were tested for lateralisation. Individuals from a high predation population used their right eye when viewing a predator, triggering an emotive response. Low predation populations preferred their right eye when viewing a blank space, for unknown reasons. It is suggested that the variation in lateralisation in a species may be mainly influenced by the habitat, or whether the individual comes from shoaling populations. Furthermore, lateralisation can be affected by personality, according to Kareklas et al. (2018). Particularly, boldness impacts the preferred direction of electrosensory inputs in the electrosensing Gnathonemus petersii, another weakly electric fish. If evolutionary pressure of predation leads to eye lateralisation, then the specialisation of the hemispheres may be to reduce the disadvantages of divided attention (Griffiths *et al.* 2004). Patterns of retinal topography in fishes have been proposed to reflect habitat variation. Eyesight in teleost reef fish is adapted for their habitats, as fish with a dense horizontal retina often live in environments with significant horizontal aspects (Collin and Pettigrew, 1988a; Collin and Pettigrew, 1988b).

Hormones modulate behaviour in animals (Soares *et al.* 2010), a method of modulation that has been well preserved throughout vertebrates (Pouca and Brown, 2017). This is achieved through affecting neural circuits and the architecture of the nodes system. Vasopressin (AVP) and oxytocin (OT) are two examples of hormones important to social behaviours. In mice, lack of OT results in mice not displaying any behaviour that indicates it recognises familiar individuals, whereas AVP-lacking rats were completely unable to recognise familiar individuals (Lim and Young, 2006). Furthermore, oestrogen is suggested to influence social learning (Markham and Juraska, 2007). The hippocampus, which is the brain area most important for spatial memory and learning, has steroid hormone receptors. This suggests that hormones may also modulate these behaviours. Evidence points towards this being apparent – a decrease in oestrogen results in a reduction in the ability to spatially learn (McEwen, 2001). Administering vasotocin into a male goldfish central brain reduces social approach behaviours, whereas isotocin increases social approach (Thompson and Walton, 2004).

### Spatial cognition

The importance of spatial memory in animals is paramount to navigation, foraging and predator avoidance. Spatial memory is an aspect of cognition that regards how animals retrieve, encode, store and present information about the external environment (Bshary and Brown, 2014). Although spatial capabilities vary throughout the animal kingdom, there is evidence for spatial memory across all taxa. Rats and pigeons are model species for the study of spatial memory, as we already have a good understanding of their capabilities, and they are easy to maintain (Bond et al. 1981). The complex spatial capabilities of rats include algorithmic foraging (learned patterns of movement; Hughes and Blight, 1999), route learning, and use of a cognitive map (Olton and Samuelson, 1976; Foreman, 1985; Wills et al. 2010). A broad range of mammals, including cows, bats, shrews and primates, also possess spatial tools in order to navigate and forage efficiently (Garber, 1989; Page et al. 2012; Zamisch and Vonk, 2012; Hirata et al. 2016). Due to the large home ranges of birds, they have a substantial need for spatial capabilities. For example, migration in birds is of a result of cultural transmission of movement patterns, cognitive maps and genetic memory, and birds that migrate have a better spatial memory than non-migrating birds (Cristol et al. 2003; Fagan et al. 2013). Pigeons are capable of altering their route mid-flight, integrating new information with old information efficiently (Blaisdell et al. 2018). Furthermore, having a well-developed spatial memory is important for foodstoring birds (Thompson and Morand-Ferron, 2019). Perceptions are changing on the abilities of reptiles, as reptiles have been shown to possess spatial memory capabilities (LaDage *et al.* 2012). Lacertid lizards, Podarcis liolepis, can navigate with a cognitive map-like environmental representation when threatened (Font, 2019). Also, red-footed tortoises, Chelonoidis carbonarius, learn mazes, utilising a win shift behaviour (Wilkinson et al. 2007; Wilkinson et al. 2009; Mueller-Paul et al. 2012). Amphibians, such as toads and frogs, use the available spatial information to navigate and forage optimally (Sotelo et al. 2015; Liu et al. 2016; Liu et al. 2019).

Some fish use tools to navigate and migrate, such as using the magnetic field and a sun-compass (Quinn and Groot, 1983; Quinn and Ogden, 1984; Quinn, 1984). However, other fish rely on behavioural adaptations to navigate, such as cognitive maps and algorithmic foraging. One method of learning a landscape is achieved by forming a cognitive map, a mental analogue of a topographic map (Wehner and Menzel, 1990). A broad range of species of amniotes have been the focal point of experiments about the presence of cognitive maps, including successful investigations into honeybees, rats and chimpanzees (Boesch and Boesch, 1984; Ellen *et al.* 1984; Cheeseman, 2014). The capability of mammals and honeybees to be able to navigate using cognitive maps hints at the possibility that it is a primitive behaviour that may be found in fish. Goldfish (*Carassius auratus*) have been subject to multiple experiments revolving around place-finding tasks, in an attempt to analyse their ability to encode featural and geometric environmental information. Goldfish can

encode featural and geometric information independently and, in the absence of one, use the other to navigate. The combination of the coding of the two types of information suggests the presence of a map-like representation of the environment. A reinterpretation of these results was suggested by Cheng (2005) that this was not the use of a cognitive map, but a combination of all possible spatial cues. This was refuted by Vargas and López (2005), who cited inconsistencies between Cheng's (2005) model for goldfish spatial awareness and previous goldfish behavioural data. A later study by Vargas *et al.* (2011) found that the findings of their third task did not suggest the use of a map-like representation of the environment but associating the goal with featural cues instead of differing spatial cues. López *et al.* (1999) found that place-learning trained goldfish utilised geometric properties over local cues, but significant changes to the geometric information available did not alter the performance of the goldfish, instead relying on cues from outside the apparatus.



Figure 2 method used by Rodriguez et al (1994). Allocentric goldfish were trained to a goal in relation to a place in the room, whereas egocentric fish learned to take a specific route/turning.

Rodriguez *et al.* (1994) ran goldfish, *Carassius auratus*, through a four-armed maze in order to train fish to navigate in different ways. Some fish were trained to use egocentric cues and the others were trained to use allocentric cues. The egocentric group were trained to only make a left/right turning, and the allocentric group were trained to only turn towards the north/south side of the room. The former learns a route, the latter learns place. The ability for goldfish to be trained allocentrically is further evidence for use of internal maps, as it demonstrates an understanding of the spatial relationships of landmarks, without the fish's starting position affecting their understanding. It is worth noting that Rodriguez *et al.* (1994) starve their subjects for two days before the experiment days, and underfeeds them during experiment days. This is to increase their drive for food, but would not pass an ethics committee at Bangor University, as this may cause unnecessary stress on the

subjects. Some studies do not have the aim of investigating the presence of cognitive maps, but recorded observations that hint at the possibility. Aronson (1951) made no direct reference to cognitive maps but found that gobiid fish use the high tide to form some spatial memory of the rock pools surrounding them, which allows them to jump into other rock pools at low tide with near-perfect accuracy. In another investigation, Reese (1989) observed that butterflyfishes make deep excursions outside of their coral reef habitats, with a swimming pattern which made it seem like it was with purpose and a meter above the reef. The contrast of the outbound movement to normal movement hints to a spatial understanding of the area, which could be evidence for a cognitive map. Reese (1989) could not rule out that the route was not novel, and since it was not the focus of the experiment, no controls or experimental design around the observed behaviour.

Zebrafish have been found to have a dynamic spatial map, using associative cues and location information to locate a past reward (Karnik and Gerlai, 2012), which is a behaviour possibly linked to their episodic-like memory (Hamilton et al. 2016). Grey bamboo sharks, Chiloscyllium griseum, have also been found to navigate via place learning, and can store this information without reinforcement for up to six weeks (Schluessel and Bleckmann, 2012). Goldfish can swim towards a constant place in a space, learning allocentric orientation, by always remembering the fastest route to their escape path (Ingle and Sahigian, 1973). Guppies went through a maze made up of six consecutive T junctions; and as time and trials increased, number of errors and time to navigate the maze decreased (Lucon-Xiccato and Bisazza, 2017a). An animal's use of landmarks varies depending on ecological demands. For example, blennies differ in home-range sizes between sexes (Fabre et al. 2014). Salaria fluviatilis were trained to navigate a maze using landmarks; males were found to be a lot more able to navigate using visual landmarks, outlining the differences in spatial abilities in genders. This was found to be due to the development of the cephalic crest, something linked to ability to solve spatial tasks. The difference in spatial abilities between sexes varies between populations. Male guppies have larger home ranges than females, requiring a more developed spatial ability (Lucon-Xiccato and Bisazza, 2017b), whilst male Azorean rock-pool blennies, Parablennius parvicornis, never leave their nesting site. Females travel long distances to mate with other males, and therefore have a greater need for spatial memory. This has led to females having a larger dorsolateral telencephalon (Carneiro et al. 2001). Not all fish have such strong spatial memory, as some have generally less need for it, and evolutionary investment into it could be detrimental. For example, as memory retention, capacity and load increases, memory flexibility decreases (Tello-Ramos et al. 2019).

Blind fish make for good test subjects for cognitive maps because visual cues are completely ruled out. In novel areas, Mexican blind cave fish, *Anoptichthys jordani*, swim at a high speed and close to the area boundaries, and a lack of exploratory behaviour indicates familiarity to an area (Teyke, 1985). Teyke (1989) explains that a stored mental representation of the space was responsible for

obstacle avoidance and the familiarity to an area, like to the findings of Hassan (1989). de Perera (2004a; 2004b), used the exploratory behaviour of Mexican blind cave fish, Astyanax fasciatus, to investigate how they code this spatial information. Using wave perturbations sensed by the lateral line organ, de Perera transformed landmarks in a familiar space to these fish and found that the landmarks were coded as a group of landmarks in relation to each other. Furthermore, the fish dishabituated to landmark transformations, expressing the disassociation between the area around them, and the mental representation of that area using landmarks as beacons of navigation (Briathwaite and De Perera, 2006). Holbrooke and De Perera (2011) trained banded tetras in a Yshaped maze to take a given route either through the down and right arm, or up and left, in an environment with both horizontal and vertical cues. Both horizontal and vertical cues facilitated training, but landmarks were ignored (horizontal more so) when they conflicted, as did such after the maze was rotated within the space. This suggests that vertical information is more important and overrides landmark cues on the horizontal axis of space. Electric fish can use just electrolocation to navigate novel locations (Graff et al. 2004). Experimental data suggests that hydrostatic pressure, due to raised water level, is key to depth orientation, and key to finding a goal at a specific elevation. A cognitive map is formed using electrolocation and hydrostatic cues, relying less on electrolocation when the location becomes more familiar and a cognitive map is formed (Cain et al., 1994; Cain, 1995). Furthermore, when Cain and Malwal (2002) tested for the importance of landmarks, it was found that if a change occurs to the water level, therefore hydrostatic pressure, then the fish rely on the landmark to navigate. In the presence of no landmark, then the internal map will be relied upon. However, larger, early-adult fish were more successful than sub-adult. This means that the ability for an individual of a species to navigate may be influenced by stage of life development.

Foraging behaviour in an uncertain environment is decided by three factors: how novel the given location is to the individual, variation in food quantities in location and recency of information regarding the first two factors. The most weight is put on the most recently obtained information about a location (Inglis *et al.* 2001). Goldfish do not randomly explore novel areas, but in a series of subsequent patterns temporally and spatially formed. As time passes since the initial exposure of environment, performance of exploratory behaviour reduces (Kleerekoper *et al.* 1974). The presence of features near food-patches greatly increases the foraging accuracy of goldfish (Warburton, 1990). Repeated visits to an empty food-patch were reduced with implementation of featural cues. A fish's reliance on spatial memory might vary in accordance with the complexity of the featural environment. Patch discrimination is also a key factor in the foraging decision making of some fish (Roberts, 1991). Stout-body chromis, *Chromis chrysura*, were investigated for searching behaviour patterns. They forage independently, but in overlapping ranges. Foraging behaviour was slow and tortuous, whereas travel between foraging regions was quick. Therefore, fish used a mixture of spatial memory and expectation of the dynamic zooplankton resource availability (Noda *et al.* 1994).

When spatial capabilities are lacking, or the situation does not suit using them, alternate behaviours help fish explore and forage areas with efficiency. Siamese fighting fish, Betta splendens, exhibit algorithmic foraging. In a radial arm maze, Siamese fighting fish were trained to find worms down an arm of an eight-arm maze, where searching through each arm once was the optimal strategy, in an algorithmic fashion of searching each adjacent arm. In the second test, a 30-second or 5-minute break was imposed after the fourth arm choice, which reduced choice accuracy post-break. The third test trained fish in either a win-stay or win-shift strategy, in which fish were much faster at training in the win-shift strategy. Roitblat et al. (1982) argued that the high level of performance in the maze does not indicate a high-capacity memory system, but algorithmic foraging behaviours and optimal strategy use. Similarly, Hughes and Blight (1999) found algorithmic foraging behaviours in fifteenspined sticklebacks, Spinachia spinachia, and corkwing wrasse, Symphodus melops. They were further tested to associate visual spatial cues with a reward in a radial arm maze. The fish displayed win-shift or lose-shift behaviour when all the arms were either full or empty. Both species learned food-cue associations more easily when a lower diversity of cues was apparent and could distinguish renewable food sources. When the cue roles reversed, foraging efficiency greatly declined, but recovered quickly as they relearned the new cues. The fish tracked food sources through sampling method foraging and could change between win-shift and win-stay when necessary. This would allow rocky intertidal fish to forage food sources from patchy disruption, as such the tidal cycle (Hughes and Blight, 2000). Similarly, win-shift strategies were also found in rats (Gaffan and Davies, 1981), hinting the strategy to be a primitive behaviour. Rats can also alter location preferences in a maze based on reward presence (Batson et al. 1986), which would be an interesting prospect to test in fish.

#### Social cognition

The definition of social learning has been a well debated topic (Reed *et al.* 2010; Whiten and Ham, 1992). The definition used for this study is that social learning is the distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning (Fragaszy and Perry, 2003). Social learning of numerous biologically important decisions for animals can be affected through observations of the behaviours of conspecifics (Galef and Laland, 2005). To understand social learning in fish, it is useful to consider the occurrences in amniotes. Rats can observe a trained conspecific pull a lever for a food reward and use that information to perform that behaviour (Heyes and Dawson, 1990). Extensive literature is present regarding how cetaceans socially learn songs from each other (McCowan and Reiss, 1997; Janik and Slater, 2000; Garland *et al.* 2011; Janik, 2014), resulting in cultural transmission of whale song. Primates are capable social learners, with both tool use (Nagell *et al.* 1993) and food preferences (Shorland *et al.* 2019) being dependent on their ability to socially learn. Birds learn key survival skills through observation of their conspecifics. Such skills include tool use (Tebbich *et al.* 2001), predator avoidance, and foraging (Slagsvold and Wiebe, 2011). Birds, too,

display a cultural transmission of songs important for mating and communication (Beecher, 2017; Beecher *et al.* 2020), as well as how to open milk bottles (Sherry and Galef, 1990). Homing pigeons navigating as a flock suggests that leader-follower relationships may not occur naturally but may be inevitable in moving groups (Pettit *et al*, 2015). Those individual animals that take on the leadership role show more consistent and effective spatial learning when travelling alone. Reptiles are a less-studied taxa for social learning, but more is being revealed about their social learning capabilities in recent years (Kis *et al.* 2015), as lizards, skinks and tortoises can socially learn foraging techniques (Wilkinson *et al.* 2010; Munch *et al.* 2018; Whiting *et al.* 2018). Amphibians, such as salamanders and frog tadpoles, have been shown to socially learn a response to a novel stimulus (Ferrari *et al.* 2007; Crane *et al.* 2018).

The topic amongst teleost fish has gained traction over recent decades, even finding social behaviours in species that are not seen as typically social (Coolen *et al.* 2005; Wilkinson *et al.* 2010; Doody *et al.* 2013; Brown, 2015; Kis *et al.* 2015). One reason to explain the spike in such research might be the benefit they provide to hatchery practices. Suboski and Templeton (1989) found that naïve juvenile rock pass, *Ambloplites rupestris*, were more likely to consume a novel food after observing a conditioned individual do so. Furthermore, training a zebra danio fish to give off an alarm reaction to an otherwise neutral stimulus, and then placing the individual in a group of naïve fish, the conditioned response is socially transmitted across the group (Hall and Suboski, 1995). These practices outline their ability to socially learn, whilst being a useful tool to train hatchery-reared fish behaviours it might miss out on by not living in the wild, such as predator recognition and food choice. Similarly, in the wild, fish in early life stages benefit from social learning, through parental care (Brown, 1984), social traditions (Helfman *et al.* 1982) and imprinting (Dobson, 1988).

French grunts, *Haemulon flavolineatum*, exhibit social traditions; individuals placed in new schooling sites were able to use the new migration routes and return to their new schooling sites (Helfman and Schultz, 1984). Schooling and shoaling behaviours greatly benefit from social learning, often with efficient social transmission taking place. Naïve fish have been found to socially learn foraging behaviour (Reebs, 2000), food patch profitability (Pitcher and House, 1987), routes (Laland and Williams, 1997; Swaney *et al.* (2001) and escape responses (Brown and Warburton, 1999) from trained fish within the shoal. Reebs (2000) conducted an experiment on species of fish that preferred to be in shade; some of these golden shiners, *Notemigonus crysoleucas*, were trained to feed in a bright area of the tank. When grouped in a shoal with naïve fish, the conditioned food-anticipatory behaviour was observed by the naïve fish, overtime displaying the same behaviours. Laland and Williams (1997) investigated social learning in guppies, *Poecilia reticulate*; untrained adult female guppies grouped with female guppies that had learned a route to a food source. After grouping during the experiment, naïve fish preferred the route their demonstrators used. Furthermore, when founding members of small groups are replaced by naïve fish, social transmission of the preferred route

continued. Only female guppies were used in this experiment, however. It is possible that this behaviour might only be present in females, or occurs to a different magnitude in males. Laland and Williams (1998) also demonstrated how much fish prioritise socially learned information. Some demonstrator guppies were trained to take an energetically costly route to a food reward; demonstrators were then grouped with naïve fish and ran the experiment. Again, when the demonstrators were replaced with more naïve fish, a social transmission of the preferred route occurred, indicating social transmission of maladaptive information can inhibit optimal strategies. The act of being in a group can affect the cognitive abilities of the individuals within the group. Fish locate food faster (Pitcher et al. 1982) and are more vigilant (Magurran and Pitcher, 1983; Morgan and Colgan, 1987) as shoal size increases, however it is found that amniotes also improve cognitive performance in a social environment (Langley et al. 2018). Grouping species also show higher social motivation, and conflict avoidance/resolution behaviours, than non-grouping species (Balshine et al. 2017). Personality also significantly impacts social learning and sociality (Trompf and Brown, 2014). Swarm intelligence is unlikely present in fish shoals, instead having alternate behaviours explaining group performance, such as high individual-level of cognition in members of a fish group and interindividual variation (Ioannou, 2017).

Most examples of social learning and behaviours in fish tend to benefit the group, but some behaviours have been developed to individually capitalise on opportunities brought about by group environments. Members of a group are typically either scroungers or producers in a group feeding model (Barnard and Silby, 1981). Fish discover food through observing other foragers (Magurran et al. 1987). Individuals do not tend to switch between strategies, but scroungers fared much better in the presence of producers, unless greatly outnumbered, as food availability was short-lived. Ninespined sticklebacks can monitor the success of other individuals to interpolate food patch quality, using cover to observe individuals in different food patches to gain social foraging information (Coolen et al. 2003). Pitcher and Magurran (1983) found that when one goldfish in a shoal was informed of the new food patch distribution, they were able to forage more efficiently than the other fish for longer in a shoal of two than five. Although fish learn collectively, groups with differing personalities are slower to decide and more likely to split (Kareklas et al. 2018). Fish have also been found to partake in by-product mutualism (Foster, 1985) and image-scoring behaviour (Bshary and Grutter, 2006) with their conspecifics. Social cooperation is not restricted to individuals of the same species. Groupers, Plectropomus pessuliferus marisrubri, and moray eels, Gymnothorax javanicus, have been recorded hunting together, as both individuals benefit from complementary predation styles (Bshary et al. 2006). In addition to this, groupers can communicate to other group hunters, including moray eels and various octopus species, to bring attention to an object of mutual interest, signalling direction of hidden prey (Vail et al. 2013).

#### Overlaps in social learning and spatial memory

With the fields of social learning and spatial memory becoming well fleshed out, the study of the overlap between the two is following suit. Brown (2011) found a social affiliation effect in rats; individuals are attracted to places if a familiar individual is there. However, the same individuals tend to avoid visiting places that were depleted of food by another individual. This shows that choices made by rats can influence the working memory of other rats. Bem *et al.* (2018) also found that rats can acquire spatial information through observing, from a fixed point, a demonstrator completing a spatial task, utilising that information to improve their own performance of the task.

Specialisation in social tasks drives adaptation in spatial memory (Lefebvre and Giraldeau, 1996). Roy and Bhat (2017) investigated if zebrafish can socially learn a maze. Their control group involved two naïve fish navigating the experiment together, followed by having to embark the maze alone.



Figure 3. The layout of the experiment by Roy and Bhat (2017) investigating social learning in a maze.

The results show that all the fish gradually improved in performance over the course of the experiment. Demonstrators performed the best, with least mistakes made. Observer fish started their solo trials faster than the naïve fish did, indicating that the presence of a demonstrator aided observers in boldness exploring the novel area. However, there was no significant difference in the performance of the last trial for both naïve and observer fish. Shoaling promotes place (over response) learning but does not facilitate individual learning of that strategy in zebrafish (McAroe *et al.* 2017). On the other hand, Port Jackson sharks, *Heterodontus portusjacksoni*, can socially learn a new foraging route by observing a trained conspecific engage the route (Pouca *et al.* 2020). Many spatial memory experiments which involve fish, including Roy and Bhat (2017), do not state that they account for the sex of their subjects, which significantly affect their spatial memory capabilities (Lucon-Xiccato and Bisaza, 2017c).

Grouping can, in certain instances, inhibit learning. An experiment on homing pigeons by De Perera and Guildford (1999) had homing pigeons trained to find a hidden food reward in one of twelve cups within an arena. Some untrained pigeons were then put into the arena with a trained bird, and some untrained pigeons were put in the arena alone. In the next stage of the experiment, all the initially untrained pigeons were put to the test in the arena, and their success and movement was tracked. The results showed that birds performed more effectively alone than they did after having the presence of a demonstrator pigeon, sometimes called the passenger effect. The passenger effect has also been found in homing pigeons, crab-eating macaques, *Macaca fascicularis*, and zebra finches, *Taeniopygia guttata* (Stammbach, 1988; Beauchamp and Kacelnik, 1991; Banks and Guilford, 2000). Interestingly, fish in a shoal prefer allocentric navigation, but when navigating alone, this preference does not occur (McAroe *et al.* 2017).

# Considerations in experiment design

There are many key factors to consider when designing an experiment revolving around the two elements of spatial memory and social learning, posing as experiment design hurdles. Variables need to be kept to a minimum, as any details from music (Chase, 2001) to numerical information (Agrillo et al. 2017; Delong et al. 2017) can be accounted for by fish to make decisions. Some less-easily controllable variables between individuals, which influence cognition, may include, sex, personality, population differences and cerebral lateralisation (Lucon-Xiccato and Bisazza, 2017c). Learning rates of cues are dependent on cue types and local ecology, as stickleback populations associated different cue types at differing speeds (Bensky and Bell, 2018). Some factors can be manipulated in order to maintain a higher rate of learning, like keeping short time intervals between stimulus and the reward (Breuning et al. 1981), and ensuring test subjects are hungry at the time of testing (Croy and Hughes, 1991a). Ability to socially learn is not directly linked to age, but life history can indirectly influence an individual's natural tendency to socially learn (Penndorf and Aplin et al. 2020). Isolation-induced stress can inhibit learning and memory formation (Laudien et al. 1986), meaning if matter of isolation is a variable in the experiment, it needs to be considered when interpreting results and data. Over the course of an experiment, fish behaviour may change and affect results not as a result of social learning and spatial memory. Handling time of prey decreases, and foraging success increases as experience with prey increases (Ranta and Nuutinen, 1986) as well as feeding efficiency (Croy and Hughes, 1991b), whereas overtraining of fish can lead to reduced resistance to extinction (Breuning and Wolach, 1981). Spatial task format affects motivation, as a more complex place increases curiosity (Schubiger et al. 2016). The variability in learned information should be kept to a minimum, as different types of learned information are maintained for different lengths of time, if some behaviours are considered more advantageous than others (Warburton, 2003). Isolated fish locate food rewards

faster than grouped fish (Hesse *et al.* 2019). We might claim that a difference in food acceptance may be a lack of social learning in the control fish, but avoidance of food is a common sign of stress in fish (Carr, 2002). Acute stress, anxiety, sleep deprivation and social isolation negatively affects learning ability (Gaikwad *et al.* 2011; Brandão *et al.* 2015; Pinheiro-da-Silva *et al.* 2017; Gibelli *et al.* 2019).

# Conclusion

It is clear that teleost fish are capable of some advanced social behaviours and spatial abilities. Furthermore, with the primitive ancestors between teleost fish and mammals having a fish-like brain, discoveries in the psychology of fish can prove fruitful for all amniotes, particularly regarding primitive functions. Combined with the ease and cost-efficiency of maintaining simple aquarium species (like goldfish and zebrafish), and our current gaps in knowledge, it is understandable to see why the field of fish cognition has gained so much traction over time. This literature review precedes an experiment investigating a possible overlap between goldfish spatial and social cognition. The aim of this study is to investigate a possible overlap between social and spatial cognition in fish. This will be done by developing our understanding of the role of social learning in the formation of spatial memory in goldfish. As well as this, we aim to see whether the presence of a trained individual will affect other facets of the learning process, such as, motivation, reward acceptance and navigation strategy used by the observer. We further aim, if there is a social effect from the observation task, to decide what future experiments might be most suited to evaluate which part of the teleost fish brain might be responsible.

The importance of such research could be important to the fisheries industry, using social learning as a tool to improve mortality of fishery-born individuals being released into the wild. In addition to this, any developments of our understanding of the cognition of a species are further arguments for the requirement of better welfare for individuals in captivity. As previously mentioned, this research may also impact our understanding of cognition within amniote species. Conducting this literature review has not provided a clear prediction as to the result of the coming experiment. It is possible that goldfish are capable of such social learning of spatial information, as found in nine-spined sticklebacks (Coolen *et al.*, 2003). There is equally a chance that the presence of a demonstrator has no/negative impact on the learning of a spatial task (De Perera and Guildford, 1999; Roy and Bhat, 2017).

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# Thesis - The effect of observing trained conspecifics on the rate of spatial learning, navigation strategy and motivation in goldfish, *Carassius auratus*

### Introduction

The importance of spatial memory in animals is paramount to navigation, foraging and predator avoidance. Spatial memory is how animals retrieve, encode, store and present information about the external environment (Bshary and Brown, 2014). Although spatial capabilities vary throughout the animal kingdom, there is evidence for spatial memory capabilities across all taxa. Avian and mammalian taxa have some well-studied spatial capabilities, with pigeons and rats often being used as model species (Bond et al. 1981). Rats have complex capabilities of spatial memory, including algorithmic foraging (learned patterns of movement; Hughes and Blight, 1999), route learning and use of a cognitive map (Olton and Samuelson, 1976; Foreman, 1985; Wills et al. 2010). Our understanding of rat spatial capabilities is so well-understood, they are a model species for a number of human afflictions, including Alzheimer's disease, and dementia (Takasaki et al. 2011; Xuan et al. 2012). Other small mammals, like bank voles, Myodes glareolus, show flexibility in their spatial cognition, altering strategies based on sex, age, and personality (Mazza et al. 2018). Bats and shrews have also been shown to use algorithmic foraging (Page et al. 2012), with bats even utilising winshift strategies (Winter, 2005). Japanese Black cows, Bos Taurus, can learn a maze and maintain the memory for up to six weeks (Hirata et al. 2016). Tamarins, Saguinus, maintain spatial information on feeding tree species within their home range (Garber, 1989). An animal's home range often reflects their spatial abilities; American black bears' (Ursus americanus) spatial memory abilities decrease when kept in captivity (Zamisch and Vonk, 2012).

Birds possess similar capabilities, often having large home ranges too. Pigeons are capable of integrating new spatial information mid-flight to navigate with improved efficiency (Blaisdell *et al.* 2018). One type of information could be the sun compass, as they learn directional relationships between stimuli in a given area (Bingman and Jones, 1994). Migration in birds often covers vast areas and is of a result of cultural transmission of movement patterns and genetic memory, and birds that migrate have a better spatial memory than non-migrating birds (Cristol *et al.* 2003; Fagan *et al.* 2013). Furthermore, spatial memory is key in food-storing birds (Thompson and Morand-Ferron, 2019). Chickens with a lower range outperformed higher range chickens during a spatial memory task (Ferreira *et al.* 2019). In line with Coppens *et al* (2010), slow-exploring, reactive animals perform better under variable and unpredictable situations than fast-exploring, proactive individuals.

More recently, reptiles have been shown to possess spatial memory capabilities (Wilkinson and Huber, 2012; LaDage *et al.* 2012; Matsubara *et al.* 2017). Lacertid lizards, *Podarcis liolepis*, can navigate with a cognitive map-like environmental representation when threatened (Font, 2019). Red-footed tortoises *Geochelone carbonaria*, are able to learn mazes, and utilise both response-based navigation strategy and win shift behaviour (Wilkinson *et al.* 2007; Wilkinson *et al.* 2009; Mueller-Paul *et al.* 2012). Research into amphibian spatial cognition has increased recently too, with poison frogs acting as a model group for the taxa (Liu *et al.* 2019). The poison frog, *Dendrobates auratus*, possesses a cognitive map to navigate; and can utilise rule-based decision strategies to optimise navigation and foraging (Liu *et al.* 2016; Liu *et al.* 2019). In another poison frog, *Allobates femoralis*, male tadpole-carriers rely on spatial memory to navigate between pool sites to deposit tadpoles (Pašukonis *et al.* 2016). The terrestrial toad, *Rhinella arenarum*, is capable of geometric orientation to find a reward (Sotelo *et al.* 2015).

Our understanding of fish spatial behaviour and learning is becoming a well-studied area, so much so that zebrafish, *Danio rerio*, are being used as a model organism for vertebrate learning and memory (Gerlai, 2016; Pouca and Brown, 2017). Some fish use tools to navigate and migrate, such as using the magnetic field and a sun-compass (Quinn and Groot, 1983; Quinn and Ogden, 1984; Quinn, 1984); other fish rely on behavioural adaptations to navigate, such as cognitive maps and algorithmic foraging.

One method of learning a landscape is achieved by forming a cognitive map, which is defined by a mental analogue of a topographic map (Wehner and Menzel, 1990). Although it is debated whether animals can definitively be proven to have cognitive maps (Bennett, 1996), a broad range of amniotes have been the focal point of experiments about the presence of cognitive maps, including successful investigations into lizards, tortoises, frogs, and most mammals and birds (Boesch and Boesch, 1984; Ellen *et al.* 1984; Jacobs, 2003; Wilkinson *et al.* 2012; Font, 2019; Liu *et al.* 2019). Honeybees have also shown evidence for the use of cognitive maps (Cheeseman *et al.* 2014). Our understanding of cognitive maps is important, as place learning is the preferred strategy across vertebrate taxonomic groups (Salas *et al.* 2003). The fact that mammals, birds, reptiles, amphibians and honeybees have the capability to be able to navigate using a cognitive map hints at the possibility that it is a primitive behaviour that may also be found in fish.

Fish create spatial maps utilising a mixture of geometric relationships, landmarks and beacons to form a cognitive map (Braithwaite and De Perera, 2006). Goldfish, *Carassius auratus*, have been subject to multiple experiments investigating for cognitive maps. Vargas *et al.* (2004) trained goldfish in a set of experiments revolving around place-finding tasks, and found that goldfish can encode featural and geometric information independently, and use one in the absence of the other to navigate. López *et al.* (1999) found that place-learning trained goldfish utilised geometric properties over local cues,

but significant changes to the geometric information available didn't alter the performance of the goldfish, instead they relied on cues from outside the apparatus. Rodriguez *et al.* (1994) trained goldfish through a four-armed maze in order for them to navigate via egocentric cues, and the others were trained to use allocentric cues. The egocentric group were trained to only make a left/right turning, and the allocentric group were trained to only turn towards the north/south side of the room. An egocentric individual encodes spatial relationships in relation between themselves and external cues/landmarks and therefore learns a route, whereas an allocentric group encodes external cues/landmarks in relation to each other, learning a place within a space. It is noting that Rodriguez *et al.* (1994) starve their subjects for two days before the experiment days, and underfeeds them during experiment days. This is to increase their drive for food, but would require a home office license, which was unfeasible at the time.

The ability for goldfish to be trained allocentrically is further evidence for use of internal maps, as it demonstrates an understanding of the spatial relationships of landmarks, without the fish's starting position affecting their understanding. Similarly, Gobiid fish, *Bathygobius soporator*, use the high tide to form some spatial memory of the rock pools surrounding them, which allows them to jump into other rock pools at low tide with near-perfect accuracy (Aronson, 1951). Zebrafish have been found to have a dynamic spatial map, using associative cues and location information to locate a past reward (Karnik and Gerlai, 2012), which is a behaviour possibly linked to their episodic-like memory (Hamilton *et al.*, 2016). Grey bamboo sharks, *Chiloscyllium griseum*, have also been found to navigate via place learning and can store this information without reinforcement for up to six weeks (Schluessel and Bleckmann, 2012). Tiger sharks, *Galeocerdo cuvier*, and thresher sharks, *Alopias vulpinus*, may use cognitive maps to move between foraging areas (Papastamatiou *et al.* 2011). Goldfish can swim towards a constant place in a space, learning allocentric orientation, by always remembering the fastest route to their escape path (Ingle and Sahigian, 1973). Guppies, *Poecilia reticulata*, ran through a maze made up of six consecutive T junctions; as time and trials increased, number of errors and time to navigate the maze decreased (Lucon-Xiccato and Bisazza, 2017a).

An animal's use of landmarks varies depending on ecological demands. For example, blennies differ in home-range sizes between sexes (Fabre *et al.* 2014). *Salaria fluviatilis* were trained to navigate a maze using landmarks. Males were found to be a lot more able to navigate using visual landmarks, outlining the differences in spatial abilities in genders. This was found to be due to the development of the cephalic crest, something linked to ability into solving spatial tasks. The difference in spatial abilities between sexes varies between populations. Male guppies have larger home ranges than females, requiring a more developed spatial ability (Lucon-Xiccato and Bisazza, 2017b). Whilst male Azorean rock-pool, *Parablennius parvicornis*, blennies never leave their nesting site, females travel long distances to mate with other males, and therefore have a greater need for spatial memory. This has led to females having a larger dorso-lateral telencephalon (Carneiro *et al.*, 2001). Not all fish have such strong spatial memory, as some have generally less need of it, and evolutionary investment into it could be detrimental. For example, as memory retention, capacity and load increases, memory flexibility decreases (Tello-Ramos *et al.*, 2019). Personality can also affect spatial learning, as spatial learning rate decreases with boldness in trout (White *et al.* 2017).

Social learning is defined as a distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time, and that new practitioners acquire in part through socially aided learning (Fragaszy and Perry, 2003). Social learning can take many forms. An individual of a group witnessing another individual in a situation and gaining novel information from it is social learning through observation, and is the most common form of social learning (Browder *et al.* 1986). Rats can learn to push a lever in a particular direction for a food reward after observation of a trained conspecific (Heyes and Dawson, 1990). Famously, the British tit family, *Paridae*, population knowledge of how to open milk bottles originated from a few individuals, and spread socially (Sherry and Galef, 1990). Imitation is a core mechanism of learning through observation, as rats benefit via social facilitation of learning a task (Zentall and Levine, 1972). Alternatively, individuals can socially learn by performing a task with a knowledgeable conspecific. Young house sparrow fledglings, *Passer domesticus*, can socially learn food-reward cues through active searching with a trained mother (Truskanov and Lotem, 2015). The active participation in the task for the fledglings was more effective than alternative methods of learning.

Social learning through listening occurs in the natural world too. Baleen whales use vocal learning to incorporate the whale songs they hear from conspecifics (Janik and Slater, 2000; Janik, 2014). Information travels socially in different ways; horizontal transmission moves between individuals in the same generation, vertical transmission moves between individuals of different generations, and cultural transmission occurs throughout a whole population (Heyes and Galef, 1996). Whale song transmission is a type of horizontal transmission, as male humpback wales, *Megaptera novaeangliae*, transmit whale songs through populations between western and central south pacific oceans (Garland *et al.* 2011). Predatory behaviour of killer whales is an example of vertical transmission. Some killer whale families hunt in groups, creating waves to push seals from ice flows (Pitman and Durban, 2012). The younger members of the killer whale family participate, socially learning the predatory behaviour from the matriarch and older members of the family (Ford, 2019). Social learning is usually favoured when using private information would be more costly than social information, such as when private information increases the likelihood of predation (\*costly information hypothesis; Webster and Laland, 2008).

Social learning has been well-documented in birds and mammals. Rats and primates, particularly humans, have served as a model species for social learning experiments (Heyes and Galef, 1996). Rats are capable of social learning and transmission of mechanisms (Laland and Plotkin, 1990) and

behaviours (Heyes and Dawson, 1990). Primates have demonstrated social learning of complex behaviours, such as food preference (Shorland et al. 2019), tool use (Nagell et al. 1993) and routine skills (Schuppli et al. 2016). This is further complicated by both sex and social rank influencing variance in social learning in primates (Botting et al. 2018). Other mammals also show strong social learning capabilities, such as both bears and cetaceans learning foraging skills socially (Sargeant and Mann, 2009; Pokrovskaya, 2015; Morehouse et al. 2016). Dolphins socially learn through vocal learning, playing a major role in acquisition of each individual species (McCowan and Reiss, 1997). Dolphins also discover play behaviours through social interactions (Kuczai et al. 2012), and are less likely to play with conspecifics they are related to – this results in cultural transmission (Cappiello et al. 2018). Birds are known to socially learn predator avoidance, foraging and mating behaviour (Slagsvold and Wiebe, 2011). Many birds rely on social learning, as learning songs of conspecifics is directly linked to survival of an individual (Beecher et al. 2020). The reliance is emphasised in the western song sparrow, who prefer to voice songs that were socially learned from conspecifics (Beecher, 2017). Giraldeau and Lefebvre (1987) recognised that pigeons can learn how to obtain food from a scrounging task when accompanied by an informed partner. Other complex behaviours, such as vigilant behaviour timing in European starlings, Sturnus vulgaris, (Butler et al. 2016), and tool use in finches (Tebbich et al. 2001), are also reliant on socially gained information.

It is important to note that social learning is not limited to social species. Non-colonial insects, nonsocial reptiles and non-grouping fish have been shown to use social learning with high effectiveness (Coolen *et al.* 2005; Wilkinson *et al.* 2010; Doody *et al.* 2013; Kis *et al.* 2015; Webster and Laland, 2017). The Italian wall lizard, *Podarcis sicula*, can socially learn a novel foraging task when observing both a conspecific and a novel different species, *Podarcis bocagei* (Damas-Moreira *et al.* 2018). Similarly, bearded dragons, *Pogona vitticeps*, socially learn through imitation (Kis *et al.* 2015). Other groups of reptiles that socially learn include tortoises, lizards and skinks (Wilkinson *et al.* 2010; Munch *et al.* 2018; Whiting *et al.* 2018). Social learning in reptiles appears to be particularly dependent on age (Noble *et al.* 2014). Amphibians such as salamanders and frog tadpoles, socially learn responses to novel stimuli (Ferrari *et al.* 2007; Crane *et al.* 2018). Insects, such as fruitflies and honeybees, socially transmit mating preferences and alarm behaviour between conspecifics (Dawson *et al.* 2016; Danchin *et al.* 2018).

Social learning in some fish is as developed as many amniotes (Brown and Laland, 2003). French grunts, *Haemulon flavolineatum*, exhibit social traditions; individuals placed in new schooling sites were able to use the new migration routes and return to their new schooling sites (Helfman and Schultz, 1984). Schooling and shoaling behaviours greatly benefit from social learning, often with efficient social transmission taking place. Naïve fish have been found to learn foraging behaviour (Reebs, 2000), food patch profitability (Pitcher and House, 1987), routes (Laland and Williams, 1997; Swaney *et al.* 2001) and escape responses (Brown and Warburton, 1999) socially from trained fish

within the shoal. Furthermore, Swain and Fagan (2019) found that the learning time of a group of guppies positively correlates with group size, and the learning rate in a group of males was learned faster than a group of females. Social learning in fish has been used for anthropogenic uses. Suboski and Templeton (1989) found that naïve juvenile rock pass, Ambloplites rupestris, were more likely to consume a novel food after observing a conditioned individual do so. Furthermore, training a zebra fish to give off an alarm reaction to an otherwise neutral stimulus, and then placing the individual in a group of naïve fish, the conditioned response is socially transmitted across the group (Hall and Suboski, 1995). The act of being in a group can affect the cognitive abilities of the individuals within the group. Fish locate food faster (Pitcher et al., 1982) and are more vigilant (Morgan and Colgan, 1987; Magurran and Pitcher, 1983) as shoal size increased, however it's found that fellow amniotes also improve cognitive performance in a social environment (Langley et al., 2018). Grouping species also show higher social motivation and conflict avoidance/resolution behaviours than non-grouping species (Balshine et al., 2017). Personality also significantly impacts social learning and sociality (Trompf and Brown, 2014). Swarm intelligence is unlikely to be present in fish shoals; instead they alternate behaviours explaining group performance, such as high individual-level of cognition in members of a fish group and inter-individual variation (Ioannou, 2017).

Fish can discover food through observing other foragers (Magurran et al., 1987). Individuals don't tend to switch between strategies, but scroungers fared much better in the presence of producers, unless greatly outnumbered, as food availability was short-lived. It has been suggested that social learning is an adaptive strategy, as there are cases of food-storing birds only able to socially learn if it was in regards to where others store their foods (Lefebvre and Giraldeau, 1996). Nine-spined sticklebacks can monitor the success of other individuals to interpolate food patch quality, using cover to observe individuals in different food patches to gain social foraging information (Coolen et al., 2003). Lemon sharks can socially learn through observing a demonstrator complete a task to make contact with a target for a food reward (Guttridge et al. 2013). Stingrays that observe a trained individual feed from an apparatus are able to learn to feed from the apparatus faster than a nonobserving conspecific (Thonhauser et al. 2013). Pitcher and Magurran (1983) found that once a goldfish in a shoal was informed of the new food patch distribution, they were able to forage more efficiently than the other fish for longer in a shoal of two than five. Fish have also been found to partake in by-product mutualism (Foster, 1985) and image-scoring behaviour (Bshary and Grutter, 2006) with their conspecifics. Social cooperation isn't restricted to individuals of the same species. Groupers, *Plectropomus pessuliferus marisrubri*, and moray eels, *Gymnothorax javanicus*, have been recorded hunting together, as both individuals benefit from complementary predation styles (Bshary et al., 2006). In addition to this, groupers can communicate to other group hunters, including moray eels and various octopus species, to bring attention to an object of mutual interest, signalling direction of hidden prey (Vail et al., 2013).

There are documented cases where animals socially learn spatial information. Panuccio et al (2012) found that juvenile short-toed snake eagles, Circaetus gallicus, socially learn migration strategies in order to override their innate direction of migration, as well as whooping cranes improving migration through social learning (Mueller et al. 2013). Similarly, horses can socially learn a route to a reward (McVey et al. 2018). Naïve rats were able to acquire spatial information by observing a trained conspecific perform a spatial task, improving their performance in the task (Bem et al. 2018). Interestingly, Leggio *et al* (2003) found that rat observers benefited from route learning rather than place learning after observing water maze trials. Social learning of spatial information may be explained by either social facilitation, local/stimulus enhancement or observational learning (Hoppitt and Laland, 2008). There is evidence of an overlap between social and spatial learning in fish. Laland and Williams (1997; 1998) found that naïve guppies travelling with guppies trained to know the route to a food source will prefer to use the socially learned route to the food when alone, even when it is a more energetically costly route. Other research found that fish learn collectively, but factors like personalities may inhibit decision making processes (Kareklas et al. 2018). Research also found that zebrafish learn places faster as a shoal than as an individual. Furthermore, this showed evidence of the presence of conspecifics affecting navigation choice (McAroe et al. 2017). Age and quantity of training can also influence place strategy choice (Packard and McGaugh, 1996; Barnes, 1979). In species like the túngara frog, *Engystomops pustulosus*, there are differences in navigation strategy between the sexes (Liu and Burmeister, 2017), females prefer allocentric cues as it may benefit them during mate assessment.

Roy and Bhat (2017) investigated whether zebrafish can socially learn a maze. All fish gradually improved in performance over the course of the experiment; however, a naïve fish paired with a demonstrator showed no significant difference in their ability to learn, whilst two naïve fish navigated and learned the maze together. Performance improved for the observers, but not the number of mistakes. This is due to the social distractions interfering with the learning experience. The main differences between Roy and Bhat's (2017) experiment and this one includes that they had the observer fish follow the demonstrators around the maze, whereas our observers watch from a fixed point, as well as the layout of the arena being different. A possible explanation for the result of another of Roy and Bhat's (2019) experiment, which should be taken into consideration for this experiment, is the passenger effect. De Perera and Guildford (1999) ran an experiment on homing pigeons, Columba livia, where trained individuals paired with untrained individuals completed an arena to find a food reward. Post-pairing period, the untrained observers took longer to learn the arena than untrained individuals without a demonstrator, which is referred to as the passenger effect. Similar behaviour has been exhibited in zebra finches and crab-eating macaques (Stammbach, 1988; Beauchamp and Kacelnik, 1991). New research investigating the overlap between social learning and spatial memory may help develop our understanding of these behaviours, as the quantity of research

taken out has been limited, despite the potential benefits of such information. The difference in the respective positions between the observers and demonstrators may outline any differences in the results found by Roy and Bhat (2017) and my own. Any differences found in the results could shed a well-nuanced light onto the coding of socially gained spatial information. Many spatial memory experiments which involve fish, including Roy and Bhat (2017), do not state that they account for the sex of their subjects, which significantly affect their spatial memory capabilities (Lucon-Xiccato and Bisaza, 2017b).

Although some studies do exist, there is a definitive gap in our knowledge of the capabilities of fish to socially learn spatial information; the little we do know does not hint at the magnitude, flexibility and ecological importance of such capabilities. This research is essential to investigate such factors, in order to go forward with more confidence and stronger foundations for future studies regarding fish cognition. One benefit of further studies into fish behaviour may be that homologous functions, which have been investigated in the spatial learning function of the telencephalon in fish, might be similar in the mammalian hippocampus. Vargas *et al* (2006) suggests that the mammalian hippocampus, amygdala and isocortex are derivatives from a primitive fish-like ancestor's lateral, medial and dorsal pallia, respectively. Homogeneity of the brain structures have been backed up by Broglio *et al.* (2003), Broglio *et al.* (2010) and Rodríguez-Expositósito *et al.* (2017). In addition to this, it is hypothesised that the common ancestor between mammals and fish had a more teleost fish-like brain, rather than a paleomammal brain. Therefore, with homologous structures and functions found in both amniotes and fish, it is possible information about the fish telencephalon may be interpolated from amniote studies.

Similarly, effects in humans should be considered in fish, given the homologous brain features. The over justification effect states that an expected external incentive, like a reward, decreases an individual's motivation to undertake a task (Tang and Hall, 1995). Furthermore, the greater our understanding of fish cognition, the more zebrafish and goldfish can be used as model organisms for studies investigating genetic diseases like dementia and Alzheimer's disease (Lieschke and Currie, 2007; Newman *et al.* 2011; Van Tijn *et al.* 2011; Willemsen *et al.* 2011; Saleem and Kannan, 2018). Bridging this knowledge gap would justify the use of zebrafish and goldfish as model species for even more advanced behavioural studies. Another benefit to further study is that a fish's ability to socially learn may be a useful tool to train hatchery-reared fish the behaviours that they might miss out on by not living in the wild, such as predator recognition and food choice (Brown and Laland, 2001). Similarly, in the wild, fish in early life stages benefit from social learning through parental care (Brown, 1984), social traditions (Helfman *et al.*, 1982) and imprinting (Dobson, 1988). Suboski and Templeton (1989) found that naïve juvenile rock pass, *Ambloplites rupestris*, were more likely to consume a novel food after observing a conditioned individual do so.

The main aim of this investigation is to develop our understanding of the role of social learning in the formation of spatial memory. Particularly, to see whether social learning has any impact on the rate of learning an environment. Other aims include understanding whether the presence of a trained individual affects other facets of the experiment, such as; reward acceptance, motivation, time taken to complete the trial and the method of navigation used by individuals. We hypothesise that the unconditioned fish, which observe a conditioned fish undergo a maze, will learn the maze faster than a fish that didn't observe a conditioned fish. We further hypothesise that the unconditioned fish undergo a maze, will use a different navigation strategy to a control fish.

#### Method

#### **Subjects**

Shubunkin goldfish, *Carassius auratus*, a social fish (Blanco *et al.* 2018), were bought from an online aquarium trader and maintained for a month before the experiment started. The goldfish lived in 40 cm x 80 cm x 45 cm glass aquaria with aerated filtered water at approximately  $22^{\circ}$ C. The experiment room used a light-dark cycle of 12 hours and the goldfish were fed flakes during this time. 100 goldfish were separated evenly and randomly between five tanks that were situated in the experiment room. These tanks were identical in contents, containing 20 goldfish, fake plants and aquarium husbandry equipment, and were assigned an experimental group each at random. Each tank was assigned a group (demonstrators, observers, control, spare goldfish #1, spare goldfish #2), which prevented any goldfish being familiar with any goldfish from any other group before any trials. Each group had 20 goldfish, with spare goldfish had profile photos taken of them, which were printed onto laminated paper, and were assigned a number for identification. Furthermore, these numbers indicated the arm the fish would be training to turn to – odd fish turn left, and even fish turn right. On experiment days, goldfish were fed bloodworms during testing, and were all fed flakes afterwards. On non-experiment days, the goldfish were fed flakes.

#### Apparatus

A four-armed maze (Figure 1) constructed with transparent glass was used. The maze was on a 1 cm thick white polystyrene sheet, which itself was on a 76 cm tall table. Each arm entrance had a slot to slide a transparent sheet of plastic to act as a door (30 cm tall). Another of these doors was used to separate the inner and outer halves of the starting arm. Three arms were used for one given trial, requiring an opaque light blue plastic door to block the one arm not in use for the respective trial. These doors were moved manually during, and outside of, testing.



Figure 4. Scale to plan view of the maze arena. The arms of the maze were 30 cm long, 30 cm tall and 15 cm wide, the centre of the maze was  $22.5 \text{ cm}^2$ .

Timing was taken using a stopwatch. Each experiment day started with putting fresh water into the maze up to a height of 22 cm. The water was approximately 20°C and was circulated around the maze between each trial. The maze was situated in the same room as they were housed in, within line of sight of the tank, but distance inhibits fish from gaining information of the maze from the tank. The experimenter positioned themselves randomly in one of five marked spots around the maze to observe the fish. Resources used during the trials, such as the doors and the bloodworms, were kept on the maze table and the shelving, respectively. The layout of the procedure room is shown in Figure 2. There are no windows to the outdoors in the room, and the adjacent room is a large aquarium room with translucent windows.



Figure 5. Plan to scale of the maze and the procedure room. X = marked spots for the experimenter to stand during the trials. N represents north.

#### Procedure

Training: To train an individual, they were placed into the inner segment of the starter arm and given two minutes to acclimatise to the maze environment. To begin the trial, the door for the starter arm was lifted and the timer started. Once the subject had completely passed across the threshold of the choice arm entrance (excluding the starting arm; as seen in Figure 3), a door was slotted into the arm entrance and the timer was stopped. If the fish got the choice correct, two bloodworms were immediately dropped into the further end of the now inhabited arm. If incorrect, the individual was given two minutes of isolation in the incorrect arm. If the subject had not made a decision by five minutes, it was considered an unmotivated trial. Each trial was recorded for success and time taken. After the trial, the individual was transported back to the starting arm via net, and water was circulated around the maze to reduce the influence of olfactory cues post-successful trial. This was repeated until the goldfish had completed ten trials - this formed a block of trials. The goldfish was then returned to the tank it came from, and the next subject was brought to the maze. Each goldfish was trained for one block of trials every weekday until it reached the learning criterion of 80% trial success rate for three consecutive trial blocks.



Figure 6. A) Illustration to show the point of which the fish was considered to have officially made a decision, as all of the fish must be over the threshold. Fish drawing is an illustration of a standard fish shape and not representative of the individuals used. B) A trial and a reverse trial of fish using an allocentric navigation strategy. C) A trial and a reverse trial of a fish using an egocentric navigation strategy

Demonstrators: Fish to become demonstrators were trained first. Once trained, they were tested for another two weeks to ensure that they could maintain the high success rate post-training, as their consistency while demonstrating was important.

Observers: Observer fish were put into the observer segment of the maze for their observation period of three blocks of trials. During this, a demonstrator, that was trained to turn the same direction that the observers were going to be trained to take, completed three blocks of trials as normal, including positive and negative reinforcement. The data about these trials were recorded. After three blocks of observations, the observer underwent training as usual.

Control: To eliminate the influence of familiarity with the maze on training, control goldfish spent 30 minutes in the observer segment for three days in a row, with no other fish in the maze. This provided control fish with as much time as observers in the maze before training, and then they too undergo training as usual.

Reverse trial: Immediately after the trial that results in the goldfish being considered trained, every fish engaged in a reverse trial, which is a normal trial except the fish began in the arm opposite the starter arm – the reverse trial arm. The preparation for this was to move the observer partition to this arm, and to move the opaque door to block the starter arm. A regular trial was then ran, with the exception of a reward/punishment, as there was no correct answer. If the fish chose the same arm that it was trained to turn into (see Figure 4), then it was recorded as allocentric. If the fish chose to make the same turning as it was trained to take in training (see Figure 4), then it was recorded as egocentric. The time taken to complete this trial was also recorded.

#### Data recording

Data was recorded during the experiment in a notebook and transferred to an excel spreadsheet at the end of each experiment day. Although video trials were considered, the vast amount of time it would take to complete all of the trials required and then to watch all the trials for data recording purposes, would far exceed the time designated for the data collection period of the MScRes. In addition to this, given the constraints of the room, the boom arm of the camera tripod might be considered an extra cue. As the main focus of the experiment is the decision making, the benefits do not outweigh the cons of drawback of the extra resources.

#### Data analysis

In order to evaluate a possible link between social learning and spatial memory, the following measures were recorded; success of trials, time taken per trial, whether the reward was accepted, and the motivation of the subject (whether it completed the trial or not). RStudio was used to process the statistical tests used. Group means for every measure required nonparametric tests for comparison, whereas only some measures also had a correlation coefficient calculated. A variety of statistical tests were used for inter-group differences. Mann-Whitney U tests were utilised to compare group performance, group rates of first trial block performance, group food acceptance likelihood, strategy performance, the effect of food acceptance on performance and group motivation. The Fisher's exact test tested for significance in strategy choice difference of the two groups, and for significance in strategy choice difference of the observers of different demonstrators. A Kruskal-Wallis rank sum test was used for the effect of strategy on group performance, with a Wilcoxon rank sum test to calculate p-values. An Independent t-test was used to calculate a significant difference on the observer performance, depending on which demonstrator was used. Spearman's rank correlation tests were used to test the correlations of time taken per trial and performance, acceptance of reward likelihood and strategy performance, subject motivation and performance, success rate of demonstrations and observer performance, and the effect of demonstrator motivation on both observer motivation and performance.

#### Statement of ethical review

Before initiating this experiment, an ethical review form was carried out, outlining the intended procedures. The experiment was submitted to, and reviewed by, College of Environmental Sciences' ethics review committee at Bangor University. The experimenting started after being provided approval by the ethics review committee by.

#### Results

#### **Control VS Observer**

The rate of training was recorded as the number of blocks of trials that were undertaken before reaching the trained threshold. The mean number of blocks it took for individuals of both groups were compared for significant difference using a Mann-Whitney U test; W = 120, P < 0.05. The control

group ( $\mu = 9.20$ ) trained, on average, in a fewer number of blocks than the observer group ( $\mu = 13.65$ ) (figure 1).



Figure 7. The number of blocks of trials taken for subjects of each group to be considered trained. The width of area represents frequency of occurrences for the respective y-coordinate. Dots on the graph indicate outliers, whereas the boxplots within the shaded areas express mean, range and the interquartile ranges. 'Wilcoxon' in this graph represents the unpaired two-samples Wilcoxon test (also known as the Wilcoxon rank sum test and the Mann-Whitney test).

Difference in performance was most emphasised within the first five blocks of trials. As seen in Fig. 5, observers started the experiment with a slightly higher success rate than control subjects. The performance of the control goldfish gradually and steadily improved, whereas the observers achieved a mean second block success rate ( $\mu = 0.48$ ) lower than the control group's first block ( $\mu = 0.495$ )

before taking on a similar incline to control. There was not a significant difference in the mean performance of the groups in the first block (Mann-Whitney U test; W = 171, P = 0.4303).



Figure 8. The mean success rate of the two groups over the course of the first five trials. On the trial success rate axis, 1 = 100% trial success rate, and 0 = 0% trial success rate. Control is represented by a solid line with circular plots, whereas observers are represented by a dashed line with triangular plots.

Individuals within the observer group were significantly (Mann Whitney U; W = 287, P = 0.01136) more likely to accept the food reward than individuals from the control group. However, there was no significant difference in the mean time taken per trial between control and observers (Mann Whitney U; W = 129, P = 0.05652, control  $\mu$  = 32.74281 seconds, observers  $\mu$  = 51.84359 seconds).

#### Egocentric VS Allocentric

The reverse trials provide insight as to which navigation strategy is used by each individual. To investigate whether an individual's group affects the possible navigation strategy utilised, a Fisher's exact test was used. Fig. 6 shows the distribution of strategy choices made between the groups, of which represents an insignificant difference (Fisher's exact test; P = 0.1128). Similarly, the performance of allocentric goldfish had shown no difference to the performance of egocentric goldfish (Mann-Whitney U test; W = 248, P = 0.1947).



Figure 9. The frequency of individuals from the different groups' choice of strategy.

The combination of the group and strategy choice allows for further scrutiny of the significant differences of mean trials to train between control and observers. A Kruskal-Wallis rank sum test shows there was a significant difference between one or more of the groups in trials to train (Kruskal-Wallis chi-squared = 9.7253, df = 3, p-value = 0.02105). A pairwise comparison using a Wilcoxon rank sum test results in Table 1.

|                   | CONTROL -<br>ALLOCENTRIC | CONTROL -<br>EGOCENTRIC | OBSERVER -<br>ALLOCENTRIC |
|-------------------|--------------------------|-------------------------|---------------------------|
| CONTROL -         | 0.094                    | -                       | -                         |
| EGOCENTRIC        |                          |                         |                           |
| <b>OBSERVER</b> - | 0.968                    | 0.094                   | -                         |
| ALLOCENTRIC       |                          |                         |                           |
| <b>OBSERVER</b> - | 0.677                    | 0.024                   | 0.572                     |
| EGOCENTRIC        |                          |                         |                           |

Table 1. Results from the Kruskal-Wallis test. Values represent p-values. P-value adjustment method: Benjamini & Hochberg (1995).

There was no significant difference between allocentric control and allocentric observers (Table 1. P = 0.968), but there was a significant difference between egocentric control and egocentric observers (Table 1. P = 0.024). On the other hand, there was no significant difference between allocentric observers and egocentric observers (Table 1. P = 0.094), nor was there between allocentric control

and egocentric control (Table 1. P = 0.094). The differences between the groups, separated by strategy, are shown in Fig. 7.



Figure 10. Boxplots representing the mean and interquartile ranges of the amounts of trials to train between the groups, separated by strategy. The plots represent the individual data points being used for the boxplots. Side-by-side data points are of the same y-value or the respective group.

Although there was a significant difference between the time taken per trial and choice of strategy (Mann-Whitney U test; W = 290, P = 0.01548), the time taken per trial did not significantly correlate with the amount of trials it took to train a goldfish (Spearman's rank correlation; S = 7974.6, P = 0.1168, rho = 0.2519157).





Figure 11. The mean time taken to undertake a trial per goldfish, measured against the number of blocks of trials it took to train the fish, separated by strategy. Colour and shape of point indicate which group the goldfish belonged to. A darker shade of plot represents two occurrences at the same point, such as (7,24 – egocentric). Correlation coefficients and their respective p-values are shown on the top right of each facet, for all the data points for the facet.

Other aspects of the experiment were recorded to provide insight into other factors that may impact the rate of learning. One such factor might be the subject's likelihood to accept the reward. There was a significant difference between the likelihood to accept the reward within the first three blocks (Mann-Whitney U test; w = 287, P = 0.01136) of control ( $\mu$  percentage chance to reject the reward in the first three blocks = 26%) and observers ( $\mu$  percentage chance to reject the reward in the first three blocks = 8%). There was only a significant correlation between percentage chance of rejecting the reward in the first three blocks and blocks of trials it took to train for the control group, not the observer group (see Fig. 9 for rho and P values). Furthermore, there was no significant difference (Mann-Whitney U; w = 175, P = 0.4734) between the percentage rejection of rewards in the first three trials between allocentric ( $\mu$  percentage chance to reject the reward in the first three blocks = 0.1406667) and egocentric ( $\mu$  percentage chance to reject the reward in the first three blocks = 0.2031667). There was also no significant correlation between the blocks of trials to be trained, and the percentage chance of rejecting the reward in the first three blocks = (Spearman's rank correlation; S = 998.26, P = 0.2889, rho = 0.2494282) or egocentric subjects (Spearman's rank correlation; S = 1211.3, P = 0.7082, rho = 0.08926873).



Figure 12. The proportion of rewards rejected per goldfish, measured against the number of blocks of trials it took to train the fish, separated by group. A proportion of "1" represents "100% percent of rewards provided rejected", and "0" represents "0%". Colour of point indicate which navigation strategy the goldfish used. The larger size of plot represents the more occurrences are present at the same point. Correlation coefficients and their respective p-values are shown on the top right of each facet, for all the data points for the facet.

#### **Motivation**

The final factor investigated was the motivation of the subjects. The proportion of motivated trials of a fish was calculated with the following equation;

$$Motivation \ percentage = \frac{Number \ of \ unmotivated \ trials}{Number \ of \ blocks \ taken}$$

The motivation of goldfish was analysed against their group, navigation strategy and how quickly the subject trained. Using a Mann-Whitney U test showed a significant difference (W = 131, P = 0.02597) between the motivation of observers ( $\mu$  percentage of unmotivated trials = 0.086%) and control ( $\mu$  percentage of unmotivated trials = 0.031%). Furthermore, there was a significant correlation (Spearman's rank correlation; S = 6969.1, P = 0.02863, rho = 0.3462384) between the percentage of unmotivated trials a goldfish had, and the amount of trials it took for them to be considered trained. Goldfish that navigated allocentrically did not exhibit a significantly different (Mann-Whitney U test; w = 251, P = 0.1007) proportion of unmotivated trials to egocentric fish.



Figure 13. The proportion of unmotivated trials per goldfish, measured against the number of blocks of trials it took to train the fish, separated by group. A proportion of "1" represents "100% percent of trials that were unmotivated", and "0" represents "0%". The larger size of plot represents the more occurrences are present at the same point. Correlation coefficients and their respective p-values are shown on the top right of each facet, for all the data points for the facet.

#### Demonstrator performance

The rate of training did not significantly differ depending on which demonstrator the observer was observing (Independent t-test; t = 0.40325, P = 0.6915). Furthermore, the mean success rate of the demonstrators over the course of the demonstrations was 92%, and any variation of success rate observed by a particular observer did not affect their rate of training (Spearman's rank correlation; S = 1571.1, P = 0.4444, rho = -0.1812576). Throughout the 600 demonstration trials that the demonstrators undertook, only 6 trials were unmotivated (1% unmotivated trial rate; Stanley five occurrences, Hobnob one occurrence), and the demonstrator unmotivated trials observed did not have a significant effect on observer motivation (Spearman's rank correlation; S = 1252.3, P = 0.8067, rho = 0.05842986) or success rate (Spearman's rank correlation; S = 1578.5, P = 0.4302, rho = -0.1868741). The demonstrator an observer was assigned had no effect on navigation strategy choice (Fisher's exact test; P = 1.0000).

## Discussion

The main takeaway from this research is that the fish that observed a trained individual learned the maze slower than their non-observing conspecifics. Therefore, it could be inferred that something about the act of observing a trained individual undertake the maze slowed down the training process for the observer. This directly contradicts with the expected results from the hypothesis, and seems to be an unusual result when considering the evidence provided for the capabilities of spatial memory in fish. More specifically, the egocentric control group trained faster than the egocentric observers. One could insinuate that the act of observing a trained individual inhibits the learning process of egocentric spatial information. To my knowledge, this is a new finding which warrants further research. Other investigations indicate that fish are able to socially learn routes, and in some cases, prefer detrimentally-longer socially learned routes (Laland and Williams, 1998). The observation process also had an effect on motivation and food acceptance, but only motivation had a significant effect on the rate of training. These are important findings that can make an impact on the design and completion of future investigations into the relationship between spatial memory and social learning in fish, particularly those which use zebrafish and goldfish as model species (Gerlai, 2017). This project also provides new information on the potential idea of using social learning in hatchery-reared fish, to improve their chances in the wild (Brown and Laland, 2001).

The difference in the progression of the first five trials (Fig. 5) shows that the observers began training with evidence of some understanding of the maze, however they drop to ~50% success rate in the second block, and improve at a slower pace than the control until block five. The approximately 50% success rate in block two for observers mirrors the 49% success rate for control - both as good as random chance. It is possible that the observing goldfish begin the maze with some socially acquired spatial memory of the maze, such as the curiosity of why the demonstrator went to one arm frequently, or the desire for the reward observed to be provided for demonstrators in that arm/the lack of reward in the other arm. It is important to consider for Fig. 5 that a small number of fish were trained in three blocks of trials and then stopped undertaking trials, which may have resulted in the drop off on the fourth trial. We can be confident that the observer subjects were able to observe the demonstrators get and eat the reward, as observers were significantly more likely to accept the reward than the control group (Fig. 9), noting that fish can socially learn to accept food (Suboski and Templeton, 1989). Arguably, the statement can be made that there has been some social transmission of information, including spatial information. The remainder of the results seem to hint that the social aspect of the experiment may be detrimental to the observing subjects in training to learn this maze. It should be reinforced, however, that the rejection/acceptance of food had no significant impact on the speed of which a fish became trained.

These results disagree with the results of Roy and Bhat's (2019) experiment with zebrafish, who found no significant difference between the performance of observer zebrafish and naïve-paired

zebrafish, as opposed to my control goldfish significantly outperforming observer goldfish. However, observer fish from both studies started with an advantage, hinting that the presence of demonstrators had aided the observers in navigation of the maze in the first solo trials. Furthermore, both sets of results effectively disprove the main hypothesis. One of the main differences between the two experiments is that in Roy and Bhat's (2019) experiment, the observer followed the demonstrator through the maze during the observation period; whereas, in our experiment, the observer was held within a fixed point for the observation period. This is unlikely to be the cause for the differences between results, as a similar experiment with Port Jackson sharks, *Heterodontus portusjacksoni*, does not agree with any of our results (Pouca et al., 2020). They found that non-social, juvenile Port Jackson sharks can socially learn a new foraging route through observation of a trained demonstrator, and that observers learned faster than individual learners and sham-observers (paired with a naïve demonstrator). Pouca et al. (2020) argue that the results occurred because the demonstrators draw attention to the route, increasing the observers learning opportunities. These contrast from both previously mentioned studies, as, although they did seem to begin with an initial advantage, this didn't translate to improved performance/learning. As the naïve Port Jackson sharks followed the demonstrators throughout the arena, the differences between my experiment and Roy and Bhat's (2017) is unlikely to be down to this factor. To further qualify this justification, Bem et al. (2018) found that rats acquire spatial information by observing demonstrators complete a spatial task from a fixed point, and then use the socially learned information to improve their performance. Similar to the Port Jackson shark experiment, the results indicate that the demonstration of correct spatial information was a prerequisite for observer improvement. It is quite apparent how unusual these findings are, considering how little they agree with the findings of others – which allows for unique opportunities in investigating the nuances of these behaviours.

One possible explanation for these results may be the occurrence of the passenger effect. De Perera and Guilford (1999) found that pigeons learned the position of the food goal more effectively when performing the task alone than after completing it with a knowledgeable companion. Similar findings were found in feral pigeons, zebra finches and crab-eating macaques (Robertson *et al.*, 1985; Giraldeau and Lefebvre, 1986; Biederman and Vanayan, 1988; Stammbach, 1988; Beauchamp and Kacelnik, 1991; Lefebvre and Helder, 1997; Banks and Guilford, 2000). A hypothesis was formed that the subjects didn't learn anything with a demonstrator, or rather that the observers are learning something different about the task compared to a control conspecific. It is possible that the presence of the demonstrator itself is an indicator of food, therefore removing the demonstrator would remove the indication that there is a food reward. Banks and Guilford (2000) suggest that spatial cues are not picked up from the demonstration by the naïve pigeon, or that the naïve pigeon fails to transfer them into the single phase, as homing pigeons can utilise knowledge observed from a demonstrator during a paired phase of a homing experiment; but fail to benefit from their initial exploitation of knowledge

of conspecific when alone. Another suggestion was that the naïve pigeons' focus was on the demonstrator in fear of exposure by desertion, therefore inhibiting encoding of information function. The perception of being transported via netting as a stressful predation event might provide a fear of desertion for my subjects, which would be further reinforced by the partition between the demonstrators and observers. However, one problem with the integration of the passenger effect into our results is that these experiments involve the naïve individual travelling with the demonstrator during observation, rather than observing from a fixed point. Unlike these experiments, this one has the naïve fish only able to observe and do nothing else, arguably making it not a passenger at all. Therefore, if the mechanism for the passenger effect is rooted in the action of following, then that would not apply to this experiment. Although, since this is not well-investigated in the fish taxa, it is a hypothesis worth considering in our interpretations. Brown (2011) found that rats were attracted to places they had seen a familiar individual visit but avoided it if they witnessed a familiar individual deplete a food source there. This fits the overall findings of how long it took for either group to train, but the initial success of the observers contradicts this.

There was slight variation between strategy choice in groups, as observers were more likely to choose the allocentric navigation strategy ( $N^A = 13$ ,  $N^E = 7$ ) and that the control were more likely to choose the egocentric navigation strategy ( $N^E = 13$ ,  $N^A = 7$ ). Analysing fish performance after splitting them up, both by group and strategy, can provide insight as to why the initial difference was found. The egocentric control group was the outlying group in the experiment. Their mean number of blocks to train was significantly different to allocentric control (P < 0.05) and egocentric observers (P < 0.05). The increase in mean trials to train from egocentric control and allocentric control may reflect a difference in difficulty of adopting the different strategies, as perhaps the allocentric strategy takes more time to train in. On the other hand, the difference between egocentric control and egocentric observers might reflect an inhibition in learning that occurs after observation of a trained individual. If both ideas were true, then the argument could be made that we would expect the allocentric observers to take significantly longer to train than any other group. However, this isn't the case. In fact, the mean number of blocks of trials to train the allocentric observers was lower than allocentric control and egocentric control and egocentric control control and egocentric control servers (Fig. 6).

The allocentric strategy of navigation has been considered as the more complex strategy (McAroe *et al.* 2016). This may also explain the significant difference in rates of learning between the groups, as the group that was more likely to learn the "more complex strategy" was the group that learned slower. The reliability of the method for the reverse trial could be improved as it is easily impacted by the small sample size it provides. This leaves a chance that some of the egocentric observers may have been allocentric observers, who impulsively turned a random way due to the stress of the reverse trial. McAroe *et al* (2017) found that individuals in shoals had shown a significant preference for the allocentric navigation strategy, whereas zebrafish that were trained as shoals showed no preference

for allocentric or egocentric when tested alone. Although they found that shoals learned quicker than individual fish, their findings on navigation strategy choice do slightly reflect the distribution of choice between the two groups, control and observers. Roy and Bhat (2017) also found that different navigation styles may have been used by social and asocial zebrafish. In mammals, it has been recorded that rats observing a water maze from a fixed point had learned the route to a platform rather than where the platform was; this preference of procedure over a cognitive map via observation, doesn't agree with the slight preference of allocentric navigation for observers and egocentric navigation for control.

The motivation of a goldfish to undertake the maze, combined with the mean speed at which goldfish completed their trials, may indicate boldness, familiarity with the situation and the strength of the attraction of the reward. Observers had a significantly higher percentage (P < 0.05) of unmotivated trials compared to control goldfish, but no significant difference (P > 0.05) in time taken per trial between the two groups. Regardless of group, each subject spent the same amount of time in the maze before commencing training, so the only difference in familiarity between the groups at the beginning of their training is that any information the observers gain socially. Ruling familiarity out, the lack of motivation for observers may be attributed to either boldness or strength of attraction to the reward. However, Roy and Bhat (2017) suggested that observers may be more comfortable in the maze because of the boldness of the demonstrators. Although increased familiarity may have influenced performance of wild-population juvenile zebrafish, this did not unearth higher learning capabilities (Roy and Bhat, 2016). If the reward was not a strong enough incentive to prompt the subject to embark the maze, then it would've been a struggle to maintain the process of training for all fish. Therefore, with this reasoning, the social aspect of the observers training might affect the boldness of the subjects. The higher the proportion of unmotivated trials a goldfish exhibited, the higher the number of blocks of trials it took for them to train (Fig. 9, P < 0.05). This could either mean that the lack of motivation affected rate of training, or these are two independent factors of observers and it just so happens that they are both slower to learn and are more unmotivated. Motivation did not significantly differ (P > 0.05) between goldfish that utilised different navigation strategies.

The use of shubunkin goldfish may have had an effect on the experiment that lead to variance. Shubunkins were used for their characteristic red, orange and black blemishes, unique to each individual, which made for easier identification with the naked eye. This variance in morphology is a product of inbreeding within the breed. This may well have also resulted in variance in spatial and social abilities between individuals. To avoid this, a more regular, wild type breed of goldfish would be needed. However, due to space and resource limitations, shubunkins were required for this instance for ease of identification. The breed choice used also made it difficult to scrutinise gender, allowing such a factor to further increase variance results. Acquiring wild-caught individuals from a single population would also eliminate any differences and influences from the aquarium industry, such as

food preference. Anecdotal evidence suggests that observers were more likely to accept food than the control, which provides further variance for rate of training as some fish came from the aquarium trade less accepting of bloodworms than others. Zebrafish may be a more suitable subject species, as if it happens to be that wild zebrafish are more accessible, it is known that they have well developed spatial and social capabilities. It should also be mentioned that when a goldfish didn't accept any rewards within the first five blocks of trials, the goldfish was discontinued from the experiment and the results were not included in analysis. Furthermore, food avoidance is a common sign of stress in goldfish (Carr, 2002), so perhaps the difference between the groups outlines a difference in stress through isolation, rather than social learning (Gaikwad *et al.* 2011). This means that the rejection of food data analysed in this experiment, does not accurately represent the acceptance/rejection of food throughout the entire experiment.

Goldfish, as well as the species they descended from, live in streams and rivers in the wild. These natural habitats often carry the threat of predation, so efficient foraging is important. Goldfish shoal in the wild. Although they don't stay in hiding, they do prefer to have a place to be able to hide in when threatened. Before having conducted this experiment, the hypothesis was based on the trail of thought that it would be beneficial for goldfish to gain spatial information whilst observing their conspecifics foraging, in order to increase own success of foraging and reduce the chance of predation. Guppies, another river species of fish, are capable of socially learning foraging sites and escape routes (Reader et al. 2003). As this is not the case with these results, alternative behaviours may be more beneficial ecologically. One could argue that, as goldfish do not stay in hiding at a passive state, they do not need to invest in the social learning of foraging information, as leaving a safe hiding spot to forage may be less stressful than for a more timid fish, like the Symphysodon *discus.* As netting may be interpreted as a predation event by the subjects, they might be choosing to avoid the correct arm where netting took place during the demonstration. It may also be possible that the goldfish are avoiding foraging areas where food depletion was observed, gambling that it would be more beneficial to forage elsewhere (Brown, 2011). This phenomenon has been studied in mammals, but not in fish. The lack of available data on this topic, particularly about fish in their natural habitat, reflects the research opportunities available, as well as the difficulty in providing accurate ecological perspectives to laboratory studies. In sum, in an ecological perspective, I hypothesise that the slower rate of learning post-observation may express a reluctance to forage at the correct arm, due to either observing a predation event, or food depletion.

It is tough to justify a particular social learning mechanism, as the poor performance compared to the controls implies that not social learning, but social distraction took place. However, it is still important to try and understand the social learning mechanisms behind the behaviours taking place. Considering how the demonstrators are having a significant effect on observer behaviour, asocial learning can be ruled out (Heyes, 1994). On the other hand, social facilitation may be responsible. Guerin (1993)

defines social facilitation as 'when there is an increase or decrease in behaviour by an animal in the presence of another animal that does not otherwise interact with the first animal'. One could argue that the slower rate of learning in observers might be considered a decrease in behaviour due to social facilitation, as well as the significant difference in likelihood of food acceptance as an increase in another behaviour. However, Clayton (1978) argues that social facilitative behaviours should not be confused with imitative behaviour, which is likely what is occurring with the social learning of food acceptance. The reduction in the rate of learning by observers could be due to cognitive distraction, where the presence of conspecifics inhibits complex task processing (Guerin, 1993; Aiello and Douthitt, 2001). Similarly, a phenomenon where being part of a group results in less motivation, called social loafing, which could account for both the lower rate of spatial learning and lower motivation (Paulus, 1983). Although these social learning mechanisms are descriptive, they are poorly studied in animals, particularly in fish.

Imitation is a novel response that is acquired through observation of a demonstrator making that response, involving a 'goal-directed' psychological mechanism (Galef, 1988). If the mechanism responsible for the behaviour is social behaviour, then imitation is likely. The increase in probability of food acceptance in observers and the slight preference to the correct arm on the first block could be due to local enhancement, which is when exposure to a demonstrator animal draws the observer's attention to the stimuli with which the demonstrator was interacting (Galef and Beck, 1985; Heyes, 1994). The observers may have had increased curiosity to the correct arm, and attention to the reward. This doesn't account for a drop in performance after the first block, however. The behaviour of socially learning through observing a conspecific traverse a binary-choice maze is seen in other experiments exploring social learning via matched-dependent behaviour (Miller and Dollard, 1941). A key difference is that in the Miller and Dollard (1941) experiment, the reward was not given to the demonstrator during demonstrations. Furthermore, matched-dependent behaviour is not strictly social learning, similar to contagious behaviour and social facilitation (Heyes, 1994).

One way to expand the questions investigated in this experiment would be to test how the observed success rate affects rate of learning. If a group of observers was exposed to a demonstrator completing 50% of the trials correct, and another group watch demonstrators that were 20% correct, it can be interpolated that either observing failures, successes, or an even mix provides the best chance for social learning. The logistics of training a demonstrator to only get 50% correct may prove challenging. A study found that starlings learned a task more effectively when observing incorrect demonstrators, in comparison to conspecifics observing correct demonstrators (Templeton, 1998). It was also considered to have the subjects only observe one demonstration trial, as this might make certain behaviours less of a factor, such as avoiding areas where conspecifics have consumed food in (Brown, 2011). The decision was made that the observers should be given a strong opportunity to socially learn so we could understand whether they have the capability to, and if successful, future

experiments could investigate the effect of differing numbers of demonstration trials on rate of social learning. Alternatively, a parallel study where the observer fish follows the demonstrator through the maze, as opposed to being restricted to the observation segment, would provide more insight into the optimal situation for goldfish to socially learn spatial tasks. Lesioning parts of the fish brain may also be responsible for the behaviours investigated in this experiment, like the lateral pallia or medial pallia. The maze itself is an adaptive tool that can be changed to expand our understanding on this topic. Demonstrators could be trained to use featural cues to navigate, such as an arrow pointing left to turn left and an arrow pointing right to turn right, and test if this alters the difficulty of social learning spatial tasks. Furthermore, increasing the observation period might increase confidence in the results, by further insuring the acknowledgement of demonstrator information for the observers, particularly with the possibility of reduced stress or increased familiarity (for control too) during the introduction stage.

The variation in strategy choice between groups brings up many questions;

There is evidence that the act of a goldfish observing (from a fixed point within the maze) a trained individual navigate the maze has an impact on spatial strategy. A possible future experiment could use demonstrators trained in using different strategies, similar to the experiment ran by Rodriguez *et al.* (1996). Observers could witness the strategy take place, and have their rate of training recorded, as well as observer strategy decision making. Alternatively, training one group of individuals allocentric navigation, and another egocentric navigation, and compare training rates. Any significant difference could reflect a difference in difficulty with learning the strategies, which would develop our understanding of the findings of this experiment.

This investigation has shed some light onto the relationship between social learning and spatial memory capabilities in goldfish, as well as the impact of observing on an individual's motivation and likelihood of food acceptance in an experimental arena setting. I hope that future studies can use this information to guide their experimental design, as well as inspire their questions, into social learning. Furthermore, experiments that will use fish as a model species for spatial memory experiments can utilise these findings to undertake their experiments with more confidence and knowledge of the potential behaviours that may be taking place.

# Conclusion

Overall, our main hypothesis was rejected, as the act of observing a trained individual resulted in a slower rate of learning. It is not clear whether the socially gained information is inhibiting the learning process, or if the observation experience alters the subject's behaviour. One could suggest that if the act of observing had influenced the subject to navigate allocentrically, the arguably more complex strategy is responsible for the differences in rates of learning. However, the available data cannot confirm nor deny this. Other explanations, which are better studied in amniotes, like the passenger effect, hint at the possibility that the act of following the demonstrator prevents social learning from taking place; yet the observer groups' significantly higher probability of accepting the food reward suggests some social information being encoded. Furthermore, the act of observing has resulted in differences in motivation and the time taken per trial between the groups, which reflects a lack of motivation or desire to complete the spatial task, or a reduction in boldness. Possible future experiments that might be able to answer some of the questions left by this study include having demonstrators that have a 50% success rate, which would allow us to see if observing negative feedback to a task would be more impactful for social learning than observing positive feedback. Alternatively, having the observer complete the task with the demonstrator would also shed light on some of the unexpected behaviour seen in this investigation. With each step, it becomes even more viable that these model fish species can be used for cognition studies for amniotes, and help us to answer important questions on the behaviour of animals in need, and ourselves. The information gained from this study can hopefully be utilised in future behavioural studies for all animals, as well as investigations into Alzheimer's disease and dementia using a fish as its model species.

# Appendix

The rights to the goldfish illustration used in Figure 3 is reserved for <a href="http://www.smallkidshomework.com/goldfish/">http://www.smallkidshomework.com/goldfish/</a>

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