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Emotional contagion and prosocial behaviour in fish: An evolutionary and mechanistic approach

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ABSTRACT

In this review, we consider the definitions and experimental approaches to emotional contagion and prosocial behaviour in mammals and explore their evolutionary conceptualisation for studying their occurrence in the evolutionarily divergent vertebrate group of ray-finned fish. We present evidence for a diverse set of fish phenotypes that meet definitional criteria for prosocial behaviour and emotional contagion and discuss conserved mechanisms that may account for some preserved social capacities in fish. Finally, we provide some considerations on how to address the question of interdependency between emotional contagion and prosocial response, highlighting the importance of recognition processes, decision-making systems, and ecological context for providing evolutionary explanations.

1. Introduction

A behaviour that benefits others is considered pro-social, as it can be used to establish and sustain social affiliation, to strengthen pair bonding, to nurture offspring, and to maintain social and cultural norms (Chudek and Henrich, 2011; Cronin, 2012; Tarsha and Narvaez, 2023). These contexts of prosocial behaviour are easy to identify in human social interactions and have been historically observed and quantified not only in humans, but also in our closest evolutionary relatives, particularly primates and other mammals (Bar-Tal, 1976; Batson, 1987; De Waal, 2008; De Waal and Suchak, 2010; Melis, 2018). In his eloquent exploration of prosociality Keith Jensen (2016) discusses how it is unlikely to have any true fitness costs to actors, and even if benefits are indirect, they still involve some level of conscious knowledge of them or some self-rewarding motivation. These self-awareness capacities have been mostly linked to cortical evolution (Fabbro et al., 2019). However, indirect fitness benefits are observed across the vertebrate phylogeny and linked to life-history processes, reproductive trade-offs and behavioural mechanisms, irrespective of any self-aware or conscious systems (Heylighen, 1992; Silk and House, 2011). Indirect fitness can be broadly derived by benefits to the genetic variation of the population. However, the selection of costly behaviour that benefits others may rely on the adaptive value of social systems across different organisational levels, from the formation of social collectives to mitigate predatory risk to socio-regulatory mechanisms purposed to maintain homeostasis (Cantor et al., 2021; Lee et al., 2021). Costly prosocial behaviour can be oriented towards relatives (kin selection), purposed for offspring survival (parental investment) or used to strengthen or establish affiliations that potentially provide later fitness benefits (cooperation, altruism or reciprocity), but can also derive from group structures and norms imposed by conspecific punishment, social norms or hierarchical systems (West et al., 2007; Simpson and Beckes, 2010; Hawley, 2014). These evolutionary components are shared across the vertebrates, and research on prosocial behaviour has exponentially increased over the last few decades and expanded to the study of domesticated animals, rodents and birds, which provided new evolutionary and mechanistic interpretations (Marshall-Pescini et al., 2016; Rault, 2019; Keysers et al., 2022; Pfattheicher et al., 2022). Thus, as we move to characterise ancestral prosocial phenotypes in even more evolutionarily distant groups, we need to look beyond higher-order cognitive functions.

A common contention is that prosocial behaviour requires empathy and concern for understanding the emotional state of others, which involves conscious self-other distinction not encountered in ancestral mirroring phenotypes, such as emotional contagion (Eisenberg and Miller, 1987; Gump and Kulik, 1997; De Vignemont and Singer, 2006; De Waal and Suchak, 2010; Jensen, 2016). Although this might hold true for humans and their closest relatives, emotional contagion does not only imply the mirroring of behaviour but also the sharing of emotional

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states, which requires some form of emotion recognition. Recognition mechanisms have long been considered for emotional contagion, and initially described to rely on self-originating feedback rather than direct recognition in others (Hatfield et al., 1993). The hypothesis is that emotional contagion initiates by an automated replication or mimicry of observed motor-sensory behaviour that then triggers afferent feedback or self-evaluation processes to instil the contagion of emotion (see evidence in humans: e.g. Doherty, 1997). Although rarely considered, similar feedback may derive from physiological changes driving the behavioural mimicry, which could explain why emotional contagion in humans and other animals is accompanied by functionally related behavioural and physiological changes (Carnevali et al., 2020; Herrando and Constantinides, 2021; Pérez-Manrique and Gomila, 2022). For instance, if an individual automatically repeats a fearful behaviour that requires changes in stress-hormone levels to occur, then the emotional state of the individual may be indirectly affected by that physiological shift. A more cognitively demanding but simpler explanation is that animals directly perceive the underlying state of a behavioural response they observe, that is sharing an emotion requires that the emotion be recognised in the behaviour of others. This direct recognition is implicit in how Darwin (1872) defined emotions as perceivable signals of internal state, and has long been described in humans (Adolphs, 2002) and increasingly supported by evidence of conserved mechanisms across the evolutionary scale (Ferretti and Papaleo, 2019). For example, oxytocinergic modulation in social decision-making brain regions, such as the amygdala, the striatum and their homologues across vertebrates, regulates the discrimination of fearful from neutral responses in humans, rodents and even fish (Satterthwaite et al., 2011; Ferretti et al., 2019, Akinrinade and Kareklas, et al., 2023).

Across these potential mechanisms, we find a common capacity to recognise and share the emotional state of others, which may explain why individuals across the vertebrate phylogeny organise prosocial behaviour that benefits others. For instance, pair-bonded prairie voles recognise the distress of their partners and increase their stress-relieving allogrooming behaviour towards them (Burkett et al., 2016), and corvids exhibit stress-relieving affiliative behaviours, such as preening and bill-twining, towards social partners that experienced aggression (Seed et al., 2007; Fraser and Bugnyar, 2010). Similarly, there are a number of cooperative or helping phenotypes in fish where responses meet the prosociality criterion of benefiting others and this directly corresponds to their emotional state, including their fear or stress. For example, cleaner wrasse (*Labroides dimidiatus*) which benefit their client fish by removing ectoparasites from their skin, have also been found to reduce the stress levels of their clients as shown by lower cortisol responses (Bshary et al., 2007). In three-spined stickleback, healthy fish are more likely to mediate their food consumption at safe distances from predators when sharing with parasitised conspecifics, meeting the risk aversive feeding needs of these diseased fish (Milinski, 1986). There are also offspring care phenotypes where prosociality can be claimed in terms of costly behaviour alleviating distress in others, such as clown fish males exhibiting more nest defence when intruders are present (DeAngelis et al., 2020) or Siamese fighting fish pausing feeding during nest guarding (Portugal, 2023). Parental phenotypes are often debatable as examples of prosociality because offspring care provides parents with direct fitness benefits. Yet environmental and genetic drivers of prosociality parallel those of parental care and in the context of evolution there is growing evidence that prosociality is determined by neuroendocrine mechanisms of "care" phenotypes, from parental to alloparental and altruistic/ helping (O'Brien, 2014; Decety et al., 2016; Marsh, 2019). Notably, one of the two most prominent hypotheses for the evolution of prosociality is the alloparental hypothesis, which is related to offspring care by third-parties, while the other is the interdependence hypothesis, which predicts elevated prosociality towards more closely related conspecifics due to direct or own benefits (Tomasello et al., 2012; Burkart et al., 2014; Tarsha and Narvaez, 2023). Thus, there is a case to be made for parental phenotypes, but also for breeding helpers and for the formation of social affiliations. In cichlids, estimated to globally represent roughly 10 % of all teleosts (Salzburger, 2018), we find a number of cooperative breeding and single parent examples, while pair bonding and monogamy are also frequently encountered. For example, in the monogamous biparental convict cichlid *Amatitlania nigrofasciata,* males preferentially share food with their female partner and increase their offspring care behaviour following the experimental removal of their partner (O'Connell et al., 2012; Satoh et al., 2021). Also, the cooperatively-breeding Lake-Tanganyika cichlid *Neolamprologus pulcher* exhibits prosocial punishment whereby dominant parents attack idle helpers, motivating them to pre-emptively care for offspring (Hidaka et al., 2024). Thus, there are a number of fish phenotypes that follow through in presenting prosociality, while their diversity, from parental care, to pair-bonding and helping, provide ample opportunity to test evolutionary hypotheses and behavioural mechanisms, such as the alloparental hypothesis and the use of punishment or incentive. However, the component of emotion recognition and contagion is less well established in fish.

More recently, evidence emerged that suggests that, following instances of emotional contagion, some forms of prosociality may be present in fish. For example, zebrafish have been shown to behaviourally and physiologically share the fear/ distress of others, and to subsequently approach and interact with others seen in distress, as compared to those remaining in a neutral state, despite the local threat risk signalled by their distress (Fernandes da Silva et al., 2019; Akinrinade and Kareklas, et al., 2023). Moreover, by approaching others, zebrafish can provide stress buffering benefits (Faustino et al., 2017; Akinrinade et al., 2023) as well as improved vigilance, attack mitigation and antipredator benefits (Butail et al., 2013; Majeed et al., 2020; Mukherjee et al., 2023; Mukherjee and Bhat, 2023), which suggests that the organisation of approach to those in distress offers direct benefits. The question we address here, is how to best quantify this relationship between emotional contagion and prosocial behaviour, and how to identify conserved neurocognitive mechanisms that can explain their evolution, in more distant vertebrate species, such as fish.

2. The evolutionary link of emotional contagion to prosociality: definitional and phenotypic grounds for their study in fish

The term "emotional contagion" has its definitional origins in the later 19th century with characterisations of the broader phenomenon of social contagion, as described by Le Bon ("behavioural contagion"; 1895) and Baldwin ("contagion of feeling"; 1897). The earliest theoretical descriptions for behavioural contagion in non-human animals include Thorndike's (1898) work on imitation-learning ("learning to do an act by seeing it being done"). Although Thorndike was unsuccessful in finding evidence of this in animals, the work comprised little distinction between imitation and goal emulation, that is reproducing the results of a behaviour rather than the behaviour itself. However, ensuing research in animal ethology identified that the transmission of sensory-motor behaviour is widespread, and as first described by Konrad Lorenz (1937), the complicated imitation of serial actions is better explained by a heritable ability for the transmission of mood, such as yawn and laughter in humans. This progressively came to contextualise emotional contagion as an evolutionary substrate of empathic behaviour (De Waal and Preston, 2017). In turn, research provided evidence for a two-step process including imitation or contagion followed by local enhancement, where the replication of behaviour observed in a particular location may then lead to local approach-avoidance responses towards others (Galef, 2013). This is in line with Levy's and Nail's (1993) review of work in humans, where they identified a separation between spontaneous and motivational features in the historical definitions of social contagion, whereby the transmission of emotion or behaviour can either elicit only replication (aka 'echo') or also disinhibition in approach-avoidance responses. A direct fitness prediction would be that individuals benefit from approaching others seen in a positive state,

which signals safety, and avoid the vicinity of those seen to exhibit distress or alarm, which signals local risk. Yet, evidence shows that avoidance is a response most commonly emulated when seen in others responding to a local cue (e.g. observing others avoiding a foot shock; Zentall, 2006), whereas approach is a more common response towards those expressing distress (e.g. mice: Ferretti et al., 2019), often after replicating the observed distress behaviour (e.g. zebrafish: Akinrinade and Kareklas, et al., 2023). This suggests that individuals tolerate local risk potentially to buffer the physiological and behavioural stress-levels of conspecifics (Kikusui et al., 2006; Gilmour and Bard, 2022). Thus, social contagion beyond simple mimicry is expected to elicit some secondary other-oriented motivational responses, which point to basal constructs of prosociality, that is benefit to others at personal cost.

In turn, prosocial behaviour is considered to involve four other-oriented contexts: informing, aiding towards a goal, ameliorating distress, and sharing resources (Tomasello, 2009). In all these contexts, we find individuals whose internal state – such as their fear, stress or hunger – is positively or negatively affected by some external stimulus (valence) and elicits some degree of physiological response (arousal) and the drive to act in a particular way (motivational intensity). This comprehensively defines emotions, whose perception by others leads them to organise a prosocial act (Dovidio and Penner, 2001; Anderson and Adolphs, 2014; Decety et al., 2016; Mendl et al., 2022). On these definitional grounds, identifying whether emotional states (i), their sharing (ii) and recognition (ii), elicit beneficial other-oriented acts (iv) relating to the expressed state (v), can establish the link between emotional contagion and prosocial response (Fig. 1). Although each of these components has been well-studied in mammals, the interplay between them has not been well defined and approaches are often limited to laboratory treatments with little ecological relevance and limited comparative potential for evolutionarily more distant groups (Marshall-Pescini et al., 2016). Below we address this by considering diverse phenotypes across fish against definitional criteria and potential experimental approaches that can test them.

2.1. A behaviour in a demonstrator represents an internal emotional state

Most animal studies examining emotional contagion, prosocial behaviour or emotion recognition, focus on negative emotional states, such as fear, distress, alarm or anxiety (Decety et al., 2016; Briefer, 2018; Pérez-Manrique and Gomila, 2022; Keysers et al., 2022; Hernandez-Lallement et al., 2022). In fish, these terms are often used interchangeably for describing the same behaviours, sometimes even under the same context. For example, in zebrafish, guppies and minnows, erratic and freezing “alarm” behaviour can be elicited by either predator cues, an “alarm" substance released from the skin of wounded conspecifics, or by observing these behaviours in others. These behaviours are often considered to indicate “fear” or “distress” (Jesuthasan and Mathuru, 2008; Speedie and Gerlai, 2008; Faustino et al., 2017; Pinho et al., 2020; Crane et al., 2020; Crane et al., 2021; Kareklas et al., 2023). However, the relatedness of these terms is that they are used for responses induced by the direct perception of danger, whereas the term “anxiety” is reserved for stress behaviour under uncertainty (e.g. edge orienting or freezing in a novel environment: Maximino et al., 2010; Stewart et al., 2012). Direct predation threat and risk under uncertainty are commonly encountered by animals in the wild, and effective physiologically driven behavioural responses provide equally transversal fitness benefits to such risky or threatening conditions (Dall et al., 2005; Schmidt et al., 2010; Németh et al., 2013). This demonstrates the ecological reliability of these negative states for comparative studies and the identification of conserved mechanisms. Positive behavioural states are more difficult to identify in animals, especially where human-derived concepts such as excitement and happiness, are neither well defined nor understood in most non-human species. Examples of what has been considered as positive states in non-human mammals include behavioural and physiological responses to social and physical environmental enrichment (Boissy et al.,2007), response to resources, such as food (Verbeek et al., 2014), and eliciting “relief” from stress, e.g. providing water to thirsty mice (Ferretti et al., 2019). This is consistent with functional definitions of emotions in fish, such as fear manifesting in escape for safety, anger manifesting in escalated aggression, or joy manifesting in repetition when gaining a desired reward. Moreover,

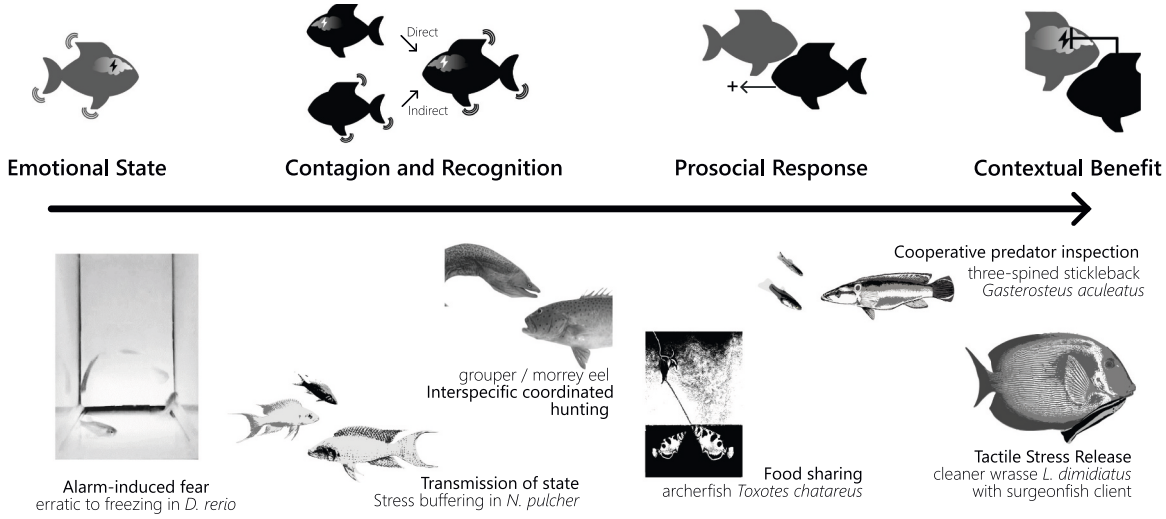

Fig. 1. Emerging components for definitionally linking emotional contagion and prosociality with illustrative examples. Emotional states are expressions stemming from internal cognitive and physiological mechanisms, such as fear-behaviour repertoires in zebrafish (*Danio rerio*). In zebrafish fear is transmitted to others that observe it and fear recognition enables animals to approach those in distress (Akinrinade et al., 2023). Similarly calm is transmitted to stressed animals in *Neolamprologus pulcher* cichlids (Culbert et al., 2019), which can be used also as a prosocial act to buffer stress in others. Recognising a partner’s state is crucial to organising a prosocial response, such as signalling individual appetitive drive for cooperative hunting by groupers and moray eels (Bshary et al., 2006). Prosocial acts are overall defined by being beneficial to others, independently if they are also beneficial to the actor (e.g. mutual resource benefit in archerfish; Nafcha et al., 2023) or if they incur costs (e.g. predation risk during cooperative inspection by sticklebacks; Walling et al., 2004). Ultimately, the link between emotional contagion and prosociality is the ability to act on the perceived emotion of others, such that the prosocial act improves or addresses the emotional state. For instance, client stress levels are lowered by the mechanosensory properties of cleaning by *Labroides dimidiatus* wrasses (Soares et al., 2011).

from goldfish, to trout and the crimson spotted rainbow fish, there is evidence of avoidance, removal and stress-release responses to pain infliction (Kittilsen, 2013). Nevertheless, even in humans, basic negative emotional states are identified as much more salient, including anger, sadness, fear, disgust, rage, grief and contempt, while positive states often include emotions such as calm and interest, which are accompanied by little behavioural salience (Plutchik, 2001; Tracy and Randles, 2011). However, as in humans, the basis of these positive emotions is change in internal state, where calm can be equated with lowered stress levels, while more prominent positive states, such as happiness and joy, are also related with increased reward signalling (Burgdorf and Panksepp, 2006; Wittmann et al., 2008; Navratilova et al., 2016; Richardson et al., 2016; Shiota et al., 2017).

The signalling activity of the hypothalamic-pituitary-adrenal/interrenal stress-axis is relatively well conserved in fish (Flik et al., 2006; Alsop and Vijayan, 2008; Gorissen and Flik, 2016). Furthermore, it presents a similar stress physiology to that of mammals, and its neural underpinnings in fear and anxiety centres, such as the amygdala and the bed nucleus of the stria terminalis (Dedovic et al., 2009; O'Connell and Hofmann, 2011a; Winter and Jurek, 2019; Janeček and Dabrowska, 2019). Notably, in zebrafish, for which genetic and molecular tools have been pioneered in the past decades, there is a unique loss of stress-axis duplicated genes, not encountered in other fish species, providing a remarkable comparative model for mammalian single stress-gene systems. Furthermore, zebrafish glucocorticoid-receptor splice variants present an exceptional similarity to those of humans, which is not encountered in other mammals (Alsop and Vajiyan, 2009). Also, reward or fear related signalling in fish telencephalic and diencephalic areas is functionally, structurally and neurochemically homologous to the mammalian mesolimbic system (O'Connell and Hofmann, 2012, 2011a). This system preserves dopaminergic, serotonergic, and glutamatergic activity (Bocchio et al., 2016; Fischer et al., 2017; Chen et al., 2021), but also socio-affective modulation by neuropeptides, such as oxytocin (Leppanen et al., 2017; Wang et al., 2020). For example, parental care in false clown anemonefish, *Amphiprion ocellaris* is triggered by oxytocin signalling, while in convict cichlids it also relies on lower androgen levels and the partners presence (Oldfield and Hofmann, 2011; O'Connell et al., 2012; DeAngelis et al., 2017; DeAngelis et al., 2020). As such, there is room for eliciting and quantifying emotional states in fish using behavioural and physiological changes, such as pharmacologically or genetically modulating neurosignalling and hormonal release or environmentally inducing fear or hunger states, and by considering consequent changes in activation across key conserved neurophysiological axes.

2.2. Observers share the demonstrator's emotional state

Emotional contagion implies a response that not only reflects behavioural imitation, but also the sharing of the internal state of demonstrators (Hatfield et al., 1993; Gallese et al., 2004). Behavioural responses may be simply directionally similar, such as in mice, where freezing in demonstrators induces decreases in observer locomotion (Ferretti et al., 2019; Ueno et al., 2020). Alternatively, responses may be highly matched or mirrored, where levels of specific responses are statistically similar between observer and demonstrator, such as the matching of freezing in rats (Pereira et al., 2012). The evidence in fish is limited, but recent work in zebrafish demonstrates that they replicate the exact phenotype, such that kinematic criteria are met for the replication of a behaviour (e.g. angular velocity and speed thresholds). These measures can reach the levels of the demonstrator's behaviour without being a complete match (Fernades da Silva et al., 2019; Akinrinade and Kareklas, et al., 2023; Kareklas et al., 2023). Interpreting contagion from behavioural imitation, on the basis transmission of emotional states, may also include fearful animals adopting the more positive state of conspecifics. For instance, in the Lake Tanganyika cichlid *N. pulcher*, individuals temporarily removed from water reduce their behavioural and hormonal stress responses in the presence of others of their group that have not been stressed, a process commonly referred to as buffering, which can also be viewed as the contagion of a "calm" state (Culbert et al., 2019). Notably, the stressed *N. pulcher* also exhibited lower social connectivity which could induce selectivity in social affiliations, such as avoidance of stressed individuals, and could also reduce the later transmissibility of stress or "calm" (Brandl et al., 2022). Different degrees of behavioural contagion could potentially indicate inhibitory regulation of emotion sharing for organising a prosocial response, i.e. controlling the extent to which shared negative emotions can overwhelm observers and limit other-oriented behaviour. For instance, the anxiolytic effects of oxytocin in human parents and lactating female mice enables the mediation of distress contagion for organising offspring-oriented care, defence and nurturing responses (Strathearn et al., 2009; Menon et al.,2018; Marsh et al., 2021). Similarly, oxytocin regulates paternal care behaviour in the monogamous convict cichlid, such as nest maintenance, offspring cleaning, transportation and fanning (O'Connell et al., 2012), while in anemonefish it drives a trade-off by elevating direct egg care and reducing nest defence (De Angelis et al., 2020). Another component is the timing and consistency of the observer's behaviour, which can indicate the transmissibility of the observed behaviour and whether motor imitation is more prevalent than the sharing of emotion. For instance, whether the observation of salient erratic distress movements elicits a fast replication of the motor responses, as opposed to the generalised sharing of distress such that it might expand to non-observed distress phenotypes, such as freezing, general anxiety levels or sensitivity to external stressors, such as pain (Martin et al., 2015). Moreover, contagion should follow direct observation or attention towards the conspecific behavioural stimulus. For fish species this may include visual attention via orientation or visual-field alignment, or mechanosensory and electrosensory attention via body alignments (Kareklas et al., 2018; Groneberg et al., 2020; Kareklas et al., 2023). However, unlike easily discernible sniffing approaches in terrestrial animals (Ferretti et al., 2019), olfactory attention in fish is limited by water-flow and hydrodynamics (Cox, 2008; Atema et al., 2012), while the perception of acoustic cues is confounded by the simultaneous pressure and particle motion component of underwater sound (Kunc et al., 2016). Finally, to ensure that any behavioural replication is indeed the product or component of emotional contagion, neurophysiological measures should also be obtained and compared to pre-exposure levels and ideally to those in demonstrators. For instance, in cooperative breeding systems, such as *N. pulcher*, juveniles that help breeders in defending and cleaning the brood increase their cortisol levels to match those of breeding females (Bender et al., 2008). Also, pairs of three-spined stickleback exhibit matched cortisol level increases under stressful conditions, such as novel environments, compared to baseline living conditions (Fürtbauer and Heistermann, 2016). The challenge here is the ability to extract such measures in controlled experiments without interrupting the test procedure, especially when the adopted paradigm is purposed for following through in testing consequent prosocial responses. For demonstrators, physiological measurements are feasible by either ensuring that an induced behaviour shows specific physiological hallmarks in a subsample, or in the case of using video-playbacks, demonstrators can be first recorded and then tested for their physiology. For terrestrial animals, observers can be physiologically monitored remotely for specific sensor-detectable measures, such as temperature (e.g. ocular thermography; Vogel et al., 2016) or heart and respiration rates (e.g. accelerometers, electrocardiograms and electromyograms with wireless technology; Jacobs et al., 2021). For fish, heart and respiration rates, as well as movement, orientation and acceleration across a three-dimensional axis is now possible by implantable biotelemetric tags (Yang et al., 2021) while non-invasive stress physiology measures, such as cortisol levels, can be sampled without interruption from holding-water (Ellis et al., 2004).

2.3. Observers directly or indirectly recognise the emotional state of demonstrators

The direct recognition of emotions in others is often ascertained by alternative forced-choice tests, where individuals need to discriminate between two competing expressions of emotional states (Bogacz, 2006; Limbrecht-Ecklundt et al., 2013). This discrimination is quantified by choices during the presentation of competing behavioural expressions, such as neutral *versus* fearful or high *versus* low intensity expressions. However, this approach may be more apt for humans expressing declarative choices, for training animals to discriminate cues, or for mammals presenting clear prosocial responses (Harms et al., 2010; Müller et al., 2015; Bellegarde et al., 2017; Ferretti et al., 2019). Conversely, interpreting choices between two stimuli presenting conflicting behavioural cues can prove problematic for probe trials or one-trial testing in fish, due to alternative explanations from attentional effects. First, the discrimination may rely simply on differences on cue salience. For example, increases in speed and angular velocity during erratic fear responses can elicit preference in others by gathering their attention, if compared to subtle neutral movement patterns. This can be directly tested by extracting attentional measures, such as head orientation and visual-field alignment towards the two contrasting cues, in addition to discrimination measures, such as approach or local interaction preferences. Alternatively, attentional preferences can be compared between behaviours of the same emotional state that diverge in salience, such as comparing neutral behaviour to both erratic and freezing (immobility) distress-responses (Akinrinade and Kareklas, et al., 2023). Second, local and attentional preferences during presentation may represent inspection, exploration or cuing, rather than recognition. For instance, archerfish exhibit faster reactions towards targets that are in the same direction as the body orientation of conspecifics, revealing social attentional cuing that could interrupt emotion recognition (Leadner et al., 2021). Similarly, attentional limitations to emotion recognition and contagion may be imposed by other social cues eliciting simultaneous responses. For instance, in the mouthbrooding cichlid *A. burtoni*, the cleaner wrasse *L. dimitiatus* and the nest-building stickleback *Pungitius pungitius*, attention to others' behaviour enables the recognition and establishment of rank, which leads subordinates to alter behaviour when observed (Pinto et al., 2011; Webster and Laland, 2013; Fernald, 2017). In dealing with this issue, social memory paradigms use probe-test trials without cues to examine if animals can recall information acquired during learning (Madeira and Oliveira, 2017). The approach relies on the underlying process of recognition memory, where differences between two conflicting sets of information can be encoded and later recalled when those differences are no longer there. As such, animals may be first allowed to observe two conflicting behaviours from a distance, and then allowed to approach demonstrators only after the cessation of conflicting sensory cues. In developing such an approach in zebrafish, we have recently used video-playbacks to ensure that conflicting cues are limited to the observation phase (Akinrinade and Kareklas, et al., 2023; Kareklas et al., 2023). Other approaches include comparing responses towards calm and distressed conspecifics, or before and after they exhibited distress (e.g. guppies and minnows: Crane and Ferrari, 2015; Crane et al., 2018; Crane et al., 2020). For indirect recognition, there has been little work in developing protocols outside the use of questionnaires in humans (Doherty et al., 1997) or the use of goal-directed mirroring tasks in humans and macaques (Rizzolatti et al., 2001). However, indirect recognition is defined by either motor-afferent feedback or self-evaluation, which are dependent on the mirrored response, such that stronger responses facilitate emotion recognition. Therefore, under indirect recognition, fish are expected to exhibit a positive correlation between the level of contagion during observation and the degree of recognition during testing. Should this involve motor-afferent feedback, then recognition should correlate only with movement levels during behavioural replication, while if this involves feedback from physiology, recognition should relate to stress-hormone or reward/fear signalling levels. Conversely, if feedback is derived from a generalised self-evaluation process, both components should be related with recognition, potentially in different degrees and with composite or additive effects. In this case an additive or composite (principal components) score of both measures should have a stronger predictive power than either measure individually.

2.4. Observers organise other-oriented prosocial acts, with or without immediate costs

A leading prosocial act is resource sharing, which is commonly encountered in fish communities. For instance, coral reef fish species exhibit food, shelter and territory sharing, both in terms of intraspecific and interspecific partitioning, and this is often attributed to mutual and reciprocal gains for niche construction. In particular, local modulation of biotic and abiotic conditions by different organisms and their socio-environmental interactions improves their collective survival (Fishelson, 1980; Laland et al., 2000; James et al., 2004; Corrêa et al., 2011). Niche construction is commonly expected to implicate social cooperation for resource access and antipredator functions, and based on these fitness benefits it is considered a substrate for human social and cultural evolution, including prosocial phenotypes such as division of labour, reciprocity, and altruism (Sterelny et al., 2007; Odling-Smee and Laland, 2009; Fuentes et al., 2010; Laland et al., 2017). Thus, similar collective fitness benefits related to niche construction could explain resource sharing in fish and provide clear examples of prosocial acts. In mammals and birds, resource sharing is most often purposed for mating or parental investment, and the phenotype comprises such resource costs that it is most often kin or dominance-status dependent, while voluntary donations tend to rely on reciprocity and mutual gains, with only a few exceptions (e.g. corvids; Cronin, 2012; Rault, 2019). Similarly, across four species of coral reef rabbitfishes (*Siganidae*), direct reciprocity in food sharing was demonstrated by the consistent, coordinated and alternating upright vigilance orientation of one fish while a partner fish was foraging on the substrate, a behaviour that incurred effort costs but improved foraging efficiency for the pair (Brandl and Bellwood, 2015). Further, instances of food and territory sharing by dominant fish are often preferential towards kin, such as in Atlantic salmon juveniles (Griffiths and Armstrong, 2002). The challenge is to identify if such phenotypes constitute active prosocial resource sharing as a function of recognising the state of others. Notably, there are a few recent examples of active prosocial food sharing in fish, but without any indication of whether these could be preferentially organised towards conspecifics under a specific stress or hunger state. In addition, these examples provide competing evidence as to whether prosocial behaviour is delimited by the selection of highly cooperative traits and the formation for strong social bonds. On the one hand, Satoh et al., (2021) found that monogamous male convict cichlids preferred choices where food was provided to them and their mate, instead of those rewarding only them. Because these cichlids exhibit biparental care, the authors interpret their findings as support for the prevalent hypothesis that proactive prosociality arises from caregiving outside parental nurturing, so-called alloparental care (Burkart et al., 2014), and from the interdependence of social partners, emphasised by their monogamous pair-bonding, which leads to shared fitness benefits (Tomasello et al., 2012). On the other hand, Nafcha et al. (2023) demonstrated the exact same "equal-payoff" prosocial choice in the highly competitive archerfish, without any effects from inter-individual familiarity, which instead suggests that proactive prosociality may arise from generalised reciprocity ("return the act to anyone"; Barta et al., 2011). The contrasting evidence provided by these two studies, regarding the selection of prosociality, is very likely a consequence of the broad variation in social behaviour exhibited by ray-finned fish, which is the largest and most phenotypically diverse group of vertebrates (Alfaro, 2018). However, the discrepancy between the social differences of the two species and their shared prosocial phenotype highlights the value of studying fish for

addressing existing questions about the evolution of prosociality.

Another extremely common phenotype in social, group-living fish, is sharing information that benefits others (Hoare and Karuse, 2003; Rieucau et al., 2015), but it is rarely characterised in terms of prosociality and the costs to the actor are oftentimes indirect and can largely vary with the situation. For example, informing others regarding potential risks, such as the presence of a predator, may only cost time and effort if it is the result of collective vigilance in close-proximity groups (Davidson et al., 2021), but if the information is provided by individuals that leave the group for a close inspection, it can implicate risk of direct predator attack. Notably, some fish species have evolved separate prosocial strategies to mitigate such risks. One example is cooperative inspection, encountered in zebrafish, cichlids and sticklebacks, and where conspecifics provide collective antipredation benefits to others by joining them in their close inspection of predator cues, a phenotype reinforced by kinship and reciprocity (Walling et al., 2004; Hesse et al., 2015; Pimentel et al., 2021). Other prosocial information-sharing acts involve prey capture and foraging, which imposes resource-sharing costs but derives mutual benefits from reciprocity, collective or cooperative foraging strategy and safety in numbers (Pitcher and Parrish, 1993; Krause et al., 2011). A notable example of intentional resource-information sharing is the interspecific cooperative hunting strategy of the grouper *Plectropomus pessuliferus* and the moray eel *Gymnothorax javanicus*, where groupers share prey to enlist the crevice-dwelling abilities of eels via communicative head-shaking signals (Bshary et al., 2006). Although the interaction is related to hunger levels and prior success in prey-capture, it is uncertain if this information on motivational state is communicated in eliciting the prosocial response of the partner.

Another category considered for prosocial responses is aiding towards a goal, often reported as helping, and several paradigms have been developed to test this in humans and other animals (Bshary and Raihani, 2017). For instance, in mice and rats, a well-developed protocol is training individuals to open an exit from a confined space and testing whether this is performed to release others, and often examples include signalling from conspecifics by stress-induced ultrasonic vocalizations, which may infer emotional contagion (Bartal et al., 2011; Mason, 2016; Ueno et al., 2019). These set-ups involve motor capacities that are limited to morphological adaptations, and which restrict their use for comparative work in fish. However, there are several types of phylogenetically persistent natural helping behaviours, a common example being that of cooperative breeding, and many hypotheses have been developed to explain its evolution (Burkart et al., 2009; Van Schaik and Burkart, 2010; Burkart et al., 2014; Takimoto-Inose, 2021). One prominent case that has been experimentally developed addressing these hypotheses is the cooperatively breeding cichlid *N. pulcher*. Earlier work in this species presented evidence for both the "territory inheritance" and "pay-to-stay" hypotheses. Namely, breeding vacancies from removing a parent were often filled by same-sex helpers while the removal and replacement of helpers resulted to their attack by third parties, which sometimes led to their eviction, but also motivated them to invest more in breeding (Balshine-Earn et al., 1998). Later evidence also demonstrated that relatedness, dominance and even group-size augmentation and maintenance influence the decision and degree of breeding help exhibited in this fish species (Stiver et al., 2005; Wong and Balshine, 2011). Helping may also extent to inter-specific interactions, such as the obligate cleaner wrasse *L. dimidiatus* that engages in the removal of parasites from client reef fish, which also reduces client stress levels (Bshary et al., 2007). *L. dimidiatus* exhibits a different nonapeptide neuronal population profile than non-cleaner wrasse (Mendonça et al., 2013). In particular, cleaning performance relies on the inhibition of vasotocin signalling to suppress appetitive drives for consuming their client's mucus instead of ectoparasites, which enables cleaners to maintain clients and avoid their punishing response (Soares et al., 2012). Given punishment is often encountered as a driver of helping, it is noteworthy that this typically implicates forms of emotion recognition without contagion, such as the appraisal of aggressive behaviour from punishers and submissive behaviour from idle helpers. For instance, the removal and replacement of helpers in the cooperatively breeding cichlid, *N. pulcher*, elicits aggression towards them and potential eviction from the group, and the level of aggression is greater when helpers exhibit increases in submissive behaviour (Hellmann et al., 2015).

More cognitively demanding complex prosocial phenotypes are often prescribed to their more "emotionally-purposed" benefit of ameliorating distress, such as non-maternal caregiving, and have been mostly studied in mammals in the form of allogrooming and in some bird species in the form of allopreening, and can have energetic, cognitive and opportunity costs without any direct benefits (Russell and Phelps, 2013). These types of other-oriented behaviours are referred to as concern, compassion or consolation, depending on the context, and are typically reserved for social partners, pair bonds and offspring, with potential indirect fitness benefits (Walker et al., 2003; Romero et al., 2010; Palagi et al., 2014; Burkett et al., 2016). Similarly, there are reproductive and parental investment contexts, with indirect fitness benefits, under which similar caregiving behaviour is found in fish species. For example, male parental care in the form of nest building, nurturing and defence is common in fish, including in the *Belontidae* family that includes the Siamese fighting fish, *Betta splendens*, reputed for their territorial contests (Lawrence, 1979; Lattal et al., 2022). The acquisition and defence of territory by *B. splendens* males is related to energetically costly offspring-oriented caregiving behaviour, purposed to alleviate distress and to reduce mortality risk from pathogenic challenges and attacks from intruders, and it is found to be evolutionarily independent from life-history and environmental pressures (Braddock and Braddock, 1959; Bronstein, 1982; Rüber et al., 2004). Namely, males invest in the production of glucose rich bubble nests purposed for safeguarding and nurturing their offspring, eggs and fry, and providing protection form lethal fungal growth and protozoan parasites (Pesaresi, 2001; Kang and Lee, 2010). Males also perform active parental defence, more readily attacking intruders that are more threatening, and choosing not to eat while eggs develop in order to guard the nest and provide oxygen supply to the nest-deposited offspring (Kareklas et al., 2019; Portugal, 2023). Parental care in terms of nest defence, or nest construction and maintenance, from algae, sand, shells or rocks, is exhibited by many gobies, sticklebacks and minnows, while many sediment brooding cichlids invest in fanning oxygen and keeping clean the brood, and in other cichlids males or females guard eggs and larvae in their mouth until free-swimming age (Svensson and Kvarnemo, 2023). Thus, there is a non-exhaustive list of such high-investment caregiving phenotypes in fish, all of which have remained underdeveloped as examples of distress-alleviating prosociality and require further study.

Across examples of prosocial behaviour, we can identify a phenotypic complexity that radically varies between species, with their ecology and adaptations, but what is transversal across the evolutionary scale are the decisions that underly prosocial acts, independent of their complexity. Most notably, a common type of distress-alleviation that is widespread in group-living species of fish, and paralleled in birds and mammals, and which could provide a shared phenotype that is ideal for comparative studies, is social buffering (Kikusui et al., 2006). Beyond a group's provision of safety and information-sharing benefits that are shared by all its members, individuals that experience stress can be behaviourally and physiologically aided in their stress-coping by the mere presence of others. This is a well recorded and theoretically developed phenomenon, whose evolutionary substrate and functional implications remain poorly understood, but have recently been probed in fish with regards to their neural mechanisms (Hennessy et al., 2009; Faustino et al., 2017; Kiyokawa and Hennessy, 2018; Culbert et al., 2019; Cohen and McKay, 2020; Gilmour and Bard, 2022; Akinrinade et al., 2023). The usefulness of this phenotype for studying the evolution of prosociality with emotional contagion is four-fold. First, it encompasses the prosocial definition of other-oriented benefit with own costs, because approaching a distressed fish comes with risks from local

threats, but also the emotional state of the actor, i.e. their valence - approach or avoid - and levels arousal in the speed of either decision (Mendl and Paul, 2020; Wu and Hong, 2022). Second, the phenotype requires little cognitive, motor or morphological specialisations for complex behaviour, and is largely dependent on environmental conditions and their effect on approach/avoid decisions. These decisions are a common component of vertebrate cognition that underlies only the direction of behavioural response and not the organisation of complex sensory-motor phenotypes, which drastically vary between species (Fawcett et al., 2014). Third, it can be explained by the motivational and local-enhancement components noted in association to emotional contagion in humans and animals (Levy and Nail, 1993; Galef, 2013). Finally, social decisions are controlled by neurocognitive systems that implicate reward and reinforcement pathways, that are well conserved across the vertebrate phylogeny (aka. Social Decision-Making Network; O'Connell and Hofmann, 2012).

2.5. Prosocial benefits to demonstrators should be related to the behaviour they presented

To ascertain that a decision for a prosocial response is related to emotional contagion, the perceived and shared emotional state should directly explain the prosocial response. In the case where others express stress, fear or anxiety, other-oriented responses should ameliorate behavioural and physiological measures related to these states, either via social buffering or from affiliative interactions, such as social touch or allogrooming (Kikusui et al., 2006; Gilmour and Bard, 2022; Lim and Hong, 2023). Although social buffering may be more common in group living fish, intra- and inter-specific interactions may include phenotypes resembling grooming responses in mammals, such as the tactile reduction of elevated cortisol levels by cleaner wrasse in previously confinement-stressed client fish (Soares et al., 2011). Other examples include faster decisions to share food when perceiving chemosensory signals of hunger in conspecifics (e.g. in rats; Schneeberger et al., 2020) or aiding others to attain perceivable but inaccessible food items, when others are observed to struggle (e.g. chimpanzees; Melis, 2018). In humans, the perception of susceptibility in others drives the sharing of information regarding potential threats, such as antisocial actors or aggressors (Feinberg et al., 2012). Similarly, when studying the evolutionary relationship between emotional contagion and prosociality in fish models, experimental paradigms and tasks should comprise contextual relevance such that the prosocial response is contingent on the initially observed state, which should also be explicitly tested. For instance, when cooperating in the defence of territory, resident *A. burtoni* males adjust their responses to the responses of their partner, which suggests that prosocial help is coordinated based on the needs of the conspecific (Weitekamp and Hofmann, 2017). However, partners do not attend to the resident's behaviour but rather respond directly to the opponent's behaviour, and this implicates extensive differences in neural activity localisation, from mesolimbic and preoptic regions in neighbours, to pallial regions in residents. This reveals that the shift from direct defence to cooperation is paralleled by a shift from risk/reward signalling to the involvement of recognition and memory structures, as a function of coordinating prosocial acts towards conspecifics, based on their state. Furthermore, the component of contagion may affect later prosocial phenotypes depending on which emotional and behavioural state is transmitted and the specific mechanisms it relies on, such as the differential expression of vasotocin between courting and aggressive contexts in *A. burtoni* males (Loveland and Fernald, 2017). According to York and Fernald (2017), the evolution of social phenotypes relies on both behaviour and neurocognitive traits, where species may evolve common phenotypes implicating the same neural mechanism or a different one, either from an identical mutation with functional redundancy (parallel evolution) or from shared ancestry and hybridization (collateral evolution). Thus, the evolution of underlying neural mechanisms is paramount to the role of emotional contagion in prosociality.

3. Traversing the phylogeny: identifying shared neurobiological mechanisms

For the organisation of emotional contagion, a leading mechanism in humans and other primates is that of mirror neurons situated in cortical premotor regions, which enable the automatic replication of behavioural and psychophysiological states observed in others and underpinned by the understanding or recognition of emotional expressions (Rizzolatti et al., 2001; Keysers, 2009). This class of neurons are purposed for goal-oriented motor responses and their replication when observed in others and linked to action-perception mechanisms of empathic behaviours (De Waal and Preston, 2017). The mechanism also involves so-called "unmediated resonance" processes, where mirrored emotional expressions are cognitively processed for recognising the experienced emotion (Goldman and Sripada, 2005). Thus, the mechanism resonates with the self-feedback processes proposed by Hatfield et al. (1993) but relies on cortical brain areas that cannot explain the replication of emotional states in non-mammalian species, like fish (Palagi et al., 2020; Hirsch et al., 2023). Similarly, prosocial behaviour in humans has been linked to empathic, affect-sharing and self-other distinction functions of cortical areas, such as temporoparietal junction, the medial pre-frontal cortex and the anterior mid-cingulate cortex (Lamm et al., 2019). The implication of emotional contagion in organising prosocial behaviour beyond these specialised cortical regions, rests on the emotive-cognitive modulation of motivational drives that defines decision-making and its broad social and ecological functions across the vertebrate phylogeny (Budaev et al., 2019; Mendl and Paul, 2020; Wu and Hong, 2022). This involves neurocognitive mechanisms for the integration and processing of social sensory information - their appraisal, recognition and reinforcement by associated costs and benefits - and ultimately their use to motivate other-oriented prosocial response (Ferretti and Papaleo, 2019; Palagi et al., 2020; Hirsch et al., 2023; Walsh et al., 2023).

The primary set of mechanisms that is paramount to emotional contagion are perceptual systems that integrate sensory information for the recognition of emotional states. Visual information is perhaps the most well-studied modality in animals, as it is the most prominent information pathway for emotion recognition and affect-sharing in humans, and thus parallels can be drawn regarding the underlying mechanisms. This also stems from the utility of facial expressions in human research on emotion recognition and mimicry (e.g. yawn contagion). Furthermore, there is evidence for similar neuromechanistic homologies in face processing in primates and other mammals (e.g. in macaques: Tsao et al., 2008) or morphological similarities in non-human primates (e.g. laughter, play or threat grimaces; Waller et al., 2017; Waller et al., 2020). The visual modality also features prominently across fish species, with adaptations responding to social and environmental demands, such as morphological reproductive signals, nocturnal or diurnal activity and predator detection strategies (Luehrmann et al., 2019; de Busserolles et al., 2020; Cortesi et al., 2020; Musilova et al., 2021). For example, the retinal structure of elephantnose fish, *Gnathonemus petersii*, comprises cone receptors grouped in photonic-crystal reflecting cups and the posterior positioning of rod receptors, enhancing sensitivity to colour-mixed stimuli and limiting spatial noise, for detecting movement in the dim-lit turbid waters they inhabit (Kreysing et al., 2012). Although such visual adaptations confirm the utility of visual tests with respect to species-specific ecological conditions, animals rely on weighted multisensory integration for improving information reliability, which is evident in emotion recognition and contagion paradigms (Fetsch et al., 2012; Munoz and Blumstein, 2012; Klasen et al., 2014). For example, distress olfactory cues can be discriminated from neutral ones, and can elicit the replication of physiological and behavioural responses in others. However, these cues can also enhance discrimination and replication of states perceived by other

modalities, such as vision (e.g. alarm substance in fish, Pinho et al., 2020; alarm pheromone in rats, Kiyokawa et al., 2004; and stress sweat in humans, Rubin et al., 2012). Other sensory modalities involved in emotion signalling across vertebrates include acoustic vocalisations, where matching or recognition has been observed for ultrasonic distress calls in rodents (Saito et al., 2016) and alarm songs in birds (Price and Yuan, 2011), and associated with physiological changes (Perez et al., 2015). Specialised sensory adaptations, such as electro-communication, may also prove to maintain the transmission of emotional states (see recent evidence of electric signal synchronisation in weakly electric fish; Worm et al., 2021). The integration of sensory inputs relies largely on the ability to attend to social information, which can have top-down effects on the recognition and contagion of emotion states as well as the organisation of other-oriented responses. The implication of attention in emotion recognition has been increasingly considered as a root of emotion recognition deficits in human social neurodevelopmental disorders, such as autism (Begeer et al., 2006; Wieckowski and White, 2020). Recently, we found that mutation to the functionally conserved paralogue of the candidate autism gene *shank3* in zebrafish, markedly reduces attention to distress behaviour such that it elicits severe deficits in both social contagion and later local preference towards distressed conspecifics (Kareklas et al., 2023). Notably, the gene transcribes the dominant SHANK3 synaptogenesis protein, and its mutation leads to the transcriptional downregulation of other interacting synaptogenic proteins, but also an apparent compensatory upregulation of neural growth and neurogenesis components. This suggests that neural plasticity is at the heart of attentional control to conspecific behaviour and its impact on emotional contagion and other-oriented response in this fish model.

A leading modulator of upstream inputs in sensory information are nonapeptides and specifically the oxytocin signalling pathway (Zheng et al., 2014; Pekarek et al., 2020). Nonapeptide regulation of social chemosensory signals is rooted in early evolutionary homologs in invertebrate reproduction (Beets et al., 2012; Garrison et al., 2012), while its implication in visual, somatosensory and auditory controls extends the vertebrate phylogeny. Examples include auditory-vocal regulation and memory in fish and songbirds, touch and pain regulation in rodents and human visual attention to facial expressions (see review by Grinevich and Stoop, 2018). Oxytocinergic controls to sensory inputs also extend to the modulation of social perceptual processes required for behavioural state recognition. For instance, oxytocin in zebrafish (see genomic validity for the common nomenclature: Theofanopoulou et al., 2021) is required during a critical period in development for the maturation of a dopaminergic cluster in the pre-tectum that is potentially involved in the visual processing of social stimuli (Nunes et al., 2021). Furthermore, oxytocin signalling is necessary for the use of visual information to discern biological motion (animacy) and conspecific form (Nunes et al., 2020), which could explain why it is also necessary for the discrimination between distress and neutral behaviour in this species (Akinrinade and Kareklas et al., 2023). Similarly, in mice, olfactory and visual discrimination of both positive ("relief") and negative (distress) emotional states is regulated by oxytocinergic projections from the hypothalamus to the central amygdala (Ferretti et al., 2019). Such conserved sensory perceptual mechanisms can explain the perception and recognition of behavioural expression of emotion, as well as their replication. For example, distress contagion in zebrafish is controlled by oxytocinergic regulations of inhibitory signalling in the telencephalic homologue of the lateral septum and excitatory signalling in the homologue of the striatum, both of which are regions implicated in oxytocinergic controls of affect sharing in humans and other mammals (Menon et al., 2018; Lamm et al., 2019; Lieberz et al., 2020).

Conserved neuromodulatory systems, such as nonapeptides, are implicated in social decisions across vertebrates, which can then explain the organisation of prosocial responses (Fig. 2). Across vertebrates, social decisions are organised by localised activity and functional connectivity across homologous areas of (1) the mesolimbic reward system, which reinforces the promotion of beneficial social behaviours and the avoidance of costly ones, (2) social behaviour areas, which control affiliation, prosociality and approach-avoidance motor responses, and (3) a set of structures linking reward and behaviour areas (O'Connell and Hofmann, 2011a, 2011b). This network exhibits a high degree of structural, topological, neurochemical, and functional conservation and comprises the most abundant and highly conserved social activity of overarching neuromodulators, such as oxytocin (O'Connell and Hofmann, 2012). Notably, across vertebrates, oxytocin the expression of receptors are highly conserved in this brain network, while the oxytocin ligand exhibits high molecular conservation (Yamashita and Kitano, 2013; Feldman et al., 2016; Carter and Kingsbury, 2022), such that distinct phylogenetic variants exhibit high cross-species receptor binding affinity (see effects of human ligand treatments in zebrafish: Braida et al., 2012). The oxytocin system exhibits three levels of neuromodualtory control, from excitatory activity via depolarisation changes, to inhibitory transmission by controls on release and interneuron spiking, and ultimately the modulation of other modulators, particularly monoamine pathways such as dopamine and serotonin (Froemke and Young, 2021). Oxytocin has been regularly implicated in emotional recognition, contagion and empathy, and prosocial behaviour, such as consolation, helping and nursing, by its activity in striatal regions, particularly the nucleus accumbens (Rodrigues et al., 2009; Shahrokh et al., 2010; Burkett et al., 2016; Yamagishi et al., 2020). Oxytocin-induced release of serotonin in this region induces social reward in mice, and the activation of presynaptic serotonin receptors elicits long-term depression of synaptic excitatory signalling for socially induced local preferences (Walsh et al., 2021). Similarly, excitatory

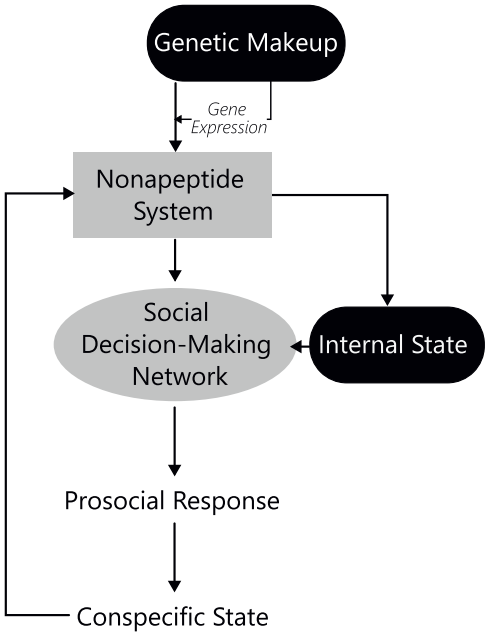

Fig. 2. Diagram of conserved systems linking emotional contagion and prosociality. At the centre we have the highly conserved neuromodulatory functions of the nonapeptide system, which include both the control of prosocial phenotypes and the regulation of social cognition, particularly motivation, memory, reinforcement and recognition. Nonapeptide cognitive functions are preserved across a set of mesolimbic-reward and social behaviour regions with high homology across vertebrates, the so-called social decision-making network (O'Connell and Hofmann, 2012). Thus, the prediction is that information on conspecific state triggers nonapeptide signalling, determined by genetic makeup at the individual, population or species level, and elicits internal state changes through neuroendocrine controls (e.g. stress or sex hormone interactions), and combined excitatory, inhibitory and monoamine modulation in the social decision-making network. This positively or negatively reinforces the expression of prosocial acts and the benefit they offer to conspecifics in response to their expressed state.

controls in the homologous region of the striatum in the zebrafish telencephalon, has similar neural decision-making controls for fear contagion and recognition, as well as the motivation of later local preferences towards those that exhibited fear (Akinrinade and Kareklas, 2023). However, these regional controls in zebrafish are situated with localised dopaminergic, rather than serotonergic, activity, which is another key modulator of striatal activity during social interactions, and oxytocin induced dopamine signalling promotes social reward (Báez-Mendoza and Schultz, 2013). The evolutionary relevance of the striatum, as well as the hippocampus, the amygdala and the bed nucleus of the stria terminalis, relates to their strong vertebrate homology that maintains their role as areas responsible for the appraisal of emotional behaviour, based on previous experience and current information, and for outputs to social behaviour areas, but also to cortical regions that could explain the extension of socio-cognitive functions in humans and other mammals (Decety et al., 2016; Tremblay et al., 2017). For example, the activation of the ventral striatum is related with that of the medial orbito-frontal cortex during the organisation of compassion in humans, while striatal inputs to the medial pre-frontal cortex linked to social memory controls may also explain the regions involvement in mentalising, the process by which humans share imagined states in others rather than observed ones (Lamm et al., 2019). Therefore, there are conserved systems that underly higher-order cognitive controls in structures exclusive to the mammalian brain, and by studying them we can delimit the evolutionary bases for the mechanistic integration of emotional contagion in the organisation of prosocial response in fish.

Based on decision-making functions, we can expect that mechanistic adaptations do not only arise for recognising emotional state in social cues but for also shifting between self-beneficial and prosocial responses towards the same cue. For example, in false clown anemonefish (*Amphiprion ocellaris*), males exhibit greater parental care behaviors than females, including nips, egg fanning, and nest visits, and this is triggered by oxytocin signalling (DeAngelis et al., 2017; DeAngelis et al., 2020). In monogamous biparental systems, such as convict cichlids, offspring defence and pair-bonding are also regulated by neuropeptides, oxytocin and vasotocin (Oldfield and Hofmann, 2011). In *L. dimidiatus*, mutualistic cleaning of client fish is driven by downmodulating vasotocin signalling, which trades off appetitive drives to consume the client's mucus for removing client ectoparasites instead (Soares et al., 2012). Across sympatric *Labridae* wrasses, genes and gene modules exhibit differential expression and co-expression patterns specific to facultative cleaning evolution in two species, and consistent with transcription in an obligate cleaner, compared to three non-cleaning species (Young et al., 2022). This illustrates how prosocial phenotypes may arise from convergent evolution and how this may be specific to the behavioural repertoire and not the underlying cognitive processes that enable social cues to trigger prosocial response, i.e. attention, recognition, memory and contagion. For instance, appetitive courtship displays are a costly other-oriented behaviour paramount to pair-bonding and reproductive fitness and in cichlids this includes bower building phenotypes evolved multiple times with thousands of associated genetic variants. Using hybrids of two cichlid species with differing bower-building phenotypes, York et al. (2018) were able to identify a differential expression of alleles specific to each species when hybrids were performing each type of building phenotype, pit-digging or castle-building. This demonstrates that genetic architecture for the transcriptional regulation of costly other-oriented behaviour with direct fitness benefits is specific to the phenotype itself.

4. Concluding remarks

In this review we aim to set the stage for comparative studies of emotional contagion and prosocial behaviour to extent from mammals and birds to the vertebrate evolutionary divergent branch of teleost fish. This approach allows us to identify and investigate similar cognitive and physiological phenotypes that underlie prosocial behaviour across phylogenetically distant species and to establish similar cognitive abilities between species as homologues (i.e. similarity by descent), or as a result of convergent evolution to similar selective pressures (aka convergent minds hypothesis). Therefore, unravelling the psychophysiological basis of cognitive abilities underlying prosocial behaviours across species is key for the understanding of the evolution of cognition and the uniqueness of prosocial behaviours observed in humans.

Declaration of Competing Interest

The authors declare that they have no competing interests or personal relationships that influence the work reported in this paper.

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