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Learning of safety by a social fish: applications for studying post-traumatic stress in humans

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As animal behaviour theory has developed over the past 70 years, much attention has gone towards social behaviour. While our basic knowledge of social systems has grown substantially, it has rarely been applied to human issues. Here, we attempted to bridge the gap between animal behaviour theory and human psychology by conducting social experiments involving fish. As in many species, minnows (family: Cyprinidae) repeatedly exposed to risky situations can develop a behavioural phenotype characterized by neophobic tendencies, pacing and stereotypic behaviours. Here, we tested whether the simple presence of calm (or un-calm) conspecific models could lead to a weakening of the high-risk phenotype in minnows that acquired fear either in isolation or within a group. We first documented that the social context of risk exposure impacted the intensity of the high-risk phenotype, with minnows exposed to risk in isolation showing stronger high-risk traits compared to those that were exposed to risk in groups. However, individuals exposed to risk in isolation were more influenced by calm models, despite their more pronounced phenotype. We argue that group exposure led to social reinforcement of risk, which in turn decreased the information transfer about safety in these individuals. We also demonstrate that a group of calm models, and not un-calm models, was required to weaken the high-risk phenotype. These findings highlight the interplay between social reinforcement of risk and safety in social groups and the impact of groups on information transmission. Moreover, our results parallel anecdotal reports of successes or failures of social therapies for post-traumatic stress (PTS) patients based on the social context of symptom acquisition, suggesting that understanding the transfer of information in social animals could prove fruitful in understanding and modelling PTS recovery.

Animal behaviour theory has developed substantially since Tinbergen (1953) published his book on social behaviour. Indeed, a tremendous amount of research has explored the social lives of animals, from acoustic communication in marmots (Blumstein, 2007) to chemical communication in insects (Wilson, 1965), interference competition in birds (Minot & Perrins, 1986) and social learning in fish (Mathis, Chivers, & Smith, 1996). While early work focused on understanding how information is transferred among group members, much of the present research, including social network theory, aims at understanding factors that affect the origin, quantity, content and reliability of information transfer in social species.

A large body of literature exists on social information transfer in the context of predation risk. A number of species, from insects to mammals, can learn about novel threats by observing experienced fearful conspecifics (reviewed in Crane & Ferrari, 2013). Factors such as size, age and experience of these conspecific 'models' are known to affect the reliability of the information learned, and this learning is not limited to risk but also extends to safety. The field of animal behaviour should thus be a crucial source of information to anyone interested in understanding factors modulating the social transfer of risk or safety-related information. Yet, applications of social learning theory outside of animal ecology, and specifically to human psychology, are relatively rare, as animal models informing human psychology are often viewed as unconvincing. Here, we present a case where the field of animal behaviour, and specifically social learning theory, can inform and provide insights into factors affecting fear severity in humans and the potential for overcoming such fear.

For decades, minnows (family: Cyprinidae) have been a classic model for understanding fear reactions because of an alarm substance in their skin, originally described as 'schreckstoff' by von

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Frisch (1938, 1941). This substance is released from injured conspecifics, and as such represents a reliable indicator of risk. When detected by nearby conspecifics, these cues elicit innate antipredator responses (e.g. freezing; Smith, 1992). Repeated exposures to alarm cues are known to induce a high-risk phenotype in a few species (e.g. Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013). In minnows, such high risk exposure induces increased freezing behaviour, a hypervigilant stereotypy, and neophobia (Crane & Ferrari, 2016), a phenomenon where animals react with fear when exposed to novel stimuli. The intensity and duration of this phenotype match the level of risk exposure (Brown, Chivers, Elvidge, Jackson, & Ferrari, 2014; Brown, Demers, Joyce, Ferrari, & Chivers, 2015; Brown, Elvidge, Ramnarine, Ferrari, & Chivers, 2015). While alarm cues alone provide little information about the attacker, the co-occurrence of specific predator cues (sound, sight, or smell) facilitates a learned association of those cues as threatening (i.e. alarm cue learning; Ferrari, Wisenden, & Chivers, 2010).

Many fish species are highly social, and in this context the fathead minnow, *Pimephales promelas*, has perhaps been the most well studied. Minnows spend much of their time engaged in social interactions, living in shoaling groups and competing for territory and mates (Martinovic-Weigelt et al., 2012; McMillan & Smith, 1974). In addition to alarm cue learning, minnows can learn by observing conspecifics (i.e. social learning; Crane & Ferrari, 2013; Mathis et al., 1996). These conspecifics are often referred to as tutors or demonstrators, but we prefer to use the term ‘model’ to remove any suggestion that the conspecific is purposefully signalling to the observing individual (Crane & Ferrari, 2013). In the context of predation risk, fear reactions provide social information to nearby individuals, although the purpose of such reactions is often to escape threats, rather than to notify others.

In one experiment with minnows, we found that the intensities of learned fear reactions were similar between alarm cue and social learning mechanisms (Crane & Ferrari, 2015). However, social information about risk was more persuasive. When minnows had prior experience with an odour as safe (repeated exposure in the absence of any negative stimuli), they failed to learn the odour as dangerous when paired with alarm cues, instead relying on their prior learning of safety (a process known as latent inhibition; Mitchell, McCormick, Ferrari, & Chivers, 2011). However, when these minnows observed an experienced model react to the odour, they learned the odour as a threat, revealing that this social information had overridden their prior individual assessment of safety (Crane & Ferrari, 2015).

When a similar social learning experiment was performed using high-risk, neophobic models, we found that the observers did not learn correctly about the novel predator odour (Crane, Mathiron, & Ferrari, 2015), and had indirectly acquired the neophobic tendencies of the models (i.e. socially transmitted neophobia; Crane & Ferrari, 2016; Crane et al., 2015). In this social learning framework, the observer and model may influence each other, with the observer potentially learning safety from the model, and the model learning risk from the observer, in a contradirectional transfer of information.

The goal in this experiment was to decrease neophobia by manipulating exposure to calm conspecific models. We sought to prioritize information transfer from the calm model to the neophobic observer, while minimizing the information transfer from the observer to the model. First, we induced the high-risk phenotype in observers via repeated exposures to alarm cues and manipulated the social context of neophobic acquisition (alone versus in group). We then manipulated the number of safe models (zero, one, or five) paired with the observer (i.e. ‘model therapy’; Fig. 1). Our previous work led us to hypothesize that the presence of more calm models would limit fear transfer to models, which would promote fear recovery in observers. We also reasoned that, as in some other animals, risk in isolation would lead to more severe symptoms (e.g. Seetharaman, Fleshner, Park, & Diamond, 2016), which we expected would be more difficult to alleviate with model therapy.

METHODS

Ethical Note

The following studies were approved by the University of Saskatchewan's University Committee on Animal Care and Supply (protocol No. 20130079) in accordance with the Canadian Council on Animal Care. We collected minnows under a Saskatchewan Ministry of Environment Special Collection Permit (SCP16-SC002). Sturgeon came from a laboratory stock colony via Genoa National Fish Hatchery, U.S.A. To obtain alarm cues from minnows, we used standard procedures for physical euthanasia rather than chemical methods that could potentially interfere with alarm cue chemistry (Ferrari, Capitania-Kwok, & Chivers, 2006; Ferrari, Trowell, Brown,

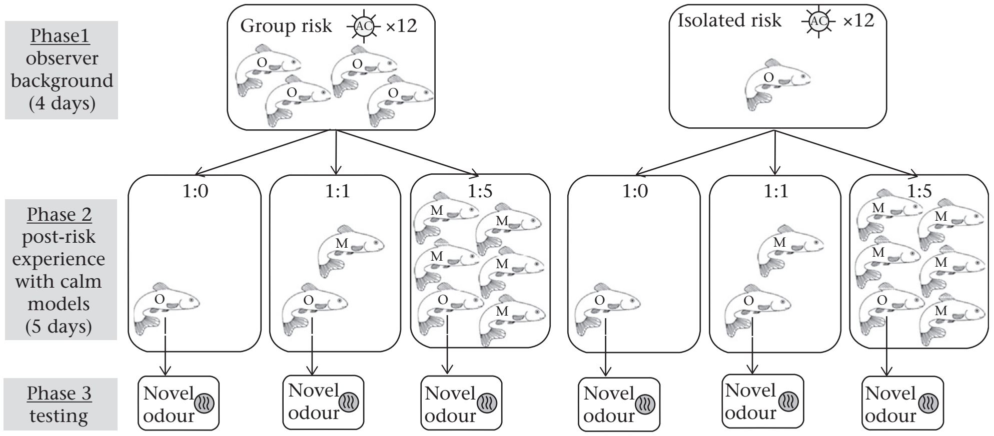

Figure 1. Experimental phases for risk-exposed individuals. Observer (O) minnows first experienced risk from 12 exposures to alarm cues (AC), either in isolation or in a group with three other fish. Then, observers had a 5-day conditioning period with the opportunity to interact with calm models (M): either zero, one, or five models. One day later, observers were tested alone, being exposed to a novel odour, to determine whether models weakened the high-risk traits of observers. Control treatments involving un-calm models were conducted but are not depicted here.