



Behavioural response of European starlings exposed to video playback of conspecific flocks: Effect of social context and predator threat



Francesca Zoratto^{a,d,*}, Leonardo Manzari^a, Ludovica Oddi^a, Rianne Pinxten^b, Marcel Eens^b, Daniela Santucci^a, Enrico Alleva^a, Claudio Carere^{c,e}

^a Section of Behavioural Neuroscience, Department of Cell Biology and Neurosciences, Istituto Superiore di Sanità, Rome, Italy

^b Laboratory of Ethology, Department of Biology, University of Antwerp, Wilrijk, Belgium

^c Centre for Statistical Mechanics and Complexity (SMC), INFN-CNR, Rome, Italy

^d Bambino Gesù Children's Hospital IRCCS, Rome, Italy

^e Department of Ecological and Biological Sciences, Università degli Studi della Tuscia, Viterbo, Italy

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ABSTRACT

We studied the behavioural response of European starlings to a socially mediated predation event. Adult starlings were exposed to either a video of a flock attacked by a peregrine falcon or a video of a flock not under attack. We investigated whether the social condition affected the anti-predator response under the hypothesis that in such a gregarious species singletons would increase their anti-predator behaviour more than individuals in groups, to compensate for potential increased risk. The video of the flock under attack caused an increase in immobility and vigilance, more marked in singletons, both during and after the exposure. The video of the non-threatened flock caused an increase in activity levels, especially during the exposure. Furthermore, we observed a marked increase in comfort activities in singletons as well as in social interactions and vocalizations in mini-flocks. Only birds in mini-flocks vocalized, which may be explained by an audience effect, a process of social cognition mediated by the social context, and not only by the stimulus. The results are in line with previous field studies, which showed that isolated starlings are exposed to a higher risk of predation compared to individuals in flocks.

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1. Introduction

A major factor in the evolution of avian flocking behaviour is predation (many eyes theory, selfish-herd theory, dilution effect, confusion effect, e.g. Cresswell, 1994; Siegfried and Underhill, 1975; reviewed in Beauchamp, 2004; Krause and Ruxton, 2002). Predation threat represents a crucial stimulus, which gives rise to a wide range of responses, such as risk assessment and decision-making processes (e.g. Devereux et al., 2006; Lima and Dill, 1990), and associated defensive/escape behaviours, such as mobbing, flight and freezing (for a review see Eilam, 2005).

Among vertebrates, a common response of preys to the direct threat of predation is freezing, i.e. remaining immobile to pass unobserved, thus diminishing the possibility of being caught by predators and increasing individual survival. Freezing is common in birds (e.g. Cade, 1965 for pigeons; Kullberg and Lind, 2002 for great tits), mammals (e.g. Wang et al., 2005 for rats) and fish (e.g. Brown

and Smith, 1998 for trouts; Lehtiniemi, 2005 for three-spined sticklebacks). For example, Siegfried and Underhill (1975) showed that, with respect to survival, it is advantageous for a single dove to remain immobile if left behind by a flock taking flight because of a predator, since falcons normally attack flying singletons.

Vocalizations are another typical response, often in the simple form of alarm calls. Whilst some aspects of anti-predator behavioural patterns (e.g. freezing) are strictly limited to individual survival, vocalizations could be signals to conspecifics that constitute a particular group and sometimes even at individuals from other species in the neighbourhood. The latter is the case of alarm signals emitted to communicate the presence of a predator, which are often non-species-specific (Klump and Shalter, 1984), while the former may depend on a phenomenon known as audience effect, documented in many species of group living vertebrates, like chickens (*Gallus domesticus*; Karakashian et al., 1988; Marler et al., 1986; Marler and Evans, 1996), zebra finches (*Taeniopygia guttata*; Vignal et al., 2004), Pinyon jays (*Gymnorhinus cyanocephalus*; Dahlin et al., 2005), Thomas' langurs (*Presbytis thomasi*; Wich and Sterck, 2003), white-headed capuchins (*Cebus apella*; Pollick et al., 2005) and Siamese fighting fish (*Betta splendens*; Doutrelant et al., 2001). This simple process of social cognition is present when emis-

* Corresponding author at: Section of Behavioural Neuroscience, Department of Cell Biology and Neurosciences, Istituto Superiore di Sanità, Viale Regina Elena, 299, I-00161 Rome, Italy. Tel.: +39 06 4990 3171; fax: +39 06 4957 821.

E-mail addresses: francesca.zoratto@iss.it, f.zoratto@gmail.com (F. Zoratto).

sion of alarm signals in response to predators is not simply a reflex but is voluntarily controlled by the individual emitting the signal and is specifically mediated by the social context, and not only by the stimulus, i.e. the presence of a predator (Dahlin et al., 2005; Mazzini et al., 2013; Wich and Sterck, 2003).

In birds, head moving typically reflects vigilance behaviours. Specifically, in feeding contexts, vigilance is classically measured as duration of head-up periods and head-down periods. However, in non-feeding contexts (as in the present study) birds always had their head up and therefore key measures of vigilance could not be obtained (Evans and Marler, 1990). In these cases head turning could provide an indication of vigilance. Indeed, head movements (i.e. rapid changes in head orientation) have been observed in many species and have been associated with antipredator vigilance (Bekoff, 1995; Cezilly and Brun, 1989; Fernandez-Juricic et al., 2011; Franklin and Lima, 2001; Jones et al., 2007; Lazarus, 1979).

A further aspect related to predation is visual lateralization. Franklin and Lima (2001), in an experiment on anti-predatory vigilance, demonstrated (by measuring birds' preferred position and head turning direction) right-eye biased lateralization in *Junco hyemalis*.

Most empirical and theoretical studies on flocking in relation to predation have been carried out in the context of foraging, focusing on vigilance and departure or escape responses (e.g. Caraco et al., 1980; Carbone et al., 2003; Hilton et al., 1999; Powell, 1974; Quinn and Cresswell, 2005; Sirot, 2006). In feeding contexts, animals joining groups face a trade-off between the antipredator advantages and the costs of increased competition (Carbone et al., 2003; Devereux et al., 2006; Krause and Ruxton, 2002). However, birds also spend a considerable time not foraging, e.g. flying, for migration and on local movements (e.g. forth and back between foraging and roosting sites) or just resting, and predation during these activities is common.

Methodologically, in laboratory studies investigating predator responses, a stuffed animal is commonly used (Cockrem and Silverin, 2002; Devereux et al., 2006; Powell, 1974), but video playbacks have, to our knowledge, rarely been used (for a review see Rieucan and Giraldeau, 2009; Woo and Rieucan, 2011). The first studies on the relationship between visual stimuli and corresponding responses were made using cardboard cut-outs (Ewert, 1987; Tinbergen and Perdeck, 1951). The advent of video technology made possible a further step forward in the presentation of visual stimuli. Evans and Marler (1990) have firstly presented video images of aerial predators to chickens proving their effectiveness in eliciting appropriate responses. Then, several experiments showed that even pigeons (Shimizu, 1998), zebra finches (Adret, 1997; Ikebuchi and Okanoya, 1999) and sparrows (Takahasi et al., 2005; Watanabe et al., 1993) reacted to video images of conspecifics. More recently it was shown that the thin film transistor (TFT), i.e. those for LCD screens, allowed zebra finches to perceive even small differences in the behaviour of conspecifics (Galoch and Bischof, 2007). Video playbacks, if effective, could be used in association with acoustic stimuli (e.g. distress calls) currently used to frighten and relocate birds that create conflicts with human activities, such as starlings in urban roosts, which constitute a major problem worldwide (Feare, 1984; Conover, 1994).

The aim of the present experiment was twofold. Firstly, we tested the hypothesis that a video of a conspecific flock under predation, projected through a beamer connected to a computer, could be effective as a stimulus in eliciting responses to predator exposure in European starlings (*Sturnus vulgaris*). We used two videos, one showing a flock of starlings in flight and the other a flying flock of starlings, similar in size, under a peregrine falcon attack.

Secondly, we tested the hypothesis that social conditions could modulate the antipredator response. The effects of the social condition have been recently investigated, in starlings, in relation

to response to novelty (Apfelbeck and Raess, 2008). Subjects that had been separated from their group had higher levels of corticosterone and were more active; however, their response to a novel object was not affected by the social condition (Apfelbeck and Raess, 2008). Here, we addressed a similar issue (i.e. the effect of the social condition) on the response to a predator by exposing to the video either birds alone or in a mini-flock.

We expected that the video with the flock under predation, compared to the video of the non-threatened flock, would be effective in eliciting fear and vigilance responses (i.e. more freezing, head turning and inactivity, less hopping, less comfort activity, less vocalizations, less social interactions, preferential use of the right eye) but differently depending on the social context: (i) birds in the mini-flocks would show reactions of fear and vigilance less marked than singletons because the former gain the advantages of being in a group; (ii) singletons would show an increase in fear and vigilance, and a decrease or absence of vocalizations, to compensate for potential increased predation risk; (iii) birds in the mini-flocks would show overall higher levels of vocalizations (audience effect).

2. Material and methods

2.1. Study species, subjects and housing

European starlings (*S. vulgaris*) are gregarious throughout the year (Cramp and Perrins, 1994; Feare, 1984). Flocks are larger in autumn and winter and smaller during the reproductive season. Also the distance between birds within the flock is wider in spring and summer aggregations than in winter flocks (Williamson and Gray, 1975). Starlings gather in flocks when flying, when foraging on the ground and when roosting in wintering grounds. Specifically, in proximity to winter roosts, birds congregate before sunset and, before landing into the roost, they form huge aggregations. In this context, flocks are usually exposed to a significant predation pressure (Carere et al., 2009; Zoratto et al., 2010).

Sixty-two captive male starlings, older than one year and individually marked with colour rings, were used in the present study. Birds had been caught near Antwerp, Belgium, in the previous years and they have been housed together in two separate flocks for at least one season (for details see Section 2.5). The experiment was conducted in September, after the breeding season and the moult period. The birds were housed in two outdoor aviaries (16 m × 8 m × 2.5 m and 18 m × 7.5 m × 3 m) at the campus of the University of Antwerp in Wilrijk, Belgium. Aviaries were visually but not acoustically separated from each other, and were provided with wooden nest boxes, small trees, and perches. Bathing water was always present in the outdoor aviaries as well as in the indoor cages. Food (Orlux paté) and water, replaced on alternate days, were supplied ad libitum.

2.2. Experimental procedure

Birds were taken from the two outdoor aviaries the day before testing and moved to the habituation room containing 15 cages (100 cm length × 45 cm width × 40 cm height) with sand on the bottom and perches fixed to the back wall. In both the habituation and experimental rooms, the temperature was always between 17 and 19 °C and an artificial 12 h light–dark cycle was set. True-light lamps with a flicker frequency of 100 Hz (i.e. fluorescent lamps that match closely the entire spectrum of natural day-light) were used. Before housing birds were identified, weighted (no significant differences in body weight were found), and randomly assigned to the social condition: subjects individually tested (called “single”) vs. subjects tested in a mini-flock of three birds (called “group”). Fourteen subjects were tested as single birds, sixteen subjects

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