Evolution of emotional contagion in group-living animals

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A B S T R A C T

Emotional contagion refers to an instantaneous matching of an emotional state between a subject and an object. It is believed to form one of the bases of empathy and it causes consistent group behavior in many animals. However, how this emotional process relates to group size remains unclear. Individuals with the ability of emotional contagion can instantaneously copy the emotion of another group member and can take relevant behavior driven by this emotion, but this would entail both cost and benefit to them because the behavior can be either appropriate or inappropriate depending on the situation. For example, emotional contagion may help them escape from a predator but sometimes induce mass panic. We theoretically study how these two aspects of emotional contagion affect its evolution in group-living animals. We consider a situation where an environmental cue sometimes indicates a serious event and individuals have to make a decision whether to react to them. We show that, as the group size increases, individuals with the ability of emotional contagion would evolutionarily weaken their sensitivity to environmental cues. We also show that a larger group yields a larger benefit to them through such evolutionary change. However, larger group size prevents the invasion of mutants with the ability of emotional contagion into the population of residents who react to environmental cues independently of other group members. These results provide important suggestions on the evolutionary relationship between emotional contagion and group living.

1. Introduction

In many animals, strong emotion manifested by an individual triggers similar emotion and associated behavior in other individuals around him/her, which is called emotional contagion. This emotional process is considered to form one of the bases of empathy and contribute to various social behavior (de Waal, 2008, 2012; Panksepp and Panksepp, 2013). However, why such an emotional process evolved in many animals is a big mystery because of its cost. Here, by cost we refer not only to the developmental and neurophysiological cost to support and maintain such ability, but also to the cost of enhancing and/or suppressing neural and physiological activity in copying other's (often negative) emotion, such as increasing blood pressure or decreasing activity level (freezing). Nakahashi and Ohtsuki (2015) constructed a mathematical model to investigate conditions for emotional contagion to evolve, and showed that copying other's emotion is more adaptive than reacting independently when the environmental similarity between individuals is larger. However, their model assumed

an interaction between two individuals only, so the condition for emotional contagion to evolve in group-living animals remains unclear. Since emotional contagion is biased toward in-group members (de Waal, 2012), there can be an evolutionary relationship between emotional contagion and group living. Therefore, how emotional contagion affects group size and how the group size affects the evolution of emotional contagion still remain an important but unsolved problem.

Why many animals form co-living groups and what affects their group size are important problems in evolutionary biology. Various merits of group formation have been proposed; for example, to keep body temperature, to cooperatively hunt preys, to resist predators, to struggle against other individuals, to find mating partners, to divide the labor, and so on (Nakahashi and Horiuchi, 2012; Nakahashi and Feldman, 2014; Nakahashi, 2016). When we study the relationship between emotional contagion and group formation, we have to consider the merit of information transmission within a group, because individuals may learn environmental information from others via emotional contagion. However, although some studies considered social learning within a group (Aoki and Nakahashi, 2008; Nakahashi et al., 2012; Ohtsuki et al., 2017), they did not study emotional contagion because the time scale of emo-

tional contagion is completely different from that of social learning assumed in these studies. In the previous studies, information is often assumed to be transmitted intergenerationally. However, information transmission occurs instantaneously, usually within seconds, through emotional contagion. Therefore, we need to develop a new framework to study the evolutionary relationship between emotional contagion and group formation.

Provided that there is no conflict of interest among group members, beneficial information to a group member should also be beneficial to other members. Since the probability that at least one member obtains beneficial information may increase as the group size increases, one may naively expect that individuals with the ability of emotional contagion obtain a larger benefit in a larger group. However, the actual situation is not so simple because individuals are error-prone. As the group size increases, the probability that at least one member obtains wrong information may also increase, which can cause harm in a group, by inducing a mass panic, for example. In fact, some breeds of chickens are too sensitive to sounds or stimuli and sometimes show panic behavior, which causes hurt (Abe et al., 2013). Therefore, it is unclear whether a larger group is beneficial for individuals with the ability of emotional contagion.

How to select information is an important problem for individuals. Although every individual should increase the probability of obtaining beneficial information and decrease that of wrong information, there is always a tradeoff between them. That is, when individuals attempt to obtain more information to receive more benefits, they inevitably obtain more wrong information at the same time. Therefore, there may be an optimum amount of information that an individual collects. The situation becomes more complex if individuals belong to a group and learn information from others via emotional contagion. There, the best strategy of information collection in each individual depends on those in other group members, and vice versa, so we need to consider a game-theoretic situation.

In this paper, we study the evolution of emotional contagion by using mathematical models. Since sensitivity to environmental information can affect the fitness of individuals, we also consider the evolution of sensitivity. We seek for the condition under which the fitness of individuals with the ability of emotional contagion is higher than that of individuals who always react independently of others (independent reaction). We also focus on the effect of group size on the evolution of emotional contagion and sensitivity.

2. Model

2.1. Overview

We suppose that individuals live in an environment where two kinds of events may happen, labeled as *trivial* and *serious*, and that the appropriate reaction to one event is inappropriate to the other. When a *serious* event happens, individuals should have strong emotion and react to it immediately, but when the event is *trivial*, they should ignore it. For example, if an individual finds a predator, he/she should have the emotion of fear and run away quickly driven by that emotion, but if it is a harmless animal or even just breeze, he/she should not react to it to avoid unnecessary cost.

We assume that if an individual takes an appropriate reaction to the event that happened (either *trivial* or *serious*), he/she suffers no fitness loss. In contrast, an actor incurs some fitness cost when he/she behaves in an inappropriate way. Although inappropriate reactions to serious events may be more costly than those to trivial ones, serious events may less frequently happen than trivial ones. Therefore, the product of event frequency and the cost of each inappropriate reaction may be in a similar order between these two. By abusing terms, we call this product (frequency times

cost of single inappropriate reaction) the "cost of events" hereafter. In particular, the cost of trivial events is normalized to unity and that of serious ones is set as c (>0), i.e., the latter is c times as large as the former.

Individuals recognize each event via an environmental cue, but they sometimes mistakenly recognize it due to recognition errors and/or environmental noise. For example, they may mistake a predator for a harmless animal, or vice versa, if those animals look similar. To model uncertainty in environmental cues, we assume for simplicity that an environmental cue is represented by a real number z and that it distributes in a one-dimensional space. In particular, we assume that trivial and serious events always send cues $z = 0$ and $z = 1$, respectively, but each individual recognizes them with normally distributed variance σ^2 due to recognition errors and noise. In other words, σ^2 indicates cognitive ambiguity between these cues. Note that values $z = 0$ and $z = 1$ do not have any special meanings here, but they are merely results of non-dimensionalization of model parameters. In particular, the distance between the positions of those two cues (which is 1) and the magnitude of noise (σ) are on a comparable scale.

Suppose that an individual has perceived a cue, y, which contains some noise in it. Then this individual has to infer if the original cue was $z = 1$ (serious) and the noise made it look y, or if the original cue was $z = 0$ (trivial) and the noise made it look y. If the individual believes the former, he/she takes an appropriate action for a serious event (for example, escaping behavior), and if he/she believes the latter he/she takes an appropriate action for a trivial event (for example, ignoring it). We, however, model decision making by individuals in a simpler and more realistic way. In particular, we assume that each individual has a rule of thumb parameterized by a threshold value, x; he/she takes an action for a serious event (escaping behavior) if the recognized cue y is larger than the threshold x, and he/she takes an action for a trivial event (ignoring the cue) if the recognized cue y is smaller than x. In other words, one's x represents his/her "insensitivity" to environmental cues. We believe that this threshold model is appropriate for a wide range of animals because it does not require sophisticated ability in inference. Rather, our approach merely assumes that individuals can have different sensitivity to environmental cues, which can be physiologically realized by having different numbers/types of receptors or by having different neural connections. Hence it is natural to assume that the threshold x is genetically encoded.

With these assumptions, the probability that an individual with threshold x takes an *appropriate* reaction to a serious event (i.e. escaping the danger) is

$$p = \int_{y=x}^{\infty} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(y-1)^2}{2\sigma^2} \right] dy \tag{1}$$

and that he/she shows an *inappropriate* reaction to a trivial event (i.e. escaping from nothing) is

$$q = \int_{y=x}^{\infty} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{y^2}{2\sigma^2} \right) dy. \tag{2}$$

In the following we will mainly consider the evolution of this continuous trait, x. Note that, q is the probability of committing a false positive error (type I error; "escaping from nothing"), the cost of which (times the frequency of trivial cues) is assumed to be 1. In contrast, $1 - p$ is the probability of committing a false negative one (type II error; "ignoring the danger"), the cost of which (time the frequency of serious cues) is assumed to be c. Obviously there is a trade-off between these two errors; if individuals attempt to decrease type I error by reducing their sensitivity, type II error necessarily increases, and vice versa, so there should be an optimal threshold x.