

From microbial green-beard effect to metazoan narrow-sense kin discrimination: the brief evolutionary history of social behaviors

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Assessment of genetic similarity is a crucial factor in social evolution. Narrow-sense kin discrimination refers to assistance toward the genealogical kin (or the damage to the non-relatives) while the kind discrimination (green-beard effect) is determined by the sharing of the specific green-beard genes regardless of the genealogical distance. In this review, I emphasize that metazoan narrow-sense kin discrimination that directly compares a wide range of genomes heavily relies on cognitive capability stemming from the nervous system. Microbial unicellular organisms, on the other hand, can perform the green-beard effect or narrow-sense kin discrimination based on spatial proximity. Consequently, the emergence of metazoan complex multicellularity is the prerequisite for the genome-wide comparison that microbes cannot perform. This illustrates the brief history of social evolution, from unicellular green-beard effects and kin discrimination based on spatial cues to cognition-involved narrow-sense kin discrimination performed by animals.

Keywords: Kin selection, Green-beard effect, Kin discrimination, Relatedness

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Introduction

Genes can promote their propagation in two ways: They can escalate the fitness of the host (where the gene resides), or they can manipulate the host to perform beneficial or harmful social behaviors toward other individuals (Hamilton 1964). A well-known example of the latter is narrow-sense kin discrimination (Strassmann et al. 2011). Animals tend to help or cooperate with genealogical kin who would share numerous genes in common. Another theoretically sound mechanism of the latter, which had been dubious for its feasibility, is the green-beard effect (Hamilton 1964; Dawkins 1976). If there is a ‘social allele’ that can manipulate the social behavior of the host, then it would be advantageous for that allele to help those who share the allele, or harm those who lack the allele. The trait that reveals the existence of that ‘social allele’ was termed the green beard (Dawkins 1976).

Narrow-sense kin discrimination relies on the estimation of the relatedness by circumstances or sampling of the traits. If a female produces an egg, then the progeny is evidently close kin of the female: No further examination is required. Therefore, the female parent can doubtlessly help and raise the progeny. Brood parasitism exploits this trait of unquestionable parental care by surreptitiously locating unrelated offspring to the nest so that the deceived parent would believe that the unrelated offspring is the actual progeny (Stevens 2013). Familiarity stemming from the small

related group can also be the reliable proxy of high relatedness (Leedale et al. 2020). When such information based on spatial proximity or familiarity is absent, which would be prevalent cases for active foragers, animals use diverse signals to examine the relatedness including olfactory cues (Mateo and Johnston 2000; Krause et al. 2012), major histocompatibility complex (MHC) (Manning et al. 1992), or visual cues (Parr and de Waal 1999; Coulon et al. 2010) (Figure 1a). Reliable cues for this narrow-sense kin discrimination should be genetically determined by multiple loci and highly polymorphic (the armpit effect) (Dawkins 1982; Grafen 1990).

Similarly, microbes help other clones in the vicinity as spatial proximity ensures high relatedness among the cells (Strassmann et al. 2011) (Figure 1b). For example, *Pseudomonas aeruginosa* provides a fitness advantage to adjacent cells by producing iron-scavenging siderophore molecules (Kümmerli et al. 2009). This mechanism of secreting diffusible elements does not require direct examination of the relatedness of recipient cells and is, therefore, susceptible to cheaters (Kümmerli et al. 2009). The relative fitness of the cheating *P. aeruginosa* that does not produce the

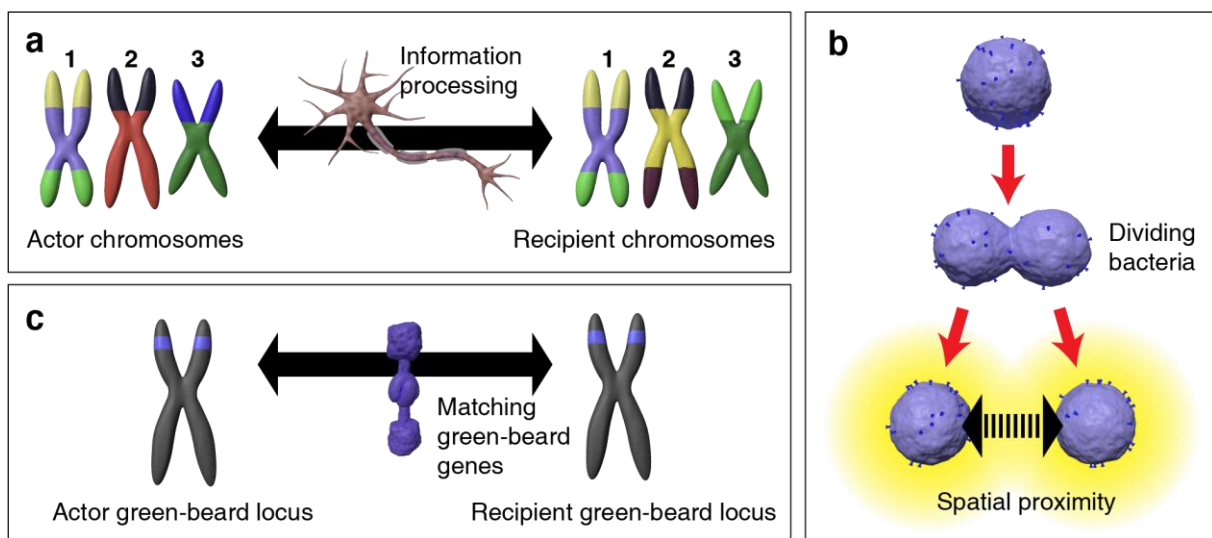


Figure 1. The illustration of the kin discrimination principles

(a) Narrow-sense kin discrimination is based on genome-wide comparisons such as olfactory or visual cues. The chromosomes of the same numbers on the top are homologous. The matching color of the homologous chromosomes from the actor and the recipient indicates that such regions are identical by descent. For example, Chromosome 1 of the actor and the recipient are identical by descent, while not all portions of Chromosome 2 are identical by descent. By analyzing the traits of the recipient and comparing such similarity with the group average, the relatedness between the actor and the recipient can be estimated. This estimation generally requires information-processing capability.

(b) Kin discrimination could be mediated by indirect cues of relatedness such as spatial proximity. Though spatial proximity is not a direct outcome of genomic similarity, the production of beneficial diffusible factors (illustrated with yellow diffusion) can elevate the fitness of the clonemates. Not demanding exquisite information-processing capability, this strategy is often adopted by microorganisms. The dashed bidirectional black arrow indicates that the relatedness is estimated by an indirect cue.

(c) If the actor and the recipient carry matching green-beard genes (blue locus of the chromosome), then exclusive helping or xenophobic harming can occur regardless of the relatedness (the genome-wide similarity). The grey regions of the chromosomes imply that genomic information of such regions does not influence the social behavior mediated by the green-beard genes.

siderophore molecules was higher if the dispersal of substances was facilitated (Kümmerli et al. 2009). Contact inhibition of *Proteus mirabilis* or *Paenibacillus dendritiformis* might be the basis for establishing partitions composed of the clones (i.e., microbial demarcation) so that altruistic cells are not exploited by the cheaters (Strassmann et al. 2011).

There is little evidence that microbes perform narrow-sense kin discrimination other than those via spatial cues (Strassmann et al. 2011). In other words, there is no known example of microbial social interaction that cells estimate the genome-wide similarity (which is not confined to the green-beard genes) of other cells. However, social behaviors of *Plasmodium chabaudi*, *Myxococcus xanthus*, and *Dictyostelium discoideum* are affected by the presence of distantly related strains (Strassmann et al. 2011). Though the mechanism is yet to be elucidated, these could be examples of microbial narrow-sense kin discrimination via genome-wide comparison. For instance, secretion and estimation of specific molecules that are related to the extensive regions of the genome could be the cue of the microbial relatedness estimation, similar to MHC or olfactory cues used by animals (Strassmann et al. 2011).

In contrast, if there is a gene (or tightly linked genes) which can (1) exhibit inimitable trait(s), (2) recognize other individuals which carry the identical allele (allorecognition); (3) perform exclusive social behaviors depending on those trait(s), then such a gene satisfies the conditions of the green-beard gene (Hamilton 1964; Dawkins 1976; Gardner and West 2010). In other words, the green-beard gene enables the hosts to perform exclusive helping among the gene-sharers or xenophobic harming to the non-gene-sharers (Gardner and West 2010). If the aforementioned three conditions are inseparable, then the green-beard gene can directly examine the presence of its copies without considering the relatedness (Biernaskie et al. 2011) (Figure 1c). For example, yeasts with flocculin-encoding gene *FLO1* can establish flocs which protect them from external stress (Smukalla et al. 2008). As yeasts without that gene are less likely to be included in the floc, *FLO1* is a facultative helping green-beard gene (Gardner and West 2010; Madgwick et al. 2019). There are numerous *traA* subtypes of myxobacteria which facilitate the outer membrane exchange (OME) (Pathak et al. 2013). *traA* satisfies the conditions of the green-beard gene as cooperation is performed among the cells with identical or similar *traA* genotypes (Pathak et al. 2013; Madgwick et al. 2019). Aggregation (e.g., yeast *FLO1*) and fusion (e.g., myxobacteria *traA*) are two well-known mechanisms of the green-beard genes which are readily found in microorganisms (Madgwick et al. 2019).

The distinction between narrow-sense kin discrimination and the green-beard effect

To avoid terminological ambiguity, it is of crucial importance to distinguish the concepts of narrow-sense kin discrimination and the green-beard effect. Here, narrow-sense kin discrimination is based on relatedness (the genetic similarity over the whole genome compared to the population average) which is determined by genealogical distance (Strassmann et al. 2011). From Darwin (1859) to Hamilton (1964, 1970), the axiomatic principle of evolution is the selection of the genes that promote its spread with all possible means. In social evolution, the straightforward mechanism for a gene to spread (gene-centered view of evolution (Dawkins 1976; Ågren 2021)) would be to help those who share identical genes and harm those who do not share the genes. This was presented in Hamilton's work (1964) as the primitive idea of the green-beard effect. However, it is mechanistically difficult (Tinbergen 1963) to figure out whether other individuals carry identical genes which was pointed out as the implausibility of the green-beard effect (Gardner and West 2010). It is also questionable whether there exists a single gene that can control the organisms to perform the social behavior (Madgwick et al. 2019). In the absence of information on whether others carry identical behavior-controlling genes, the optimal alternative is to infer the probability to share genes that are inherited from the

common ancestor (identical by descent) (Hamilton 1964), which has been the foundation of the narrow-sense kin discrimination.

Recently, empirical examples of the green-beard genes are accumulating, especially in microbes (Madgwick et al. 2019). It is common that such genes facilitate adhesion, aggregation, or fusion among the sharers of the genes. As pointed out by Gardner and West (2010), (narrow-sense) kin discrimination by the armpit effect and green-beard effect are different. Green-beard social interaction is determined mostly by the existence of the compatible green-beard gene, while there could be errors in the recognition (Choi et al. 2023). Narrow-sense kin discrimination and the green-beard effect (kind discrimination) comprise broad-sense kin discrimination (Strassmann et al. 2011).

A complication arises due to the correlation between relatedness and the probability to share the green-beard gene. High relatedness indicates that two individuals or strains are more likely to share identical genes including the green-beard gene. It was also theoretically expected that narrow-sense kin discrimination is in the same line with the green-beard effect in certain conditions (Biernaskie et al. 2011). If the social interaction is solely mediated by the green-beard gene, however, cooperation among microorganisms with higher relatedness does not ensure that they are performing narrow-sense kin discrimination.

Beneficial green-beard interactions between two distantly related organisms (or the absence of damage for the harming green-beard genes (Gardner and West 2010)) may occur if such a green-beard allele is frequent. In contrast, closely related organisms may not cooperate due to the mutation in the green-beard alleles. If the social behavior is the outcome of the narrow-sense kin discrimination accompanied by the genome-wide comparison, mutations in several alleles would have little impact on the social interaction.

The role of the neurons in the genome-wide comparison for narrow-sense discrimination

Complex multicellularity was accompanied by the differentiation of the somatic cells to perform specific roles (Grosberg and Strathmann 2007) including the signal relay. The emergence of the signal-relaying neurons and the collective neural system enabled the organisms to gather and store multimodal information for decision-making. To estimate the relatedness not based on spatial proximity but on the comparison of phenotypes, sensory cues should be gathered, estimated, and compared. Most examples of the animal narrow-sense kin discrimination unreliant on spatial proximity employ cognitive capability. Armpit effect, the comparison of the genetically determined odor to estimate the kinship (Mateo and Johnston 2000), would be unattainable unless sensory neurons relay the signals. Visual examination of the phenotypic similarity also requires memory and inferential capability (Parr and de Waal 1999). Generally speaking, suppose that there are traits of an organism that directly represent genome-wide attributes, wider than a single or several genes as in the case of the green-beard genes. For narrow-sense kin discrimination based on genome-wide comparison to occur, the signals stemming from those traits should be transmitted to other individuals. Furthermore, the signal should affect the behavior of the organisms. Nervous systems which can collect information, make inferences, and act accordingly satisfy the requirements to perform narrow-sense kin discrimination based on genome-wide comparison. For example, in cooperative breeding (Griffin and West 2002), the parents would need to recognize and remember which are the progeny of their relatives. It was also pointed out that the distinction of individuals is essential for the evolution of cooperation (Crowley et al. 1996).

Another reason that neurons would be the prerequisite for the optimal narrow-sense kin discrimination based on

genome-wide comparison is the adjustability of the behavior. Although the genome-wide similarity is accurately measured, this similarity does not directly represent the relatedness. If the frequency of most alleles is high, two organisms could be genetically and phenotypically similar though they are distantly related. In other words, identity by state does not always guarantee identity by descent as the similarity of the phenotypes is a bivariate function of the genealogical distance and the allele frequency. If the population is nearly homogeneous with respect to genotypes (e.g., as a consequence of continuous inbreeding, exclusive cooperation (Crozier's paradox) (Crozier 1986), genetic drift (Kimura 1968), or selection pressure (Landis et al. 2024)), then a high match of the cues may not represent high genealogical relatedness. To disentangle the genealogical distance from the allele frequency, the overall similarity within a group should be considered. This would be the reason that equations concerning social behavior consider the average genealogical distance of the population. For example, relatedness is defined as $(\phi_2 - \bar{\phi})/(\phi_1 - \bar{\phi})$ by Taylor et al. (2007) where ϕ_2 is the coefficient of consanguinity between the actor and the recipient (Malécot 1948), ϕ_1 is the coefficient of consanguinity of the actor to the self, and $\bar{\phi}$ is the average coefficient of consanguinity within the population. The cognitive capability enables the organisms to gather the population-wide similarity of a group that should function as the reference of the similarity. The similarity between individuals should be higher than this population reference to ensure high relatedness.

To evaluate the effect of the neurons on narrow-sense kin discrimination, the social behaviors of the plants and microbes can be compared to those of the animals with the nervous system. As explained in the previous section, there is no evidence that microbes perform narrow-sense kin discrimination except for the estimation based on spatial proximity (Strassmann et al. 2011). There is ample evidence that plants perform social behavior based on kin discrimination. The growth of roots is curtailed in the presence of kin in the vicinity, leading to reduced competition (Biedrzycki et al. 2010; Biedrzycki and Bais 2010). Similarly, the competition among zygotes in plant ovaries is

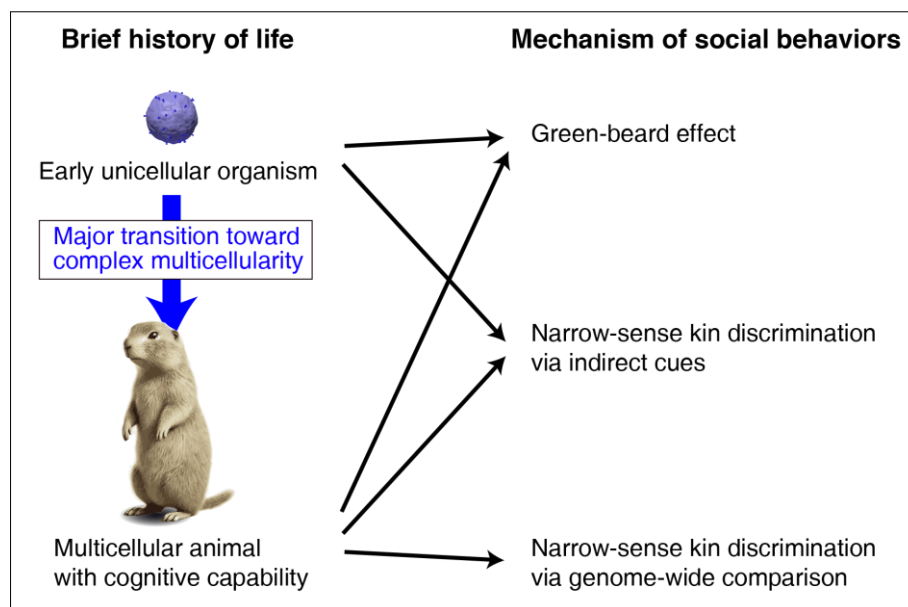


Figure 2. The brief evolutionary history of social behaviors

The early unicellular organisms would have performed social behavior mediated by the green-beard gene or spatial proximity. There is no convincing example that unicellular organisms perform social behavior based on explicit genome-wide comparison. Complex multicellular animals emerged as an outcome of the major transition in evolution. Animals with cognitive capability can perform narrow-sense kin discrimination by directly comparing the genome-wide similarity.

reduced if zygotes are closely related (Bawa 2016). The density-dependent reduction of the competition is comparable to microbial quorum sensing (Diggle et al. 2007). Although the molecular mechanism of how plants recognize the kin is yet to be elucidated, diffusion of the volatile substances or exudates is speculated to be the possible mechanism (Biedrzycki et al. 2010).

Suppose that the substances that mediate the kin discrimination in plants are determined by the genome-wide structure similar to the MHC or visual appearance, and receptors of other plants can measure the relatedness based on the difference in the substances. Then, kin discrimination through these substances can be categorized as narrow-sense kin discrimination utilizing the genome-wide comparison. On the other hand, the substances that plants emit for social behaviors may not reflect the genome-wide information but might be determined by one or several (polymorphic) genes. Otherwise, if there is a bundle of highly linked genes that emit the substances, recognize the substance, and act differentially according to the recognition, then it may satisfy the condition of the green-beard genes. To my knowledge, there is no convincing evidence to date that narrow-sense kin discrimination based on direct genome-wide comparison is performed without the mediation of neurons.

Concluding remarks: the brief history of social evolution

The traits of kin selection and the green-beard effect provide implications to the general history concerning the evolution of social behaviors (Figure 2). Social behavior of early unicellular organisms would have been based on the green-beard effect or the narrow-sense kin discrimination reliant on spatial proximity. Aggregation of the gene-sharers or the cooperation among adjacent cells would be examples of the former and the latter forms of social behaviors.

As an outcome of major transitions in evolution, metazoan multicellularity has obtained a higher degree of differentiation and constant aggregation (Smith and Szathmary 1995; Knoll 2011). Rooted from metazoan multicellularity, the emergence of the nervous system and the corresponding capability to process the information brought about individual-level social behavior. Animals can perform narrow-sense kin discrimination based on genome-wide comparison via diverse cues. The elaborate distinction and classification of social behaviors enable us to appreciate how different types of social behaviors appeared during the course of evolution.

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