Self-Organization in Primates: Understanding the Rules Underlying Collective Movements

Cédric Sueur · Jean-Louis Deneubourg

Abstract Patterns of collective movements, such as the distribution of leadership and the organization of individuals, may be either homogeneously (no leader, no specific order), or heterogeneously (1 or several leaders, and a highly stable order) distributed. Members of a group need to synchronize their activities and coordinate their movements, despite the fact that they differ in physiological or morphological traits. The degree of difference in these traits may affect their decision-making strategy. We demonstrate how a theoretical model based on a variation of a simple mimetic rule, i.e., an amplification process, can result in each of the various collective movement patterns and decision-making strategies observed in primates and other species. We consider cases in which 1) the needs of different individuals are identical and social relationships are equivalent between group members, 2) the needs of individuals are different and social relationships are equivalent, and 3) the needs of individuals are different and social relationships are different. Finally, 4) we assess how the synergy between 2 mimetism rules, specifically the probability of joining a movement and that of canceling an initiation, allows group members to stay synchronized and cohesive. Our models suggest that similar self-organized processes have been selected as reliable and well-adapted means for optimal collective decisions across species, despite differences in their biological and social characteristics.

Keywords Cancellation · Cohesion · Collective decision · Consensus · Initiation · Leadership · Mimetism · Quorum · Rule of thumb

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Introduction

When a team of carpenters build a house, they follow a blueprint of specifications to achieve the final structure successfully, and have a metal representation of what they do. However, when ants build their nest, there is no leader or blueprint to guide them in their collective nest-building actions. They do not base their behaviors on a global overview of the building but simply interact locally with the closest neighboring ants or with pheromones left by other ants (Deneubourg and Goss 1989). These local interactions between individuals without a global referent give rise to self-organization, a process in which patterns at the global level of a system emerge solely from numerous interactions among the lower level components of the system (Camazine *et al.* 2003; Deneubourg and Goss 1989; Sumpter 2006). The rules specifying interactions among the components of the system are applied using local information, without reference to a global pattern (Camazine *et al.* 2003). Such self-organized processes imply positive feedback, such as amplification (or mimetism), or negative feedback that constrains the system. These simple, local rules have been well described for schools of fish, flocks of birds, migrating locusts, and ungulates (Amé *et al.* 2006; Bazazi *et al.* 2008; Couzin and Krause 2003; Couzin *et al.* 2005; Gautrais *et al.* 2007; Gueron *et al.* 1996), all of which live in large groups without global communication and individual recognition between all individuals. However, self-organized processes also exist in species that live in smaller groups and show high cognitive abilities, including nonhuman primates and humans (Dyer *et al.* 2009; Helbing *et al.* 1997; Hemelrijk 1999; Meunier *et al.* 2006; Petit *et al.* 2009; Sueur *et al.* 2009). This suggests that the rules underlying collective decisions do not differ with individual or system complexity (Detrain and Deneubourg 2006; Sueur *et al.* 2009), and that simple rules can result in different collective patterns.

Complex patterns may arise where individuals have different needs. Almost all primate species live in groups and hence enjoy the benefits of sociality, such as lower predation risk and better food search efficiency (Alexander 1974; Krause and Ruxton 2002; Wrangham 1980). Group members must therefore synchronize their activities and coordinate their movements despite differences in physiological or morphological traits such as sex, age, body size, or reproductive status (Conradt and Roper 2005; King and Cowlishaw 2009; Petit and Bon 2010). For example, in baboons (*Papio ursinus*), chimpanzees (*Pan troglodytes*), and zebras (*Equus burchellii*), males or lactating females, which have the highest nutrient requirements, initiate more collective movements or are located at the front of the movement progression more often than their conspecifics (Fischhoff *et al.* 2007; Hockings *et al.* 2006; Prins 1996; Rhine, 1975). In contrast, individuals that are more vulnerable to predation, such as juveniles, are located more frequently in the middle of the progression (Fischhoff *et al.* 2007; Hockings *et al.* 2006; Prins 1996; Rhine 1975).

The need to resolve conflicts of interest between individuals with different needs may result in the emergence of complex patterns including specific organization of group members during movements, fission–fusion dynamics, or specific communication signals (Conradt and Roper 2005; King and Sueur, this issue; King *et al.* 2009; Sueur *et al.* 2010a). The greater the differences between group members, the more complex the decision-making process will be. In the context of collective movements, we can study these patterns by observing the distribution of leadership,

the order of individuals during the progression, or other types of organisation such as the existence of subgroups, either within the same progression or moving separately. In primates the distribution of leadership and the organization of individuals may be randomly or homogeneously distributed, with no leader and no specific order, or heterogeneously distributed, with 1 or several leaders and a highly stable order (Hockings *et al.* 2006; Jacobs *et al.*, this issue; Meunier *et al.* 2006; Rhine 1975; Sueur *et al.* 2009). [A leader is "an individual eliciting strong follower behavior/ exerting social influence on others, by its rank into the progression, its behavior or its social status" (Pyritz *et al.*, this issue)]. This raises the question of whether different rules underlie these different patterns, or whether they can be explained by a single rule in which the parameters, such as the probability of initiating a movement or the probability of following, vary according to individual character-istics (quantitative modulation instead of qualitative modulation, Pillot and Deneubourg 2010).

In previous modeling studies, researchers attempted to understand how ecological constraints affect collective decision making (Sellers *et al.* 2007; Zappala and Logan 2009) but did not focus on individual or social mechanisms underlying these decisions. Here, we use data from previous studies and a simple mathematical model involving a theoretical group of 10 individuals to show how varying the parameters of a simple mimetic rule, i.e., an amplification process, can result in all the patterns observed during collective movements in primates and other species. First, we examine the simple case in which the needs of different individuals are identical and social relationships are equivalent between group members, as discussed by Pillot and Deneubourg (2010), and show that this physiological and social homogeneity results in strong anonymous mimetism when joining a movement. Second, we examine how biased leadership in favor of some individuals emerges through differences in the needs of group members. Third, we include differentiated social relationships between individuals, as observed in most primate species, and demonstrate that this assortativity in the social network results in the emergence of a specific order of individuals. Fourth, we show how the synergy between 2 mimetism rules, i.e., positive and negative feedback, can lead to synchrony between individuals. In each case, we provide a general description of the process underlying the joining of group members to a collective movement (each case is explained by an equation in which parameters vary), then we give a theoretical example to explain better how to find such processes in primates, and lastly we review previous studies in primates wherein each mimetic process was already shown.

Anonymous Process and Identical Needs

General Description

In anonymous mimetism (allelomimetism), the probability of displaying a behavior (in this case, joining a movement) depends on the number of individuals already performing this behavior, whatever their identities. This is found in species in which group members are unable to recognize and identify their conspecifics, or in species in which the social network is equal, i.e., all individuals are connected by

relationships having the same value (a hypothetical true egalitarian species in which an individual interacts with all its partners at the same frequency). It could also occur in species in which social relationships differ between individuals but do not have any impact on the amplification process. For instance, white-faced capuchins (*Cebus capucinus*), which are more egalitarian than brown capuchins (*Cebus appela*), displayed an anonymous mimetism when joining a collective movement (De Marco *et al.* 2008; Leca *et al.* 2002, 2003, 2007; Meunier *et al.* 2006). Individuals with identical needs have the same probability of going in the same direction at the same time. The synergy of anonymous mimetism and identical needs results in a process wherein all individuals have the same weight in the decision, i.e., the same influence on the probability of making their conspecifics move. In this process, the probability λ per time unit that an individual goes in one direction is:

$$\lambda = \alpha + \frac{\beta X^q}{S^q + X^q} \tag{1.1}$$

wherein α is the intrinsic probability that an individual starts. All individuals have the same intrinsic probability. β is a mimetic coefficient. The higher this mimetic coefficient is, the faster individuals will join the movement (also called a chain reaction or snowball effect, Fig. 1a). Because λ is a probability ranging from 0 to 1, $\alpha + \beta$ is always <1. Because the system is anonymous, β is the same for all group members, whatever the identity of the individual that moves or that of any individuals already moving. X is the number of individuals already moving. If no individual is moving, $X=0$ and $\lambda=\alpha$. This is the case for the probability λ_{01} of the initiator (λ_{01} because the initiator is the first individual to move). The departure of the initiator is not influenced by any moving individual. q is a coefficient representing the degree of sensitivity of individuals to the system and affects the slope of the sigmoid curve that has been fitted to the data. Higher values of q correspond to sigmoid curves with a steeper slope, particularly around the threshold value (Fig. 2a). In essence, a higher q results in a faster transition between resting and departing and therefore in higher discrimination (Amé *et al.* 2006; Dussutour *et al.* 2005). S is a threshold. The higher it is, the longer it will take to reach a decision and the higher the number of individuals involved will be (Fig. 2b). Mimetism as described is linear (Fig. 1a). This linearity may be explained by considering $q=1$ in Eq. 1.1. For example, in white-faced capuchins, the probability of joining a movement is anonymous and linear (Petit *et al.* 2009) and the values of Eq. 1.1 are: $\alpha=1/162.3$ s, $\beta=1/74.5$ s, $q=1$, $S = N-X$ (where N is the number of group members).

In a mimetic process, α must be lower than $\frac{\beta X^q}{S^q + X^q}$ (except for the initiator of the movement wherein $X=0$, then $\frac{\beta X^q}{S^q + X^q} = 0$). If α is always greater than $\frac{\beta X^q}{S^q + X^q}$, individuals will not remain cohesive because their need to go in one direction is higher than their need to stay with their conspecifics. Where the intrinsic probability of a single individual is higher than the mimetic process, the costs of living in groups are greater than the potential advantages, and the individual decides against following its group. If this applies to several individuals, it can result in irreversible group fission.

Equation 1.1 is the most common rule explaining amplification in animals, as well as in chemical and physical systems (Deneubourg and Goss 1989; Nicolis and Prigogine 1977). Values of the different parameters (α, β, S, q) are calculated by comparing theoretical distributions from Eq. 1.1 with an observed distribution, usually the distribution of latencies, in the study group. Because the process is
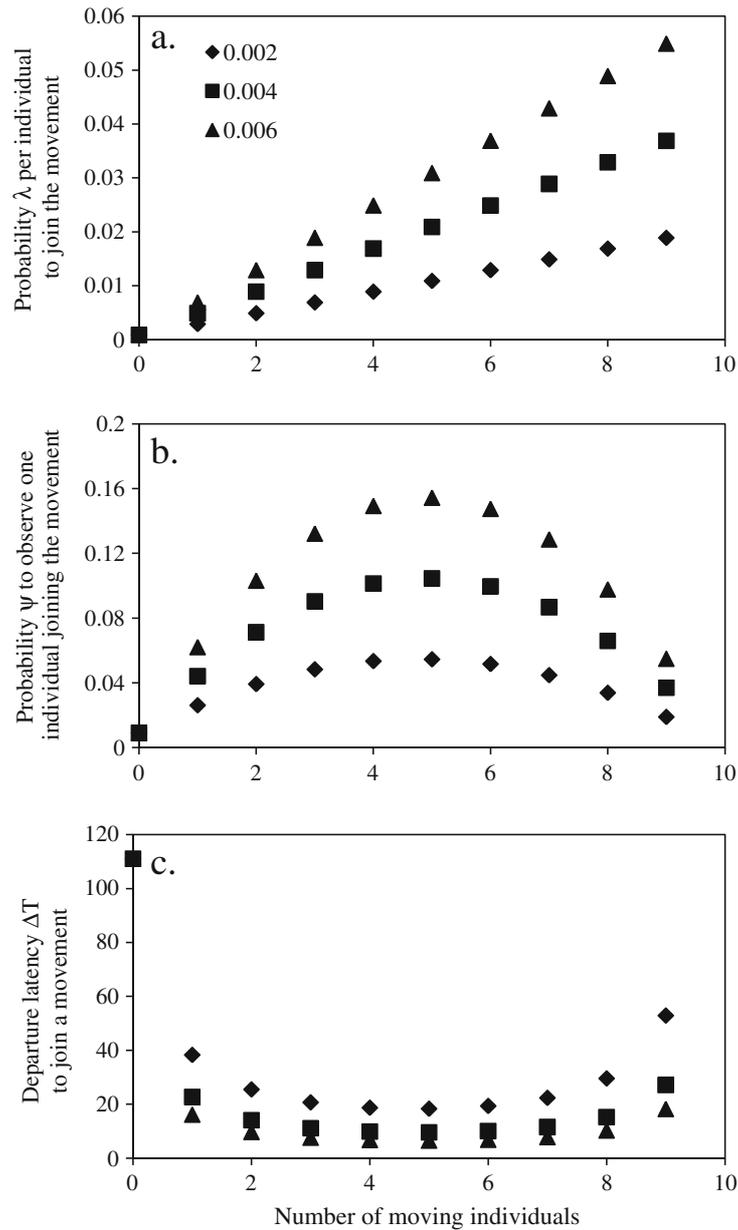
Fig. 1 **a** Individual probability λ of joining a movement. **b** Probability ψ of 1 individual joining a movement. **c** Departure latency ΔT of joining a movement according to the number X of individuals already moving (0 for the initiator, 9 for the last follower) in a group of 10 individuals. We tested 3 different mimetic coefficients β per individual (0.002, 0.004, and 0.006).

anonymous ($\frac{\beta X^q}{S^q + X^q}$ not different between individuals) and all individuals have the same intrinsic probability α, λ can be calculated easily manually or using a tabulator, as in Figs. 1 and 2. However, agent-based modeling software, such as Netlogo 3.14 (Wilensky 1999), allows iteration of the calculation and, more importantly, the introduction of stochasticity into the model, i.e., an error margin for each individual. For example, at each time step in the stochastic model each resting agent can be randomly attributed a number between 0 and 1; when this number is lower than λ, the individual leaves the resting area for the foraging area; if this number is higher than λ, the agent does not move. Different values of β give different theoretical distributions (Fig. 1 for 3 different values of β). We consider the theoretical value of
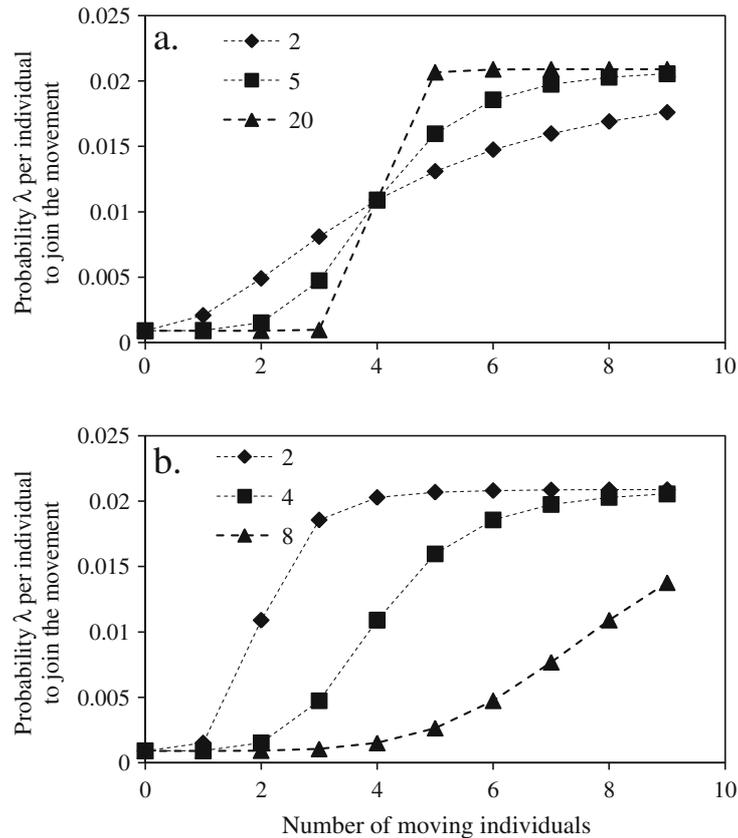
Fig. 2 Probability λ per individual of joining a movement according to the number X of individuals already moving (0 for the initiator, 9 for the last follower) in a group of 10 individuals. **a** Threshold S is fixed ($S=4$) but the degree q of sensitivity changes ($q=2$, 5, and 20). **b** The degree q of sensitivity is fixed but threshold S changes ($S=2$, 4, and 8).

the mimetic coefficient for which the distribution of latencies best fits the distribution of latencies observed in a focal group as accurate. This procedure was followed in studies on Tonkean and rhesus macaques (*Macaca tonkeana*, *M. mulatta*), brown lemurs (*Lemur fulvus*), and white-faced capuchins: authors tested different mimetic coefficients and considered as right the one for which the theoretical latencies' distribution best fits with the one observed in each studies group. For example, this value is 0.002 in Tonkean macaques, 0.003 in rhesus macaques, 0.004 in brown lemurs, and 0.001 in white-faced capuchins (Jacobs *et al.*, this issue; Petit *et al.* 2009; Sueur *et al.* 2009, 2010a).

Equation 1.1 gives the probability of moving per individual. We obtain the probability of observing an individual moving by correcting for the number of resting individuals. At each time step, we are 9 times more likely to observe 1 individual starting to move in a group in which 9 individuals are resting than in a group in which 1 individual is resting (Fig. 1b for a theoretical example). The probability ψ per time unit that one of the Y resting individuals will move and become the $(X+1)^{th}$ follower therefore becomes:

$$\psi = \lambda * Y = \left(\alpha + \frac{\beta X^q}{S^q + X^q} \right) * Y \tag{2.1}$$

The distribution of the probabilities ψ for Eq. 2.1 is a parabolic curve (Fig. 1b).

The departure latency ΔT of an individual is the inverse of its probability of moving, λ. The departure latency ΔT_{01} of the initiator of a movement is defined as the time between the end of the previous collective movement and the departure of the initiator of the current movement. This is also called the stationary period because subjects are engaged in an activity other than moving, such as foraging or resting. ΔT_{01} is given by:

$$\Delta T_{01} = \frac{1}{\psi_{01}} = \frac{1}{\alpha} \text{ as } X = 0 \qquad (3.1)$$

The departure latency $\Delta T_{x,x+1}$ of the $(X+1)^{th}$ follower is defined as the time between the departure of the previous follower x and the departure of this follower $x+1$, and is given by $\Delta T_{x,x+1}$ of the :

$$\Delta T_{x,x+1} = \frac{1}{\psi_{x,x+1}} \qquad (3.2)$$

The distribution of these departure latencies also follows a parabolic curve, inverse to the curve illustrating the probability of moving (Fig. 1c). This shape suggests a mimetism rule underlying a collective phenomenon that results in an all-or-nothing process, meaning that either no individual will join the movement at all, or all the group members will follow (parabolic curve, or U-shape function, Fig. 3a). There are no or few intermediate situations. This pattern occurs in Tonkean and rhesus macaques (Sueur *et al.* 2009, 2010a), brown lemurs (Jacobs *et al.*, this issue), and white-faced capuchins (Meunier *et al.* 2006), suggesting a mimetic process in each of these species (anonymous or nonanonymous). The higher β and q are, the stronger the all-or-nothing effect is. These probabilities are constant per time unit. However, the time spent in a state (resting or moving) may influence the probability ψ of changing state (Pillot and Deneubourg 2010).

Considering the Number of Moving Individuals and the Number of Resting Individuals

Equation 1.1 considers that the probability λ of going in one direction depends only on the number X of individuals already moving in this direction. However, λ might also depend on the number Y of resting individuals, i.e., the individuals that have not already moved. This is the case, e.g., in sheep (*Ovies aries*: Pillot and Deneubourg 2010; Pillot *et al.* 2010). In this case, the probability λ of an individual going in one direction is:

$$\lambda = \alpha + \frac{\beta X^q + \beta' Y^q}{S^q + X^q + Y^q} \qquad (1.2)$$

wherein β' is the mimetic coefficient influencing individuals not to move. Y is the number of resting individuals. If individuals do not take into account the resting individuals but only the moving individuals in their probability λ of starting, Y always equals 0 and Eq. 1.2 is the same as Eq. 1.1. If $\beta > \beta'$, then an individual is more influenced by the number X of moving individuals than by the number Y of resting individuals. If $\beta < \beta'$, then an individual is more influenced by the number Y
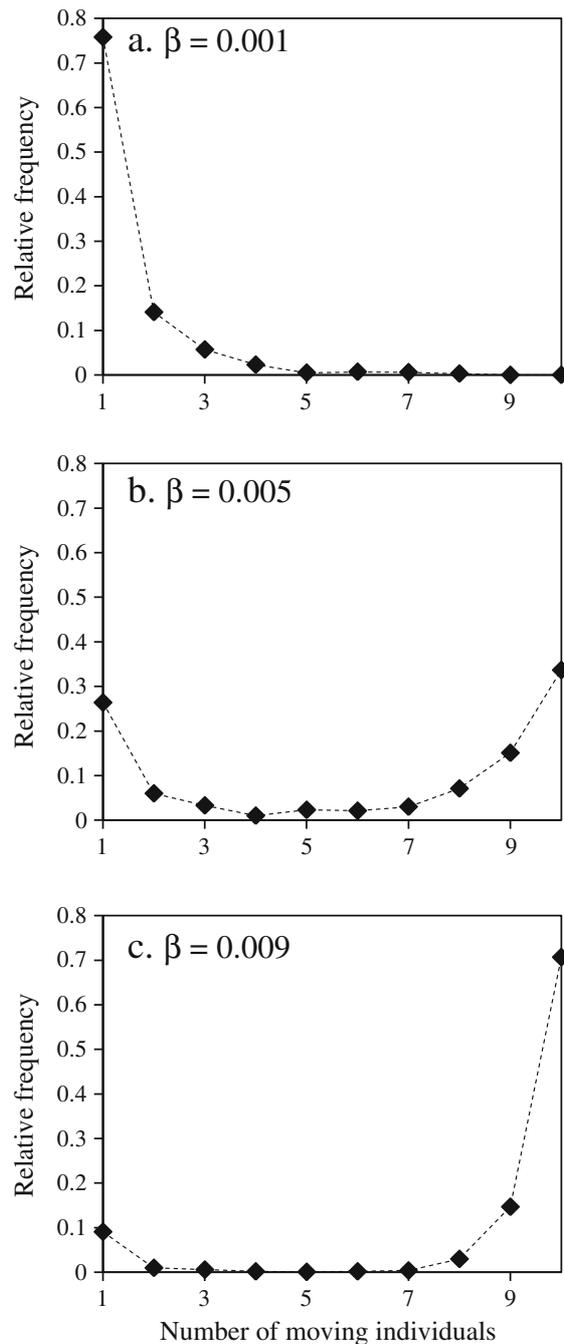
Fig. 3 Distribution of the number of moving individuals (relative frequency of observations according to the number of moving individuals). 1 moving individual means a failed start attempt; 10 individuals mean all group members follow the initiator. The time after which the start attempt is considered to have failed is fixed at 300 s (Sueur *et al.* 2009, 2010a). The mimetic process is an all-or-nothing process but the shape of the curve depends on the mimetic coefficient. Here, we illustrate 3 theoretical examples. **a** $\beta=0.001$: the distribution is composed of a maximum of failed start attempts and appears to be a power distribution. **b** $\beta=0.005$: the distribution has a U-shape (parabolic curve), meaning that either all individuals are following the initiator or none are following at all. **c** $\beta=0.009$: the distribution is still a U-shape but with more movements in which all individuals move.

of resting individuals. We tested these different rules, taking into account the number of resting and moving individuals, in Tonkean and rhesus macaques and in brown lemurs, and in all 3 species, subjects are influenced only by the number of individuals already moving (Jacobs *et al.*, this issue; Sueur *et al.* 2009, 2010a, 2011).

In the rest of this article, therefore, we consider only the situation where the probability of moving is influenced by the number of individuals already departed.

Quorum Response and Voting Process

The probability of displaying a behavior may also depend on a quorum response ($q \neq 1$, Fig. 2a). In this case, the phenomenon is nonlinear (Pratt *et al.* 2002; Seeley and Visscher 2004; Pratt 2005; Ward *et al.* 2008; Sumpter and Pratt 2009; Bousquet *et al.* 2010; Sueur *et al.* 2010b, 2011) and depends on 2 characteristics: value q representing the sensitivity of the system (Fig. 2a) and value S for reaching the threshold (Fig. 2b). This quorum response, also termed a voting process, has been shown in ants (Pratt 2005), bees (Seeley and Visscher 2004), Tonkean macaques (Sueur *et al.* 2010b, 2011) and meerkats (*Suricatta suricatta;* Bousquet *et al.* 2010). In Tonkean macaques, the probability of initiating a movement depends on the number of individuals displaying preliminary behaviours. The q value of sensitivity in Eq. 1.1 was 5 in both groups studied, while the threshold S was 9 for one group and 5 for the other (Sueur *et al.* 2010b, 2011). In meerkats, the moving speed increased with the number of moving calls according to a q value of 1.03 and a S value of 2.57 (number of callers) (Bousquet *et al.* 2010). A similar quorum response occurs when capuchins (Meunier *et al.* 2008) and macaques (Sueur and Petit 2010) recruit followers. The initiator emits a recruitment signal until at least three individuals follow. When 3 individuals have joined the movement, the number of signals emitted by the initiator is *ca.* 0. The quorum process in primates (Sueur *et al.* 2010b, 2011) also shows a higher degree of sensitivity ($q \geq 5$) than that observed in insects or fish ($q = 2$) in experimental tests in the laboratory (Amé *et al.* 2006; Ward *et al.* 2008). The discrimination is higher because primates are not only able to estimate, but can also count and subtract (Hauser *et al.* 2000), resulting in more accurate decisions, with fewer mistakes (Sueur *et al.* 2010b, 2011; Sumpter and Pratt 2009). This quorum process enables individuals to take more accurate decisions (Sumpter and Pratt 2009; Sueur *et al.* 2010b, 2011). A higher q value means a more sensitive system, with less risk of error when choosing a direction, for example. A higher threshold S means more individuals participate in the decision, which therefore provides more information about where to go and the motivation of the group, hence resulting in a more accurate decision.

Anonymous Process but Different Needs

Here, social relationships between individuals still all have the same value, meaning that individuals do not need to recognize their conspecifics individually. However, the intrinsic probability α and the mimetic coefficient β in Eq. 1.1 can differ according to the characteristics of the individual choosing to move. Differences in the intrinsic probability α might correspond to the time chosen to move (1 or several individuals do not want to move at the same time as their conspecifics) or to the direction chosen (1 or several individuals do not want to move in the same direction as their conspecifics). However, a group may remain cohesive if the costs of splitting are outweighed by the benefits of grouping. In such a situation individuals cannot

reach a consensus. For example, if half the group want to go to area A in an easterly direction, and the rest of the group want to go to area B in a westerly direction, they cannot resolve the conflict by going north (Conradt and Roper 2010). If the intrinsic probability α of 1 individual or more is higher than its mimetic coefficient β, he will split from the group. We develop the case in which individuals differ in the probability of moving in the same direction.

All Individuals Display Different Probabilities

In most species all individuals have a different intrinsic probability α because they all have different needs. For instance, all individuals initiate movements but at different frequencies in white-faced capuchins (Leca *et al.* 2003), chacma baboons (Stueckle and Zinner 2008), Tonkean and rhesus macaques (Sueur and Petit 2008; Sueur *et al.* 2009), and lemurs (Jacobs *et al.* 2008, this issue). The distribution of initiations per individual is more or less homogeneous depending on individual differences.

The probability ψ_i that an individual i moves is:

$$\psi_i = \alpha_i + \frac{\beta X^q}{S^q + X^q} \tag{2.2.1}$$

wherein α_i is different for each individual i.

These differences in intrinsic probability between individuals may result in stability in the progression order. If $\alpha_A > \alpha_B > \alpha_C > \alpha_D > \alpha_E$ in all cases of departures, then there is a high probability of observing $\psi_A > \psi_B > \psi_C > \psi_D > \psi_E$, meaning a high probability that individual A will be the initiator, individual B the first follower, C the second, etc. However, this situation is extreme because it means that the intrinsic probability α_i of an individual i is always the same whatever the context. However, α_i depends on both the individual i and on the departure and arrival area, modifying the progression order depending on the departure or arrival area. Implementing stochasticity in our agent-based model allows us to take this variance of probabilities α_i into consideration.

We can also consider the case in which all individuals have the same intrinsic probability α of moving but different mimetic coefficients β_i. In this case, the probability ψ_i that an individual i moves is:

$$\psi_i = \alpha + \frac{\beta_i X^q}{S^q + X^q} \tag{2.2.2}$$

wherein β_i is different for each individual i (only the mimetic coefficient differs between individuals, while the social relationships remain unchanged, meaning that an individual has the same relationships with all other group members).

According to Eq. 2.2.2, all individuals have the same probability of initiating a movement but not the same probability of following. The variance of the mimetic coefficient β_i also depends on the environmental context: β_i might be different for each departure and arrival area. It might also differ between individuals according to their sociality or cohesiveness, independent of social relationships. Each individual can have a different cohesiveness value (also called index of independence) based on intrinsic characteristics or life history.

One Individual Displays a Different Probability from That Shown
by Its Conspecifics

In some species, a single individual has more needs than its conspecifics. This is the
case in primate species displaying high sexual dimorphism or a 1-male, multifemale
social structure, e.g., hamadryas baboons (*Papio hamadryas*: Kummer 1968) and
mountain gorillas (*Gorilla berengei berengei*: Watts 2000). In these species, we
expect the intrinsic probability that the male moves to be higher or lower than that of
other group members, according to the situation. In the first case, the male wants to
move to another area while other group members want to stay in the current area,
whereas in the second, the male wants to stay and continue foraging while other
individuals want to leave the area. We therefore have 2 different probabilities of
movement:

$$\psi_M = \alpha_M + \frac{\beta X^q}{S^q + X^q} \qquad (2.2.3)$$

for the male

$$\psi_i = \alpha_i + \frac{\beta X^q}{S^q + X^q} \qquad (2.2.4)$$

for other individuals i, with α_i the same for all individuals i

This kind of situation may result in leadership biased toward the individual that
shows a different intrinsic probability to the rest of the group without any need to
recognize group members. He will initiate more movements according to the value
of the intrinsic probability. This can also result in a certain stability in the
progression order, with this individual located more often at the front or back of
movements. Accordingly, the consensus is termed unshared (or the leadership as
personal; Conradt and Roper 2005; Leca *et al.* 2003), although the male has no
intention of being the leader and there is no individual recognition between group
members (Pyritz *et al.*, this issue). In the case in which individuals have the same α
but not the same β, we expect a homogeneous distribution of initiation between
group members, but in the majority of cases 1 individual will be the first or the last
follower.

Leadership is also influenced by factors other than body mass or nutrient
requirements, such as the information that individuals possess (King and Sueur, this
issue; King *et al.* 2009; Petit and Bon 2010). If individuals want to eat a specific
item to satisfy a specific need, they must know where this item is located. This
problem does not occur in a homogeneous and certain environment. However, some
species live in environments where dry seasons could be very intense, over a number
of years, making waterholes very rare and dispersed. This is the case for elephants,
where the matriarch and some other members of the troop know the location of these
waterholes while other group members do not (McComb *et al.* 2001). The matriarch
is described as the main leader of the group, initiating most group movements (King
and Sueur, this issue; King *et al.* 2009; McComb *et al.* 2001). This emergence of a
leader based on information possessed can be explained easily using Eq. 2.2.1,
wherein $\alpha_i = \gamma_i * \delta_i$. γ_i is a value related to the information the individual possesses
about its environment and δ_i is a value based on food motivation, for example. γ_i

ranges from 0, if an individual has no knowledge of any area in its environment, to 1, complete knowledge of the environment. Even if 1 individual has a high δ_i—a high motivation to move and go to a waterhole—it will not initiate a movement if $\gamma_i=0$ because it has no knowledge about its environment. Only the matriarch that possesses the highest γ_i would initiate movements and lead the group.

Subgroups of Individuals Sharing the Same Probability

Segregation may occur between different sexes or age classes. For example, the sexual segregation observed in red deer (*Cervus elaphus*) is influenced by individual differences in nutrient requirements between males and females (Conradt 1998; Conradt and Roper 2000; Ruckstuhl and Kokko 2002). Here again, we have 2 different probabilities of movement:

$$\psi_M = \alpha_M + \frac{\beta X^q}{S^q + X^q} \tag{2.2.5}$$

for males, with all α_M equal between males

$$\psi_F = \alpha_F + \frac{\beta X^q}{S^q + X^q} \tag{2.2.6}$$

for females, with all α_F equal between females

In the case where $\alpha < \beta$, whatever the sex, the group will stay cohesive but segregation will occur in both the time chosen to move and the progression order (all males together and all females together). However, if too great a difference occurs between individuals the group will split, with 1 single-sex group moving and the other staying in the current area. This may also explain subgroups of juveniles or of females with infants, as observed in baboons and zebras (Fischhoff *et al.* 2007; Prins 1996; Rhine 1975; Rhine and Tilson 1987; Rhine and Westlund 1981). β may also change during a short period for 1 individual or a category. For example, in male–female consortships a male and a female synchronize their movements during a short period around ovulation. We suggest that in this condition, the social relationship is not affected but that the coefficient β of the male or of the female are affected by the reproductive state of the female.

Selective Mimetism and Different Needs

Selective mimetism is defined as an amplification process by which the probability of performing a behavior relies not only on the number of individuals displaying this behavior but also on their identities (Sueur *et al.* 2009, 2010a, 2011; Jacobs *et al.*, this issue). It requires the ability to recognize conspecifics. This recognition can be visual, acoustic, or pheromonal (Fellowes 1998; Johnston 1998; Sorensen *et al.* 1998). Whereas processes in insects or ungulates seem to be more like allelomimetism (Amé *et al.* 2006; Detrain and Deneubourg 2006; Gautrais *et al.* 2007), those observed in primates are more selective (Jacobs *et al.*, this issue; Sueur *et al.* 2009, 2010a, 2011) because primates have complex social relationships influenced by kinship, dominance, affiliation, and interindividual recognition

(Alexander 1974; Boinski and Garber 2000; Byrne and Whiten 1988; Sueur *et al.* 2009; Tomasello and Call 1997; Wrangham 1980, 1987). The strength of social relationships also differs between dyads. In selective mimetism, the probability ψ_i that an individual i joins a movement is:

$$\psi_i = \alpha_i + \frac{z^q}{S^q + z^q} \qquad (2.3)$$

wherein $Z = \sum_{j=1}^{N} \beta_{ij}\varepsilon_j$. ε_j is the state of individual j. If j is already moving, $\varepsilon_j=1$. If j is still resting, $\varepsilon_j=0$. β_{ij} is the strength of the social relationship between i and j.

We consider the case in which each dyad has a different mimetic coefficient that corresponds to their social relationship. Values of social relationships may be absolute or relative (Cairns and Schwager 1987; Sueur *et al.* 2009; Whitehead 2008). The value for an individual i must be corrected such that $\sum_{j=1}^{N} \beta_{ij} = N - 1$, wherein N is the number of group members (Table I). Affiliative relationships are commonly used for this selective mimetism, i.e., the number of times 2 individuals were observed together, but we can also use the same equation (Eq. 2.3) to test kinship relationships (β_{ij} is the degree of relatedness between individual i and individual j) and dominance or age relationships (β_{ij} is the difference in hierarchical rank or age between i and j) (Jacobs *et al.*, this issue; Sueur *et al.* 2009, 2010a). Selective mimetism based on affiliative relationships occurs in Tonkean and rhesus macaques (Sueur *et al.* 2009, 2010a, 2011), brown lemurs (Jacobs *et al.*, this issue). In these species, only mimetism based on affiliation explains either the departure latencies of individuals or their order and associations (who follows whom), while other hypotheses (allelomimetism, selective mimetism based on kinship or dominance) are not supported. Moreover, the variance of departure latencies for a rank/position is higher in selective mimetism than in allelomimetism. For example, in an anonymous process, all individuals have the same probability of joining the initiator. In contrast, in selective mimetism an individual that has a strong relationship with the initiator

Table I Values of relationships between individual A and other group members (B–J)

Relationship (A, X)	Absolute frequency	Relative frequency	Corrected frequency
B	5	0.0390625	0.3515625
C	23	0.1796875	1.6171875
D	0	0	0
E	6	0.046875	0.421875
F	15	0.1171875	1.0546875
G	13	0.1015625	0.9140625
H	36	0.28125	2.53125
I	2	0.015625	0.140625
J	28	0.21875	1.96875
Sum	128	1	9

The absolute frequency is the number of times we observed 2 individuals together. The relative frequency is the ratio of the number of observations for 1 dyad divided by the total number of times A was observed. The corrected frequency is the relative frequency multiplied by the number of relationships shown by A, i.e., $N-1$, where N is the number of group members

will join the latter quickly, while individuals having no or little relationship with the initiator will not follow it or will do so after a long time. This selective mimetism coupled with different intrinsic probabilities between group members results in a stable progression order more often than the processes described previously. Group members can be associated through their social relationships as well as by similarities in nutrient requirements. Associations and order of individuals are amplified if there is a synergy between social relationships and differences in nutrient requirements, i.e., individuals with the same needs associate more than individuals with different needs (Croft *et al.* 2003, 2004, 2005). The distribution of the number of followers may show great variation and adopt different shapes according to the social relationships of individuals. In a cohesive group, the distribution will still have a U-shape (parabolic curve, Fig. 3). This is the case in Tonkean macaques (Fig. 4a). In a group clustered in 2 subgroups, the parabola will be inversed. Lastly, in a group with a range of different social relationship strengths, we would expect to observe movements going from no follower to all group members, with almost all intermediary cases. This is the case, e.g., in brown lemurs (Fig. 4b) and rhesus macaques (Fig. 4c) The curve for rhesus macaques suggests that the group is not very cohesive because most movements include only less than half of the group.

Synergy Between Different Mimetic Rules

Positive feedbacks such as the amplification process described in the preceding text are often associated with negative feedbacks. These are regulatory mechanisms that enable equilibrium to be achieved within the system. For instance, an animal cannot always behave according to the "do the same as your neighbor" rule of thumb, or the group would always be in a single state: moving or resting (Detrain and Deneubourg 2006). Different feedback loops occur in the context of collective movements. Throughout the day, individuals change between moving and resting activities, resulting in an oscillation between the 2 phases. The same amplification process occurs from moving to resting.

The probability $\psi_{i,m}$ that an individual i moves is:

$$\psi_{i,m} = \alpha_{i,m} + \frac{\beta X^q}{S_m^q + X^q} \qquad (2.4.1)$$

while the probability $\psi_{i,r}$ that an individual i rests (stops moving) is:

$$\psi_{i,r} = \alpha_{i,r} + \frac{\beta Y^q}{S_r^q + Y^q} \qquad (2.4.2)$$

wherein X is the number of moving individuals and Y is the number of resting individuals.

The probability of changing from one state to another therefore depends on a ratio of the number of individuals in each state:

$$\psi(r, m) = \frac{X^q}{Y^q} \qquad (2.5.1)$$

Fig. 4 Distribution of the number of moving individuals (relative frequency of observations according to the number of moving individuals) in **a** a group of 10 Tonkean macaques (Sueur *et al.* 2009), **b** a group of 11 brown lemurs (Jacobs *et al.* this issue), and **c** a group of 15 rhesus macaques (Sueur 2010; Sueur *et al.* 2010a). In these 3 species, affiliative relationships influenced the mimetic process to join a movement. The shape of the curve gives insight into group cohesion. Tonkean macaques and brown lemurs are shown here to be more cohesive than rhesus macaques, as the highest frequency in these 2 species concerns the maximum number of followers. In brown lemurs and rhesus macaques, the high number of movements involving about half of group members illustrates the possible existence of subgroups.
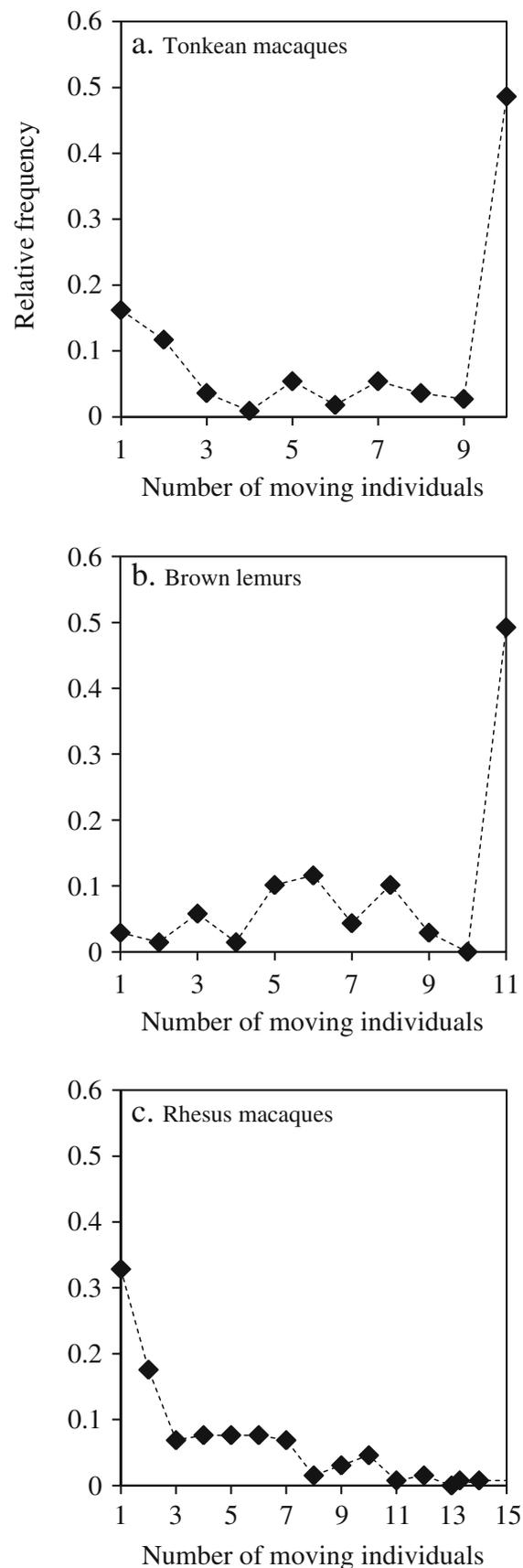
for the probability of changing from resting to moving

$$\psi(m,r) = \frac{X^q}{Y^q} \tag{2.5.2}$$

for the probability of changing from moving to resting

Another case of a feedback loop concerns recruitment signals (Detrain and Deneubourg 2006). In Tonkean macaques, the initiator pauses after emitting calls used to recruit conspecifics (Sueur and Petit 2010). When a threshold of 3 individuals joining the movement is reached, it stops emitting these signals. Thus the initiator's behavior influences future followers, and the followers' behavior influences the initiator. The same process occurs in capuchins, with back glances instead of pauses (Meunier *et al.* 2008). Here, the probability ψ_i that an individual i joins the movement is the same as that described in Eq. 2.1. The probability ψ_s that the initiator stops emitting signals is:

$$\psi_s = \alpha_s + \frac{\beta_s X^q}{S^q + X^q} \tag{2.6}$$

wherein α_s is the intrinsic probability of stopping signaling, β_s is an inverse mimetic coefficient, X is the number of individuals that have joined the movement, and S is a threshold number of moving individuals.

In capuchins, the initiator comes back to the group and cancels its initiation if not followed by its conspecifics (Petit *et al.* 2009). The cancelation process in this species is also an amplification process in which the probability ψ_c that the initiator gives up and returns to the group is:

$$\psi_c = \alpha_c + \frac{\beta_c X^q}{S^q + X^q} \tag{2.7}$$

wherein α_c is the intrinsic probability of canceling (α_c=0.009 in Petit *et al.* 2009), β_c is an inverse mimetic coefficient (here, the probability of cancelling, i.e., of stopping the initiation of a movement, depends on the number of followers; β_c=−0.009), X is the number of followers, S is a threshold number of followers (S=2), and q is the degree of sensitivity of the system (q=2.3).

Conclusion

Mimetic rules can be applied to various processes in various species. Here we have reviewed the case of collective movements, but the same amplification process applies to the spread of diseases, the transmission of traditions in primates, collective construction in insects, and collective panic or applause in human beings (Camazine *et al.* 2003; Detrain and Deneubourg 2006; Dyer *et al.* 2009; Helbing *et al.* 1997, 2000; Voelkl and Noë 2008). We have shown that the modulation of the parameters of a simple equation results in the emergence of totally different patterns, from personal to distributed leadership (Leca *et al.* 2003), and from randomly homogeneous organization of joiners to a highly structured and stable organization. Understanding how the parameters of this mimetic rule can be modified enables us to understand better the complexity of species.

The study of self-organization originated from physics and chemistry (Nicolis and Prigogine 1977, 1989) and was then applied to insects and species living in large groups (Camazine *et al.* 2003; Couzin and Krause 2003) and finally to primates (Hemelrijk 1999; Petit *et al.* 2009; Sueur *et al.* 2009). This leads us to believe that these simple and local rules can underlie complex systems, whatever the species and the individual complexity. Although biological and social characteristics differ between species, similar self-organized processes have been selected as reliable and well adapted means for optimal collective decisions.

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