

Sequence of quorums during collective decision making in macaques

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Received: 7 March 2010 / Revised: 2 May 2010 / Accepted: 25 May 2010
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Abstract Synchronization of activity is one of the major challenges of any society, and to what extent social animals reach a consensus still remains to be established. In the case of group movements, recent studies have underlined the importance of the pre-departure period and suggested that some individuals in a group express their motivation to move by showing a preference for a specific direction. However, how do other group members really choose the time and direction of movement? This study shows that in

two semi-free ranging Tonkean macaque (*Macaca tonkeana*) groups, several individuals propose different directions for movement by displaying unique behavior. The whole group eventually moves in the choice of direction supported by the majority of individuals according to a sequence of three quorum rules. Moreover, when the number of individuals choosing another direction is higher than their own group, individuals that proposed alternative directions eventually renounce and follow the majority. Despite conflict of interests, group members reach a consensus before the actual start of group movement. This demonstrates that processes of this type, which can be considered to be voting processes, are not exclusive to human societies and may be explained by a complex sequence of simple rules.

Communicated by: M. Beekman

Electronic supplementary material The online version of this article (doi:10.1007/s00265-010-0999-8) contains supplementary material, which is available to authorized users.

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Keywords Consensus · Voting process · Vote · Threshold · Primates · Group movement · Self-organization

Introduction

Animal group decision making for group movement (Buhl et al. 2006; Conradt and Roper 2005; Couzin 2007; Danchin et al. 2004; Parrish 1999; Sumpter 2006; Ward et al. 2008) has mainly been studied using the concept of leadership (Couzin et al. 2005; Biro et al. 2006; Norton 1986). Several authors have suggested that one or a few individuals decide about the time and the direction of movement and subsequently “lead” the group (Biro et al. 2006; Couzin et al. 2005; Sueur and Petit 2008a, b). However, other studies have shown that even if some individuals consistently lead the group, the period preceding the decision can be crucial with regards to making the leader depart: other group members may display specific

behaviors (in one or several directions) that consequently influence its departure probability (Kummer 1968; Prins 1996; Sueur and Petit 2008a, b). It has often been claimed that a decision depends on a quorum threshold as in the case of fish, ants or bees (Pratt et al. 2002; Seeley and Visscher 2004; Sumpter 2006; Ward et al. 2008). A response to a quorum (or to a threshold) is observed when the probability of animals exhibiting a particular behavior is dependent on the number of individuals already performing the behavior, whatever the process underlying the estimation of this number (Pratt et al. 2002; Seeley and Visscher 2004; Sumpter 2006; Ward et al. 2008). In *Temnothorax* ants, the probability that an ant will immigrate to a specific nest chosen from two or several new nests depends on the number of ants already present in this nest (Pratt et al. 2002). Similarly, a quorum threshold was described in honey bees (*Apis mellifera*) when they selected a new nest site (Seeley and Visscher 2004). An experimental study on three-spine sticklebacks (*Gasterosteus aculeatus*) showed that a quorum response could also explain group movement decisions in fish and how they choose between two proposed directions (Ward et al. 2008).

When mammals proposed different directions for movement using specific behaviors (Kummer 1968; Prins 1996), more complex processes called “voting behaviors” are evident (Conradt and Roper 2005; Kummer 1968; Prins 1996; Sueur and Petit 2008a, b). These processes seem to imply a more global type of communication (Conradt and Roper 2005). A well-known study suggesting the existence of concurrent proposals by group members was carried out on hamadryas baboons (*Papio hamadryas hamadryas*) during movement from the sleeping area to waterholes in the morning (Kummer 1968). In that species, males, supported by their harem, repeatedly tried to influence other group members to follow their direction using a specific posture called “notifying behavior” (“an individual soothingly presents his hindquarter in the fleeting manner customary between males,” Kummer 1968). At the end of the decision-making process, the entire troop went in the direction taken by the majority of group members. In a study on African buffalo (*Syncerus cafer*), individuals were usually seen to be resting several minutes prior to the group's departure towards a new grazing location. Adult cows intermittently stood-up and oriented their heads and bodies in a particular direction. After such reorientation, animals often resumed resting or grazing locally until departure. Thus, the reorientation was clearly not a sign of immediately impending behavior. However, the direction taken for the eventual grazing location was the most frequently observed direction in all notifying behaviors before movement (Prins 1996). While the study on baboons or that carried out on African buffalo provided descriptive evidence for voting behavior, the quantitative data were

insufficient to establish whether group members truly counted votes and decided according to the majority (Conradt and Roper 2005; Kummer 1968; Prins 1996). Our study provides quantitative evidence that similar processes exist in Tonkean macaques.

Tonkean macaques are considered to be a tolerant species (Anderson 2007; Thierry 2007) in which individuals of every status can express their motivations before, during, and after the start of group movements (Sueur and Petit 2008a). All group members therefore take part in the decision-making process, which reflects an equally shared consensus (Conradt and Roper 2005; Sueur and Petit 2008a). We have previously shown that “preliminary behaviors” (Sueur and Petit 2008a, 2009) displayed before departure favor the recruitment of group members to the group movement. The more preliminary behaviors occurred, the more individuals joined the movement (Sueur and Petit 2008a). The preliminary behaviors looked like preparation for the future group movement and on rare occasions occurred in two different directions. However, we still do not know how this decision is taken prior to departure. Given these previous findings on collective decision making and the egalitarian basis of their society, Tonkean macaques seem to be an ideal choice for the study of voting processes. Here, we address this question in two semi-free ranging groups of Tonkean macaques using observations of behavior when two concurrent directions for movement were proposed.

Methods

Subjects and environment

The two study groups of Tonkean macaques were bred in semi-natural conditions at the Strasbourg University Centre of Primatology. They ranged in a 0.5 ha park (fenced field), containing different patches of vegetation between which individuals could collectively switch. The first Tonkean macaque group studied (November 2005 to March 2006) consisted of ten individuals: one adult male (over 5 years), five adult females (over 4 years), and four juveniles (from 1 to 3 years). The second group (study carried out from December 2003 to April 2004) consisted of 22 individuals: seven adult males (27, 15, 11, 9, 7, 6, and 5 years old), eight adult females (33, 25, 24, 21, 21, 14, 12, and 11 years old), one subadult male (4 years old), and six juveniles (1 year old). The composition of both groups was similar to that found in wild groups (Supriatna et al. 1992; Whitten et al. 1987). Animals had free access to an inside shelter with commercial pellets and water ad libitum. Fruit and vegetables were distributed once a week, outside the observation sessions.

Observational protocol

The beginning of a group movement was defined by the first departure of an individual who walked more than 10 m in less than 40 s. This criterion was the same as that used by Leca et al. (2003), Jacobs et al. (2008), and Sueur and Petit (2008a, b), and it allowed us to discriminate first departures (i.e., initiations) from other movements such as foraging movements or preliminary behaviors (Sueur and Petit 2008a). The departure of the first individual over a distance of more than 10 m was an obvious signal for other group members (Jacobs et al. 2008; Leca et al. 2003; Sueur and Petit 2008a, b). A “joiner” was defined as any individual walking for more than 5 m in a direction that formed an angle less than 45° with the direction of the first individual to depart. We considered a group movement to be finished when no individual joined the movement within 5 min of the departure of the first individual or the last individual to join (Sueur and Petit 2008a, b; Sueur et al. 2009). The park of each group was marked with reference points, and the position (± 1 m) of each animal as well as the distance it walked was recorded. Group movements occurring in agonistic or sexual contexts were discarded from the analysis. Conflicts or consorts could induce non-spontaneous movements. Events were only taken into account if more than 2/3 of group members were present in or around the starting zone when they occurred. We defined the starting zone to be the area ≤ 10 m from the starting point of the first departed individual. With this criterion, both groups were clumped in the majority of cases; the diameter of the group was less than 10 m in both cases, whatever the study group (Sueur and Petit 2008a). Using video scoring, C.S. recorded the identity as well as the frequency of any behavior displayed by each group member. Measurements were taken using the *all-occurrence* sampling method, both during the twenty minutes prior to a group movement, and after the start of the group movement (Altmann 1974). A *back glance* is defined as an individual turning its head and looking in the direction of other group members. In the cases in which the eyes of animals could not be observed, we used the direction of the head—with an angle greater than 135° from the direction of the movement—to determine a back glance (see Sueur and Petit 2009 for more details). An *intention movement* is defined as the walking of an individual, for between 1 to 5 m, in a specific direction. A stop of more than 2 s after an advance was considered to show the end of the behavior. This definition corresponds to that of Kummer (1968) and Prins (1996). Indeed, the direction of the body axis of individuals indicated the direction of the future group movement (Prins 1996). We considered the back glances as preliminary behaviors when an individual had previously made some intention movements (at least one) and moved away from the group. Back glances and intention move-

ments were recorded and named as “preliminary behaviors” when exhibited before departure (Sueur and Petit 2008a). We called individuals displaying preliminary behaviors *notifying individuals*. We considered a *direction* to exist when there were at least two preliminary behaviors (two intention movements or one intention movement coupled with one back glance) for that direction, performed by the same individual or different ones. If the directions of at least two individuals displaying preliminary behaviors formed an angle greater than 45°, we considered these directions to be different (*direction 1* and *direction 2*). We considered direction 1 as the direction eventually chosen by the entire group (i.e., the direction of the future group movement) and direction 2 as the direction that was not chosen by the group at departure. A *switch in direction* was considered to have occurred when an individual displaying preliminary behaviors in one direction changed its direction towards another one. The pre-departure period was defined as the time between the first preliminary behavior and the departure of the initiator.

Assessing dominance rank

To establish the dominance hierarchy of each group, we recorded data in two contexts: during spontaneous aggressive interactions, and during drinking competition around a single source of orange juice. We ranked individuals over the age of one in a matrix according to the avoidance and unidirectional aggression observed. We carried out an analysis of hierarchical rank order using MatMan and verified the hierarchy linearity (de Vries et al. 1993) for both species (Group 1: $h^2=0.79$, $p<0.0006$; Group 2: $h^2=0.81$, $p<0.0001$).

Statistical analysis

Even though many routes were available and taken by the group in the enclosure, no event was recorded in which more than two directions were displayed before the departure of a group. We conducted two-tailed sign tests to investigate whether the frequencies of behaviors, number of notifying individuals, the mean hierarchical rank, and the mean age of notifying individuals differed between direction 1 and direction 2. A positive difference given by the sign test is the number of cases in which the value of direction 1 exceeds that of direction 2. A null difference is the number of cases in which the value of direction 1 is equal to that of direction 2. A negative difference is the number of cases in which the value of direction 1 is less than that of direction 2. Differences in the rate of notification between individuals were tested using a Chi-square test. The same procedure was used to test whether the initiator was more highly ranked or older than other

individuals in the movement. Departing in one direction involves two different decisions: the time decision (when) and the direction decision (where). We decided to study these two decisions separately in order to understand the rules underlying the initiator's choice, i.e., whether the initiator first decided on the departure time, and then on the direction to follow, or the converse. Analyses of first departure probability distributions (probability of being the first to depart and probability of choosing one direction according to the number of notifying individuals and behaviors) and switches in direction were carried out using exponential, logarithmic and sigmoid curve estimation tests (R^2) and Spearman's rank correlation tests (r_s). The study of probability distributions reveals how the rate of observations—the probability—evolves according to a certain variable (here, we tested the duration of the pre-departure period, the number of preliminary behaviors, and the number of notifying individuals for each direction).

Survival analysis, or analysis of probability distribution, is the best statistical framework for quantifying time-structured behaviors (Cox and Oakes 1984). This method has already been successfully applied in numerous ethological studies (Amé et al. 2006; Dussutour et al. 2005; Meunier et al. 2006; Nicolis et al. 2003; Sueur et al. 2009; Theraulaz et al. 2002). We used this methodology to assess how the probability to switch direction or to depart in a specific direction is influenced by different variables in the pre-departure period: the duration of the pre-departure period, the number of preliminary behaviors, and the number of notifying individuals for each direction. The sigmoid and logarithmic curves show a threshold that may correspond to a quorum. This threshold is the value of the independent variable—here, the number of preliminary behaviors or of notifying individuals—for which the probability that individuals exhibit a behavior equals 0.5. On the other hand, the exponential curve shows that the probability of displaying a specific behavior is not dependent on the number of notifying individuals and/or number of preliminary behaviors (Meunier et al. 2006; Sueur et al. 2009; Sumpter and Pratt 2009). Only the values of the model fitting best with the observed data are indicated in the results. Tests were performed using SPSS 10 (SPSS inc., Chicago, USA). α was set at 0.05. Means were \pm S.E.M.

Results

Among the 146 group movements recorded in group 1 and the 119 recorded in group 2, 44 and 36, respectively, were preceded by preliminary behaviors before departure. Among these events we found 13 group movements in group 1 and 14 in group 2 where several individuals displayed preliminary behaviors in two different directions

before departure. A total of 9.6 ± 0.3 and 18.0 ± 4.4 individuals in groups 1 and 2, respectively, participated in these movements with two proposed directions. With regards to other movements for which no preliminary behavior was displayed, the process of decision making was only based on initiations, and fewer individuals participated (Sueur and Petit 2008a, b; Sueur and Petit 2009; Sueur et al. 2009). Displaying preliminary behaviors in two different directions reflects a conflict of interest between group members and is a good opportunity to study the decision-making process. In such cases, while the group was stationary, at least two animals displayed preliminary behaviors in two different directions (Fig. 1a, b). At a given time, one individual (the initiator) initiated a movement in one of the two proposed directions and was followed by all group members (Fig. 1c). We called direction 1 the direction taken by the initiator (the direction of the future group movement) and direction 2 the other direction. We conducted different analyses in order to investigate how the initiator decided on its choice of direction for movement, and how cohesion was maintained within the group.

Deciding on direction

Which direction was chosen, and how?

Before the initiator's departure, $66.1 \pm 5.4\%$ of members of group 1 and $35.4 \pm 3.3\%$ of members of group 2 had already displayed preliminary behaviors. More precisely, $38.5 \pm 5.9\%$ of individuals in group 1 and $24.3 \pm 3.1\%$ in group 2 notified direction 1 (i.e., displayed intention movements in direction 1) while $27.7 \pm 3.6\%$ in group 1 and $11.1 \pm 1.2\%$ in group 2 notified direction 2. The duration of the pre-departure period, i.e., the time elapsed between the first preliminary behavior and the departure of the initiator, was 242 ± 51 s for group 1 and 131 ± 22 s for group 2. For group 1, the number of preliminary behaviors ($N=13$, $P=0.0063$, sign tests, Table 1) and the number of notifying individuals ($N=13$, $P=0.038$, sign tests, Table 1) were higher for direction 1 than for direction 2 on departure of the initiator. We obtained similar results for group 2, both for the number of preliminary behaviors ($N=14$, $P=0.0009$, sign tests, Table 1) and for the number of notifying individuals ($N=14$, $P=0.0063$, sign tests, Table 1). In only one case, group 1 moved in the direction notified by the less common behavior. It never happened in group 2. There was no case in which the majority of individuals notified one direction but more preliminary behaviors occurred in the other direction; the number of preliminary behaviors was always the highest for the direction in which the highest number of notifying individuals was. Moreover, only on one occasion did groups 1 and 2 move in the direction notified by the lower number of individuals. This suggests that the initiator

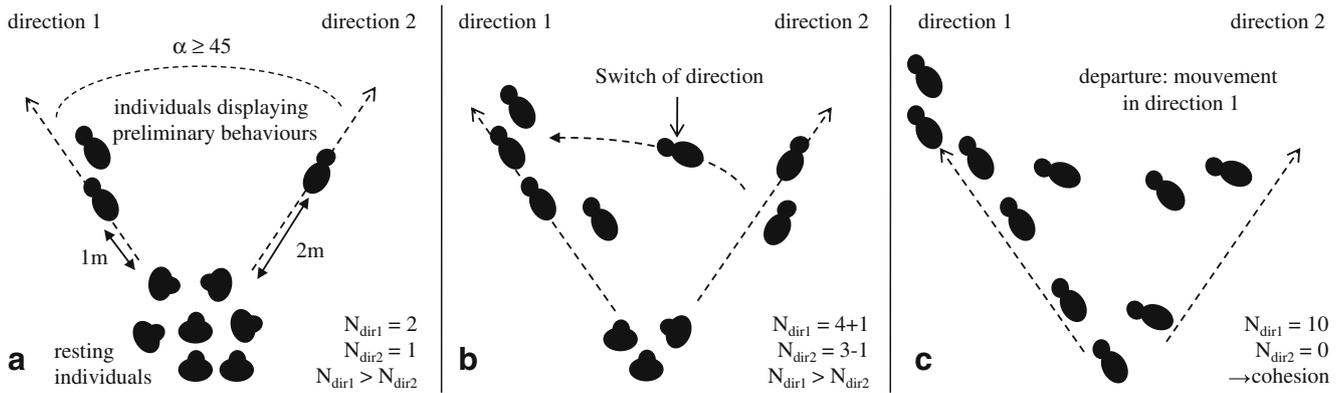


Fig. 1 Illustration of the decision-making process in Tonkean macaques: **a** one sub-group of macaques proposes a direction (direction 1) using preliminary behaviors, another individual proposes an alternative direction (direction 2); **b** some individuals decide to switch their direction, and the majority of these switches are from

direction 2 to direction 1; **c** the initiator departs and the movement starts in direction 1, the choice of the majority of notifying individuals; the remaining individuals notifying direction 2 join the movement in direction 1 and then maintain cohesion with other group members

took the number of preliminary behaviors and/or number of notifying individuals into account when choosing the direction in which to move (Fig. 1c, analyses of the role of the initiator in the pre-departure process are shown below). The initiator chose the direction for which there were the most preliminary behaviors and notifying individuals.

The probability (number of observations for each independent variable divided by the total number of observations) of the initiator choosing direction 1 according to the difference in the number of preliminary behaviors between direction 1 and direction 2 is a sigmoid function ($y = \frac{1}{1+s^{-\lambda x}}$ with $\lambda=5$, where y is the probability to choose direction 1 and x is the difference in the number of preliminary behaviors between direction 1 and direction 2) for group 1 ($N=22$; $r_s=0.93$, $P<0.00001$) and for group 2 ($N=22$; $r_s=0.89$, $P<0.00001$). We obtained the same result for the number of notifying individuals ($y = \frac{1}{1+s^{-\lambda x}}$ with $\lambda=17$, where y is the probability to choose direction 1 and x is the difference in the number of notifying individuals between direction 1 and direction 2; $N=26$; $r_s=0.87$, $P<$

0.00001 , Fig. 2a for group 1; $N=28$; $r_s=0.87$, $P<0.00001$, Fig. 2b for group 2). For both groups, the threshold was 0 for both the number of preliminary behaviors and the number of notifying individuals. The difference in the number of preliminary behaviors and/or notifying individuals between direction 1 and direction 2 only needs to equal one for the initiator to choose the direction with the majority of preliminary behaviors and/or notifying individuals. However, the value of λ —representing the power factor influencing the sigmoid curve slope and showing the non-linearity of the phenomenon—was higher for the number of notifying individuals, indicating a likely higher discrimination than for the number of preliminary behaviors. However, this result should be treated with caution, as only a minimal difference can be seen in the influence of the number of preliminary behaviors and notifying individuals. λ affects the slope of the sigmoidal curves that have been fitted to the data. Higher values of λ correspond to the fitted curves having a steeper slope, particularly around the threshold value of x (zero in this case). In essence a higher value of λ

Table 1 Number of cases in which each group of Tonkean macaques moved in direction 1 (direction finally chosen by the group) when the value of the independent variable in direction 1 is less than that in

direction 2 ($D1 < D2$), when the value in direction 1 is equal to that in direction 2 ($D1 = D2$) and when the value in direction 1 is greater than that in direction 2 ($D1 > D2$)

	Number of cases for which the direction 1 was chosen					
	Group 1			Group 2		
	D1 < D2	D1 = D2	D1 > D2	D1 < D2	D1 = D2	D1 > D2
Number of preliminary behaviors	1	1	11	0	3	11
Number of notifying individuals	1	2	10	1	2	11
Mean hierarchial rank	7	0	6	7	0	7
Mean age	8	1	4	8	0	6

D1 direction 1, D2 direction 2

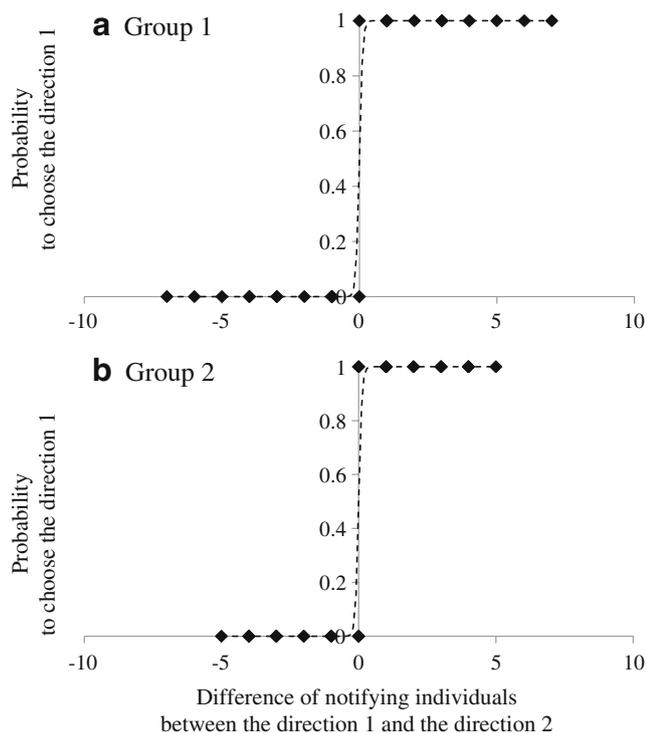


Fig. 2 Direction decision. The probability of the choice of direction being based upon the difference of notifying individuals observed in the two possible directions (direction 1–direction 2 and direction 2–direction 1). Squares represent the observed data. The dashed line represents the theoretical sigmoid function

results in a quicker transition between not choosing direction 1 and choosing direction 1 as the difference between notifying individuals for both directions increases (Amé et al. 2006; Dussutour et al. 2005; Nicolis et al. 2003). Interestingly, we observed the only case of group splitting (group 2) when the number of preliminary behaviors was the same in each direction (2 vs. 2). In this case, the direction advertised by two individuals was then preferred by the larger sub-group (12 individuals) whilst the other direction, promoted by only one animal, was chosen by only four followers.

Individuals notifying direction 1 were not higher- or lower-ranking (group 1: $N=13$, $P=1$; group 2: $N=14$, $P=1$; sign tests, Table 1), or younger or older than those notifying direction 2 (group 1: $N=13$, $P=0.387$; group 2: $N=14$, $P=0.790$; sign tests, Table 1). There was no difference in the rate of notification between individuals (group 1: $\chi^2=2.75$, $df=9$, $P=0.979$; group 2: $\chi^2=23.227$, $df=16$, $P=0.113$). These results suggest that the group—i.e., the initiator followed by the other group members—chose the direction of movement according to the number of notifying individuals rather than their specific status. The initiator did not depart in the direction shown by the last preliminary behavior or notifying individual (eight movements in the direction of the last behavior vs. five movements in the direction not notified by the last behavior for group 1; eight

movements in the direction of the last behavior vs. six movements in the direction not notified by the last behavior for group 2). This latter result seems to indicate that the initiator did not depart according to the number of preliminary behaviors and/or notifying individuals in one direction, but rather took into account the number of preliminary behaviors and/or notifying individuals in both directions before deciding (this assumption is confirmed by our results in the section “Deciding on departure time”).

Which role did the initiator play during the pre-departure period?

The future initiator was involved in the pre-departure period in 57.1% of cases in group 1 and 23.1% in group 2 (based on cases where two directions are proposed). It displayed the first preliminary behavior in 38.4% of cases (five out of 13 individuals) in group 1 and 21.4% (3 out of 14) in group 2, whereas the theoretical, expected probability ($1/N$ with N being the number of individuals in each group) of displaying the first preliminary behavior was 10% (about 1.3 out of 14) for group 1 and 4.5% (about 1.96 out of 14) for group 2. It therefore appears that the future initiator was more involved in the pre-departure period (i.e., displayed preliminary behaviors) than other group members. Interestingly, this individual notified the direction it would take later when initiating (direction 1) more than the other (direction 2) (group 1: $N=13$, $P=0.001$, positive differences=11, negative differences=0, null differences=2; group 2: $N=14$, $P=0.031$, positive differences=6, negative differences=0, null differences=8; sign tests). On average, this initiator was neither higher-ranking nor older than other group members (group 1: $N=13$, $P=0.612$ for hierarchical rank and $P=0.343$ for age; group 2: $N=14$, $P=0.790$ for hierarchical rank and $P=0.145$ for age, sign tests) and was not observed to be a male any more frequently than a female (group 1: $N=13$, $n_{\text{female}}=7$, $n_{\text{male}}=6$; group 2: $N=14$, $n_{\text{female}}=8$, $n_{\text{male}}=6$). These results on the initiator's identity are similar to those of Sueur and Petit (2008a, b). In the latter study, Tonkean macaques initiated movements at the same frequency, whatever their age, sex, or social status.

Deciding on departure time

Having investigated how the initiator chose the direction in which to move (i.e., where), we then investigated how the initiator chose the time to move (i.e., when).

Was the initiator's departure dependent on the length of the pre-departure period?

We checked whether the probability of the initiator's departure was dependent on time, i.e., if the probability of departure

increased (or decreased) with time. The results showed that the departure probability did not depend on the duration of the pre-departure period (i.e., did not increase or decrease with time), but was constant per-unit-time (exponential curves estimation; group 1: $R^2=0.99$, $F_{1,11}=806$, $P<0.00001$; group 2: $R^2=0.92$, $F_{1,12}=371$, $P<0.00001$).

Did the probability of the initiator's departure depend on the number of preliminary behaviors and/or notifying individuals?

As the mean number of notifying individuals at the end of the pre-departure process was higher for the smaller group than for the larger group (see above for details), it seems that the initiator's decision to depart depended on the number of notifying individuals rather than on the number of remaining individuals (those not involved in the pre-departure process). If the initiator decided to depart according to the number of remaining individuals, then the number of notifying individuals in the smaller group must be less than that in the larger group (Amé et al. 2006; Dussutour et al. 2005; Nicolis et al. 2003). We therefore studied the probability of departure by analyzing the departure probability distribution according to (1) the number of preliminary behaviors and (2) the number of notifying individuals for direction 1, for direction 2, and for the sum of the two directions.

The question asked was as follows: How many notifying individuals were taken into account by the initiator (for direction 1, direction 2 or in both directions) when making its decision to depart, and did this departure respond to a threshold? The data fit a sigmoid function: $y = 1 - \frac{1}{1+(\frac{x}{S})^n}$;

where y is the probability to depart first, x is the sum of the notifying individuals in direction 1 and direction 2, S is the threshold of the sigmoid curve and n is the power influencing the sigmoid curve slope (see Table 2 for equation parameters and statistical values). These results suggest that the initiator departed after a specific threshold was reached. However, considering the power n (representing the degree of discrimination, sensitivity of individuals), it seems that the initiator discriminated and took into account the number of notifying individuals in both directions (i.e., their sum) in order to depart rather than the number of individuals in direction 1 alone, as suggested above (Fig. 3a, b). This difference is weak but confirms the previous results about the influence of the sum of notifying individuals in both directions instead of the number in only one direction.

Switch in direction

Individuals that notified direction 2 changed their direction and joined the majority in 100% of cases in group 1 and 80% in group 2 (one group fission). These switches in direction (from direction 2 to direction 1) occurred 46 and 14 times in groups 1 and 2, respectively. Switches from direction 1 to direction 2 occurred less frequently (group 1: 11 cases, $N=13$, $P=0.0002$; group 2: 3 cases, $N=14$, $P=0.01$). We observed that the switches from direction 2 to direction 1 occurred before and after the departure of the initiator. More interestingly, these switches occurred before departure 63.7% and 50% of the time in groups 1 and 2, respectively. These individuals changed their minds before the departure of the initiator when the number of

Table 2 Results of comparisons between the observed initiator departure probability curves and a theoretical sigmoid function

	Variables	Direction	S	Number	R^2	F	P
Group 1	Number of preliminary behaviors	D1	12	4	0.98	(1.9) 420	<0.00001
		D2	4	2	0.99	(1.6) 837	
		D1 + D2	16	3	0.99	(1.10) 679	
	Number of notifying individuals	D1	6	5	0.98	(1.9) 503	
		D2	3	3	0.99	(1.9) 686	
		D1 + D2	9	5	0.99	(1.19) 1,825	
Group 2	Number of preliminary behaviors	D1	4	3	0.99	(1.7) 650	
		D2	2	3	0.97	(1.4) 144	
		D1 + D2	7	3	0.98	(1.9) 397	
	Number of notifying individuals	D1	3	3	0.98	(1.19) 1,020	
		D2	1	3	0.99	(1.19) 3,397	
		D1 + D2	5	5	0.99	(1.19) 1,448	

Numbers in brackets are the degrees of freedom for the curve estimation test. These degrees of freedom are not based on the number of events for each group (13 and 14, respectively) but on the number of values for each independent variable

S is the sigmoid curve threshold, n is the power of the sigmoid function, D1 direction 1, D2 direction 2

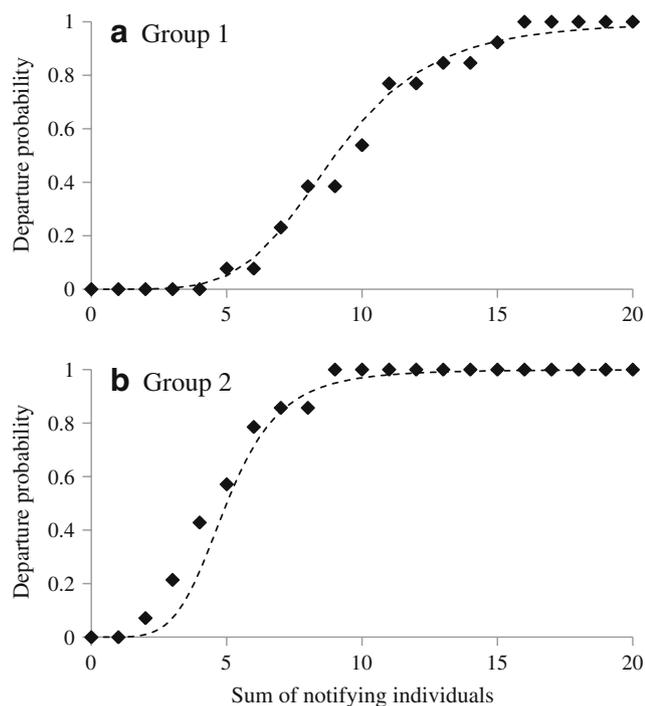


Fig. 3 Time decision. Probability that the initiator will depart according to the sum of notifying individuals in each direction. Squares represent the observed data. The dashed line represents the theoretical sigmoid function

preliminary behaviors prior to their switch was higher for direction 1 than for direction 2 (group 1: $N=46$, $P<0.0001$, positive differences=36, negative differences=7, null differences=3; group 2: $N=14$, $P=0.001$, positive differences=11, negative differences=0, null differences=3; sign tests). Thus, the rallying of these individuals from direction 2 to direction 1 may already take place before the start of the movement. Moreover it seems that these switches in direction also depended on a threshold. We checked whether the probability of switching direction was dependent on the total number of preliminary behaviors in direction 1 and direction 2, and this relation also followed a sigmoid function ($y = 1 - \frac{1}{1+(\frac{x}{S})^n}$; group 1: $S=15$, $n=3$, $R^2=0.99$, $F_{1,20}=1,384$, $P<0.00001$; group 2: $S=6$, $n=5$, $R^2=0.97$, $F_{1,4}=148$, $P<0.00001$). The probability of switching direction also depended on the number of preliminary behaviors in direction 1 ($y = 1 - \frac{1}{1+(\frac{x}{S})^n}$; group 1: $S=9$, $n=2$, $R^2=0.97$, $F_{1,17}=646$, $P<0.00001$; group 2: $S=2$, $n=2$, $R^2=0.95$, $F_{1,4}=87$, $P<0.001$) but the power n was higher when considering both directions than when considering only one direction. Notifying individuals seemed to take into account both the number of preliminary behaviors in direction 1 and those in direction 2 before switching direction. Also, the change from a probability of 0 to a probability of 1 to switch direction is rapid when the threshold is reached, given the value of the power n .

Discussion

We only observed two concurrent directions for 8.9% of group 1 and 11.7% of group 2 movements. These low figures were probably due to the low probability that two individuals would simultaneously display preliminary behavior in different directions. The semi-free ranging breeding conditions may also affect this rate because these conditions rarely lead to true conflicts of interests. However, this process should not be underestimated at the group level because in all instances except for one, group members reached a consensus for a single direction and thus remained cohesive. Moreover, other behaviors such as manipulations, reconciliations, innovations, or altruism are very rare in nature, and may be rarer than the voting process, but we cannot stipulate that displaying these behaviors has no effect on individual fitness or species evolution (Byrne and Whiten 1988; Hamilton 1964; Reader and Laland 2002; Thierry 2007). Group members finally moved together: even the individuals notifying direction 2 joined the movement. Moreover, the similarities in the results of the two study groups suggest a general rule of decision making, and only important costs and/or benefits for group members can lead to the highly discriminative system that the Tonkean macaques displayed.

In order to decide which direction to follow, Tonkean macaques notified their preferred directions in the same way as hamadryas baboons (Kummer 1968), and the movement started in the direction supported by the highest number of behaviors and individuals, despite divergent motivations. This departure implied a sequence of three quorums, one concerning the decision of direction changes before departure and two concerning the initiator's departure. This implies that the initiator and the notifying individuals assessed the number of preliminary behaviors and/or number of notifying individuals in each direction in order to choose between them. Several animal species are able to count or at least estimate quantities, ranging from fish to primates (Agrillo et al. 2008; Brannon and Terrace 1998; Hauser et al. 2000; Pepperberg 2006). Some studies have even shown that macaques are able to order numbers, and also add or subtract numbers or quantities (Agrillo et al. 2008; Hauser et al. 2000). Therefore, in the context of this study and according to our results the initiator could probably perceive the difference in terms of preliminary behaviors and/or notifying individuals between the two proposed directions. The results also suggest that the number of notifying individuals is more significant than the number of preliminary behaviors for making the decision. Nevertheless, when the number of notifying individuals was the same in both directions, individuals seemed to take the number of preliminary behaviors into account when deciding which direction to follow (one case).

We found that the departure of the initiator in one direction (direction 1) depended on two decisions: the time decision and the direction decision. One may argue that we have one single quorum response. However, results show that animals display three different behaviors, i.e., switching direction, choosing the departure time and choosing the departure direction. These behaviors are not variants of a same behavior, did not occur simultaneously and are not different responses to a same quorum rule. The probabilities of displaying each of these three behaviors follow different sigmoid curves with different parameters. For instance, if the direction decision was dependent on the same quorum as the time decision, then individuals would not choose the direction taken by the majority of individuals but would randomly choose one of the two directions. However, individuals always choose the direction taken by the majority of individuals because there is another process, a second quorum allowing this direction decision. The two decisions, that of direction and that of time, are therefore different. In this study case, having two quorum responses may lead to a more accurate decision than having only one quorum response where the time decision and the direction decision are mixed. Indeed, the decision-making process for a departure in direction 1 may follow one of the following sequences: (1) the initiator decides to depart when the total number of notifying individuals reaches a specific threshold and then chooses the direction shown by the majority of notifying individuals; in this case, the time decision precedes the direction decision; (2) the initiator decides to depart in the direction for which the threshold of notifying individuals has been reached; (3) the initiator decides to depart in the direction shown by the highest number of notifying individuals. In the latter two cases, the time decision is dependent on the direction decision. Based on our results, we can dismiss sequence (3) because it involves no more than one or two notifying individuals on departure of the initiator, whereas our results showed that this threshold was six for group 1 and three for group 2 (see *S* values in Table 1). Sequence (2) can also be dismissed. Indeed, both sequences (2) and (3) involve the initiator's departure in the direction illustrated by the last preliminary behavior. We did however find that the initiator did not systematically start to move in the direction of the last behavior in both groups. The more likely scenario is therefore that the initiator first decided to start departure by taking into account the total number of notifying individuals—our results confirmed this hypothesis—and *then* decided on the direction by comparing the number of notifying individuals in each direction. This assumption is strongly confirmed by the analysis of the temporal sequences, the threshold for choice of direction, which equalled 0, and the high power n or λ of the sigmoid function. This suggests high discrimination between both

directions and great non-linearity of the phenomenon (Pratt et al. 2002; Seeley and Visscher 2004; Sumpter 2006; Ward et al. 2008). This partition between decision and action (i.e. the departure) makes consensus building and group cohesion possible (Conradt and Roper 2005; Sueur and Petit 2008a).

We found the same threshold function in Tonkean macaques as that seen in ants, bees and fish (Pratt et al. 2002; Seeley and Visscher 2004; Sumpter 2006; Ward et al. 2008). However, the mechanism underlying the departure of the whole group appears to be more complex because it implies three quorums—one quorum for the switch in direction, one for the departure choice, and the last quorum for the direction choice—and a sharp difference in the number of notifying individuals and the number of preliminary behaviors. Moreover, the process seems to be flexible, as the decision to move may also rely on the number of notifying individuals or preliminary behaviors, according to the situation. Nevertheless, group members seemed to be more sensitive to the number of notifying individuals, in most cases. Hence, the quorum is a mechanism allowing trade-off between the time taken for decision making, the accuracy of the latter, and group cohesion (Austen-Smith and Feddersen 2009; King and Cowlshaw 2007; List 2004). The more the collective decision involves thresholds—as we found in our study—the more it enables optimal decisions to be taken by pooling information from many individuals (List 2004), thus increasing the accuracy of the decision (Austen-Smith and Feddersen 2009; King and Cowlshaw 2007; List 2004). Indeed, taking into account the number of notifying individuals in both directions, and not just one, increases the decision threshold and therefore decreases the probability of making a mistake by selecting the wrong direction. However, it would be interesting to study larger groups in order to understand how discrimination between two directions could both evolve with a higher number of notifying individuals and depend on the cognitive abilities of the species (Agrillo et al. 2008; Hauser et al. 2000). We are aware that since food access was *ad libitum*, the possibilities for discussing how the mechanism we found allows better accuracy about information are limited. This mechanism nevertheless ensures that animals maintain group cohesion.

Even if the mechanisms underlying collective decision making are threshold dependent, this study shows that the way Tonkean macaques select movement direction recalls not only the voting process of hamadryas baboons and African buffalo (Kummer 1968; Prins 1996), but also the vote described in bees when choosing a new nest site (Seeley and Visscher 2004; Sumpter 2006). According to the Oxford English dictionary, a vote is defined as a formal indication of a choice between two or more candidates or

courses of action. Prins (1996) defined body posture or intention movement as formal indications. This definition includes all phenomena implying a choice between different propositions, whatever the underlying mechanism, the species or its cognitive abilities (Seeley and Visscher 2004; Sumpter 2006; Tomasello and Call 1997). In the present study, Tonkean macaques, whatever their status, voted for a given direction using preliminary behaviors. However, finding a quorum in Tonkean macaques does not mean that the mechanisms underlying the same global phenomenon (choosing between different propositions) are simple and similar to those in insects or fish. Even if the changes in behavior observed in Tonkean macaques are based on a quorum, their decisions may include complex mechanisms such as high discrimination, intentions reflecting the motivations of individuals, insight, and recognition of social relationships. This has already been shown in previous studies in primates (Tomasello and Call 1997).

This type of voting process has probably emerged because of the egalitarian basis of the Tonkean macaque society, where decisions are distributed among all group members (Anderson 2007; Conradt and Roper 2009; Dyer et al. 2009; Fowler and Schreiber 2008; Sueur and Petit 2008a; Thierry 2007). Tonkean macaques are known to display the democratic skills usually found in human beings: they use peaceful interventions to stop aggression (Petit and Thierry 1994) and reconcile after conflict (Thierry 2007). Similarly, voting to reach a consensus does not seem to be limited to human societies alone and may help understand the origin of politics in humans (Conradt and Roper 2009; Dyer et al. 2009; Fowler and Schreiber 2008; List 2004).

Acknowledgments The authors are grateful to M. Pelé and J. Dubosq for the video analyses. We thank N. Poulin for statistical advice as well as L. Conradt, E. Danchin and R. Bon for helpful comments on this manuscript. This work was supported by the European Doctoral College of Strasbourg Universities, the French Research Ministry, the French Foreign Ministry, the Franco-American Commission, the Fyssen Foundation, and the Belgian National Funds for Scientific Research.

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