$v_{esc} \sim 0.7$ m/s, assuming a bulk density of 470 kg/m^3 (*17*), placing 67P well within the modeled BLF regime for impact velocities up to 1.5 m/s (as represented by Fig. 1). The accreted body is spun up to a final rotation period $P_{rot} \sim 10$ to 12 hours for $M_t/M_p = 2$ and $P_{rot} \sim 10$ to 14 hours for $M_t/M_p = 4$, depending on initial angular momentum and final shape and elongation of the resulting structure. Although consistent with $P_{rot} = 12.7$ hours for 67P, this is perhaps not meaningful because P_{rot} increased by 0.4 hours before and after the comet's 2009 perihelion (*31*).

A relatively narrow range of comet nuclei have been observed by spacecraft: ~10-km radius at largest (1P/Halley and 19P/Borrelly) and ~1 km at smallest (103P/Hartley). For these sizes the outcomes of collisions would be comparable to those presented here, for a normalized impact velocity v_{imp}/v_{esc} and normalized angular momentum L/L_{ref} to define the boundaries. For bodies much larger than ~10 to 100 km, compaction of a weak interior is expected (*32*) (fig. S1); this would strongly influence the outcomes of collisions by increasing the deep interior binding energy.

In simulations of BLF collisions, traces of the projectile are smeared onto the target and piled along the equator, suggesting the possibility of distinguishing features in remote sensing. We also consider the effect of successive collisions, as these could potentially bury, cover, or otherwise modify a preexisting structure. For this, we first produced a cohesionless BLF collision target (shape held by friction) with initial rotation $P_{rot} = 12$ hours, followed by a large splat-forming collision (Fig. 3). Splat formation is clearly possible without destroying the preexisting bilobate structure. We also consider tensile strength at the resolution scale (*23*) for cometesimals of mass ratio 1/2, 1/4, and 1/8 (figs. S4 to S6). Initially cohesive bodies are partly or fully damaged by the collisions (fig. S7), meaning that final shapes are maintained only by friction, as in Fig. 1. For tensile strength ~100 Pa, the results are comparable to identical collisions with zero tensile strength, and the distinct neck of 67P might be better reproduced with some tensile strength (Fig. 4). Greater tensile strength allows smaller "heads" to form, as opposed to cohesionless bodies and lumpy splats. There appears to be a tendency to form more binaries and small satellites with small tensile strength, although we have not evaluated the dynamical stability of pairs.

The major structural features observed on cometary nuclei—evidence for layers and bilobed shapes—can be explained by the pairwise accretion of icy bodies with little tensile strength on ~10- to 100-m scales. Our analysis is compatible with the low bulk densities of comets: Low tensile strength implies high original porosity, while the collisions result in only minor compaction. These slow mergers might represent the quiet, early phase of planet formation (*3*), before large bodies excited the system to disruptive velocities, supporting the idea that cometary nuclei are primordial remnants of early agglomeration (*33*). Alternatively, the same processes of coagulation might have occurred among debris clumps ejected from much larger parent bodies. Apart from requiring the latter scenario to be consistent with the cosmochemistry of nuclei, these clumps would have to be similar in size to produce BLF collisions, and nearly cohesionless, aspects for which there is evidence in simulations of larger collisions (*12*, *34*). In either case, these structures would have to avoid catastrophic disruption until the present.

REFERENCES AND NOTES

1. B. Donn, D. Hughes, "A fractal model of a cometary nucleus formed by random accretion," in *Proceedings of the 20th ESLAB Symposium on the Exploration of Halley's Comet* (European Space Agency, Paris, 1986), vol. 3, pp. 523–524.
2. P. R. Weissman, *Nature* **320**, 242–244 (1986).
3. S. J. Weidenschilling, *Icarus* **127**, 290–306 (1997).
4. D. Durda, S. A. Stern, *Icarus* **145**, 220–229 (2000).
5. P. R. Weissman, E. Asphaug, S. C. Lowry, "Structure and density of cometary nuclei," in *Comets II*, M. C. Festou, H. U. Keller, H. A. Weaver, Eds. (Univ. of Arizona Press, Tucson, AZ, 2004), pp. 337–357.
6. M. J. Mumma, P. R. Weissman, S. A. Stern, "Comets and the origin of the solar system - Reading the Rosetta Stone," in *Protostars and Planets III* (Univ. of Arizona Press, Tucson, AZ, 1993), pp. 1177–1252.
7. H. F. Levison, M. J. Duncan, L. Dones, B. J. Gladman, *Icarus* **184**, 619–633 (2006).
8. H. E. Schlichting, C. I. Fuentes, D. E. Trilling, *Astron. J.* **146**, 36 (2013).
9. A. Morbidelli, W. F. Bottke, D. Nesvorný, H. F. Levison, *Icarus* **204**, 558–573 (2009).
10. J. N. Cuzzi, R. C. Hogan, W. F. Bottke, *Icarus* **208**, 518–538 (2010).
11. R. M. Canup, *Astron. J.* **141**, 35 (2010).
12. Z. M. Leinhardt, R. A. Marcus, S. T. Stewart, *Astrophys. J.* **714**, 1789–1799 (2010).
13. E. Asphaug, W. Benz, *Nature* **370**, 120–124 (1994).
14. H. Boehnhardt, "Split comets," in *Comets II* (Univ. of Arizona Press, Tucson, 2004), pp. 301–316.
15. M. J. S. Belton, *Icarus* **210**, 881–897 (2010).
16. M. F. A'Hearn, *Annu. Rev. Astron. Astrophys.* **49**, 281–299 (2011).
17. H. Sierks et al., *Science* **347**, aaa1044 (2015).
18. M. J. S. Belton et al., *Icarus* **187**, 332–344 (2007).
19. N. Thomas et al., *Science* **347**, aaa0440 (2015).
20. W. Benz, E. Asphaug, *Comput. Phys. Commun.* **87**, 253–265 (1995).
21. M. Jutzi, W. Benz, P. Michel, *Icarus* **198**, 242–255 (2008).
22. M. Jutzi, *Planet. Space Sci.* **107**, 3–9 (2015).
23. Materials and methods are available as supplementary materials on Science Online.
24. Y. Skorov, J. Blum, *Icarus* **221**, 1–52 (2012).
25. M. Arakawa, M. Yasui, *Icarus* **216**, 1–9 (2011).
26. M. Jutzi, K. Holsapple, K. Wüenneman, P. Michel, "Modeling asteroid collisions and impact processes." in *Asteroids IV*, in press; preprint available at http://arxiv.org/abs/1502.01844 (2015).
27. P. Tanga et al., *Astrophys. J.* **706**, L197–L202 (2009).
28. Z. Leinhardt, D. C. Richardson, T. Quinn, *Icarus* **146**, 133–151 (2000).
29. E. Asphaug, C. B. Agnor, Q. Williams, *Nature* **439**, 155–160 (2006).
30. M. Jutzi, E. Asphaug, *Nature* **476**, 69–72 (2011).
31. S. Mottola et al., *Astron. Astrophys.* **569**, L2 (2014).
32. W. B. Durham, W. B. McKinnon, L. A. Stern, *Geophys. Res. Lett.* **32**, L18202 (2005).
33. M. J. S. Belton, *Icarus* **231**, 168–182 (2014).
34. E. Asphaug, A. Reufer, *Icarus* **223**, 544–565 (2013).

GROUP DECISIONS

Shared decision-making drives collective movement in wild baboons

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Conflicts of interest about where to go and what to do are a primary challenge of group living. However, it remains unclear how consensus is achieved in stable groups with stratified social relationships. Tracking wild baboons with a high-resolution global positioning system and analyzing their movements relative to one another reveals that a process of shared decision-making governs baboon movement. Rather than preferentially following dominant individuals, baboons are more likely to follow when multiple initiators agree. When conflicts arise over the direction of movement, baboons choose one direction over the other when the angle between them is large, but they compromise if it is not. These results are consistent with models of collective motion, suggesting that democratic collective action emerging from simple rules is widespread, even in complex, socially stratified societies.

Individuals living in stable social groups may often disagree about where to go but must reconcile their differences to maintain cohesion and thus the benefits of group living. Consensus decisions could be dominated by a single despotic leader (*1*), determined by a hierarchy of influence (*2*), or emerge from a shared democratic process (*3*). Because decisions are typically more accurate when information is pooled (*4*, *5*), theory predicts that shared decision-making should be widespread in nature (*6*). However, in species that form long-term social bonds,

considerable asymmetries in dominance and social power often exist, and some have proposed that these differences give high-ranking individuals increased influence over group decisions (1, 7, 8). Determining how consensus is achieved in these types of societies remains a core challenge for understanding the evolution of social complexity (6, 9, 10).

We studied the collective movement of a troop of wild olive baboons (*Papio anubis*) at Mpala Research Centre in Kenya to examine how group members reach consensus about whether and where to move. Baboons, long a model system for studying the evolutionary consequences of social bonds (11–13), live in stable multi-male, multi-female troops of up to 100 individuals (11). Despite differing needs, capabilities, and preferred foraging strategies (14–16), troop members remain highly cohesive, traveling long distances each day as a unit, while foraging for diverse and widely dispersed foods. How troops make collective movement decisions, and whether specific individuals determine decision outcomes, remain unclear. Attempts to identify influential individuals by observing which animals initiate departures from sleeping sites (17, 18) or are found at the front of group progressions (19) have yielded conflicting results (9). Studying collective decision-making events requires many potential decision-makers in a group to be monitored simultaneously—a significant logistical challenge.

To tackle this "observational task of daunting dimensions" (8), we analyzed data from 25 wild baboons (~80% of our study troop's adult and subadult members, table S1), each fitted with a custom-designed global positioning system (GPS) collar that recorded its location every second [Fig. 1 and movies S1 and S2 (20)]. We developed an automated procedure for extracting "movement initiations" based on the relative movements of pairs of individuals (20). These were defined as sequences in which one individual (the initiator) moved away from another (the potential follower) and was either followed (a "pull," Fig. 1 inset, left) or was not and subsequently returned (an "anchor," Fig. 1). This definition is agnostic to individual intention and motivation. Although any particular movement sequence may or may not reflect a causal relationship between initiator and follower (supplementary text), analyzing aggregate patterns across many sequences nonetheless yields insight into the processes driving collective movement.

Our method is based on finding all minima and maxima in the distance between pairs

of individuals, allowing it to capture pulls and anchors occurring over a range of time scales, from seconds to minutes [fig. S8 (21)]. It also detects simultaneous movement initiations. We

aggregated concurrent pulls and anchors on the same potential follower into "events" (20). We then examined the behavior of potential followers during these events, including whether
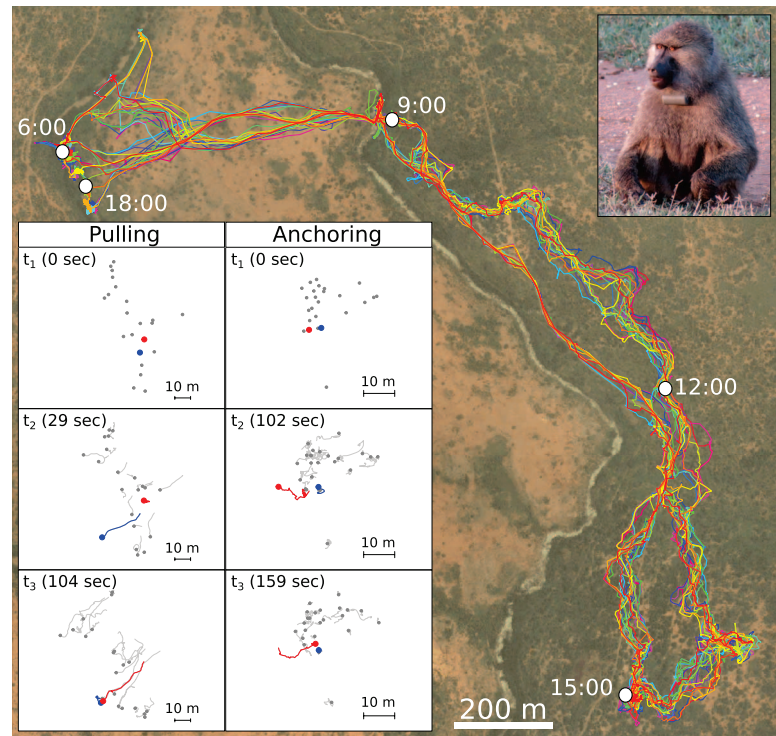

Fig. 1. Extracting pulls and anchors from movement data. Baboon trajectories (25 individuals) during the first day of tracking. (**Inset, left**) Successful initiation (pull), where the initiator (red) recruits the follower (blue). (**Inset, right**) Failed initiation (anchor), where the initiator (red) fails to recruit the potential follower (blue). Other individuals' trajectories are in gray.
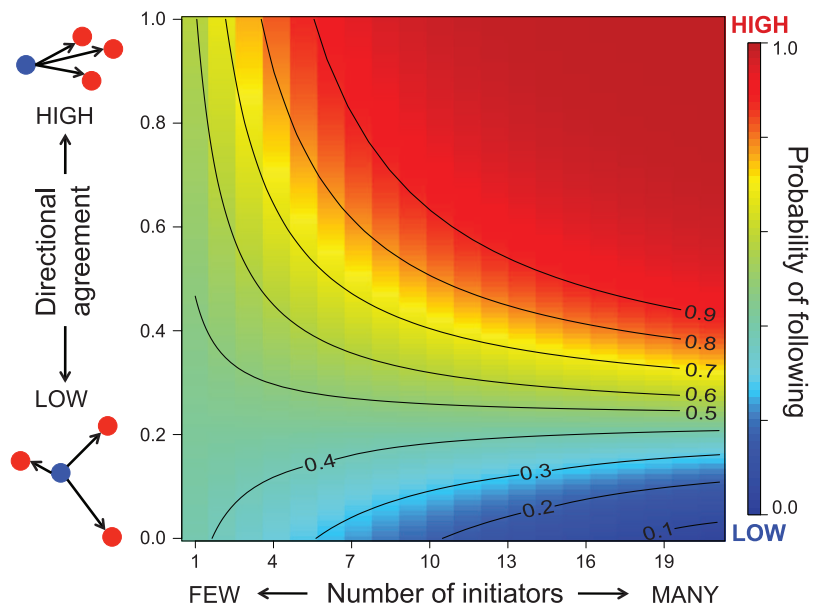

Fig. 2. The probability of following depends on the number of initiators and their directional agreement. Baboons are most likely to follow when there is high agreement among many initiators. When agreement is low, additional initiators do not improve the chances of following and may decrease them. The surface plot shows a GEE fit to the data (table S2).

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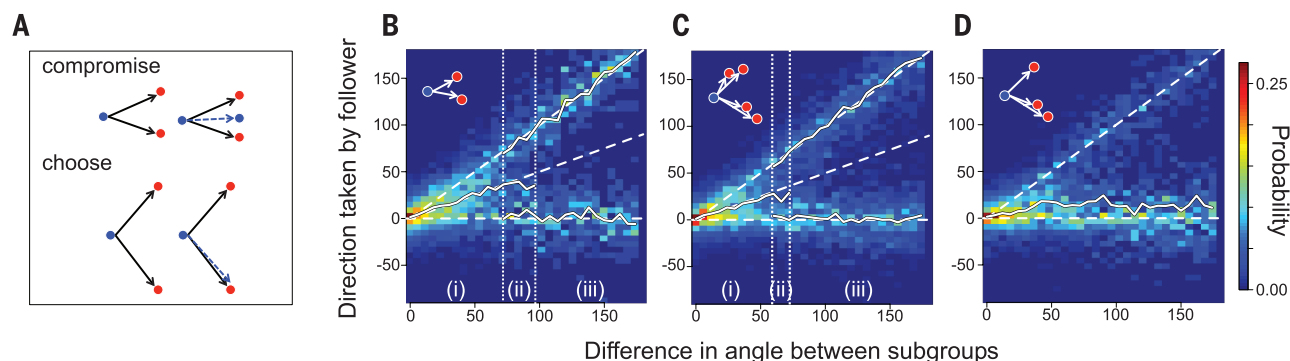
Fig. 3. As predicted by collective movement models (A), as the angle between initiation directions increases, baboon followers exhibit a transition from compromising (moving in the average of the two directions) to choosing one direction over the other. (**B** to **D**) Plots show the empirical distribution of follower movement directions as a function of the angle of disagreement between two initiators (B) or two subgroups of initiators (C). Regions divided by dotted lines are statistically assigned to (i) compromise, (ii) transitional, and (iii) choose (fig. S9). Solid white lines show the median of the directions taken for each mode. Dashed white lines represent the expected direction when compromising (middle line) or choosing (top/bottom lines). When the number of individuals in the clusters differs by 1, followers are more likely to move toward the majority (i.e., along the horizontal line) (D).

they followed any initiators, and if so, in which direction they moved.

Our data show that the probability of following depends on both the number of initiators and their level of directional agreement. To quantify directional agreement among concurrent initiators in an event, we calculated the circular variance (*cv*) of the unit vectors pointing from the potential follower to each initiator and defined agreement as 1 – *cv*. This measure approaches 0 when individuals initiate in opposing directions (low agreement) and 1 when all individuals initiate in the same direction (high agreement). Fitting a binomial generalized estimating equation (GEE) model revealed that a baboon's probability of following depends on an interaction between the number of initiators and their directional agreement (Fig. 2 and table S2). Overall, baboons are most likely to follow when there are many initiators with high agreement. However, when agreement is low, having more concurrent initiators decreases the likelihood that a baboon will follow anyone. This pattern suggests that decisions are delayed when opinions are split.

If social dominance plays a role in determining the outcomes of movement decisions (*1*), the disproportionate influence of high-ranking animals should be easiest to observe when single individuals make movement initiations (single-initiator events). We found no evidence of this. The dominant male did not have the highest probability of being followed, dominance rank (*20*) did not correlate with initiation success, and no sex differences existed in initiation success (fig. S1, binomial GLMM: coefficient (male) ± SE = –0.222 ± 0.159, *z* = –1.402, *P* = 0.161, initiator and follower fit as random effects), despite males being dominant over females (*11*). Instead, we found that baboons are more likely to follow initiators who move in a highly directed manner (fig. S2), which is consistent with the findings of a previous study (*17*).

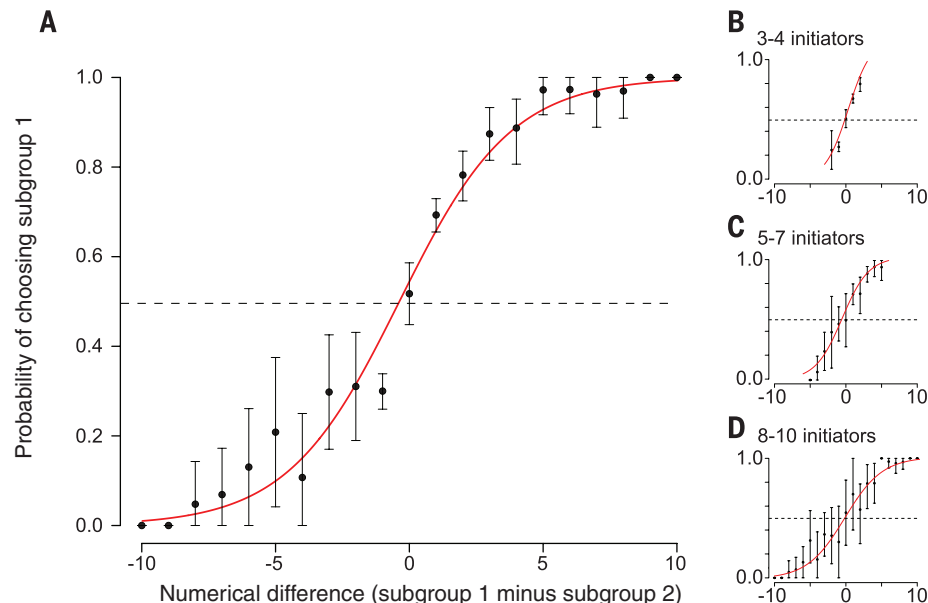When multiple members of the troop initiate movement simultaneously, followers must de-

cide in which direction to move. Theory (*22*) predicts that, when preferred directions conflict, the type of consensus achieved will depend on the angle between these directions (angle of disagreement, Fig. 3A). When this angle is large, the group travels in one direction or the other ("choose"). Below a critical angle, the same individual rules result in the group moving in the average of preferred directions ("compromise"). Our data reveal that baboon followers exhibit these two predicted regimes. In events with two initiators, followers consistently choose one direction or the other when the angle between the initiators' directions is greater than approximately 90°, but they compromise when the angle falls

below this threshold (Fig. 3B, (*20*)). The same pattern emerges in events with multiple initiators clustered into two subgroups (Fig. 3C).

When initiators have strongly conflicting directions, how do followers choose which direction to take? When facing a choice between two subgroups of initiators, followers are more likely to move toward the direction of the majority. This tendency grows stronger as the numeric difference between the two subgroups increases (Fig. 4), which is consistent with theoretical (*3, 6, 22*) and empirical studies (*3, 5, 23*). Individuals' choices also scale up to group movement. After such conflicts, the troop's travel direction is positively correlated with the direction

Fig. 4. When initiation directions conflict, followers choose the direction of the largest subgroup of initiators. (**A**) Empirical data are in black; error bars are 95% confidence intervals estimated by 1000 bootstrapped replications of the data. The red line shows a sigmoidal fit to the data. The tendency to follow the majority is maintained regardless of the total number of initiators (**B** to **D**) or whether the troop is moving or stationary (fig. S6).

associated with successful (but not failed) subgroups of initiators (fig. S4). Thus, failed initiators ultimately move in the direction of the majority (away from their original initiation directions), maintaining cohesion with others.

The failure of high-ranking individuals to dominate movement decisions highlights an important distinction between social status and leadership in wild baboons. Although field-based experiments suggest that dominant individuals, when highly motivated, can shape group movement patterns to their advantage (*1*), our results provide evidence that the decision-making process driving day-to-day movement patterns in baboons is fundamentally shared. Our study emphasizes the power of using high-resolution GPS tracking data to uncover the interdependencies of animal movements. In conjunction with the rich individual-level data that long-term observational studies provide, these methods open up a new window into the social dynamics of wild animal groups.

REFERENCES AND NOTES

1. A. J. King, C. M. S. Douglas, E. Huchard, N. J. B. Isaac, G. Cowlishaw, *Curr. Biol.* **18**, 1833–1838 (2008).
2. M. Nagy, Z. Akos, D. Biro, T. Vicsek, *Nature* **464**, 890–893 (2010).
3. I. D. Couzin *et al.*, *Science* **334**, 1578–1580 (2011).
4. L. Conradt, C. List, *Philos. Trans. R. Soc. London Ser. B* **364**, 719–742 (2009).
5. D. J. T. Sumpter, J. Krause, R. James, I. D. Couzin, A. J. W. Ward, *Curr. Biol.* **18**, 1773–1777 (2008).
6. L. Conradt, T. J. Roper, *Trends Ecol. Evol.* **20**, 449–456 (2005).
7. A. J. King, G. Cowlishaw, *Commun. Integr. Biol.* **2**, 147–150 (2009).
8. R. W. Byrne, in *On the Move*, S. Boinski, P. A. Garber, Eds. (Univ. of Chicago Press, Chicago, 2000), p. 501.
9. A. J. King, C. Sueur, *Int. J. Primatol.* **32**, 1245–1267 (2011).
10. A. J. King, D. D. P. Johnson, M. Van Vugt, *Curr. Biol.* **19**, R911–R916 (2009).
11. D. L. Cheney, R. M. Seyfarth, *Baboon Metaphysics* (Univ. of Chicago Press, Chicago, 2008).
12. J. B. Silk, *Science* **317**, 1347–1351 (2007).
13. R. M. Sapolsky, *Science* **308**, 648–652 (2005).
14. S. E. Johnson, J. Bock, *Hum. Nat.* **15**, 45–62 (2004).
15. J. Altmann, *Baboon Mothers and Infants* (Univ. of Chicago Press, Chicago, 1980).
16. A. J. King, G. Cowlishaw, *Anim. Behav.* **78**, 1381–1387 (2009).
17. A. J. King, C. Sueur, E. Huchard, G. Cowlishaw, *Anim. Behav.* **82**, 1337–1345 (2011).
18. S. Stueckle, D. Zinner, *Anim. Behav.* **75**, 1995–2004 (2008).
19. S. A. Altmann, *Foraging for Survival: Yearling Baboons in Africa* (Univ. of Chicago Press, Chicago, 1998).
20. Materials and methods are available as supplementary materials on *Science* Online.
21. O. Petit, J. Gautrais, J.-B. Leca, G. Theraulaz, J.-L. Deneubourg, *Proc. Biol. Sci.* **276**, 3495–3503 (2009).
22. I. D. Couzin, J. Krause, N. R. Franks, S. A. Levin, *Nature* **433**, 513–516 (2005).
23. C. Sueur, J.-L. Deneubourg, O. Petit, *Behav. Ecol. Sociobiol.* **64**, 1875–1885 (2010).

SIGNAL TRANSDUCTION

Structural basis for nucleotide exchange in heterotrimeric G proteins

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G protein–coupled receptors (GPCRs) relay diverse extracellular signals into cells by catalyzing nucleotide release from heterotrimeric G proteins, but the mechanism underlying this quintessential molecular signaling event has remained unclear. Here we use atomic-level simulations to elucidate the nucleotide-release mechanism. We find that the G protein α subunit Ras and helical domains—previously observed to separate widely upon receptor binding to expose the nucleotide-binding site—separate spontaneously and frequently even in the absence of a receptor. Domain separation is necessary but not sufficient for rapid nucleotide release. Rather, receptors catalyze nucleotide release by favoring an internal structural rearrangement of the Ras domain that weakens its nucleotide affinity. We use double electron-electron resonance spectroscopy and protein engineering to confirm predictions of our computationally determined mechanism.

G protein–coupled receptors (GPCRs), which represent the largest class of drug targets, trigger cellular responses to external stimuli primarily by activating heterotrimeric G proteins: An activated GPCR, upon binding an inactive, guanosine diphosphate (GDP)–bound G protein, dramatically accelerates GDP release, thus allowing guanosine triphosphate (GTP) to bind spontaneously to the vacated nucleotide-binding site (*1*, *2*). This nucleotide exchange initiates G protein–mediated intracellular signaling. Despite breakthroughs in GPCR structure determination (*3*–*5*), key aspects of the molecular mechanism by which GPCRs accelerate GDP release remain unresolved.

Heterotrimeric G proteins undergo a dramatic conformational change upon binding activated GPCRs (Fig. 1, A and B). Double electron-electron resonance (DEER) spectroscopy has demonstrated that the Ras and helical domains of the G protein α subunit (Gα), which tightly sandwich the nucleotide in all nucleotide-bound G protein crystal structures, separate by tens of angstroms upon GPCR binding and GDP release (*6*). A crystal structure of a GPCR–G protein complex (*4*), and accompanying deuterium-exchange and electron microscopy data (*7*, *8*), confirmed this dramatic domain separation.

These observations have raised several unresolved questions (*4*, *9*). What is the role of domain separation in GDP release? Does a GPCR catalyze GDP release by forcing the domains to separate, or does the GPCR force out GDP, with the absence of GDP leading to subsequent domain separation? More generally, what is the structural mechanism by which a GPCR brings about GDP release?

To address these questions, we performed atomic-level molecular dynamics (MD) simulations of heterotrimeric G proteins with and without bound GPCRs. We initiated simulations from crystal structures of nucleotide-bound G protein heterotrimers [in particular, G_i (*10*) and a

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Science

Shared decision-making drives collective movement in wild baboons

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Baboons follow the pack, not the leader

How do groups of animals, including humans, make decisions that affect the entire group? Evidence collected from schooling animals suggests that the process is somewhat democratic, with nearest neighbors and the majority shaping overall collective behavior. In animals with hierarchical social structures such as primates or wolves, however, such democracy may be complicated by dominance. Strandburg-Peshkin *et al.* monitored all the individuals within a baboon troop continuously over the course of their daily activities. Even within this highly socially structured species, movement decisions emerged via a shared process. Thus, democracy may be an inherent trait of collective behavior.

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