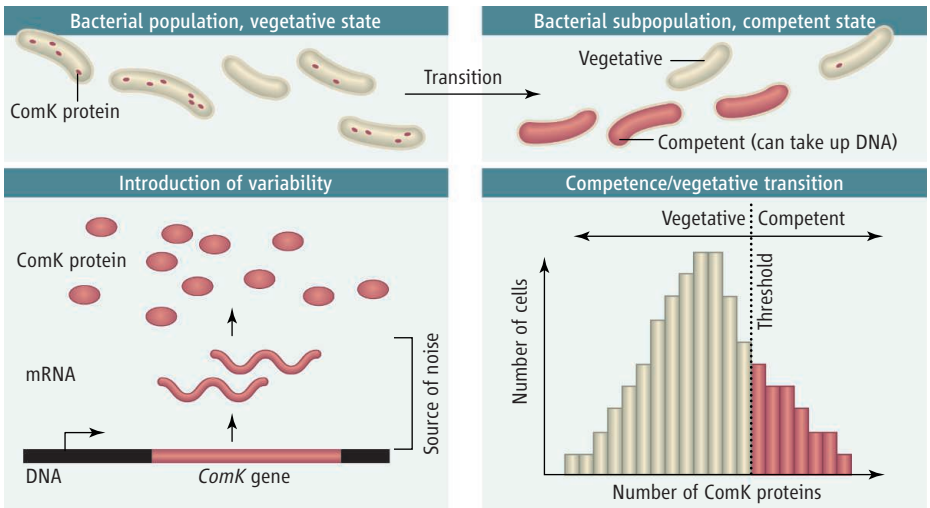

Randomly flipping a cell-fate switch. A population of bacteria can express variable amounts of ComK protein. Only cells that express greater than a threshold concentration of ComK become competent. Cell-to-cell variation in ComK protein expression ("noise") arises from variations in comK mRNA concentration across the cell population.

find that noise in ComK protein expression comes mainly from random production and/or degradation of *comK* mRNA, rather than from external factors (such as variability in ribosome numbers from cell to cell).

To demonstrate that noise in *comK* gene expression is the key factor causing cells to transition to competence, Maamar *et al*. modifed a strain (which has an increased basal *comK* mRNA production) by decreasing the rate of translation initiation. This reduces noise (*6*) while keeping the average comK protein concentration fixed. In the modified strain, low noise levels caused cells to transition into the competent state less frequently than wild-type cells. In other words, the reduced-noise strain produces more mRNA, but less protein from each mRNA. This reduces the amount of variability in mRNA expression levels, and thus variability in protein concentration.

In a complementary study, Süel *et al.* (*7*) create a strain in which bacteria cannot complete cell division, causing multiple cells to share cytoplasm. In this strain, cell-to-cell variability is reduced because connected cells share proteins, averaging away differences in protein concentrations between cells. Like Maamar *et al*., they find that a decrease in cell-to-cell variability leads to a decrease in transitions to the competent state.

Maamar *et al*. and Süel *et al.* provide a comprehensive microscopic view of how stochastic fluctuations in gene expression can cause cells to change their phenotype. An even clearer picture of such cell decision-making might be attained by coupling real-time measurements of mRNA and protein concentrations (*8*, *9*) with switching events in single living cells. There remains the nagging question of why the population only allows a fraction of its cells to become competent. By splitting the population into two phenotypes, *B. subtilis* may use naturally occurring noise to increase population diversity and enhance survival in the face of environmental uncertainty (*10*–*12*). It is possible that evolution has been using a strategy of modifying transcription and translation rates to fine-tune the noise levels (*5*, *6*) of key genes that underlie phenotypic diversity in a population.

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10.1126/science.1146747

ECONOMICS

Spying on Others Evolves

Watchful eyes induce altruistic behavior and an "arms race" of signals between observers and the observed.

Manfred Milinski and Bettina Rockenbach

When reputation is at stake, animals as well as humans switch from selfish to altruistic behavior, because only the latter is socially rewarded (*1, 2*). But how do they assess whether their actions are observed? Recent investigations into human behavior have shown that subtle cues of being watched such as two stylized eye-like shapes on a computer screen background suffice to change behavior (*3*). A picture showing a pair of eyes attached to a cafeteria collection box significantly raises the donated amount compared to a flower symbol; in fact, the eyes were most effective when looking directly at the observer (*4*).

Although just ink on paper, these eye-shaped cues seem to elicit unconscious hard-wired reactions. Indeed, electrophysiological responses recorded from the scalp of normal subjects showed responses to isolated eyes that are even larger than the responses to full faces (*5*). Brain imaging studies in humans have also highlighted a role for the superior temporal sulcus (STS) and amygdala in gaze processing; the STS is likely to be essential for recognizing the eyes, head, and body as stimuli used in social communication, whereas the amygdala is likely to be essential for attaching social and emotional significance to these stimuli (*6*). Interestingly, even birds respond strongly to eye-like shapes, especially when two eyes are staring at them (*7*).

What is the benefit of watching someone? Spying on others seems widespread in animals and humans (*8*). By snooping on one another's social life, animals and humans can work out how to behave when they meet in the future. Recent experiments

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showed that even fish gain sophisticated information from watching members of the same species (*9*). Some fish can infer the social rank of others by observation alone and use this information to their own advantage in future encounters (*10*). So it comes as no surprise that both humans and animals try to deceive observers by behaving as they want to be seen by others to secure future gains.

For example, the cleaning wrasse fish grooms its client fish in the friendliest way when other clients watch, but without an audience it prefers to bite off pieces of its client's skin (*11*). In a dictator game experiment, only one player (the dictator) is endowed with money and may share it with a second player. Although unidentifiable human "dictators" share almost nothing (*12*), face-to-face identification increases the share rate to 50% (*13*). Consequently, in order to gain accurate information, observers should avoid being recognized: Indeed, some social birds have eyes concealed in dark areas or stripes, ensuring that the observed individual cannot detect being the target (*14*).

Are you being naughty or nice? Totem poles put up in villages in North America several hundred years ago standing vigilant at attention, with ever-watchful eyes. Unlike natural goats, the stylized goat has "human eyes" with white sclera stressing the direction of his gaze.

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This is where humans differ from most animals. We have large white sclera on either side of the dark central iris when looking directly at the observer. This seems to be an honest signal of where we watch (*6*). Obviously there has been a net selective advantage of signaling the direction of our gaze in social interactions. However, having such eyes should be disadvantageous when trying to observe others' "unobserved" behavior, because we should take into account that the observed person turns altruistic as soon as our observing gaze is recognized.

Can we escape being watched? Whenever a person can be recognized by any cue, bad conduct may incur costs. Instead of behaving altruistically, people sometimes avoid having to justify their behavior by masking their faces, for example, at a masked ball, when robbing a bank, etc. Interestingly, the usual way to remove the identity of people on photos is to cover their eyes by a black stripe. Visual cues of faces seem to be of prime importance. Thus, either masking such cues or paying attention to being watched may be socially selected.

Thus, a new dimension arises when issues of reputation are present in human social dilemmas. An "arms race" of hiding signals between observers and observed may result: Observer Alice should take into account that the behavior of Bob (the observed) changes and therefore should conceal her watching; Bob should be very alert to faint signals of being watched by Alice, but he should avoid any sign of having recognized Alice's watching when switching from selfish to altruistic behavior. He should avoid turning his gaze in the direction of the recognized observer. On the other hand, as soon as Alice sees that Bob has recognized that he is being observed, she should eventually not reward the observed altruistic behavior.

An arms race between observing and being observed has implications for the large body of recent research on human altruism. Observed altruistic behavior may often be less the expression of a personal trait than an optimal response to the faint feeling of being observed. Would altruism then function as a potential deceit? For example, what we expect for the efficient interaction between reputation and costly punishment in social dilemmas—where individual and social interests are at odds—might depend on the recognized state of the signaling arms race (*15*). When cues revealing that the observed person has discovered the observation are indeed so subtle that altruism is a successful deceit, the positive effects of reputation can be expected to be present to a much greater extent. However, when the observer can conceal his spying, reputation is subjectively not at stake and thus will not induce altruism.

Does the observer thus really want to see "unobserved" behavior? Yes, but only if the social partner interacts with the observer mostly anonymously and she profits from seeing his "normal" behavior and reacts accordingly. Otherwise she should try her best to generate the impression that her social partners always feel observed so that their "normal" behavior is altruistic. Perhaps this is achieved in some societies by the ever-present watchful eyes of totem poles (see the figure) or a god that "sees through everything." Even actors on billboards, a modern form of ink on paper, may elicit unconscious social reactions in our amygdala and thus influence our behavior.

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10.1126/science.1143918

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