Development of a Signaling Network

Eleanor Brush
July 9, 2012

1 Model as a Stochastic Differential Equation

1.1 Derivation of the SDE from microscopic events There are three processes that can cause an animal's estimate of its dominance with respect to another to change:

1. an error can be made so that the animal's estimate randomly changes from one point in time to the next without an external stimulus

2. external observations provide evidence about each animal's dominance, e.g. by fighting each other they gather evidence about their relative strength

3. receiving a signal provides evidence that the receiver is dominant to the signaler

Assumption: For now, we will assume that the two animals have access to the same external observations, which would be the case, for instance, if they only gather evidence from fights that they both are engaged in. We can relax this assumption in the future.

Let $X_t^{(i)}$ denote animal i's estimate of its dominance at time t. We can write down equations describing how these estimates change over time:

$$X_{t+\tau}^{(1)} = X_t^{(1)} + \sum_{i=0}^{N_{e_1}(\tau)} E_i^{(1)} + \sum_{i=0}^{N_f(\tau)} F_i + b_{s_2} S_2(X_t^{(2)}, \tau)$$

$$X_{t+\tau}^{(2)} = X_t^{(2)} + \sum_{i=0}^{N_{e_2}(\tau)} E_i^{(2)} - \sum_{i=0}^{N_f(\tau)} F_i + b_{s_1} S_1(X_t^{(1)}, \tau)$$

where

- $E_i^{(j)}$ describes the magnitude of an error in estimate for animal j, which are identically distributed over time; $N_{e_j}(\tau)$ describes the number of error events in an interval of length τ so that $\sum_{i=0}^{N_{e_j}(\tau)} E_i^{(j)}$ gives the total magnitude of errors in an interval of length τ

- F_i describes the magnitude of a piece of external evidence, which are identically distributed over time; $N_f(\tau)$ describes the number of external observations in an interval of length τ so that $\sum_{i=0}^{N_f(\tau)} F_i$ gives the total magnitude of external evidence in an interval of length τ (and the evidence gathered changes the animal's estimate in opposite directions, i.e. if a fight is won, one animal's estimate is increased while the other's is decreased by the same amount)

- $S_j(X_t^{(j)}, \tau)$ gives the number of signals emitted by individual j in an interval of length τ and b_{s_j} describes the boost that each of those signals would give to animal $j + 1$'s estimate of its dominance

The fact that the two animals are privy to the same external observations is captured by the identity of the second sums in the above equations. **Assumption:** The above equations assume that τ is small enough so that X_t does not change significantly enough in the interval $[t, t + \tau)$ that signaling rates would change. (Error and fighting rates do not depend on the estimates– another assumption.) We could write the evidence from signals as a sum over several events in the interval $[t, t+\tau)$ as with errors and observations, but this is equivalent to the formulation above since we assume the size of a signal and the strength of a boost from receiving a signal is constant over time.

We can now describe the distributions from which these events are drawn:

- $N_{e_j}(\tau) \sim \mathcal{P}(r_{e_j}, \tau)$

- $E_i^{(j)} \sim \mathcal{N}(\mu_{e_j}, \sigma_{e_j}^2)$, i.i.d.

- $N_f(\tau) \sim \mathcal{P}(r_f, \tau)$

- $F_i \sim \mathcal{N}(\mu_f, \sigma_f^2)$, i.i.d.

- $S_j(X_t^{(j)}, \tau) \sim \mathcal{P}(f(X_t^{(j)}), \tau)$

where $\mathcal{P}(\lambda, \tau)$ denotes a Poisson process with rate λ and $\mathcal{N}(\mu, \sigma^2)$ denotes a Normal distribution with mean μ and σ^2. $f(x)$ gives the rate (probability) of emitting a signal as a function of the estimate x, which is decreasing in x.

We now make two approximations:

1. If Y_i, i.i.d., are drawn from some distribution and $N(\tau) \sim \mathcal{P}(\lambda, \tau)$, then $Z(\tau) = \sum_{i=0}^{N(\tau)} Y_i$ is a compound Poisson process with

$$\mathbb{E}[Z(\tau)] = \mathbb{E}[N(\tau)]\mathbb{E}[Y] = \lambda\tau\mathbb{E}[Y]$$
$$\text{and } Var(Z(\tau)) = \mathbb{E}[N(\tau)]\mathbb{E}[Y^2] = \lambda\tau\mathbb{E}[Y^2]$$

For computational convenience, we will approximate the distribution of $Z(\tau)$ by $\mathcal{N}(\lambda\tau\mathbb{E}[Y], \lambda\tau\mathbb{E}[Y^2])$. (HOW VALID IS THIS?)

2. If τ is big enough that enough events happen, then we can approximate the Poisson process $\mathcal{P}(\lambda, \tau)$ with $\mathcal{N}(\lambda\tau, \lambda\tau)$.

This allows us to rewrite our equations for X_t as:

$$X_{t+\tau}^{(1)} = X_t^{(1)} + Y_{e_1}(\tau) + Y_f(\tau) + b_{s_2}Y_{s_2}(X_t^{(2)}\tau)$$
$$X_{t+\tau}^{(2)} = X_t^{(2)} + Y_{e_2}(\tau) - Y_f(\tau) + b_{s_1}Y_{s_1}(X_t^{(1)}\tau)$$

where

- $Y_{e_j}(\tau) \sim \mathcal{N}(r_{e_j}\tau\mu_{e_j}, r_{e_j}\tau(\sigma_{e_j}^2 + \mu_{e_j}^2))$

- $Y_f(\tau) \sim N(r_f\tau\mu_f, r_f\tau(\sigma_f^2 + \mu_f^2))$

- $Y_{s_j}(\tau) \sim \mathcal{N}(f(X_t^{(j+1)})\tau, f(X_t^{(j+1)})\tau)$

Finally, if we define the following constants:

$$m_{e_j} = r_{e_j}\mu_{e_j},$$
$$n_{e_j}^2 = r_{e_j}(\sigma_{e_j}^2 + \mu_{e_j}^2),$$
$$m_f = r_f\mu_f,$$
$$n_f^2 = r_f(\sigma_f^2 + \mu_f^2),$$

then we get the following equations:

$$X_{t+\tau}^{(1)} = X_t^{(1)} + \left[m_{e_1} + m_f + b_{s_2}f(X_t^{(2)})\right]\tau + n_f\sqrt{\tau}Z^{(1)} + n_{e_1}\sqrt{\tau}Z^{(2)} + b_{s_2}\sqrt{f(X_t^{(2)})}\sqrt{\tau}Z^{(3)}$$
$$X_{t+\tau}^{(2)} = X_t^{(2)} + \left[m_{e_2} - m_f + b_{s_1}f(X_t^{(1)})\right]dt + n_f\sqrt{\tau}Z^{(1)} + n_{e_2}\sqrt{\tau}Z^{(4)} + b_{s_1}\sqrt{f(X_t^{(1)})}\sqrt{\tau}Z^{(5)}$$

where $Z^{(1)}, \ldots, Z^{(5)} \sim \mathcal{N}(0,1)$, i.i.d., which are equivalent to the stochastic differential equations:

$$dX_t^{(1)} = \left[m_{e_1} + m_f + b_{s_2} f(X_t^{(2)}) \right] dt + n_f dW_t^{(1)} + n_{e_1} dW_t^{(2)} + b_{s_2} \sqrt{f(X_t^{(2)})} dW_t^{(3)}$$

$$dX_t^{(2)} = \left[m_{e_2} - m_f + b_{s_1} f(X_t^{(1)}) \right] dt + n_f dW_t^{(1)} + n_{e_2} dW_t^{(4)} + b_{s_1} \sqrt{f(X_t^{(1)})} dW_t^{(5)}$$

where $W_t^{(1)}, \ldots, dW_t^{(5)}$ are independent Brownian motions.

We could make a few simplifying assumptions to reduce the number of parameters. **Assumptions:**

- $r_{e_1} = r_{e_2}$
- $\mu_{e_1} = \mu_{e_2}$, and even simpler would be to have both equal 0 (expected error is 0)
- $\sigma_{e_1}^2 = \sigma_{e_2}^2$
- $b_{s_1} = b_{s_2}$
- and combining the above would give $m_{e_1} = m_{e_2}$ and $n_{e_1} = n_{e_2}$

1.2   Evolution of probability distribution over time More generally, consider a system

$$dX_t = a(X_t)dt + \sum_{i=1}^{5} \sigma_i(X_t)dW_t^{(i)}$$

with $W_t^{(1)}, \ldots, W_t^{(5)}$ independent Brownian motions. If $a, \sigma_1, \ldots, \sigma_5 : \mathbb{R}^2 \to \mathbb{R}^2$, are "nice" enough functions, and the random variable X_t has a "nice" enough density function (i.e. $\mathbb{E}[g(X_t)] = \int g(x)p(t,x)dx$ for every bounded measurable function g), then according to the Fokker-Planck / Kolmogorov forward equation

$$\frac{\partial p}{\partial t} = -\sum_{i=1}^{2} \frac{\partial}{\partial x_i}(a^{(i)}(x)p(t,x)) + \frac{1}{2} \sum_{i,j=1}^{2} \sum_{k=1}^{5} \frac{\partial^2}{\partial x_i \partial x_j}(\sigma_k^{(i)} \sigma_k^{(j)} p(t,x))$$

$$\Rightarrow \frac{\partial p}{\partial t} = -(m_{e_1} + m_f + b_{s_2} f(x_2)) \frac{\partial p}{\partial x_1} - (m_{e_2} - m_f + b_{s_1} f(x_1)) \frac{\partial p}{\partial x_2}$$

$$+ \frac{1}{2}(n_{e_1}^2 + n_f^2 + b_{s_2}^2 f(x_2)) \frac{\partial^2 p}{\partial x_1^2} + n_f^2 \frac{\partial p}{\partial x_1 \partial x_2} + \frac{1}{2}(n_{e_2}^2 + n_f^2 + b_{s_1}^2 f(x_1)) \frac{\partial^2 p}{\partial x_2^2}$$

using the functions a and σ_i as for our particular model. Note that this requires the function $f : \mathbb{R} \to \mathbb{R}$ be C^2.

1.3   Statistics of the Process WITHOUT Signaling Feedback For simplicity, we start with the case where there is no feedback from signaling to the estimates so that the model becomes

$$dX_t^{(1)} = [m_{e_1} + m_f] dt + n_f dW_t^{(1)} + n_{e_1} dW_t^{(2)}$$

$$dX_t^{(2)} = [m_{e_2} - m_f] dt + n_f dW_t^{(1)} + n_{e_2} dW_t^{(4)}$$

This is a simple drift-diffusion model. We can consider the dynamics of each estimate separately. We will show results for $X_t^{(1)}$, which follow similarly for $X_t^{(2)}$. As derived in [1], the expected time until $X_t^{(1)}$ reaches either $-T$ or T is

$$\frac{T}{m_e + m_f} \tanh\left(\frac{T(m_e + m_f)}{n_f^2 + n_e^2} \right)$$

and the probability that $X_t^{(1)}$ reaches $-T$ before it reaches T is

$$\frac{1}{1 + \exp\left(\frac{2T(m_e + m_f)}{n_f^2 + n_e^2} \right)}$$

(assuming $X_t^{(1)} = 0$).

1.4 Ornstein-Uhlenbeck Variant The dynamics are more interesting if the estimates don't just keep increasing or decreasing more or less deterministically. To add negative feedback and prevent this from happening, we can make the size of an error proportional to the current estimate:

$$dX_t^{(1)} = \left[m_{e_1}X_t^{(1)} + m_f + b_{s_2}f(X_t^{(2)})\right]dt + n_f dW_t^{(1)} + n_{e_1}dW_t^{(2)} + b_{s_2}\sqrt{f(X_t^{(2)})}dW_t^{(3)}$$

$$dX_t^{(2)} = \left[m_{e_2}X_t^{(2)} - m_f + b_{s_1}f(X_t^{(1)})\right]dt + n_f dW_t^{(1)} + n_{e_2}dW_t^{(4)} + b_{s_1}\sqrt{f(X_t^{(1)})}dW_t^{(5)}$$

The Fokker-Planck equation now becomes

$$\frac{\partial p}{\partial t} = -(m_{e_1}x_1 + m_f + b_{s_2}f(x_2))\frac{\partial p}{\partial x_1} - m_{e_1}p - (m_{e_2}x_2 - m_f + b_{s_1}f(x_1))\frac{\partial p}{\partial x_2} - m_{e_2}p$$

$$+ \frac{1}{2}(n_{e_1}^2 + n_f^2 + b_{s_2}^2 f(x_2))\frac{\partial^2 p}{\partial x_1^2} + n_f^2\frac{\partial p}{\partial x_1 \partial x_2} + \frac{1}{2}(n_{e_2}^2 + n_f^2 + b_{s_1}^2 f(x_1))\frac{\partial^2 p}{\partial x_2^2}$$

If we ignore signaling feedback for the moment and look for a stationary distribution, we want to solve the equation

$$0 = (m_{e_1}x_1 + m_f)\frac{\partial p}{\partial x_1} - m_{e_1}p - (m_{e_2}x_2 - m_f)\frac{\partial p}{\partial x_2} - m_{e_2}p$$

$$+ \frac{1}{2}(n_{e_1}^2 + n_f^2)\frac{\partial^2 p}{\partial x_1^2} + n_f^2\frac{\partial p}{\partial x_1 \partial x_2} + \frac{1}{2}(n_{e_2}^2 + n_f^2)\frac{\partial^2 p}{\partial x_2^2}$$

$$= (m_e x + m_f)\frac{\partial p}{\partial x} - (m_e y - m_f)\frac{\partial p}{\partial y} - 2m_e p + \frac{1}{2}(n_e^2 + n_f^2)\frac{\partial^2 p}{\partial x^2} + n_f^2\frac{\partial p}{\partial x \partial y} + \frac{1}{2}(n_e^2 + n_f^2)\frac{\partial^2 p}{\partial y^2}$$

if we assume $m_{e_1} = m_{e_2}$

2 Simulating the Learning / Signaling Process

A Gillespie algorithm allows us to simulate the process as described by the model above (ORNSTEIN-UHLENBECK VARIANT). We are interested in the effect of signaling feedback, i.e. the b_s parameter, on the dynamics of the model. We run the algorithm 1000 times so that we obtain, at each point in time, a distribution of each animal's estimates. We then compare these distributions when there is and isn't signaling. In both regimes, each animal's estimates reach a relatively stationary distribution fairly quickly so that we can pick a typical time point at which the distributions are not changing any more. (A Kolmogorov-Smirnov test for the differences between distributions at different points in time does not allow us to reject the null hypothesis that the distributions are the same, at a significance level of $p = 0.05$.) In Figure (1), we plot the distribution of each animal's estimates at $t = 200$ when there is and isn't signaling feedback ($b_{s_1} = b_{s_2} = 0$ and $b_{s_1} = b_{s_2} \gtrsim 0$). We find that the distributions with and without signaling feedback are quite different. They are, in fact, statistically distinguishable (K-S test statistic $D = 0.68$, $p < 2.2 \times 10^{-16}$ for Animal 2 and $D = 0.21$, $p < 0.05$ for Animal 2). In both cases, the most noticeable affect of increasing the signaling feedback is increasing the variance of the distributions (from 1.55 to 81.44 for Animal 1 and from 1.23 to 7.02 for Animal 2). While the mean for Animal 2 is similar in the two cases (-10.03 without feedback and -9.36 with feedback), the mean for Animal 1 noticeably increases from 10.04 to 17.25.

By comparing distributions of the estimates at a given point in time, we compare the behavior of the stochastic process over many realizations. We can also compare the behavior of individual trajectories over time. We hypothesize that by increasing the strength of signaling feedback, we should increase the stability of signaling behavior and it should be less likely that the dominant animal's estimate sink to such an extent that it becomes subordinate. To test this hypothesis, we count, for each run of the simulation, the number of switches between dominance regimes. A dominance regime is defined by one animal's estimate being below the signaling threshold $-T$ and the other animal's estimate being above the positive threshold T. If a dominance regime is established with Animal i's estimate above the threshold (dominant) and Animal $i + 1$'s estimate below the threshold (subordinate) and subsequently

Animal 1's Estimate at t= 100

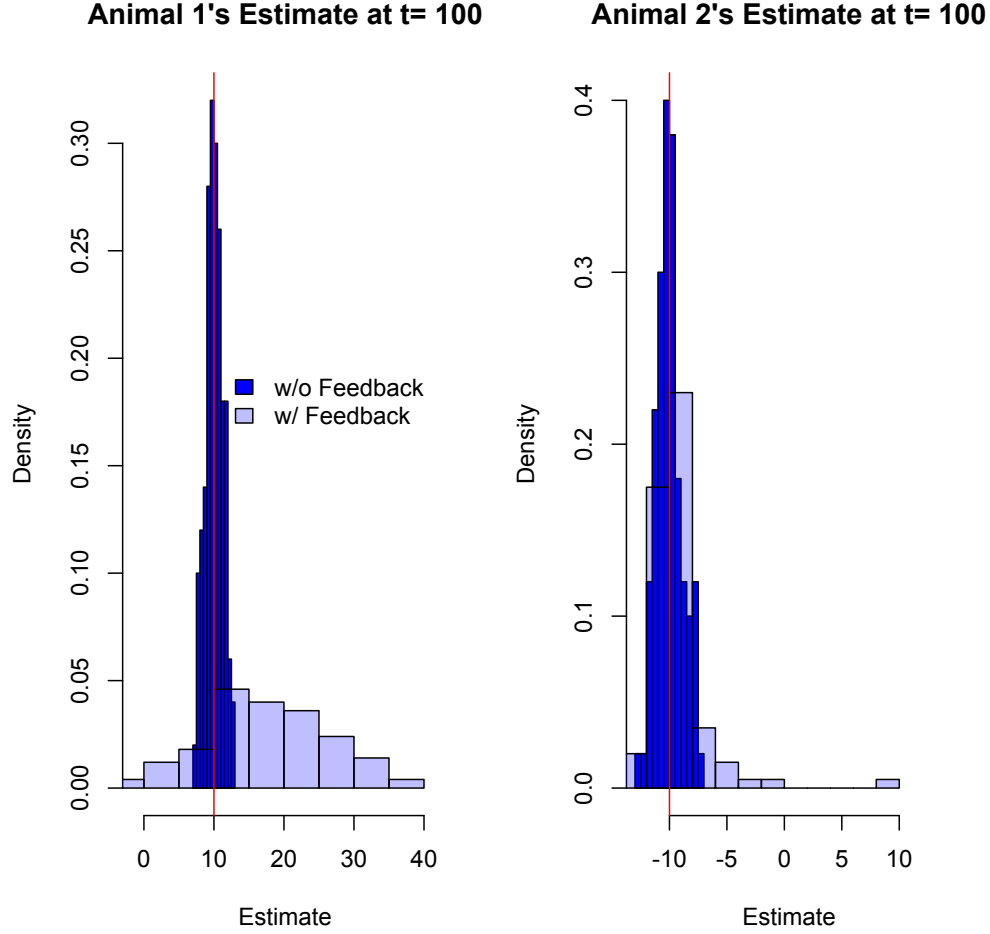**Animal 2's Estimate at t= 100**

Figure 1: The distribution of estimates for each animal at time 200, for no signaling feedback and for signaling feedback $b_{s_1} = b_{s_2} = 3$. Other parameters are set as follows: threshold $T = 5$, $m_{e_1} = m_{e_2} = -.5$, $n_{e_1} = n_{e_2} = 1$, $m_f = 5$, $n_f = .5$. Vertical red lines indicate predicted mean for process without feedback, $-m_f/m_{e_1}$ for Animal 1 and m_f/m_{e_2} for Animal 2.

a dominance regime is established with Animal i subordinate and Animal $i+1$ dominant, we count this as one switch. Fixing the other parameters of the model, for each difference in fighting ability m_f and level of signaling feedback $b_{s_1} = b_{s_2}$, we can find the average number of switches that occur in a run of the model. This is shown in Figure (2). As expected, as the difference in fighting ability increases fewer switches occur since Animal 1 is dominant the vast majority of the time. However, what is less expected is that increasing signaling feedback actually decreases stability.

References

[1] Rafal Bogacz, Eric Brown, Jeff Moehlis, Philip Holmes, and Jonathan D. Cohen. The physics of optimal decision making: A formal analysis of models of perforamnce in two-alternative forced-choice tasks. *Psychological Review*, 113(4):700–765, 2006.

Numbers of switches, me= -0.5 se= 1 sf= 0.5
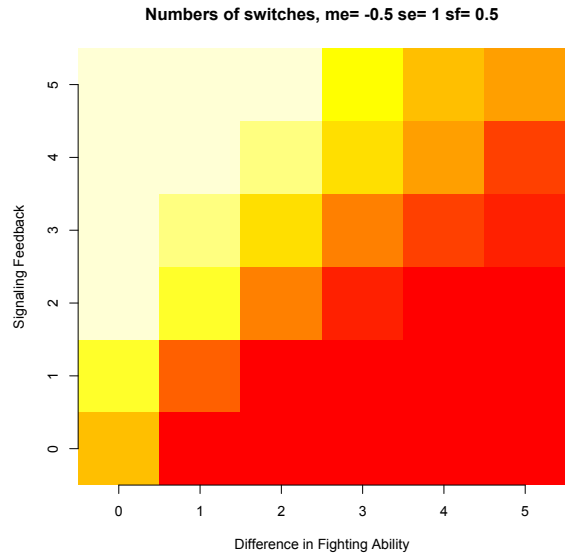
(a)

Figure 2: The number of switches between dominance regimes as a function of the difference in fighting ability, m_f, between the animals and the degree to which receiving a signal affects an animal's estimate of its dominance, $b_{s_1} = b_{s_2}$. Lighter colors correspond to a higher number of switches.