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increase physical and chemical weathering, pulling more CO_2 out of the atmosphere and so cooling the global climate[8].

The near-consensus of papers in a volume devoted to this topic[9] makes the uplift–weathering hypothesis a leading explanation for global cooling during the past 20 Myr. Still, ignorance of uplift histories across much of Tibet has made the hypothesis difficult to evaluate in full. In particular, with little direct evidence for uplift before 20 Myr ago, it is hard to claim that Tibetan uplift caused, or was even involved in, the global cooling that began 55 Myr ago and led to Antarctic glaciation by 36 Myr ago[10].

If large-scale uplift did occur in northeastern Tibet as early as 37–33 Myr ago, chemical weathering of this high terrain could have contributed to global cooling then. Other evidence supports this idea. A striking increase in the global-ocean $^{87}Sr/^{86}Sr$ ratio began 40 to 35 Myr ago, and the extra ^{87}Sr probably came from the Tibet–Himalaya complex[11], from both accelerated weathering and the exposure of rocks rich in ^{87}Sr. The early uplift inferred for northeast Tibet matches the initial upturn in this signal.

Now the question is whether further exploration of Tibet will find evidence of even earlier uplift, especially during the cooling between 55 and 40 Myr ago[10]. □

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Neurobiology

Making smooth moves

Terrence J. Sejnowski

Whether reaching, throwing, running or dancing, our natural tendency is to make smooth and precise movements. Out of the infinite number of ways that we could have made a particular movement, we generally pick the one that is the smoothest. The current thinking in the field of motor control is that the smooth, stereotyped trajectories made by our motor system are specially chosen to minimize jerkiness[1,2] and to maximize efficiency[3]. Or could it be that smoothness is a by-product of a more fundamental computational goal of the motor system, a goal that only makes us look graceful by accomplishing something else?

On page 780 of this issue[4], Harris and Wolpert propose an alternative to the principle of maximum efficiency: the principle of maximum precision. On the face of it, making a precise movement does not seem to imply smoothness. Imagine that the goal is to touch an object as precisely as possible in a fixed amount of time. Getting to the spot as

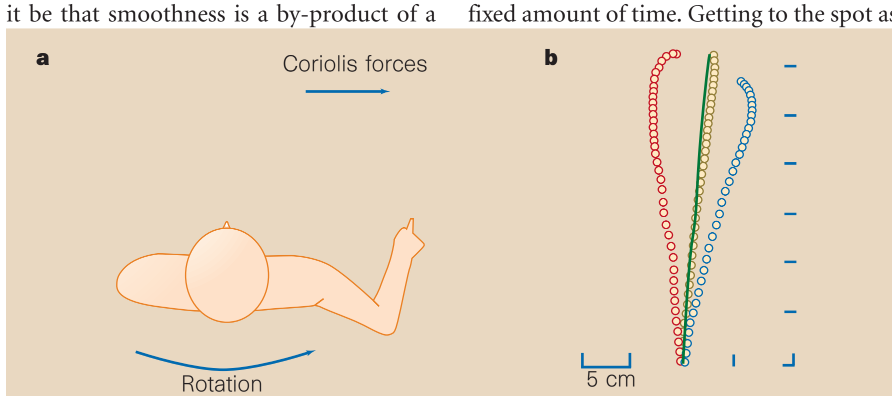

Figure 1 **Hand trajectories for reaching before and after rotation of the body, showing that smooth movements are made even after adaptation in an altered environment.** a, **The subject was on a turntable and slowly rotated.** b, **View from above of average reaching movements, made in darkness to the position of a visual target that was extinguished just before the subject reached for it. The initial trajectories after the start of rotation (blue circles) were seriously affected by Coriolis forces, but after 40 arm movements (yellow circles) the accuracy and velocity profile of the trajectory was almost identical to that of the original movement (green line). After the rotation stopped, the initial trajectory (red circles) shows the after-effects of rotation. (Adapted from ref. 7.)**

quickly as possible and making a careful landing might be a better way to ensure precision rather than making the arm movement as smoothly as possible. What this high-acceleration strategy does not take into account, however, is that the motor neurons that control the arm are noisy and cannot be counted on to get the arm to the same place for the same command. In particular, giving your muscles strong commands is exactly the wrong thing to do because the variability in the muscle output increases with the strength of the command. When they take activity-dependent motor neuron noise into account, Harris and Wolpert find that optimizing the precision of the endpoint of a movement produces smooth movements with exactly the properties of those that we tend to make.

The velocity profiles of arm movements are highly symmetrical around the midpoint of the movement. Simulations of a simple arm controlled by signals that have the same noise characteristics as our motor neurons have similar bell-shaped trajectories when the controller is optimized for maximum precision, over a wide range of parameters such as the inertia, viscosity and time constants. Robustness of the shape of the velocity curve to the details of the arm model is particularly important because the universality of this property[5] originally inspired the minimum-jerk model of motor control. Not only does smoothness apply to arm movements under normal conditions, it also holds after adaptation in altered environments (Fig. 1). The maximum-precision model also accounts for other universal laws of arm movements, such as those that relate the duration of a movement to the maximum precision attained[6], and how the speed of movement scales with the radius of curvature. It is also impressive that the model can account for a broad range of movements including saccadic eye movements, pointing movements and rhythmic arm movements.

This explanation is satisfying for three reasons. First, reducing uncertainty should clearly be a primary concern of any movement controller, whereas smoothness might reduce wear and tear but is more of a luxury. Second, the motor system is constantly calibrating itself to improve performance[7] (Fig. 1), and it is much easier to compute the endpoint error than the degree of smoothness. Finally, grace is a reward for virtue, a bonus for being as accurate as you can possibly be. So we may move through the world smoothly neither by chance nor necessity, but rather because of noise in our motor neurons.

Noise is ubiquitous in the nervous system and is often ignored. The response of a neuron to a sensory stimulus or the output of a motor neuron during an action is highly variable from one experimental trial to the next, so responses are typically averaged over dozens of trials to reduce the variability. However, we can see clearly and move accurately on a single trial, so it is of interest to look more closely at the limits and possible benefits of neural variability. The existence of invertebrate brains that work at a much higher level of precision and repeatability with many fewer neurons, and the exceptional precision in the timing of spikes in the peripheral auditory and electrosensory systems of vertebrates, suggest that noise is not an inevitable consequence of sloppy components.

To a first approximation, the variance in the firing rate of a neuron is proportional to its rate; in the cortex of the brain, the ratio of the variance to the rate is close to 1, making the spike trains of cortical neurons about as variable as radioactive decay. One possible benefit of having this degree of variability is to keep a neuron poised at its most sensitive region, near the threshold and ready to fire a spike whenever a suitable excitatory signal appears[8]. A neuron that fires with a high degree of variability can carry more information than one that fires at a constant rate, like a metronome[9]. But it is not yet clear how brains take advantage of the bandwidth in the spike timing. There may be other reasons for neural variability that we do not yet fully appreciate. The observation that, because of noisy motor neurons, we may have to move more smoothly in the outside world, could have a counterpart for internal brain functions that also tend to run smoothly[8,10]. Noise may not be a problem for neurons, but a solution. □

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Pollination

Sunbird surprise for syndromes

Jeff Ollerton

Interactions between plants and their pollinators include some of the most striking and sophisticated of ecological affiliations[1]. On page 731 of this issue, Anton Pauw[2] describes the relationship between the South African plant *Microloma sagittatum*, a member of the milkweed family, and its pollinator, the lesser double-collared sunbird (*Nectarinia chalybea*; Fig. 1). The importance of this work lies not only in the description and experimental demonstration of a surprising interaction — it also highlights the danger of assuming that a pollinator is known from an analysis of a pollination 'syndrome'.

Pollination syndromes are suites of flower characteristics (morphology, colour, nectar and odour) that supposedly attract particular pollinators to specific flowers, and allow them to forage at the exclusion of 'illegitimate' visitors that would take the floral reward without executing pollination[1,3]. This idea is superficially tidy, and it appeals to the classifying minds of many biologists. Indeed, some authors have used this concept to infer the pollinators of species even without field data and then to draw far-reaching conclusions about the historical ecology and evolution of such relationships[4].

But there are problems associated with the syndrome approach. First of all, most flowering plants are pollinated by a wide taxonomic range of pollinators[5], and cannot be shoehorned into neat syndromes. Second, the jaw-cracking terminology of the syndrome concept is often imprecise and confusing. For instance, the luridly coloured, foul-smelling flowers associated with 'sapromyiophily' (literally, flowers that mimic decaying organic material and are 'loved' by flies) are often beetle pollinated. An example is the now famous *Amorphophallus titanum*[6], one of which flowered this June at Miami's Fairchild Tropical Garden. Finally, and surprisingly (given their wide acceptance), the predictive value of pollination syndromes has never really been tested — there has been little attempt to use these descriptions as hypotheses to verify the usefulness of floral characteristics in predicting what might pollinate a particular plant. The syndrome of 'ornithophily' (bird pollination), for example, is typified by tubular, red, scentless flowers. Although many ornithophilous flowers fit this description, many do not; hummingbirds, for instance, can visit a range of flowers, regardless of morphology or colour[7].

Some workers have recently begun to take a healthily sceptical approach to the syndrome concept[5,8]. However, there are no published examples in which communities