

Collision-avoidance: nature's many solutions

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How does the brain sense looming danger? A new study shows that specialized visual neurons in pigeons carry out several different computations in parallel to analyze signals from approaching objects such as predators.

Anyone who was led to believe that catching a bird simply requires sprinkling salt on its tail can probably testify that this method does not work well. Whether or not salt on the tail has a paralyzing effect, live birds rarely give you the opportunity to test the method. In fact, most animals have evolved many parallel warning systems to escape such undesirable encounters with predators. The smell of coyote urine makes wild mice freeze, the sound of bat calls makes flying crickets dive, and the sight of an approaching car makes humans run (or brake). Among warning signals, those coming from moving predators present a complex challenge to the brain: how can their

dynamic physical characteristics indicate with little ambiguity that they represent a looming danger? Work by Sun and Frost¹ on page 296 of this issue of *Nature Neuroscience* proposes a set of solutions expressed by the dynamic responses of specialized visual neurons in pigeons. What makes this work all the more interesting to us is that it indicates, first, that several different computations—each with its own advantages and disadvantages—are carried out in parallel in the same region

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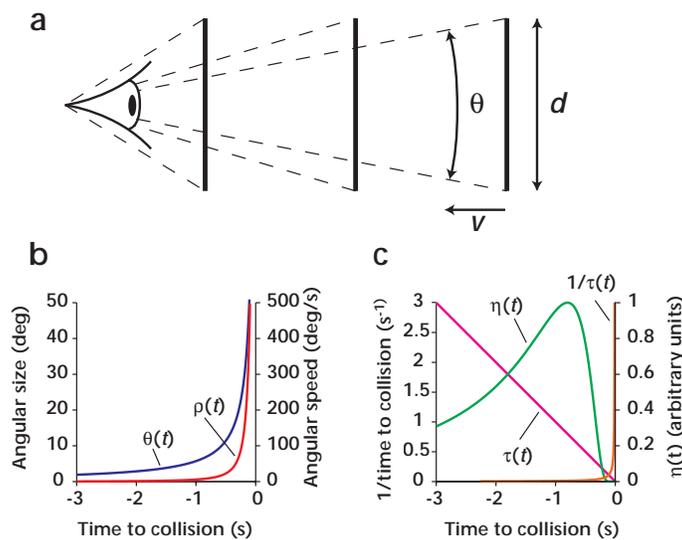


Fig. 1. Elementary kinematics of object approach on a collision course (a) Schematics of a typical looming experiment¹. An object of fixed size d approaches the eye at a constant velocity v . During approach, the angle $\theta(t)$ subtended by the object and its rate of increase [$\rho(t) = \theta'(t)$] both grow nonlinearly. (b) Time course of $\theta(t)$ and $\rho(t)$ during approach ($v = 300$ cm per s, $d = 30$ cm). (c) Corresponding time course of the functions $\tau(t)$, $\tau^{-1}(t)$ and $\eta(t)$ (with $\alpha = 16$, see eq. 2 in ref. 1).

of the brain and, second, that one of these solutions, despite its apparent complexity, is found unchanged in very different animals (birds¹ and insects²).

An approaching object on a collision course projects an expanding image on the retina (Fig. 1a). If the approach velocity is constant, the angle $\theta(t)$ subtended by the object grows nonlinearly in a near-to-exponential fashion. This can be seen in Fig. 1a, where the growth of θ is greater over the late than over the early half of the object's approach. Similarly, the rate at which this angle expands ($\rho(t) = \theta'(t)$) itself increases nonlinearly (Fig. 1b). For a given object approach velocity, specific attributes of angular expansion (size, velocity, acceleration) are thus projected on the reti-

na. From these variables, an observer can derive some of the characteristics of the object's motion, as well as predict the time of impending collision. The big question is, how does the brain behind the exposed retina do it?

One possibility is that neurons (or neuronal circuits) compute $\rho(t)$, the rate of angular expansion, thus indirectly tracking object approach. This solution is reasonably simple and could lead to an appropriate avoidance command when the firing rate of these neurons crosses a certain threshold. It also has an advantage: because large objects start to appear big earlier than small ones, the threshold will be crossed earlier during approach of large objects, leaving

more time for escape. The solution has its downside too, in that the rate of expansion increases faster as collision approaches. If this parameter (the rate of expansion) is represented by a firing rate, the neuron's firing may saturate close to the critical time.

To avoid this, Mother Nature found a solution: the fast expansion can be slowed down by dividing the rate of angular expansion by an exponential function of the object's angular size [$\eta(t) = \theta'(t) / e^{\alpha \cdot \theta(t)}$] (Fig. 1c). When the object is far away, the growth of the numerator dominates and $\eta(t)$ (or the firing rate of the neuron representing it) increases. When the object comes nearer, the denominator gains relative influence because of its exponentiation

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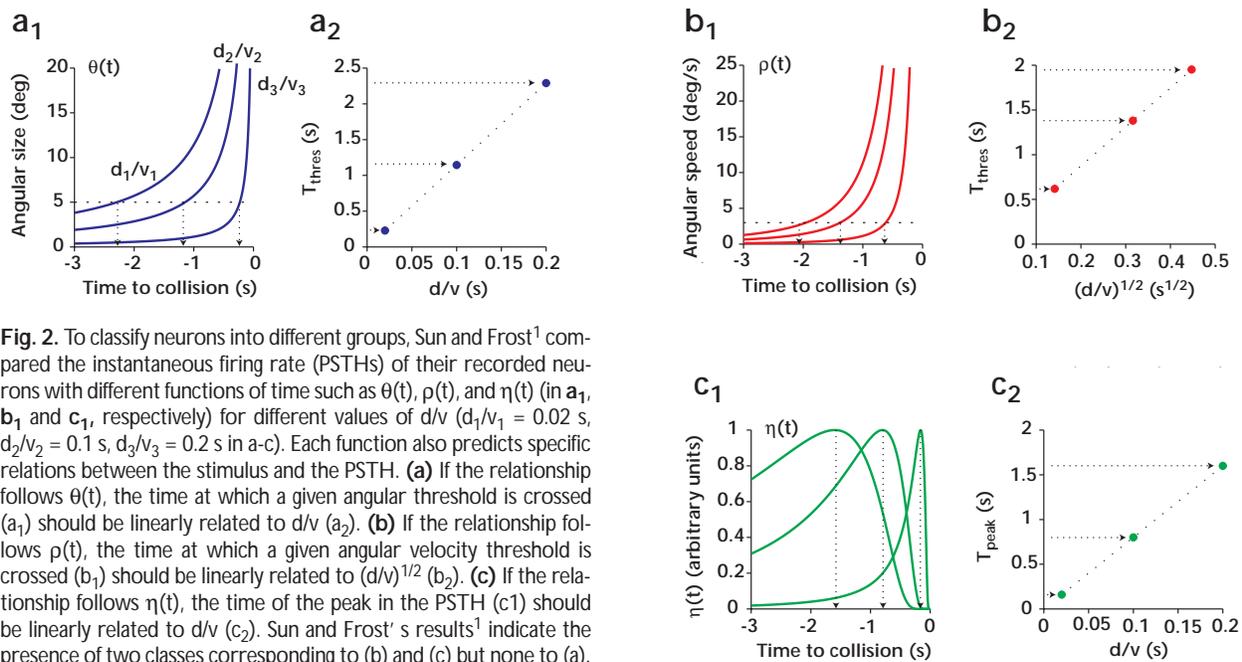


Fig. 2. To classify neurons into different groups, Sun and Frost¹ compared the instantaneous firing rate (PSTHs) of their recorded neurons with different functions of time such as $\theta(t)$, $\rho(t)$, and $\eta(t)$ (in **a**₁, **b**₁ and **c**₁, respectively) for different values of d/v ($d_1/v_1 = 0.02$ s, $d_2/v_2 = 0.1$ s, $d_3/v_3 = 0.2$ s in a-c). Each function also predicts specific relations between the stimulus and the PSTH. **(a)** If the relationship follows $\theta(t)$, the time at which a given angular threshold is crossed (**a**₂) should be linearly related to d/v (**a**₂). **(b)** If the relationship follows $\rho(t)$, the time at which a given angular velocity threshold is crossed (**b**₁) should be linearly related to $(d/v)^{1/2}$ (**b**₂). **(c)** If the relationship follows $\eta(t)$, the time of the peak in the PSTH (**c**₁) should be linearly related to d/v (**c**₂). Sun and Frost's results¹ indicate the presence of two classes corresponding to (b) and (c) but none to (a). In addition, a third class has a constant firing threshold, consistent with a τ computation.

and slows down the increase in firing rate. Another advantage is that, at a critical time preceding collision, $\eta(t)$ reaches a peak. This peak occurs when (and thus signals that) the object subtends a particular angle, given by $2\text{tg}^{-1}(2/\alpha)$, constant for a given neuron. There are two problems associated with η , however. First, to know that this angle has been reached, downstream circuits need to detect a peak firing rate. This is not trivial, and because peak detection requires comparing successive values, this operation requires time, when time is in short supply. Second, the peak signals an angle, not an actual size; it thus confounds a large object that is farther away with a small object that is near. Less time would therefore be available for escape from a small and rapidly approaching object than from a large, slow moving one.

Here also, there is a potential solution. It consists of calculating yet another variable, the time-to-contact $\tau(t)$ or its inverse (Fig. 1c). Tau is relatively easy to compute when $\theta(t)$ is small and when the approach velocity is constant: $\tau \approx \theta(t)/\theta'(t)$. This measure, introduced by Gibson³ and studied behaviorally in diving birds by Lee and Reddish⁴, has the advantage that it is independent of the object size or approach velocity. Tau or $1/\tau(t)$ gives a running value of the

time before collision. By setting an appropriate threshold, it becomes possible to trigger a motor reaction at a constant delay prior to the anticipated collision. The downsides of the τ computation are that it provides no information about object size or velocity and that the mathematical approximation $\tau \approx \theta/\theta'$ is not valid when θ is large.

Remarkably, each of these three potential solutions is reflected in the properties of neurons in *nucleus rotundus* of pigeons¹, an area homologous to the mammalian inferior caudal pulvinar⁵—a thalamic nucleus with visual inputs from the superior colliculus and which projects to occipital, parietal and temporal cortices. Sun and Frost¹ identified three groups of neurons that respond to approaching objects on a collision course by comparing the dynamics of their firing rates with kinematic functions such as $\theta(t)$, $\rho(t)$ or $\eta(t)$ for different object sizes and approach velocities. (See Fig. 2 for a summary of their methods.) One group of neurons shows firing profiles that are best described by a ρ computation. A second group shows peaked firing profiles, best fitted by a η computation. This is particularly interesting to us because the η algorithm was first derived² to describe the responses of DCMD, a looming-sensitive neuron in locusts⁶⁻⁸. To find such

a remarkably similar solution in such distant species (which interestingly have similar predators) supports the idea that similar problems engender similar computational solutions. Finally, Sun and Frost describe a third group of neurons whose onset of activity during approach is independent of object size or velocity, suggesting a τ -style computation. The existence of this last class of neurons was previously reported by Frost's group⁹. The properties of these neurons were confirmed in this report and analyzed further, allowing their clear distinction from the other two neuronal and computational clusters.

Why are these results important? First, they focus on the dynamics of neuronal responses—rather than mean responses—as relevant neuronal signals. An early attempt at this was made by Rind and Simmons⁸ in their study of locust DCMD responses. Second, the results indicate that the brain reconstructs object approach using several parallel (and possibly serial) computations. Each one provides a different piece of information about the state of the environment, and the animal thus presumably makes an informed decision on the basis of these different inputs. But how? It will be interesting to study how downstream circuits interpret these parallel messages, so as to make the best motor

decision (for example, “duck, but not too early, so as to prevent course correction by predator”). Does one signal dominate the others (see ref. 9)? If so, under what circumstances? Or does some combination of these signals guide behavioral responses? It will also be fascinating to study the cellular mechanisms by which these different computations are carried out. Do the ρ neurons for example, provide inputs to the τ and η neurons, allowing size and velocity signals to be combined? If so, how are these opera-

tions implemented biophysically? If the τ neurons really fire when the variable τ crosses a given threshold, how is this threshold set and held constant? These are some of the many interesting questions that remain to be answered, but Barrie Frost and colleagues are getting us closer to this target.

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