PERSPECTIVES: BEHAVIOR

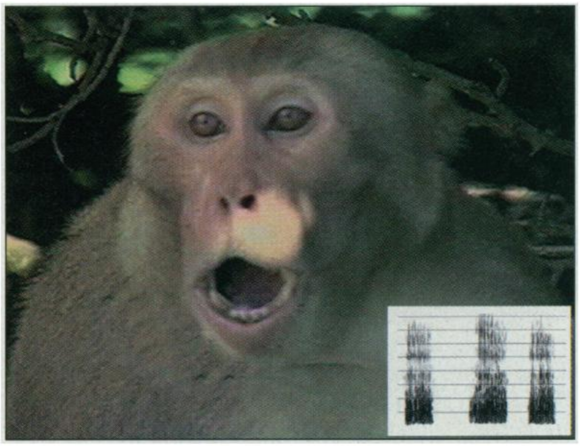
# Communication Goes Multimodal

**Sarah Partan and Peter Marler**

The signals that organisms exchange as they communicate are often very complex. Understanding how these signals are perceived poses special problems both for physiologists who study neural integration and for behavioral scientists interested in communication. This "binding problem"—how an organism creates a coherent percept from parts of a stimulus analyzed separately—is especially acute when several sensory modalities are used. Communication researchers tend to categorize signals by the primary sensory channel involved, but in reality multiple channels are often engaged simultaneously, especially in highly social, group-living creatures. Despite predictions that multiple, concurrent stimuli should be important (*1*), their influence on signal efficacy and meaning has only recently been fully appreciated (*2, 3*). For example, human speech perception is influenced by visual stimuli (*4*), and signals as diverse as threat expressions of macaques (see upper figure) and recruitment signals of ants have different consequences, depending on the combination of sensory modalities used (*5, 6*).

Behavioral neuroscientists find that integration of information from multiple sensory channels is crucial for attention and perception in humans, monkeys, birds, and insects, particularly in the processing of stimuli associated with posture and movement (*7*). The communicative consequences of combining signal components from different sensory channels remain poorly understood, and we lack a theoretical framework for dealing with them. Here we offer a classification system for categorizing and comparing the effects of multimodal signals (see lower figure).

The components of a multimodal signal may be either redundant or nonredundant in meaning. Redundancy is common (*8*) and ensures that the message will get through in the face of environmental noise (backup signals) (*9*). Nonredundant components have the advantage of providing more information per unit time (multiple messages) (*10*). Both types can be distinguished empirically by the behavior they elicit from a recipient. When presented separately, redundant signal components should have equivalent effects on a receiver, whereas nonredundant components should have different effects (*5*).

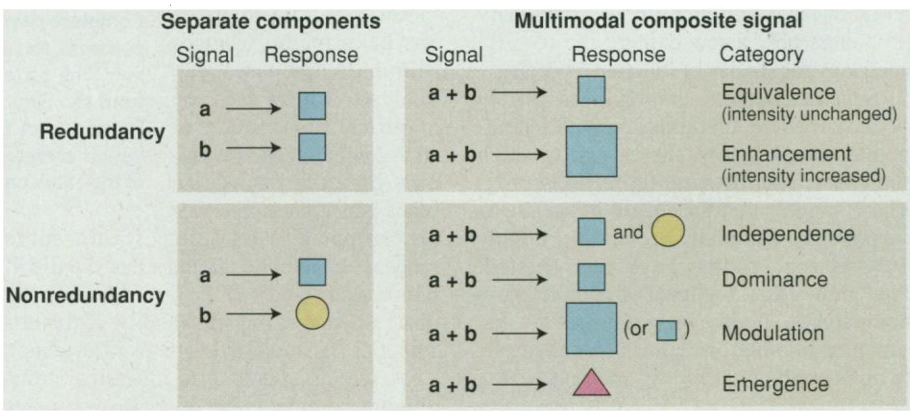


**Visual and vocal.** Bimodal threat display of an adult male rhesus macaque (*Macaca mulatta*) combining a facial expression (open-mouth threat) with a vocalization (bark). Image was digitized from videotape. Insert depicts the bark (*y* axis, frequency 0 to 8 kHz; *x* axis, time 0 to 2 s) taken from videotape at the same moment as the picture.

When components are combined simultaneously into a multimodal signal, several outcomes are possible (see lower figure). Redundant components might result in the same response as each component alone. Courting male moths (*Cycnia tenera*) elicit equivalent responses from females regardless of whether their pheromones and ultrasonic sounds are presented separately or together (*11*). More commonly, the combination of redundant components results in an enhanced response. *Aphaenogaster* ants recruit help for carrying prey by emitting pheromones, but with large prey they also stridulate, producing a substrate-borne vibrational signal. The stridulation has a small effect alone, but both components together recruit more workers (*6*). Similar multiplicative effects occur during neural processing of simultaneous visual and auditory stimuli in the superior colliculus of cats (*12*).

Combinations of nonredundant components yield other outcomes. The two components could be independent, eliciting distinct responses even when combined. Pheromones from female *Cupiennius salei* spiders alert males to the presence of a potential mate. Concomitant vibrational signals from the female then direct males to her location (*13*). These two components function independently whether they are perceived simultaneously or not. Alternatively, one component may dominate the other. Dogs signal play behavior visually with a bow, and sometimes also growl, normally a threat. Separately, these signals are contradictory, but their combination elicits play, the visual component taking precedence (*14*).

One nonredundant component may modulate the effect of the other. Male *Alpheus heterochaeli* shrimp respond aggressively to visual cues alone, such as an open claw, but do not respond to chemical cues alone. When the two are combined and the pheromone is from a female, male




**Classification of multimodal signals**. Redundant signals are depicted above, nonredundant signals below. **(Left)** Responses to two separate components (a and b) represented by geometric shapes (the same shape indicates the same qualitative response; different shapes indicate different responses). **(Right)** Responses to the combined multimodal signal.

The authors are in the Center for Animal Behavior and Department of Neurobiology, Physiology and Behavior, University of California, Davis, CA 95616, USA. E-mail: srpartan@ucdavis.edu

aggressive responses are suppressed (*15*). Neural analogs for modulation include cells in the cat superior colliculus that respond to visual stimuli alone but not to auditory stimuli alone. Auditory and visual stimuli together elicit enhanced responses in some neurons, leave some unchanged, and leave others depressed (*12*).

Finally, the combination of two nonredundant components can produce an entirely new response (emergence). When a vocal stimulus (human phoneme "ba") is mismatched with a visual stimulus (face articulating "ga"), subjects may perceive a new phoneme, "da" (*4*). Aromatic pyrazines and red and yellow coloration are commonly associated with noxious insects. Presented alone, neither cue produces aversion in chicks; aversion appears only when the odor and color occur simultaneously (*2*). Here, multimodal stimuli evoke a response not elicited by the unimodal components. Similarly, some cat superior colliculus cells respond to multimodal but not unimodal stimuli (*12*). The provision of a common terminology for discussion of multimodal signaling and its underlying integrative neural processing may encourage efforts to unify physiologic and behavioral research in this area.


**References and Notes**

1. C. Darwin, *The Expression of the Emotions in Man and Animals* (Murray, London, 1872); N. Tinbergen, *Behaviour* **15**, 1 (1959); P. Marler, in *Primate Behavior: Field Studies of Monkeys and Apes*, I. DeVore, Ed. (Holt, Rinehart and Winston, New York, 1965), pp. 544–584.
2. C. Rowe and T. Guilford, *Nature* **383**, 520 (1996).
3. S. J. Scheffer, G. W. Uetz, G. E. Stratton, *Behav. Ecol. Sociobiol.* **38**, 17 (1996); L. Fusani, R. E. Hutchison, J. B. Hutchison, *Behaviour* **134**, 321 (1997).
4. H. McGurk and J. MacDonald, *Nature* **264**, 746 (1976).
5. S. R. Partan, thesis, University of California, Davis (1998).
6. B. Hölldobler, *J. Comp. Physiol. (A)*, in press.
7. E. Horn, Ed., *Multimodal Convergences in Sensory Systems* (Fischer, Stuttgart, 1983); M. Brainard and E. I. Knudsen, *J. Neurosci.* **13**, 4589 (1993); J. Driver and P. Grossenbacher, in *Attention and Performance XVI: Information Integration in Perception and Communication*, T. Inui and J. McClelland, Eds. (MIT Press, Cambridge, MA, 1996); R. A. Andersen, *Philos. Trans. R. Soc. London Ser. B* **352**, 1421 (1997).
8. E. O. Wilson, *Sociobiology* (Harvard Univ. Press, Cambridge, MA, 1975); J. R. Krebs and R. Dawkins, in *Behavioral Ecology*, J. R. Krebs and N. B. Davies, Eds. (Sinauer Associates, Sunderland, MA, 1984), pp. 380–402.
9. R. A. Johnstone, *Philos. Trans. R. Soc. London Ser. B* **351**, 329 (1996).
10. A. P. Moller and A. Pomiankowski, *Behav. Ecol. Sociobiol.* **32**, 167 (1993).
11. W. E. Conner, *Experientia* **43**, 1029 (1987).
12. B. E. Stein, M. T. Wallace, M. A. Meredith, in *The Cognitive Neurosciences*, M. S. Gazzaniga, Ed. (MIT Press, Cambridge, MA, 1995), pp. 683–702.
13. J. S. Rovner and F. G. Barth, *Science* **214**, 464 (1981).
14. M. Bekoff, *Q. Rev. Biol.* **47**, 412 (1972).
15. M. Hughes, *Anim. Behav.* **52**, 247 (1996).
16. Thanks to K. Britten, J. Capitanio, J. Endler, C. Greene, W. Mason, K. Partan, and R. Wylie.


PERSPECTIVES: CLIMATE CHANGE

# Solving the Aerosol Puzzle

Jeffrey T. Kiehl

How do aerosol particles affect climate? This is one of the key questions that has to be answered if we are to understand how humans influence Earth's climate. The burning of fossil fuels and biomass (in natural and man-made fires) leads to the production of substantial amounts of aerosols in the atmosphere. These particles increase the reflection of sunlight back to space directly and also indirectly by increasing the brightness of clouds. Both of these effects reduce the amount of solar energy available to the climate system, a phenomenon called negative climate forcing (that is, a cooling of the atmosphere). On page 1299 of this issue, Haywood *et al.* (*1*) use a new approach to determining the direct effect of aerosols on Earth's climate. By combining satellite data of reflected sunlight with results from numerical models, they calculate how aerosols alter the amount of solar radiation available to Earth's climate system. Their unique integration of observations and models shows how a better understanding of the aerosol problem can be reached.

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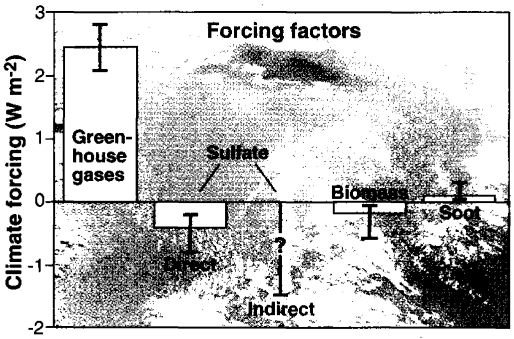
Emissions from industry are a major source of aerosols in the atmosphere. In fact, studies indicate that the cooling effect of these anthropogenic aerosols could offset a substantial amount of the forcing by greenhouse gases, which causes global warming. Unfortunately, the magnitude and spatial extent of the anthropogenic aerosol forcing effect are highly uncertain (see figure), and this uncertainty is a major hurdle in advancing our understanding of how humans have altered, and may in the future alter Earth's climate.




**A question of uncertainties.** Climate forcing from 1850 to the present, based on (*6*). Positive forcing corresponds to warming and negative forcing to cooling of the atmosphere. Large uncertainties exist, particularly in the aerosol forcing.

The complexity of this problem seems to grow with each new study. Uncertainties in the direct effect arise from the amount and distribution of aerosols in the atmosphere and their chemical and physical properties, which determine their effectiveness at reflecting sunlight back to space. Interactions between different types of aerosols may also affect the magnitude of direct forcing. Recent observation and modeling studies (*2*, *3*) indicate that gas phase sulfur species readily attach to sea-salt particles, leading to composite particles that are larger in size than pure sulfate particles. Larger particles reflect less sunlight, and formation of sulfate on sea salt therefore reduces the overall magnitude of the sulfate forcing. Sulfate formation can also occur on mineral dust and carbon aerosols, again reducing the sulfate forcing. At present, there is little information on how this masking effect alters estimates of sulfate aerosol forcing. Despite these caveats, direct forcing by sulfate aerosols is clearly an important factor in anthropogenic climate forcing.

The indirect effect is plagued with even greater uncertainties. Field observations indicate that an increase in sulfate below a cloud leads to an increase in the number of cloud droplets within the cloud. A higher number of small cloud droplets increase the cloud's brightness; that is, more sunlight is reflected back to space. Unfortunately, the predicted number of cloud droplets for a given amount of sulfate aerosol varies widely from model to model, leading to a fivefold uncertainty in indirect forcing by aerosols (*4*), due to the uncertainty in predicted cloud drop number for a given below-cloud sulfate mass. The variability may result from many factors, such as the chemical properties of the aerosol, sources of other particles that can make cloud droplets, and variations in cloud properties.

How can we better understand the ways in which aerosols affect climate? Satellite

J. T. Kiehl is at the National Center for Atmospheric Research, Climate Modeling Section, Boulder, CO 80307, USA. E-mail: jtkon@ncar.ucar.edu

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