

which in the "animal literature" are referred to as the development of hierarchies of sets (14).

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15. Supported by NIMH grant MH 12970 and research career award MH 15, 214 to K. H. Pribram.

22 May 1967

Erratic Display as a Device against Predators

Abstract. *Prey animals in many different taxonomic groups behave erratically when attacked by predators. This reaction is not accidental, but acts as a specific antipredator device. Observational data and theoretical considerations indicate that such protean displays function to confuse and disorient the predator and to increase its reaction time. Thus the survival of the prey is assisted, and the selective advantage whereby such erratic patterns of the prey animals may have evolved is created.*

When attacked by predators, many prey animals do not flee in a straight line; their behavior is highly erratic and unpredictable, taking the form of zigzagging, looping, spinning, or wild bouncing. This phenomenon is often briefly noted in the literature, but with no explanation of its significance; it has been recorded separately in several taxonomic groups including many mammals and birds (1, 2), noctuid and geometrid moths (3), grasshoppers (4), and the marine copepod *Calanus* (5). It occurs in many other types of animals including dipterous insects, cladoceran crustaceans, voles, the stickleback *Gasterosteus*, shore hoppers, and fleas. We now propose a unifying theory.

The audiogenic seizures of small mammals provide the first clue. It has been suggested (6) that the phase of intense erratic activity at the beginning of such seizures might have survival value if it were to occur in the wild during predatory attack. On the basis of this suggestion Chance and Russell (7) coined the term protean behavior, and proposed that patterns of erratic behavior may exist having the function of confusing predators. Here we point out that such patterns are in fact very common (see the foregoing list), and that they pose some interesting and important theoretical problems. We shall

show that the basis for understanding their confusing effect upon predators is provided by modern psychological conflict theory.

We define protean behavior as behavior that is sufficiently unsystematic to prevent a reactor from predicting in detail the position or actions (or both) of the actor. It includes many reactions that are released only when the animal is in immediate and obvious danger. For example, if small insects resting on tree bark are disturbed, they usually take to the wing in a characteristically erratic spinning and looping action; there is no known aerodynamic or physiological reason for such flight. The flight path is much more direct and simple when the insect leaves its resting place of its own accord. Similarly, noctuid and geometrid moths show a bewildering variety of unoriented maneuvers when exposed to the ultrasonics of hunting bats; their behavior has been shown to have a selective advantage of about 40 percent (8).

The protean nature of such single erratic displays may be enhanced by changes in color; Huxley (4) notes that flash coloration and zigzag fleeing are associated in some grasshoppers. Swift changes in color also occur in the squid *Sepioteuthis* when zigzagging during

escape (9), and in the reef fishes *Haemulon flavolineatus* and *Epinephalus striatus* (10). In the latter example the display is further complicated by a series of percussive sounds (11).

In many species of birds, including waders, gulls, ducks, and starlings, the erratic pattern is shown by whole flocks and may then be termed a united erratic display; it acts as a deterrent (1) against the attacks of aerial predators like the peregrine falcon. On appearance of the predator the birds draw together into a tight group, which zigzags unpredictably in swift flight, sometimes splitting into subgroups, with the individuals continually shuffling their relative positions.

Certain animals move very erratically even when undisturbed, especially insects that spend considerable periods on the wing, for dispersal or feeding movements, during daylight hours; they are highly vulnerable to predation by birds that feed on aerial plankton, and their erratic flight may well be a form of protean insurance against sudden attack.

In all the foregoing examples the function of the erratic displays appears to be to disorient the predator's attack. Some protean displays, however, seem to be designed to switch the predator's motivation from attack to escape, having in this respect the same function as certain systematic responses like eyespot displays in Lepidoptera (4, 12). Erratic, convulsive movements, combined with intermittent flashing of colored surfaces, occur in several species of butterflies and moths when disturbed while in a cryptic posture. Swift and complete changes in color, associated with darting movements, occur in the cuttlefish *Sepia officinalis* (13). The luminescent "berserking" display of sea pansies, although static, seems to be a similar phenomenon. Such displays have an effect of startling and may arouse escape tendencies because of the sudden unexpected changes in the predator's visual field (13). Sudden movements are known to evoke escape reactions in many vertebrates (14).

We propose that the essential feature of all protean displays is that they are likely to arouse mutually incompatible tendencies in the reactor. These tendencies may be of simple orienting components or of fundamental behavioral categories like escape or defense. The theories of Berlyne (15) on arousal and conflict are highly relevant to an understanding of the effect on the

predator. He shows that the greater the number and novelty of stimuli, and the less expected and more variable their sequence, the greater is the conflict induced. He also demonstrates that the amount of conflict is directly related to increase in reaction time.

Protean displays involve all the above factors, so, besides the possibility that a predator may be confused into making an incorrectly directed attack, it will in any case suffer a delay in its reaction time. Any such delay is bound to be of survival value to the prey. Therefore, unlike cryptic, mimetic, or warning displays, the protean display does not systematically deny or falsify information; instead it creates confusion by simultaneously arousing conflicting responses. Furthermore, to the extent to which it is unsystematic, it is resistant to defeat by learned modification of responses in the predator.

There is thus both theoretical (15) and observational (8) evidence that erratic movements during antipredator displays have survival value. In terms of evolutionary theory, therefore, their unpredictability is not accidental but has appeared as a result of natural selection during phylogeny. Protean display is an entirely distinct principle in antipredator behavior—a principle that awaits more detailed and exact analysis.

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17 April 1967

Brain Catecholamines: Relation to Defense Reaction Evoked by Acute Brainstem Transection in Cat

Abstract. *The concentration of noradrenaline, but not serotonin, in the brainstem of cats is reduced 3 hours after the production of a defense reaction by supracollicular decerebration, even when movements and changes in blood pressure are abolished by transection of the spinal cord. After midcollicular decerebration, which does not elicit a defense reaction, noradrenaline concentrations do not change. The decrease in its concentration accompanying the defense reaction produced by brain lesions probably reflects activity, in this behavior, of neurons containing noradrenaline.*

When the defense reaction (or sham rage) is elicited by electrical stimulation of the amygdala or hypothalamus in the cat, it is accompanied by a decrease in the concentration of noradrenaline (NA) in the brain and of NA and adrenaline (A) in the adrenals, without change in the amounts of dopamine and serotonin (5HT) in the brain (1). Furthermore, with fluorescence histochemistry it has been demonstrated that the decrease in the NA in the brain is the result of depletion of NA located within axon terminals of neurons containing NA (NA neurons) (2). Since concentrations of NA do not change when electrical stimulation fails to elicit the defense reaction, we previously suggested a relationship between activity in these NA neurons and this behavior (1).

To determine if the defense reaction elicited without electrical stimulation is accompanied by a decreased concentration of NA in brain, we produced recurrent spontaneous outbursts of rage in cats by decerebrating them above the colliculi and preserving the posterior hypothalamus (high decerebration). Concentrations of NA and 5HT in the medulla, pons, and the lower part of the mesencephalon and of NA and A in adrenals have been compared with

those in identical regions of the lower brainstem and in the adrenals of cats decerebrated by transection between superior and inferior colliculi (low decerebration). These cats do not show spontaneous rage.

Mature cats of both sexes were anesthetized with ether, cannulas were placed in one femoral artery and in the trachea, the common carotid arteries were bilaterally ligated, and the cat was then placed in a stereotaxic frame. Decerebration was performed with a spatula and completed by suction. Blood pressure measured by a Statham pressure transducer, heart rate measured by a cardiometer triggered by the arterial pulse, expired CO₂ measured by an infrared CO₂ meter, and respiration and chest movements measured by a pneumograph were amplified and displayed on channels of an Offner-Beckman polygraph. Body temperature was maintained at 37°C by an infrared lamp thermostatically controlled by the rectal temperature. After the transection of the brainstem was completed, administration of the anesthetic was discontinued. The animals were decapitated 3 hours later, the brains were rapidly removed, the levels of transection were noted, and a piece of lower brainstem extending from 1 cm be-

Table 1. Changes in mean concentration (\pm standard error) of catecholamines in cat brainstem and adrenal glands and of serotonin in brainstem 3 hours after decerebration at midcollicular (low decerebrate) or supracollicular (high decerebrate) levels. Figures in parentheses are the numbers of observations. Abbreviations: NA, noradrenaline; 5HT, serotonin; A, adrenaline. The differences between the nonoperated and ether controls and between the nonoperated and low decerebrate cats are not significant.

Group	Brainstem (ng/g)		Adrenal gland (ng/g)	
	NA	5HT	NA	A
<i>Control animals</i>				
Nonoperated	227 \pm 13 (10)	516 \pm 47 (4)	512 \pm 32 (10)	484 \pm 30 (9)
Ether	216 \pm 6.8 (5)	512 \pm 28 (2)	505 \pm 38 (5)	473 \pm 65 (5)
<i>Operated animals</i>				
Low decerebrate (no defense reaction)	200 \pm 9.5 (5)	648 \pm 45 (6)	542 \pm 45 (7)	459 \pm 55 (7)
High decerebrate (defense reaction)	149 \pm 10† (7)	531 \pm 39 (4)	325 \pm 46* (8)	258 \pm 50* (8)

* Difference from nonoperated controls significant, $P < .01$. † Difference from nonoperated controls significant, $P < .001$.

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Science **156** (3783), 1767-1768.
DOI: 10.1126/science.156.3783.1767

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