

Successive negative contrast in the consummatory responding of didelphid marsupials

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In a consummatory experiment patterned after previous work with rats and goldfish, successive negative incentive contrast was sought in didelphid marsupials of two species (*Lutreolina crassicaudata* and *Didelphis albiventris*). Half of the subjects of each species were trained from the outset with a 32% sucrose solution and shifted occasionally to a 4% sucrose solution; the rest, which served as controls, were trained only with the 4% solution. The positive results obtained (less response to the 4% solution in the shifted subjects than in the controls) fit the hypothesis, based on comparative work with descendants of older vertebrate lines, that the mechanism of successive negative incentive contrast evolved in a common reptilian ancestor of birds and mammals.

Although the fashion of recent years among ethologists and comparative psychologists with little knowledge of learning has been to denigrate "general process" theory, there are many phenomena of learning that can reasonably be assumed, on the basis of the taxonomic diversity of the animals in which they are found, to be common to vertebrates and understandable in terms of common principles. Competent evidence of evolutionary divergence in learning is, in fact, far more the exception than the rule, and of special interest for that very reason.

Our concern here is with "successive negative incentive contrast," a phenomenon well known in rats that has failed to appear in animals of certain older vertebrate lineages (Flaherty, 1982). The phenomenon is important, of course, as the first, and still perhaps the most powerful, evidence of learning "about" reward and of the control of behavior by remembered (associatively reinstated) consequences of previous actions (Hull, 1952; Tolman, 1932). When rats are shifted to a less preferred reward after instrumental training with a preferred reward, they perform more poorly for a time than do control animals

trained from the outset with the less preferred reward (Crespi, 1942; Elliott, 1928), but the performance of shifted goldfish may continue to be better than that of the controls or, if impaired at all, does not fall below the control level (Bitterman, 1984; Gonzalez, Ferry, & Powers, 1974; Gonzalez, Potts, Pitcoff, & Bitterman, 1972; Lowes & Bitterman, 1967; Mackintosh, 1971). Corresponding results have been obtained in consummatory experiments. Rats given access to 32% sucrose in a series of daily sessions and then shifted either to 4% sucrose (Flaherty, Becker, & Checke, 1983) or to 32% sucrose adulterated with quinine (C. F. Flaherty, personal communication, 1985) do not take as much of it as do control animals that have experienced only the less preferred food, but goldfish continue to take more of an attractive food after it has been adulterated with quinine than do control animals that have experienced only the adulterated food (Couvillon & Bitterman, 1985). Successive negative incentive contrast has been found in monkeys (Tinklepaugh, 1928) and chimpanzees (Cowles & Nissen, 1937) as well as in rats, but has failed to appear not only in goldfish, but also in toads (Schmajuk, Segura, & Ruidiaz, 1981) and painted turtles (Pert & Bitterman, 1970; Pert & Gonzalez, 1974).

On the basis of these comparative results together with a demonstration of the spaced-trials partial reinforcement effect in pigeons (Roberts, Bullock, & Bitterman, 1963), it is tempting to speculate that successive negative incentive contrast reflects the operation of a mechanism that evolved in some common reptilian ancestor of birds and

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mammals (Bitterman, 1986). Three assumptions underlying this hypothesis should be made explicit. One is that the failures with fishes, toads, and turtles are not due merely to insensitive or otherwise inappropriate experimental methods, and a second is that the results for the particular species studied can be generalized to the lineages they are taken to represent (cf. Mayr, 1968). Skeptics may wish to look further for the effect with different methods or in different species of the same lineages. A third assumption is that successive negative incentive contrast is an important component of the spaced-trials partial reinforcement effect (more rapid extinction in consistently than in inconsistently rewarded animals), which occurs only with large rewards and reflects precipitous decline in the performance of the animals confronted with nonreward for the first time (Gonzalez & Bitterman, 1969; Hulse, 1958; Wagner, 1961). As is understandable on the basis of the same assumption, the spaced-trials partial reinforcement effect has failed to appear in goldfish (Schutz & Bitterman, 1969), African mouthbreeders (Longo & Bitterman, 1960), or painted turtles (Pert & Bitterman, 1970).

It was Romer's view that the reptiles (especially the dominant dinosaurs) contributed indirectly to the development of the intelligence he regarded as "the hallmark of mammalian progress" by making it necessary for mammalian survival (Romer & Parsons, 1986, pp. 82-83), but our speculation is that the contribution was more direct—that whatever advance is represented by the mechanism of successive negative incentive contrast can be credited to the reptiles themselves. In this view, the effect should be found not only in birds (where it has not yet been sought directly), but also in crocodilians (sole survivors of the ruling reptiles from which birds are descended), and in monotremes and marsupials as well. The easiest experiments to contemplate, of course, are with pigeons or birds of some other species for which efficient training techniques already are available, but in the special circumstance of our collaboration in Argentina it seemed reasonable to turn—despite a paucity of information about their learning (Kirkby, 1977; Papini, 1986)—to marsupials. The two species we studied, both of the family *Didelphidae*, adapt reasonably well to laboratory conditions and come fairly readily to take food in a small enclosure. We chose, therefore, to begin with a simple consummatory experiment. Half the subjects of each species were given repeated access to a preferred food and then shifted occasionally to a less preferred food, while the rest served as controls, being given only the less preferred food.

METHOD

Subjects

The subjects were 13 red opossums (*Lutreolina crassicaudata*)—9 males, 4 females—and 9 white-eared opossums (*Didelphis albiventris*)—8 males, 1 female. The weights of the animals varied considerably, with no overlap between species. The red opossums weighed between 240 and 980 g (with males tending to be heavier than females); the white-eared opossums weighed between 1,040

and 3,320 g (showing no sexual dimorphism in body size). All of the animals were adults, captured in the wild, and maintained in individual cages under laboratory conditions for at least 2 months before the beginning of the experiment. After their free-feeding weights had stabilized, the animals were put on a 24-h feeding schedule, which resulted in a temporary weight loss of about 10%. The red opossums, which were lighter in weight and took food less readily than the white-eared opossums, had 2 h of access to food and water each day; in the interim, they were deprived of both food and water to encourage drinking in the experimental situation. The white-eared opossums, which took food more readily, had only 1 h of access to food each day and unrestricted access to water. The natural day-night cycle prevailed in the windowed animal room, where a temperature of 22°C was maintained.

Apparatus

The experimental chamber was 54 cm long, 33.5 cm wide, and 31 cm high. The longer (lateral) walls were of clear Plexiglas; the other walls and the ceiling were of aluminum. The floor was made of aluminum bars. The chamber was dimly illuminated from above by a 3.6-W lamp, and a small speaker produced a 70-dB white background noise. Mounted on the front wall was a drinking tube—its orifice 2.5 cm above the floor—which contained sucrose solution. The tube was graduated to provide a measure of the amount of solution consumed in each experimental period. Aluminum plates were situated at either side of the orifice just far enough apart to admit the animal's head, and a photocell was used to detect proximity of the head to the orifice. The photocell relay connected the output of a pulse generator to a digital counter, thus providing a measure of drinking time. The control equipment was located in an adjoining room, from which the animal in the chamber could be observed through a one-way window.

Procedure

The subjects of each species were divided into 2 groups that were designated Group 4-4 and Group 32-4. Because of the sexual dimorphism in the body size of the red opossums, 2 of the 4 females were assigned to each group. The subjects of Group 4-4 were trained throughout (in all 44 daily sessions) with a 4% sucrose solution, which was determined in preliminary tests to be the lowest sucrose concentration that the animals would take with some consistency. The subjects of Group 32-4 were trained from the outset with a 32% sucrose solution and tested from time to time with a 4% solution. There were 4 such down-shifts. In Shift 1, there were 4 4% sessions following 12 32% sessions, and the same was true of Shift 2. In Shift 3, there were 2 4% sessions following 4 32% sessions, and the same was true of Shift 4. For each animal, there was a single pretraining session consisting of a 10-min period of habituation to the chamber. Sucrose solution of appropriate concentration was available from the outset of each subsequent training session, which lasted for 5 min after the first activation of the photocell circuit by the animal. The total amount (in milliliters) of the solution consumed and the total drinking time (in seconds) in each session were measured.

RESULTS

In Figure 1, the results for the two species are plotted in terms of the mean amount consumed in each session. The white-eared opossums, which drank more than the smaller red opossums, did not show as strong a preference for the higher sucrose concentration, evidence perhaps of a performance ceiling. Successive negative contrast is not, of course, precluded, even where there is no difference at all in preshift behavior (Gonzalez,

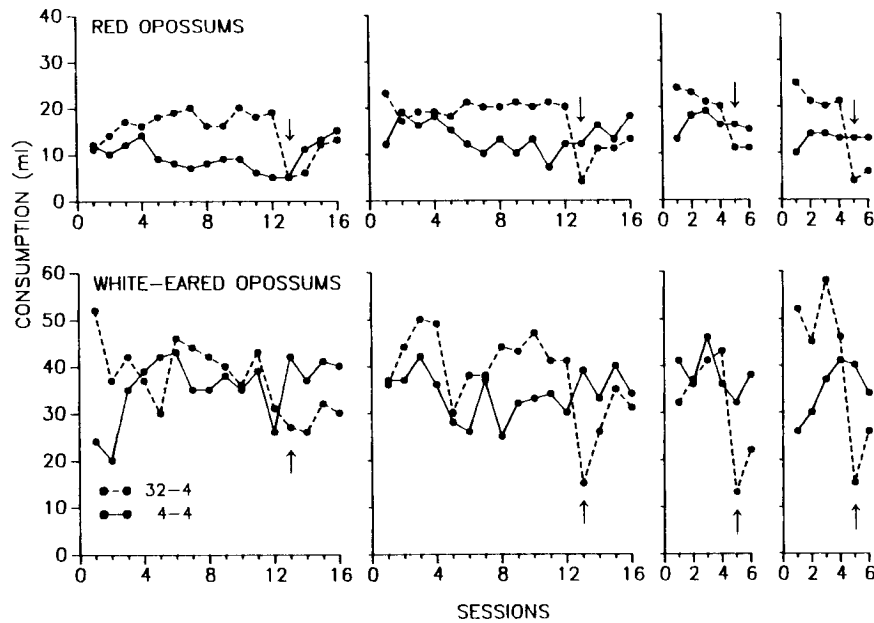


Figure 1. Mean amount of sucrose solution consumed in each session by the two groups of each species. The arrows show the points at which the concentration of sucrose for the contrast animals (32-4) was down-shifted.

Gleitman, & Bitterman, 1962), but actually may be more evident under such conditions because of the greater remove of the control behavior from the performance floor. In any case, each of the shifts showed contrast (less consumption by Group 32-4 than by Group 4-4) except the first for the red opossums, where the control animals still were drinking very little. An overall analysis of variance based on amount consumed in the first session of each of the 4 shifts for both groups of both species shows the contrast effect to be statistically significant [$F(1,18)$ for groups = 6.64, $p = .0190$]. Consumption of sucrose was significantly greater for the white-eared than for the red opossums [$F(1,18)$ for species = 14.48, $p = .0013$], but the magnitude of the contrast effect did not vary significantly with species [$F(1,18)$ for the interaction of groups $\times$ species = 2.48, $p = .1323$], or as a function of repeated shifts [$F(3,54)$ for the interaction of groups $\times$ shifts = 1.92, $p = .1370$].

In Figure 2, the results for the two species are plotted in terms of mean drinking time. These curves are very much the same in pattern as those for amount consumed, with negative contrast appearing in every shift except the first for the red opossums. An overall analysis of variance again shows a significant contrast effect [$F(1,18)$ for groups = 5.53, $p = .0303$], a significant species effect [$F(1,18) = 18.17$, $p = .0005$], and an insignificant groups $\times$ species interaction ($F < 1$). For the time scores, however, the magnitude of the contrast effect varied significantly as a function of repeated shifts [$F(3,54)$ for the interaction of groups $\times$ shifts = 3.45, $p = .0331$]. It should be noted explicitly as an exceptional case that the

distributions of the time scores were such as to permit analysis of variance without transformation.

DISCUSSION

This experiment with marsupials provides both direct and indirect support for the hypothesis that successive negative incentive contrast reflects the operation of a mechanism that evolved in some common reptilian ancestor of birds and mammals. The support is direct in that the positive results obtained are predicted by the hypothesis. The support is indirect in that the positive results add to our confidence in the negative results obtained in work with other species. Since there is no reason to believe that the method employed here is more powerful than all of the various methods employed in experiments with fishes, toads, and turtles, we are encouraged in the belief that the effect failed to appear in those animals because it was not there.

In contributing to the meaningful pattern of results obtained in these comparative experiments on contrast—meaningful with respect to the evolutionary relationships among the species compared—the present work serves also to support the underlying strategy (Bitterman, 1960, 1975). It has been suggested that comparisons of such distantly related animals as “teleost fish, turtles, pigeons, rats, and monkeys . . . do not permit generalizations to be made about the evolution of intelligence or any other characteristic of these organisms” (Hodos & Campbell, 1969, p. 345); that if the results of comparative studies “are to be meaningful in terms of present-day interpre-

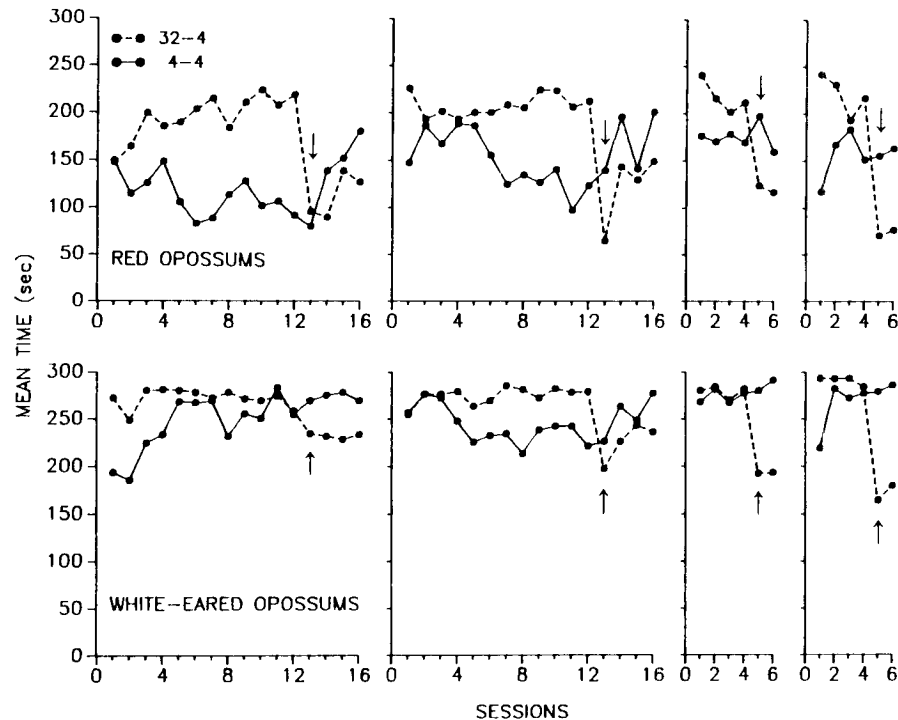


Figure 2. Mean drinking times in each session for the two groups of each species. The arrows show the points at which the concentration of sucrose for the contrast animals (32-4) was down-shifted.

tations of the evolutionary history of vertebrates," the animals compared "should be descendents of a common lineage" (Hodos, 1970, p. 37); and that "we must not expect to find smooth progressions from one major taxon to the other" (Hodos, 1982, p. 53). The contrast results, fragmentary as they are, clearly permit a meaningful generalization about a smooth progression, which may, of course, at any moment be proved incorrect by new experiments with other species of the same or different lineages—generalizations are born to be contradicted. There may in fact be no such progressions, but if there are (which we simply have no good reason to doubt), they will not be found until we look for them in comparative experiments with animals of different lineages.

REFERENCES

- BITTERMAN, M. E. (1960). Toward a comparative psychology of learning. *American Psychologist*, **15**, 704-712.
- BITTERMAN, M. E. (1975). The comparative analysis of learning. *Science*, **188**, 699-709.
- BITTERMAN, M. E. (1984). Migration and learning in fishes. In J. D. McCleave, G. P. Arnold, J. J. Dodson, & W. H. Neill (Eds.), *Mechanisms of migration in fishes* (pp. 394-420). New York: Plenum.
- BITTERMAN, M. E. (1986). La evolución del aprendizaje: Generalidad y divergencia [The evolution of learning: Commonality and divergence]. *Revista Latinoamericana de Psicología*, **18**, 247-262.
- COUVILLON, P. A., & BITTERMAN, M. E. (1985). Effect of experience with a preferred food on consummatory responding for a less preferred food in goldfish. *Animal Learning & Behavior*, **13**, 433-438.
- COWLES, J. T., & NISSEN, H. W. (1937). Reward expectancy in delayed responses of chimpanzees. *Journal of Comparative Psychology*, **24**, 345-358.
- CRESPI, L. P. (1942). Quantitative variation of incentive and performance in the white rat. *American Journal of Psychology*, **55**, 467-517.
- ELLIOTT, M. H. (1928). The effect of change or reward on the maze performance of rats. *University of California Publications in Psychology*, **4**, 19-30.
- FLAHERTY, C. F. (1982). Incentive contrast. A review of behavioral changes following shifts in reward. *Animal Learning & Behavior*, **10**, 409-440.
- FLAHERTY, C. F., BECKER, H. C., & CHECKE, S. (1983). Repeated successive contrast in consummatory behavior with repeated shifts in sucrose concentration. *Animal Learning & Behavior*, **11**, 407-414.
- GONZALEZ, R. C., & BITTERMAN, M. E. (1969). Spaced-trials partial reinforcement effect as a function of contrast. *Journal of Comparative & Physiological Psychology*, **67**, 94-103.
- GONZALEZ, R. C., FERRY, M., & POWERS, A. S. (1974). The adjustment of goldfish to reduction of magnitude of reward in massed trials. *Animal Learning & Behavior*, **2**, 23-26.
- GONZALEZ, R. C., GLEITMAN, H., & BITTERMAN, M. E. (1962). Some observations on the depression effect. *Journal of Comparative & Physiological Psychology*, **55**, 578-581.
- GONZALEZ, R. C., POTTS, A., PITCOFF, K., & BITTERMAN, M. E. (1972). Runway performance of goldfish as a function of complete and incomplete reduction in amount of reward. *Psychonomic Science*, **27**, 305-307.
- HODOS, W. (1970). Evolutionary interpretation of neural and behavioral studies of living vertebrates. In F. O. Schmidt (Ed.), *The neurosciences: Second study program* (pp. 26-47). New York: Rockefeller University Press.
- HODOS, W. (1982). Some perspectives on the evolution of intelligence and the brain. In D. R. Griffin (Ed.), *Animal mind-human mind* (pp. 33-56). Berlin: Springer.
- HODOS, W., & CAMPBELL, C. B. G. (1969). *Scala naturae*: Why there is no theory in comparative psychology. *Psychological Review*, **76**, 337-350.
- HULL, C. L. (1952). *A behavior system*. New Haven: Yale University Press.
- HULSE, S. H., JR. (1958). Amount and percentage of reinforcement and

- duration of goal confinement in conditioning and extinction. *Journal of Experimental Psychology*, **56**, 48-57.
- KIRKBY, R. J. (1977). Learning and problem-solving in marsupials. In B. Stonehouse & D. Gilmore (Eds.), *The biology of marsupials* (pp. 193-208). Baltimore: University Park Press.
- LONGO, N., & BITTERMAN, M. E. (1960). The effect of partial reinforcement with spaced trials on resistance to extinction in the fish. *Journal of Comparative & Physiological Psychology*, **53**, 169-172.
- LOWES, G., & BITTERMAN, M. E. (1967). Reward and learning in the goldfish. *Science*, **157**, 455-457.
- MACKINTOSH, N. J. (1971). Reward and aftereffects of reward in the learning of goldfish. *Journal of Comparative & Physiological Psychology*, **76**, 225-232.
- MAYR, E. (1968). The role of systematics in biology. *Science*, **159**, 595-599.
- PAPINI, M. R. (1986). Psicología comparada de los marsupiales [Comparative psychology of marsupials]. *Revista Latinoamericana de Psicología*, **18**, 215-246.
- PERT, A., & BITTERMAN, M. E. (1970). Reward and learning in the turtle. *Learning & Motivation*, **1**, 121-128.
- PERT, A., & GONZALEZ, R. C. (1974). Behavior of the turtle (*Chrysemys picta picta*) in simultaneous, successive, and behavioral contrast situations. *Journal of Comparative & Physiological Psychology*, **87**, 526-538.
- ROBERTS, W. A., BULLOCK, D. H., & BITTERMAN, M. E. (1963). Resistance to extinction in the pigeon after partially reinforced instrumental training under discrete-trials conditions. *American Journal of Psychology*, **76**, 353-365.
- ROMER, A. S., & PARSONS, T. S. (1986). *The vertebrate body* (6th ed.). Philadelphia: Saunders.
- SCHMAJUK, N. A., SEGURA, E. T., & RUIDIAZ, A. C. (1981). Reward downshift in the toad. *Behavioral & Neural Biology*, **33**, 519-523.
- SCHUTZ, S. L., & BITTERMAN, M. E. (1969). Spaced-trials partial reinforcement and resistance to extinction in the goldfish. *Journal of Comparative & Physiological Psychology*, **68**, 126-128.
- TINKLEPAUGH, O. L. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology*, **8**, 197-236.
- TOLMAN, E. C. (1932). *Purposive behavior in animals and men*. New York: Century.
- WAGNER, A. R. (1961). Effects of amount and percentage of reinforcement and number of acquisition trials on conditioning and extinction. *Journal of Experimental Psychology*, **62**, 234-242.

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