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Auditory quality cues are more effective than auditory location cues in a R - no R (go - no go) differentiation: the extension of the rule to primitive mammals (American opossum, *Didelphis virginiana)*

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Abstract. Discrimination learning of instrumental responses to auditory compound stimuli was investigated in opossums using the R - no R (go - no go) differentiation. Each compound stimulus consisted of two factors: quality and location. Each correct response performed to the conditioned positive, or "safe" stimulus, was rewarded by food and never punished. Each incorrect response performed to the conditioned negative, or "warning" stimulus, was punished by an electric shock. In subsequent testing, each opossum proved to use only the quality cues to solve the task even though later testing showed them capable of using the location cues. Thus, the rule discovered in higher mammals, that the efficacy of auditory stimuli in differentiation depends on the perceptual ability of the animal as well as the type of the behavioral response with which the animal is confronted, may be extended to neurologically primitive mammals and also to a joint conditioned approach-avoidance method.

Key words: conditioned avoidance, conditioned approach, auditory quality, auditory location, R - no R (go - no go) differentiation, opossum

Short communication

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In the natural environment an animal is confronted with sounds of several physical attributes (e.g., intensity, frequency, spectrum) from sound sources with their own set of attributes (e.g., direction, distance and character). Recently, physiological experimentation on the mammalian central auditory system has shown that sound-quality discriminations (such as frequency analysis) rarely show a deficit after any central auditory lesion while sound-source discriminations (such as sound localization) almost always show deficits after the same central lesion (Masterton 1992). It follows that sound-source discriminations require auditory analytical mechanisms beyond that of the ear. The question arises as to the relative efficacy of these two classes of stimuli in auditory learning and particularly in approach-avoidance learning (e.g., Jane et al. 1965).

The goal of the present research was to compare the effectiveness of sound-quality cues with sound--source location cues in a discrimination learning task, using the same avoidance learning task usually used for testing the perceptual abilities of mammals (e.g., see Heffner and Heffner 1995). The experiment has been performed on opossums, which are neurologically primitive mammals in the evolutionary aspect (see Frost and Masterton 1992).

Four wild-born adult female American opossums (*Didelphis virginiana*) were trained daily in a sound-proof chamber. Two loudspeakers, one 60° to the left (L) and the other 60° to the right (R), were used as "location" cues. Two other cues, one a continuous white noise (C) and the other a 5 per s pulsing white noise (P), were used as "quality" cues. Each training stimulus was a compound of the two types of cues consisting of a quality factor (C or P) and a location factor (L or R). The intensity of each stimulus was presented at random intervals from X s to Y s, always at 51 dB SPL with a 3 s duration. The background noise level was 54 dB.

To remove possible sensory or motor biases, the compound stimuli were counterbalanced. The animals were divided into two groups. In one group of two animals (designated "C"), the positive (or "safe") stimulus was a continuous noise "C", from the left "L" and can be referred to as "LC" while the negative or warning stimulus was a right (R) pulsing (P) noise designated "RP". After this training, these opossums were tested for their responses to the two other compounds: that is, the animals trained on LC safe and RP warn received test trials on LP and RC. The other group of animals (designated "P"), trained on LP safe vs. RC warn, was tested on LC and RP (Table I).

The opossums were trained to maintain contact with a metal food trough in order to receive a flow of pureed food. As long as the opossum was in contact with the spout, food was continuously delivered. This method is a variation of one described previously for cats (Masterton and Granger 1988, Masterton et al. 1992).

After the opossum learned to lick the food trough continously for long periods of time (10-20 min), the entire daily session was divided into 3-s periods. The last one second of each period was used to determine whether cessation of contact with the food trough had occurred for that period. The computer divided this last second into ten bins and recorded contact for each bin. Therefore, a time-in-contact score from zero to ten could be recorded for every period throughout the session. Either the "safe" or "warning" stimulus was then presented at random intervals but only when the opossum had been in contact with the spout during the preceding two periods.

Each animal was trained to perform the instrumental response of touching the spout during the last one second of the safe stimulus; this response was reinforced by continuation of the food delivery. Response to the warning stimulus was reinforced by an electric shock of 0.4 mA (see Masterton

TABLE I

Training and testing on groups C and P

	Group C		Group P	
	L	R	L	R
C	train	test	test	train
P	test	train	train	test

et al. 1992 for details) delivered through the trough itself. The duration of the shock was restricted to one second, delivered during the last (third) second of the warning stimulus. Because the opossum could break contact with the trough at any time, the shock was both avoidable and escapable.

The opossums learned to perform the instrumental licking response on safe trials and to refrain from this response on warning trials, according to the R - no R procedure (Stasiak and Ławicka 1991). Consequently errors on safe trials consisted of response omission and were designated as "false alarms". Errors on warning trials consisted of touching the spout and were designated as "misses".

The training involved four stages. In Stage I the opossums were trained with only safe stimuli; each session consisted of 12 trials. In Stage II the warning stimulus was introduced; each session consisted of 12 safe and 12 warning trials presented in a pseudo-random order. In each of the first two stages the animals were trained to a minimum 90% correct performance in 5 successive daily sessions; hence, with 60 trials in Stage I and 120 trials in Stage II.

In Stage III, the unreinforced test trials were introduced (Table I). This testing of the novel compound stimuli lasted 5 sessions with 6 additional trials per session. Thus, each session now consisted of 30 trials, 24 reinforced trials using the same stimulus compounds with which the opossums had been trained and 6 unreinforced test trials with the new stimulus compounds. In Group C the test trials were RC (3 trials in each session) and LP (3 trials in each session); in Group P the test stimuli were RP and LC. In the test trials the shock was never delivered. It is important to note that these same combinations of quality and location cues had never been delivered previously.

Finally, to be sure the opossums were capable of discriminating the location cues (i.e., Left vs. Right) in Stage IV, the quality factor was not varied leaving only location as a cue. In Group C the safe stimulus was presented from the left (L) loud--speaker (LC), and the warning stimulus was presented from the right (R) loudspeaker (RC). In Group P the safe and warning stimuli were LP and RP, respectively. For Stage IV a softened criterion was used; the criterion was limited to only one session with a maximum of two errors: one "false alarm" and one "miss".

In each session the intertrial intervals lasted between 10 and 30 periods, i.e., between 0.5 and 1.5 min. The daily session usually lasted from 30 to 40 min and was divided into two parts. During the first part the trials occurred. In the second part, the opossum was allowed to lick the spout *ad libitum*.

The opossums attained the criterion in Stage I almost immediately (Table II), and only one animal (DD3) needed one additional session. Introducing negative compound stimuli in Stage II lowered the animals' performance level on safe trials, which was reflected in an increase in "false alarms" (Table II). The majority of errors were on warning trials: that is, in "misses" (Table II).

Introducing test trials in Stage III did not change the performance level on regular trials (i.e., with the pre-trained compounds). The performance level continued at 90% correct responses for each opossum.

The important result, however, is that in the test trials each animal responded almost exclusively to quality cues (Table III) and neglected the location cues. That is, the safe stimulus placed in the position of the warning stimulus, maintained its safety signalling value (Table III); the opossums approached the spout to the new compound stimulus. In addition, the warning stimulus placed in the locus of the safe stimulus, retained its warning significance

TABLE II

Individual error scores (including criterion sessions) on the first two stages of the training

Group	Opossum	Stage I		Stage II		
		Trials	False alarms	Trials	False alarms	Misses
C	DD1	60	1	840	39	158
	DD2	60	1	1296	51	368
P	DD3	72	8	120	4	2
	DD$	60	0	1104	32	188

TABLE III

Results of test trials introduction in Stage III: number of unreinforced responses to quality (Q) and to direction (D)

Group	Opossum	Reversed location of safe		Reversed location of warning	
		Q	D	Q	D
C	DD1	12	3	14	1
	DD2	14	1	11	4
P	DD3	15	0	15	0
	DD4	14	1	13	2
C+P	Total	55	5	53	7

(Table III) and the opossums avoided the trough during the new compound stimulus. In general, the opossums reacted according to the quality of the conditioned stimulus in 90% of the test trials.

Finally, removing the quality cue in Stage IV resulted in rapid and long-lasting deterioration of the performance. Two opossums were unable to achieve the one-session criterion (Table IV) within the limit of 15 sessions (360 trials). The two other animals required 240 and 216 trials, respectively (that is, 10 or 9 sessions) to achieve the softened criterion (Table IV).

The results show that normal opossums are able to solve a simple R - no R differentiation task involving auditory compound stimuli (consisting of both quality and location factors), when conditioned approach-avoidance method is used. In training involving both safe and warning stimuli the animals were able to solve the differentiation by a discrimination of two auditory compound stimuli - one positive and one negative. The answer to the question whether the opossums' learning was based on the detection of difference between the continuous and pulsing white noise, or on detection of the difference between the two locations of the noises was unequivocal. Although capable of using either quality or direction, the opossums invariably choose quality over location or direction as the salient cue (Table III).

TABLE IV

Stage IV: the L-R differentiation. The same quality delivered from the L loudspeaker as well as from the R loudspeaker. The asterisk indicates that the criterion was not achieved within the 15 sessions. Percentage in the parenthesis denotes the score in the last session

Group	Opossum	Trials	False alarms	Misses
C	DD1	360*	73 (50%)	110 (50%)
	DD2	240	31	63
P	DD3	216	5	65
	DD4	360*	58 (42%)	102 (58%)

It is known that the nonsymmetrically reinforced the R - no R (go - no go) differentiation of instrumental responses (Stasiak and Ławicka 1990) is difficult to achieve when the only auditory location cues are presented and food reinforcement is used (see Konorski 1973 for discussion). On the contrary, the R_1 - R_2 differentiation, where instead of positive and negative stimuli only positive stimuli are applied, is very easy to achieve when auditory location stimuli are presented and food reward is used (Ławicka 1964, 1969). This case of learning extends to a triple-choice situation (e.g. Stasiak and Żernicki 1993). Alternatively, the R - no R differentiation is easy when the quality cues are presented, and the R_1 - R_2 (go left - go right) differentiation is difficult when the quality cues are used (Ławicka 1964, 1969, Ławicka et al. 1975). Hence in general, the differentiation of instrumental responses depends not only on the perceptual ability to discriminate between the stimuli, but also on the type of used behavioural task required.

The present results using a conditioned approach-avoidance method show that opossums invariably utilize quality cues to solve the R - no R differentiation task (see Table III). Furthermore, after quality was removed as a cue and only location remained, opossums show great difficulty in relearning the same task (see Table IV).

These data are consistent with the results obtained on dogs using conditioned approach methods (Dobrzecka et al. 1966, Ławicka 1969). They too,

exhibit difficulties in the stage of that training (see Table IV). These difficulties are understandable, however, since in approach methods the different auditory localization cues are related to the different motor acts (responding to left, responding to right) while in the present task only one instrumental response is required: non-directional withdrawal (see Ławicka 1969 for discussion).

In conclusion, the general rule that higher mammals use auditory quality cues and not auditory location cues to solve the R - no R differentiation may be extended to neurologically primitive mammals and approach-avoidance learning. Nevertheless, some opossums are able to solve the R - no R differentiation with the location cues alone when both the perceptual requirements of the task and the criteria are markedly softened (Masterton and Stasiak, in preparation).

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