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THE COMBINATION OF APPETITIVE AND AVERSIVE REINFORCERS AND THE NATURE OF THEIR INTERACTION DURING AUDITORY LEARNING

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Abstract—Learned changes in behavior can be elicited by either appetitive or aversive reinforcers. It is, however, not clear whether the two types of motivation, (approaching appetitive stimuli and avoiding aversive stimuli) drive learning in the same or different ways, nor is their interaction understood in situations where the two types are combined in a single experiment. To investigate this question we have developed a novel learning paradigm for Mongolian gerbils, which not only allows rewards and punishments to be presented in isolation or in combination with each other, but also can use these opposite reinforcers to drive the same learned behavior. Specifically, we studied learning of tone-conditioned hurdle crossing in a shuttle box driven by either an appetitive reinforcer (brain stimulation reward) or an aversive reinforcer (electrical footshock), or by a combination of both. Combination of the two reinforcers potentiated speed of acquisition, led to maximum possible performance, and delayed extinction as compared to either reinforcer alone. Additional experiments, using partial reinforcement protocols and experiments in which one of the reinforcers was omitted after the animals had been previously trained with the combination of both reinforcers, indicated that appetitive and aversive reinforcers operated together but acted in different ways: in this particular experimental context, punishment appeared to be more effective for initial acquisition and reward more effective to maintain a high level of conditioned responses (CRs). The results imply that learning mechanisms in problem solving were maximally effective when the initial punishment of mistakes was combined with the subsequent rewarding of correct performance.

Key words: reinforcement learning, rodent, reward, punishment, shuttle-box.

Conditioning involves the association of neutral stimuli with appetitive or aversive reinforcers. Animals direct their behaviors, in both natural and laboratory situations (e.g. instrumental conditioning experiments), in such a way as to obtain appetitive reinforcers (“rewards”) and avoid aversive reinforcers (“punishments”). In most animal conditioning experiments, behavioral measures of conditioning and of brain systems have been studied with one type of reinforcer (appetitive or aversive) only. Hence, the nature of the interaction between appetitive and aversive reinforcers during associative learning in the same experimental situation is not well understood. Scrutinizing this interaction experimentally meets with substantial difficulties (see Dickinson, 1976; Mackintosh, 1983; Magoon and Critchfield, 2008 for an overview of the underlying theoretical problems). On the procedural side there has been a lack of learning paradigms that train the same behavior using both appetitive and aversive reinforcers delivered with the same temporal contingency and titrated to achieve comparable effects, such that their combinatorial influence can be quantified. Consequently, most classical work on the subject has relied on indirect methods, typically utilizing sequential interaction between reward-driven and punishment-driven tasks.

Early work by Konorski and collaborators on stimulus approach and withdrawal proposed that the interaction between appetitive and aversive reinforcers is mutually inhibitory in nature (Konorski and Szwejkowska, 1956; Konorski, 1967). Subsequent studies addressed the behavioral influence of stimuli associated with one type of reinforcer on stimuli associated with the other, using summation, retardation and counter-conditioning procedures (Dickinson and Pearce, 1977; Dickinson and Dearing, 1979; Mackintosh, 1983). Here also, an aversive stimulus was observed to suppress an appetitive response, and an appetitive stimulus was observed to suppress an aversive response (Estes and Skinner, 1941; Dickinson and Pearce, 1977).

Scavio (1974) demonstrated that preconditioning stimuli with shock impaired the further development of an appetitive response in rabbits. Appetitive conditioning and avoidance learning using the same stimuli indicated that appetitive and aversive conditioned motivational states interact substractively (Bull, 1970). A conditioned stimulus (CS) associated with shock can inhibit the association of a CS paired with the omission of expected food reward (Dickinson and Dearing, 1979). The underlying motivational states of reinforcer interaction were also investigated using stimulus preexposure or preconditioning with one reinforcer. Fear conditioning was greatly enhanced if the CS was previously paired with food (Dickinson, 1977).

The above studies strengthen the argument that appetitive and aversive reinforcers can indeed interact. How-

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Abbreviations: BSR, brain stimulation reward; CR, conditioned response; CS, conditioned stimulus; FS, foot shock; RT, reaction time; VTA, ventral tegmental area.

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ever, once the behavior is learned, intrinsic motivation also drives and strengthens associative learning (cf. Rolls, 2008). It has been demonstrated that, irrespective of reinforcer presentation, response-contingent neutral stimuli also can have intrinsic reinforcing properties (Reed et al., 1996). Stimulus generalization gradients in appetitive and aversive reinforcement investigated with two different responses showed that gradients of effect were different for the two types of reinforcers (Hearst, 1960).

In order to compare the potentially different roles of reward and punishment, it is desirable to develop behavioral procedures which can incorporate both types of reinforcers within the same training session (e.g. Magoon and Critchfield, 2008; Morrison and Salzman, 2009) as most previous experiments measured the effect of one reinforcer on the previously established conditioned response (CR) by the other reinforcer. Previous work had studied excitatory or inhibitory interactions between sequential reward- and punishment-driven learning processes (Dickinson, 1976, 1977; Dickinson and Mackintosh, 1978), concurrent schedules of reward and punishment without conditioned stimuli (Kelleher and Cook, 1959; Olds and Olds, 1962), combinations with secondary reinforcers associated with the opposite valence (Morris, 1975; Baron et al., 1977), and non-contingent schedules of aversive and appetitive reinforcers (Stein, 1965; Margules and Stein, 1968; Carder, 1970; Castro-Alamancos and Borrell, 1992). The design of the present set of experiments allowed us to demonstrate an equivalence of reward and relief from punishment in the sense of two forces acting towards a convergent effect. At the same time we could dissociate their different contributions to the early and late phases of a learning process.

Conventional reinforcers such as food and footshock (FS) involve different behavioral contingencies which are not easily combined in the same experiment and involve different forms of information processing. Also, a principal difference between appetitive and aversive reinforcers is that the effect of appetitive reinforcers typically saturates with prolonged presentation while the effect of aversive reinforcers does not. If we assume that avoidance responses must come under the control of additional positive incentives, the concept of combining "carrot and stick" arises: how effective is learning if an aversive stimulus is experienced upon unsuccessful avoidance and an appetitive stimulus is experienced upon successful avoidance?

Efforts have already been made to demonstrate the facilitation of learning using non-contingent application of positively reinforcing brain stimulation on aversive avoidance behavior (Margules and Stein, 1968; Castro-Alamancos and Borrell, 1992). Also, rewarding brain stimulation reduced the aversive reinforcing property of electric shock when both reinforcers were paired (Cox and Valenstein, 1965; Carr and Coons, 1982). Positively reinforcing posterior hypothalamic brain stimulation was used as a CS to signal the aversive FS; however, it further reduced the self stimulation performance during the post-conditioning sessions (Mogenson and Morrison, 1962). Facilitation of shuttle-box avoidance learning was observed if the animals were allowed to self-stimulate for lateral hypothalamic brain stimulation immediately after the avoidance learning sessions (Aldavert-Vera et al., 1997). The difference between earlier studies and our investigation is the following: we deliver the internal reward for successful avoidance in a similar contingent way as the FS for unsuccessful avoidance and thereby address the nature of their interaction.

Here, we addressed the interaction of appetitive and aversive reinforcers in Mongolian gerbils (*Meriones unguiculatus*) during 2-way hurdle crossing in a shuttle box using auditory stimuli as CS, FS as an aversive reinforcer and brain stimulation reward (BSR), that is electrical stimulation of the ventral tegmental area (VTA), as an appetitive reinforcer. Our previous studies have demonstrated that Mongolian gerbils are suitable animal model to investigate auditory learning (Wetzel et al., 1998, 2008; Ohl et al., 1999, 2001). In preparatory experiments, current strengths for FS and VTA stimulation were separately calibrated to produce the same asymptotic level of behavioral performance in individual animals. After studying the effect of both reinforcers separately, we addressed reinforcer integration using FS as an aversive reinforcer upon each unsuccessful trial and BSR as an appetitive reinforcer upon each successful trial. This matched power of the reinforcers, in principle, allowed us to determine any possible type of interaction in combined experiments. FS-reinforced learning is initially dominated by aversive experience which leads to subsequent relief upon successful avoidance. Therefore, the primary question we addressed was whether effects from punishment and rewards inhibit each other, or alternatively, whether the relief from punishment and receipt of reward input facilitate the learning process (equivalence hypothesis) (Dinsmoor, 2001).

The dopamine signal from the midbrain substantia nigra pars compacta (SNc) and the VTA contributes to associative learning processes in which the exact timing of the reinforcement is vital (Schultz et al., 1997). Consistent with the role of dopamine as an encoder of stimulus-response associations which drive an instrumental act, dopamine medications in neuropsychiatric patients improved learning from success (Frank et al., 2004).

To obtain a comprehensive understanding of the effects of combining appetitive and aversive reinforcers to drive the associative learning we studied (1) acquisition and extinction using separate and combined reinforcers, (2) omission of one reinforcer in the combination experiment after animals had reached maximum performance followed by omission of the remaining reinforcer (extinction), and (3) omissions after partial reinforcement procedures.

EXPERIMENTAL PROCEDURES

Animals

A total of 80 adult male Mongolian gerbils (Meriones unguiculatus) obtained from Tumblebrook Farms, West Brookfield, MA, USA (age: 3–6 months, weight: 85–105 g) were used in this study. Gerbils were individually housed 3 days before experiments started and maintained on a 12 h light/dark cycle (light on 7:00–19:00 h) throughout the experiment. All experimental procedures