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Discrimination: From behaviour to brain

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Abstract

Discrimination is a skill needed by many organisms for survival: decisions about food, shelter, and mate selection all require the ability to distinguish among stimuli. This article reviews the how and why of discrimination and how researchers may exploit this natural skill in the laboratory to learn more about what features of stimuli animals use to discriminate. The paper then discusses the possible neurophysiological basis of discrimination and proposes a model, based on one of stimulus-association put forth by Beninger and Gerdjikov (2004) [Beninger, R.J., Gerdjikov, T.V., 2004. The role of signaling molecules in reward-related incentive learning. Neurotox. Res., 6, 91–104], to account for the role of dopamine in how an animal learns to discriminate rewarded from non-rewarded stimuli.
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1. Introduction

This paper examines the possible role of dopamine (DA) in learning appropriate responses to rewarded and unrewarded stimuli used in discrimination tasks, whether in a laboratory or natural setting. I first present a review of discrimination learning: why it is important to so many organisms, how animals discriminate, and how aspects of discrimination may be manipulated by researchers to discover such things as stimulus features used for discrimination or specialized abilities to discriminate. I then discuss the neurophysiological basis of discrimination learning, with specific attention given to the role that DA may play in signaling the presence of rewarded and unrewarded stimuli. I present a model, originally introduced by Beninger and Gerdjikov (2004) of the proposed neural circuitry involved in associative learning, but modified and expanded to explain changes that may occur during discrimination learning. This model is supported by evidence from several species showing that DA is active during discrimination learning, and varies depending on whether the animal experiences reward or no reward. Finally I discuss the predictions the model makes and future research needed to address these predictions.

2. Why discrimination?

Learning about the environment in which you exist is critical for adjusting behaviour for survival. One form of learning, viz., associating a positive outcome with otherwise neutral stimuli, can be applied to many human and non-human behaviours, such as identifying a particular location (an otherwise neutral stimulus) to obtain food (positive outcome). This learning could be of two types: pavlovian (stimulus-outcome), or instrumental (stimulus-response; see Day and Carelli, 2007 for review). However, associative learning only accounts for part of the story: what about other stimuli encountered that produce different results, such as punishment, less reward, or even neutral outcomes? Animals must be able to discriminate between different stimuli in their environment as a pre-requisite for differentially associating them with an outcome. Decisions based on discrimination of stimuli can affect survival, for example, what food to ingest (is this poisonous or nutritious?), where to build a home (is this a safe or dangerous location?) and what conspecific is the best mate (which male will produce the strongest offspring?). If an organism could not discriminate among stimuli and associate them with particular consequences, they would risk ingesting the wrong food, nesting in the wrong place, or mating with the wrong mate or even species, thereby decreasing chances of survival of the organism and ultimately, the species. Therefore, discrimination, as well as association, is an important skill that most organisms must use daily.

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3. How do they do it?

Discrimination relies on an organism's ability to perceive features of stimuli, features we can label as "cues". Organisms can then use these cues to distinguish among stimuli with those features. Cues may be of any modality; one needs only to think of the five senses to begin the list: visual, acoustic, somatosensory, gustatory or olfactory. There are also cues within these categories and outside the human range of perception, such as ultraviolet light (e.g. chickadees: Doucet et al., 2005), ultrasonic vocalizations (e.g. rats: D'Amato et al., 2005), electroreception (e.g. weakly electric fish: Zhou and Smith, 2006), or magnetic fields (e.g. migratory birds: Mouritsen and Thorston, 2005). Cues may be used singly or in combination with other cues of the same modality (i.e. two visual cues such as motion parallax and occlusion for monocular depth perception) or cross-modal cues (e.g. both visual and auditory cues for localization). Multiple cues may elicit maximal behavioural response, for example, mother rats oriented most quickly to a pup when both ultrasonic vocalizations played from a speaker and olfactory cues from a pup near the speaker were present, compared to vocalizations or the pup alone (Farrell and Alberts, 2002). The availability of multiple cues may also enhance accuracy in (natural) discrimination tasks (e.g. human beings, Kunnapas, 1968; spiders, Uetz and Roberts, 2002; songbirds, Naguib, 1998).

What do organisms need in order to discriminate features of stimuli? First, they require the ability to perceive the feature or cue in the modality presented: humans, for example, are physiologically unable to hear ultrasonic vocalizations and can therefore not discriminate among them. As a corollary of the behavioural importance of a cue modality, species may show superior discrimination performance when using cues of the modality in which they specialize, such as rats' superiority at performing tasks using olfactory, rather than visual or auditory, information (see Slotnick, 2001 for review). Within a modality, certain types of cues may be better discriminated than others (e.g. position vs. feature cues in whiptail lizards, Day et al., 2003). Further, certain species may be much better at discriminating cues in a specific modality than other species. For example, when comparing the performance of humans, rats, and songbirds in the same auditory discrimination task, songbirds far out-performed both rats and humans when discriminating tonal frequencies divided into rewarded and non-rewarded ranges (Weisman et al., 2004). Even within species there may be specialization: comparison of two songbird species, chickadees and zebra finches, on a distance cue discrimination task revealed superior performance by chickadees (Phillmore et al., 1998).

In order to perform discriminations based on stimulus features, animals must have enough resolution in their perceptual/neural systems to distinguish feature differences in the stimuli. Weisman et al. (1998) used a connectionist model to compare performances of songbirds and humans on a multi-frequency range discrimination task. Both zebra finches and humans were presented randomly on each trial with one of 40 pure tones ranging from 980 to 5660 Hz in a go/no-go operant discrimination task. Frequencies were grouped into alternating rewarded (go) and non-rewarded (no-go) sets of 5 adjacent tones each. On any given trial, a subject/participant must decide if the tone was rewarded, and therefore respond, or non-rewarded, and therefore withhold response. After thousands of trials, songbirds discriminated precisely among all individual frequencies, regardless of location in the range. Humans, however, could report accurately only on the highest and lowest frequencies. Weisman et al. explained this by proposing that the spread of excitation from sensory input was wider across tonotopic units connected to outcome units in humans than in zebra finches. This meant that in humans, a greater proportion of outcome units was activated for each individual frequency presented compared to songbirds, and therefore humans displayed less ability to resolve accurately the differences between individual tones; in turn, human beings could not respond appropriately within the borders of rewarded and unrewarded frequency ranges. Research comparing frequency tuning in cochlear neurons of humans and another species of songbird, the European starling (Sturnus vulgaris), shows that songbirds do not have more finely tuned frequency responses (Ruggero and Temchin, 2005). However, narrower frequency tuning, or some other change in stimulus representation, could be further up in the ascending sensory system, such as in neurons of the primary auditory cortex, and could be different in other species of songbirds.

Besides having the perceptual/neural capability to distinguish features of stimuli, the organism must also be able to associate stimuli with behaviour. In other words, it must be able to respond to the differences in the cues they have perceived. For example, songbird mating strategies usually involve female sexual selection. A female songbird must first be able to perceive features of a male that are indicative of quality, such as song repertoire size (Searcy and Yazukawa, 1996), performance of difficult songs (Ballentine et al., 2003) or feather markings (e.g. Cordero et al., 1999). However, a female songbird must not only perceive the difference between two conspecifics based on these features, but must also choose to mate with the male of better quality. Unless she actually mated with the male with the better song repertoire, discriminative ability would have no bearing on what would become, essentially, random choice.

Finally, the animal must have the ability to appropriately link their responses to stimuli with consequence. For example, in an operant discrimination paradigm, a songbird must link the response it makes to S+s with the delivery of food (e.g. "near" vocalizations", and the absence of that reward with S−s (e.g. "far" vocalizations") in order to successfully obtain food when it is available. Evidence that this link has been made can be demonstrated by asymptotic measures of performance, and generalization to similar stimuli (e.g. Phillmore et al., 1998).

4. How can we understand it?

In order to understand the process of discrimination further by studying it in a laboratory setting, researchers can exploit both the ability to perceive differences in stimuli and the ability to associate stimuli with responses. Researchers can set up contingencies based on discrimination of cues: responses to stimuli with particular features result in a particular outcome, either positive (reward) or negative (punishment or non-reward).

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