Neuroscience and Biobehavioral Reviews 71 (2016) 829–848

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

# Appetitive Pavlovian-instrumental Transfer: A review

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ARTICLE INFO

*Article history:*
Received 7 February 2016
Received in revised form
23 September 2016
Accepted 23 September 2016
Available online 28 September 2016

*Keywords:*
Pavlovian conditioning
Instrumental conditioning
Transfer
PIT
Review

ABSTRACT

Reward-related cues are an important part of our daily life as they often influence and guide our actions. This paper reviews one of the experimental paradigms used to study the effects of cues, the Pavlovian to Instrumental Transfer paradigm. In this paradigm, cues associated with rewards through Pavlovian conditioning alter motivation and choice of instrumental actions. The first transfer experiments date back to the 1940s, but only in the last decade has it been fully recognised that there are two types of transfer, specific and general. This paper presents a systematic review of both the neural substrates and the behavioral factors affecting both types of transfer. It also examines the recent application of the paradigm to study the effect of cues on human participants, both in normal and pathological conditions, and the interactions of transfer with drugs of abuse. Finally, the paper analyses the theoretical aspects of transfer to build an overall picture of the phenomenon, from early theories to recent hierarchical accounts.



**Contents**

1. Introduction ..... 830
   1.1. Scope and purpose of the review ..... 831
2. The transfer paradigm ..... 831
3. Behavioral results – variables influencing transfer ..... 833
   3.1. Pavlovian factors ..... 833
   3.2. Instrumental factors ..... 834
   3.3. Other factors and results ..... 835
4. Neural substrates ..... 835
   4.1. Amygdala and nucleus accumbens ..... 835
   4.2. Molecular processes in nucleus accumbens ..... 836
   4.3. Dorsal striatum ..... 837
   4.4. Midbrain structures ..... 837
      4.4.1. Dopamine ..... 837
   4.5. Prefrontal cortex ..... 838
   4.6. Neural correlates ..... 838
5. Interaction with drugs of abuse ..... 838
6. Human transfer ..... 840
7. Theoretical aspects of transfer ..... 841
8. Conclusions and future directions ..... 844
   References ..... 845

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http://dx.doi.org/10.1016/j.neubiorev.2016.09.020

**Glossary**

*Pavlovian conditioning*: During Pavlovian conditioning a neutral stimulus, such as a sound, becomes a conditioned stimulus (CS) by pairing its occurrence with an unconditioned stimulus (US) that naturally elicits some response. For example, a sound (CS) might be paired with food (US) by delivering food only when the sound is present. At the end of training, the animal/participant will have learned that the CS predicts the US and so it will approach the site of food delivery when it hears the sounds.

*Instrumental conditioning*: During instrumental conditioning an animal/participant is trained to make a response by delivering an attractive outcome. For example, a hungry rat might be trained to press a lever that delivers food. This training can lead to two kinds of instrumental behavior: habits, controlled by antecedent stimuli through the formation of stimulus-response (S-R) associations or goal-directed actions, controlled by the consequences of the action through the formation of action-outcome (A-O) associations.

*Devaluation*: Outcome devaluation is a procedure where the US or the outcome (O) value is altered. For example, the value of a certain food might be altered by feeding it to satiation or by pairing it with illness (the latter induced by lithium-cloride injections).

*Extinction*: A training session where the US predicted by a CS or the outcome (O) predicted by an action is no longer delivered, thus promoting the extinction of the Pavlovian conditioned response or the instrumental action.

## 1. Introduction

Predictive cues are an important part of our life that continuously influence and guide our actions. Hearing the sound of a horn makes us stop before we attempt to cross the street. Seeing an advertisement for fast food might make us hungry and lead us to seek out a specific type and source of food. In general, cues can both prompt us towards or stop us from engaging in a certain course of action. They can be adaptive (saving our life in crossing the street) or maladaptive, leading to suboptimal choices, e.g. making us eat when we are not really hungry (Colagiuri and Lovibond, 2015). In extreme cases they can even play a part in pathologies such as in addiction, where drug associated cues produce craving and provoke relapse (Belin et al., 2009).

One particular paradigm used to study the effect of such cues is the Pavlovian to Instrumental Transfer paradigm. In this paradigm, Pavlovian predictions and instrumental actions are first trained in separate experimental phases. The instrumental actions are then tested in both the presence and the absence of the Pavlovian cues to assess the effect of the latter on the former.

The first Pavlovian to instrumental transfer studies date back to the 1940s, reporting that stimuli paired with food were able to augment instrumental actions directed towards food (Estes and Skinner, 1941; Walker, 1942; Estes, 1943). Transfer effects can either promote or discourage actions, with the presence of cues increasing/decreasing the frequency of an action or biasing choice in favour of certain actions. Amongst other factors, the type of effect obtained depends on the valence of the Pavlovian US, i.e., whether it is appetitive or aversive. For example, a Pavlovian cue associated with an aversive shock might promote actions leading to shock avoidance but decrease actions leading to food (Rescorla and Solomon, 1967).

Our understanding of transfer has naturally developed with our understanding of Pavlovian and instrumental conditioning. At the same time, studying the interaction of Pavlovian and instrumental conditioning has often yielded new insights into these individual processes. At the time of the earliest studies, for example, it was not clear if Pavlovian and instrumental conditioning constituted different forms of learning. Gradually, however, two-process theories emerged that separated Pavlovian and instrumental processes (see Rescorla and Solomon (1967) for a review). Transfer effects were, at that stage, understood as the result of Pavlovian cues generating general appetitive or aversive emotional states and, indeed, the transfer paradigm was typically used to study the influence of conditioned emotional responses (Rescorla and Solomon, 1967). Subsequent studies refined this general emotional state finding that, in many conditions, transfer was better characterised as controlled by primary motivational processes than emotional states. So, for example, Dickinson and colleagues demonstrated in studies of the so called irrelevant incentive effect that a cue predicting sugar solution would enhance instrumental actions both when rats were hungry and when they were thirsty whereas a cue associated with dry food pellets would only elevate performance when hungry. These effects were generally interpreted as suggesting that primary motivational processes could modulate the production of conditioned emotional states, much as suggested by Bindra (Dickinson and Dawson, 1987; Balleine, 1994; Bindra, 1974). However, none of these accounts explained the influences of Pavlovian cues on choice: i.e., how Pavlovian cues could sometimes be found to enhance actions tied to a specific outcome, e.g. how a CS associated with grain pellets enhanced lever pressing for grain pellets but not for other food outcomes (such as sugar). One possibility is that both Pavlovian and instrumental conditioning lead to the formation of associations: stimulus-outcome associations (S-O) in one case and response-outcome associations in the other case (R-O), and that the common outcome mediates the interaction (Trapold and Overmier, 1972). In the 1980s and 90s much experimental work was devoted to establishing that instrumental conditioning could be subdivided into two types: habitual actions, controlled by stimulus-response (S-R) associations, and goal-directed actions, controlled by response-outcome (R-O) associations (Balleine and Dickinson, 1998). In parallel, a series of articles examined the ability of Pavlovian cues tied to a specific outcome to bias choice between specific actions (Colwill and Rescorla, 1988; Colwill and Motzkin, 1994; Rescorla, 1991, 1994a,b; Delamater, 1995, 1996). At the beginning of the century, investigation of the neural substrates of transfer began: some initially contrasting results led at that stage to the realisation that transfer effects come in two different forms and so had to be subdivided as well. These studies divided the phenomenon into specific and general transfer, each characterized by a different neural substrate (Corbit and Balleine, 2005, 2011, see Section 4). Specific transfer refers to the ability of cues to enhance specific actions associated with the same outcome as the cue, whereas general transfer refers to the ability of cues to enhance also actions paired with different outcomes.

Most data on transfer come from animal studies,[1] however in recent years the transfer paradigm has also been adapted for human participants. In general, human studies have produced similar results to animal studies both in terms of the behavioral factors

[1] Studies mostly involved rats, however other species have been used as well, such as mice (see Lederle et al., 2011 in different mice strains), monkeys (Stebbins and Smith, 1964), dogs (Rescorla and LoLordo, 1965), pigeons (Morse and Skinner, 1958) and even horses (Lansade et al., 2013).