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Review

The integrative function of the basal ganglia in instrumental conditioning☆

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ABSTRACT

Recent research in instrumental conditioning has focused on the striatum, particularly the role of the dorsal striatum in the learning processes that contribute to instrumental performance in rats. This research has found evidence of what appear to be parallel, functionally and anatomically distinct circuits involving dorsomedial striatum (DMS) and dorsolateral striatum (DLS) that contribute to two independent instrumental learning processes. Evidence suggests that the formation of the critical action–outcome associations mediating goal-directed action are localized to the dorsomedial striatum, whereas the sensorimotor connections that control the performance of habitual actions are localized to the dorsolateral striatum. In addition to the dorsal striatum, these learning processes appear to engage distinct cortico-striatal networks and to be embedded in a complex of converging and partially segregated loops that constitute the cortico-striatal thalamo-cortical feedback circuit. As the entry point for the basal ganglia, cortical circuits involving the dorsal striatum are clearly in a position to control a variety of motor functions but, as recent studies of various neurodegenerative disorders have made clear, they are also involved in a number of cognitive and executive functions including action selection, planning, and decision-making.

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In instrumental conditioning an animal's actions are, procedurally speaking, instrumental to the occurrence of some consequence or outcome. For most of the, now quite lengthy, period since it was first described, however, theories of instrumental learning have referred not to the consequences of actions but to their antecedents, regarding instrumental actions as a form of acquired reflex. Thorndike [1], for example, characterized this learning as 'trial and error' and formulated an associative theory of its acquisition encapsulated within the, so-called, 'law of effect'. According to this view, responses in a situation that result in satisfaction (later, more ambiguously, referred to as reinforcement, e.g. by Hull [2]) become more firmly (and responses resulting in dissatisfaction more weakly) connected with that situation; the probability of performing a response reflects, therefore, the strength of the situation–response (S–R) association.

Although there were quibbles over various aspects of S–R theory (e.g. [3,4]), its dominance over research in instrumental conditioning went unassailed for much of the 20th Century. Over the last

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two decades, however, this theoretical framework has been substantially and quite radically revised. It is now generally accepted that instrumental conditioning engages two distinct learning processes, one that can be characterized in S–R terms and a second, fundamentally different process through which animals encode the consequences of their actions and that we have proposed is critical to the acquisition and deployment of goal-directed actions [5–12]. Although S–R association can sometimes dominate (when actions become habitual), it now appears that, in most circumstances, the probability of a response is a product of associations with both its antecedents and its consequences, i.e. that these learning processes can exert a cooperative influence on the selection and initiation of instrumental actions. Indeed, at a neural level we have argued that managing the interplay between these two associative processes is the primary function of the basal ganglia [11–13].

In what follows we will briefly review the behavioral and neural evidence for these claims before considering two important issues involving, first, evidence for the distinct sources of these influences on performance at both a cortical and a striatal level and, second, the evidence demonstrating their integration in implementing a course of action and the role of the basal ganglia in this process. It will be noted that we plan here to focus primarily on the processes contributing specifically to instrumental conditioning. Other recent reviews have discussed the relationship between instrumental and Pavlovian conditioning processes and their neural bases in more detail and the interested reader is referred there for further discussion (cf. [7,14–16]).

1. Goal-directed action

1.1. Cognition, behavioral control and Pavlovian conditioning

Paradoxically, although the cognitive control of behavior has been of increasing interest to neuroscientists, research in this area has focused predominantly on predictive learning in Pavlovian conditioning paradigms such as fear conditioning and eye-blink conditioning. There is, however, no necessary relationship between cognition and the performance of the Pavlovian conditioned response (CR). Indeed, although it is not generally recognized, at an adaptive level a cognitive mechanism is of little *functional* value to a purely Pavlovian animal because the production of the CR is under the control of the CS–US association and is demonstrably not determined by a direct relationship between the CR and the US (e.g. [17–19]). As a consequence, although the production of the CR is clearly influenced by the nature of the CS–US association, no amount of refinement in the cognitive representation of the CS, US or their relationship can increase the ability of an animal to control the *direction* of the CR. In fact, a cognitive mechanism can only exert a functional effect on behavior when coupled to a process capable of modifying, withholding or reversing the direction of actions on the basis of that information, something that demands greater behavioral control than the system mediating Pavlovian conditioning provides (cf. [20,21] for further discussion).

For similar reasons, the Pavlovian paradigm can provide only a limited animal model of the effects of neuropathology on, so-called, executive functions in humans and that evidence suggests depend upon the integrity of various prefrontal-subcortical circuits [22–24]. Deficits in executive function have been generally described as comprising multiple components usually including volition, planning, and purposive action [25], capacities that fall outside the Pavlovian domain. The limbic cortices appear to be particularly heavily affected in executive dysfunction and several investigators have proposed that distinct constellations of symptoms may reflect the disconnection of this cortical area from specific subcortical regions such as the mediodorsal thalamus (in Alzheimers, e.g. [26]), areas of the striatum (in Parkinsons, Huntingtons and obsessive compulsive disorders, e.g. [27–31]), and the amygdala (in various emotional disorders, e.g. [32]). A disturbing feature highlighted in recent work is the increasing evidence for the early onset of many of the dysfunctions associated with these disorders, something that suggested to Brown and Marsden [27], amongst others, that even quite substantial motor deficits involving tremor and choreic symptoms may partially reflect a disorder in the sustained functioning of a prefrontal-basal ganglia-cortical feedback network engaged during planning, response selection and initiation. However, studying normal and pathological executive functions will require models of behavioral control that go beyond predictive learning to capture the processes engaged during the acquisition and implementation of new behavioral strategies.

1.2. Cognitive and motivational control of actions

Given these limits of Pavlovian processes, it is important to note that instrumental conditioning in rodents has been found to provide an alternative and quite accurate model of executive control generally and of human goal-directed action in particular. Models of human action (e.g. [33–36]) have tended to focus on two critical determinants of goal-directed actions: (1) their dependency on the experienced causal relation between acting (or not acting) and the occurrence of some consequence; and (2) the sensitivity of these actions to changes in the desirability of the consequences or goal of an action. From this perspective, actions that persist even when causally unrelated to their consequences or when those consequences are demonstrably no longer valued should not be regarded as goal-directed.

As we pointed out some time ago [5], this “desire plus belief” characterization of human actions can be used to distil two criteria, what we have called the contingency and the goal criteria, for the detection of goal-directed actions in any species. Since that time we have accumulated considerable evidence suggesting that, for the most part, the performance of instrumental actions by rodents satisfies these criteria. Not only are these instrumental actions highly sensitive to changes in the value of their associated outcome, i.e. post-training devaluation often produces profound changes in the subsequent rate of performance (cf. [6,7,10] for reviews), there is also considerable evidence suggesting that, unlike Pavlovian CR’s, these actions are sensitive to changes in the causal relation to their consequences; generally, rats will stop responding if performance no longer delivers the instrumental outcome and will stop responding even faster if their responding now cancels an otherwise freely available food [37,38]. Furthermore, using a schedule developed by Hammond [39], in which the probability of an outcome given a response (i.e. $p(\mathrm{O/R})$) and the probability of an outcome in the absence of that response ($p(\mathrm{O/noR})$) can be independently manipulated, we, amongst others, have reported clear evidence that performance declines as the latter probability increases, even when action–outcome contiguity (i.e. $p(\mathrm{O/R})$) is kept constant and at a rate that ordinarily maintains substantial levels of performance [8,9,40–43].

Given the clear sensitivity of actions to changes in the probability of outcome delivery it might also be expected that performance would also be sensitive to information concerning the likelihood of earning a particular outcome. And, indeed, there is considerable evidence that stimuli associated with rewarding events can exert quite specific effects on outcome selection and on choice in studies assessing Pavlovian-instrumental transfer. What has also become clear, however, is that this effect does not depend on the mere asso-