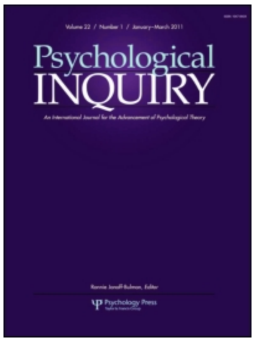

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Considering the Influence of the Pavlovian System on Behavior: Appraisal and Value Representation

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Introduction

Current theories of emotion vary with respect to many aspects such as the nature and function of emotion components, or the role of appraisal mechanisms in eliciting emotion responses (e.g., Coppin & Sander, 2016). Because most reviews of emotion theories tend to focus on differences and oppositions, Agnes Moors's (this issue) focus on similarities and shared ideas between two major theories of emotion represents an important and rare contribution to the field. Indeed, Moors's thoughtful and convincing attempt to integrate dimensional appraisal theory and psychological construction theory is a conceptual tour de force that is likely to advance our understanding of emotion: She clearly describes specific aspects that are critical to both theories, allowing to set some priorities for empirical research as it is arguably particularly important to test ideas that are shared by two of the most prominent theories of emotion. But Moors goes beyond bringing together these two theories. She brings a third approach into the conceptual analysis of the nature of appraisal mechanisms: general behavior theories, with an emphasis on a goal-directed mechanism (as opposed to a stimulus-driven mechanism). The aim of this commentary is to focus on this contribution to theories of emotion, in particular with respect to the appraisal of concern-relevance. Moors presents dual theories proposing that behavior is guided by two parallel and competing mechanisms, a goal-directed mechanism and a stimulus-driven mechanism. The goal-directed mechanism assesses the utility of one or multiple action options; the utility of these action options is based on the value that the outcome has for the individual as well as the expectancy that the action will lead to the outcome. Moors hypothesizes that this mechanism is dominant, as it is more likely to produce optimal behavior. In contrast, the stimulus-driven mechanism, which consists of an association between the representation of a specific stimulus's features and an action or response, is more basic and determines behavior only under certain circumstances such as poor operating conditions. Here we wish to complement this theoretical background by showing how it can be useful to consider the Pavlovian system (see, e.g., Clark, Hollon, & Phillips, 2012) as a third source of control on behavior and cognition. We also illustrate how the Pavlovian system's associative nature is conceptually similar to the stimulus-driven mechanism to some respect, but at the same time how it critically differs in the sense that it can be strongly influenced by outcome representation like the goal-directed mechanism Moors presented. Moreover we delineate the role the representation of the outcome value plays in eliciting an emotional response by highlighting possible underlying psychological mechanisms involved in the Pavlovian system such as incentive salience and the appraisal of concern-relevance.

Learning and Behavior: Goal-Directed, Habitual, and Pavlovian Systems

As previously mentioned, Moors (this issue) presents a popular theory that distinguishes two types of mechanisms to explain behavior: a goal-directed mechanism and a stimulus-driven mechanism. With respect to Moors's inspiring integrated theory, an important research tradition has led to the proposal that there exists at least three—rather than two—parallel and competitive learning systems that influence behavior: the goal-directed, the habitual, and the Pavlovian systems (e.g., Daw & O'Doherty, 2013; Rangel, Carmer, & Montague, 2008). First, the goal-directed system, which is similar to Moors's goal-directed mechanism, is in charge of the learning of an action in relation to its valued outcome; for example, one learns that if a coin is inserted in the vending machine, then one will receive a treat. This system involves learning an association between a specific action (e.g., inserting a coin) and valuable outcome (e.g., the treat; action–outcome learning). The ability to select goal-directed actions requires a representation of the states, actions, and goals available and involves a flexible computation of action plans. Second, the habitual system is in charge of learned associations between stimuli and actions (e.g., stimulus–action learning), which will result in a certain outcome; this system is related to the stimulus-driven mechanism mentioned by Moors. Indeed, unlike goal-directed behaviors, habitual behaviors are reflexively elicited by the stimulus without considering the current goals of the individual. This implies that actions can be selected even if the outcome of the action is no longer relevant to or valued by the individual. Thus, under the control of the habitual system, the action is not performed with the intention of obtaining or avoiding the outcome,

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whereas in the goal-directed system, the representation of the outcome is critical. Finally, a third distinct system has been proposed: the Pavlovian system. The Pavlovian system has an associative nature consisting in the learning between a stimulus and its associated outcome (e.g., stimulus–outcome learning); for example, learning the association between a vending machine sign and the reception of a treat. For a long time, the Pavlovian system was presumed to be stimulus driven, by learning simple stimulus-value associations (Doll, Simon, & Daw, 2012); however, recent evidence suggests that the Pavlovian system is capable of building a more complex representation of the stimulus and its associated outcome (Dayan & Berridge, 2014; Prévost, McNamee, Jessup, Bossaerts, & O'Doherty, 2013; Robinson & Berridge, 2013). Furthermore, although the neural basis of these systems is not fully established (Rangel, Camerer, & Montague), it has been proposed that these systems potentially rely on separate neural networks (Balleine & O'Doherty, 2010). More precisely, the goal-directed system has been suggested to rely on a neural circuit involving brain areas such as the medial prefrontal cortex, the dorsomedial striatum, and the mediodorsal thalamus, whereas the habitual system has been suggested to rely on a network involving the sensory-motor cortex, the dorsolateral striatum, and the posterior thalamus. Finally, the Pavlovian system has been suggested to rely on brain areas such as the orbitofrontal cortex and the ventral striatum.

It is interesting to note that these systems can interact but also are in competition with one another to determine behavior. The pull for power between these systems can sometimes lead to maladaptive behavior, in which an inappropriate action such as a habit is selected instead of a goal-directed behavior, to use Moors's example: a Belgian driver driving on the wrong side of the road in the United Kingdom. Importantly, there can be an interaction between the Pavlovian and the other instrumental systems, resulting in the learning of an action that is invigorated by the perception of a Pavlovian cue (Campese et al., 2014; Daw & O'Doherty, 2013); this phenomenon is known as a Pavlovian-instrumental transfer (PIT). Over the last couple of decades, it has been brought to the forefront that this interaction between the Pavlovian system and the other instrumental systems might provide useful insights in the understanding of maladaptive behaviors (e.g., Corbit & Balleine, 2015).

Whereas the Pavlovian system shares similarities with both the habitual and the goal-directed systems, it is in fact different from them. We develop these points further hereafter by using appetitive learning literature to compare the different systems. It is important to note that these learning systems are conceived to be similarly involved in both appetitive and aversive learning (Rangel et al., 2008). However, in the present commentary, we focus on appetitive learning as changes in the valuation systems are more easily studied using rewards.

The Pavlovian and Habitual Systems: The Role of the Outcome Value Representation

As previously mentioned, the Pavlovian system has an associative nature and is driven by the perception of stimuli, just like the habitual system. However, the association learned is between a stimulus and its associated outcome (e.g., stimulus–outcome learning) rather than a stimulus and an action (e.g., stimulus–action learning). Even though the Pavlovian system is in charge of learning associations between stimuli and outcomes, Pavlovian learning still produces behaviors (e.g., Dayan, Niv, Seymour, & Daw, 2006). Once the associative learning is completed, the Pavlovian stimulus acquires the ability to evoke behaviors originally triggered by the outcome. Therefore, both habitual and Pavlovian behaviors are triggered by the stimulus perception, and for a long time these two systems were assumed to make similar computations by simply storing caches of stimulus-value or action-value associations (Doll et al., 2012). However, there is a fundamental difference between these two kinds of behaviors: Whereas habitual behaviors are completely independent from the representation of the original outcome associated with the action, Pavlovian behavior can be highly sensitive to the value of the outcome. A clear illustration of this phenomenon can be found in the outcome devaluation literature. Devaluation procedures consist in decreasing the value of an outcome or a stimulus-associated outcome through satiation (procedure used on humans and animals) or by associating the outcome with an illness (procedure used on animals), resulting in the modification of the behavior related to the outcome (Balleine & O'Doherty, 2010). For instance, in a study by Hogarth and Chase (2011), young adult smokers learned to press keys that would allot them either tobacco points or chocolate points. The participants subsequently underwent a devaluation procedure either for the tobacco or for the chocolate, where they had to smoke a cigarette or eat chocolate to satiation. Finally, in a choice task, the young adult smokers were less likely to press on the keys associated with the outcome that was specifically devalued.

A large corpus of literature has consistently shown that the influence of Pavlovian stimuli on behavior is highly sensitive to outcome devaluation procedures (e.g., Holland & Staub, 1979; Lex & Huber, 2010). For example, Pool, Brosch, Delplanque, and Sander (2014) found that chocolate lovers' attention was involuntarily oriented toward a Pavlovian stimulus associated to a chocolate odor, resulting in the participants being quicker to discriminate the position of a line when it was preceded by the Pavlovian stimulus compared to a neutral stimulus. However, after a devaluation procedure in which the participants were satiated with chocolate, the cue associated with the chocolate odor no longer involuntarily oriented participants' attention and in turn no longer affected the participants' behavior. This study shows that the cue no longer being relevant to the chocolate lovers was crucial in determining their behavior.

In contrast, the influence of the habitual system on behavior is completely insensitive to changes in the outcome value (e.g., Adams, 1982; de Wit et al., 2012; Tricomi, Balleine, & O'Doherty, 2009). In a famous experiment, Adams showed that depending on the amount of training a rat receives to press on a lever to receive a reward, it will either stop reproducing the action to receive the outcome or continue the action after an outcome devaluation procedure. Indeed, two groups of rats were trained to press on a lever to receive sucrose. The first group received a small amount of training, inducing goal-directed behavior, whereas the second group was overtrained, inducing habits. After the sucrose was associated with an illness in both groups, the first group of rats stopped pressing on the lever to receive the now-devalued sucrose; however, the second group of overtrained rats continued to press on the lever to obtain the devalued sucrose. These findings demonstrate that, unlike the goal-directed mechanism and the Pavlovian system, habits are not dependent on the representation of the outcome value.

As just shown, the Pavlovian system and the habitual system are quite different even if they share a similarity in that they both involve the learning of an association of a stimulus and an outcome or action, respectively. Already, the type of association is different: The former is in charge of associations between a stimulus and an outcome, and the latter is in charge of associations between a stimulus and an action. In addition, the behavior produced by the Pavlovian system relies on the outcome value, whereas the habitual system is insensitive to outcome value.

The Pavlovian and Goal-Directed Systems: The Roles of Incentive Salience and Expected Pleasantness

A major way in which the Pavlovian and goal-directed systems are similar is that the representation of the outcome value, which can be subject to devaluation in both cases, plays a key role in the control of behavior. However, it has been suggested that changes in the representation of the outcome value do not affect the behavior produced by these systems in the same manner. These systems have different behavior productions because they rely on distinct incentive processes (e.g., Ostlund & Balleine, 2008).

The goal-directed mechanism is dependent on the hedonic experience related to the outcome to determine the performance of the goal-directed actions (Balleine & O'Doherty, 2010). In contrast, according to the incentive salience hypothesis, the incentive processes underlying the Pavlovian system in appetitive behaviors do not depend on the pleasure experienced due to the outcome. The incentive salience hypothesis proposes that reward processing is composed of multiple components including *wanting* and *liking* (Berridge & Robinson, 2003). Reward pursuit behaviors are said to be guided by the *wanting* component, which consists of the effort one is willing to mobilize in order to obtain a reward, rather than the *liking* component, the pleasure experienced during the consumption of the reward (Berridge & Robinson, 2003). In general, *wanting* and *liking* are positively correlated, that is, if one likes a particular reward, then one will put in a proportional amount of effort to obtain said reward. However, under certain circumstances such as addictions (Berridge, Robinson, & Aldridge, 2009) or stress (Pecina, Schulkin, & Berridge, 2006; Pool, Brosch, Delplanque, & Sander, 2015), *wanting* and *liking* can be dissociated, meaning that an individual will work very hard to obtain a reward that is not necessarily liked anymore. The incentive salience hypothesis proposes that the influence of Pavlovian stimuli does not depend on the hedonic properties of the associated outcome but rather relies on a different mechanism consisting of the synergetic interaction between an individual's brain (e.g., level of mesolimbic dopamine) or physiological state (e.g., hunger or satiety) and the Pavlovian stimulus (Zhang, Berridge, Tindell, Smith, & Aldridge, 2009). After the perception of the Pavlovian cue, behavior is not determined by the pleasantness expected of the associated outcome but is directly modulated by the relevant physiological state. Although the incentive salience hypothesis only makes predictions about the physiological relevance of a stimulus to the organism, we proposed that this concept could be expanded, using appraisal theory, to the psychological construct of affective relevance (Pool, Sennwald, Delplanque, Brosch, & Sander, 2016). Affective relevance consists in the interaction between the perception of a stimulus and an individual's current concerns (Sander, Grandjean, & Scherer, 2005). These concerns, which are affective representations, encompass both physiological and psychological concerns (e.g., needs, values). For a reward-associated stimulus to trigger a motivational state (i.e., wanting), it has to be relevant for the current concerns of the individual (Pool et al., 2016; Robinson & Berridge, 2013; Tindell, Smith, Pecina, Berridge, & Aldridge, 2006; Zhang et al., 2009). Essentially evidence suggests that the goal-directed system relies on the experienced pleasantness of the outcome and the Pavlovian system depends on the affective relevance the outcome has for the individual's current concerns.

In addition, whereas the Pavlovian system's conditioned behavior ceases once an outcome has been devalued (Robinson & Berridge, 2013), the goal-directed system requires explicit feedback that the outcome has been devalued through reexperience to reduce behavior, therefore updating the expectations of the outcome pleasantness (Balleine & Dickinson, 1991; Ostlund & Balleine, 2008; Pool et al., 2016). These differences between the systems can be illustrated with Balleine and Dickinson's (1991) study. In this study, rats were taught to press on a lever in order to receive sucrose. Once the sucrose was associated with illness in a devaluation procedure, their behavior did not stop under extinction. The rats had to consume the devalued sucrose to stop pressing on the lever, revealing that to adapt their goal-directed actions, rats needed to update the value representation of the outcome through the direct consumption experience. Therefore, whereas the goal-directed mechanism relies on memory updates of the outcome pleasantness, the Pavlovian system relies on an online valuation of the outcome relevance for the current state of the individual, meaning as soon as the outcome has been devalued, the behavior produced by the Pavlovian stimuli will cease. Evidence of this phenomenon can be seen in Robinson and Berridge's (2013) study, in which they taught rats to turn their repulsion toward a cue associated with an unpleasant salty sensation into an attraction toward it. Robinson and Berridge demonstrated that when the rats were put in a sodium depletion state, the cue associated with the unpleasant salty sensation became relevant, in turn making the rats want the cue associated with the previously unpleasant salty sensation. This study shows that the relevance of the outcome associated with the Pavlovian stimulus is key in influencing behavior.

In brief, though outcome value is important for both the Pavlovian and the goal-direct system, they rely on different incentive processes. Unlike the latter, the former does not seem to rely on the hedonic properties of the outcome but rather on its relevance for the current concerns of the individual. Moreover, the behavior the Pavlovian system produces seems to be dependent on an online valuation of the outcome relevance, whereas the goal-directed system requires a memory update of the value of the outcome to modify behavior.

Conclusion

Moors's (this issue) integration of two key emotional theories leads to both conceptual improvement and promising avenues for empirical research. We found of particular interest Moors's integration of classical theories explaining behavior considering two competing and parallel systems that guide behavior: the stimulus-driven system and the goal-directed system. We showed that it could be worth complementing Moors's new integrated theory with a third system, namely, the Pavlovian system. We feel that it is important to take into consideration this third system, as it can also control emotional behavior independently of the goal-directed or habitual systems. It is not like either of the mechanisms Moors presented, as it has an associative nature and is driven by the stimulus perception, but it relies heavily on the representation of the outcome. With this respect, it could be argued that the cognitive component, as a causal eliciting mechanism shaping the other components of emotion, should be "stretched" (to use Moors's words) to include not only the goal-directed mechanism but also the Pavlovian mechanism. Given the valuation function of appraisal mechanisms (see Brosch & Sander, 2014, 2015), we would not see this "stretching" as leading to an exclusion of either the goal-directed mechanism or the Pavlovian mechanism from the dynamics of appraisal processes.

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