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Pavlovian feed-forward mechanisms in the control of social behavior

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Abstract: The conceptual and investigative tools for the analysis of social behavior can be expanded by integrating biological theory, control systems theory, and Pavlovian conditioning. Biological theory has focused on the costs and benefits of social behavior from ecological and evolutionary perspectives. In contrast, control systems theory is concerned with how machines achieve a particular goal or purpose. The accurate operation of a system often requires feed-forward mechanisms that adjust system performance in anticipation of future inputs. Pavlovian conditioning is ideally suited to subserve this function in behavioral systems. Pavlovian mechanisms have been demonstrated in various aspects of sexual behavior, maternal lactation, and infant suckling. Pavlovian conditioning of agonistic behavior has been also reported, and Pavlovian processes may likewise be involved in social play and social grooming. Several further lines of evidence indicate that Pavlovian conditioning can increase the efficiency and effectiveness of social interactions, thereby improving their cost/benefit ratio. We extend Pavlovian concepts beyond the traditional domain of discrete secretory and other physiological reflexes to complex real-world behavioral interactions and apply abstract laboratory analyses of the mechanisms of associative learning to the daily challenges animals face as they interact with one another in their natural environments.

Keywords: aggression; biological theory; control theory; feed-forward mechanisms; learning theory; nursing and lactation; Pavlovian conditioning; sexual behavior; social behavior; social grooming; social play

1. Introduction

Many of the things that animals do, they do together. This makes the analysis of social behavior a central problem in behavioral science. Our goal in this target article is to expand the conceptual and investigative tools that are used in the analysis of social behavior by integrating three different theoretical perspectives: biological theory, control systems theory, and learning theory (in the form of Pavlovian conditioning). We discuss how the integration of these three perspectives provides insights into important proximate mechanisms of social behavior that increase the efficiency and effectiveness of social interactions.

The three theoretical approaches addressed in this paper have developed mostly independently of one another, and two of the three (control theory and learning theory) have had little to say about social behavior. The biological approach has focused on ecological and genetic factors that shape social behavior but has largely ignored the role of learning or learned associations. Control systems theory developed as a discipline in engineering, and although it has been used in the analysis of some biological systems (e.g., McFarland 1971), it has not been extended to social behavior. Pavlovian conditioning theory originated in investigations of digestive physiology and since then has been applied to a variety of other areas including cardiovascular and immune functioning, placebo effects, substance abuse, ingestive behavior, and language and memory (Hollis 1997;

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Turkkan 1989). However, most of the research on Pavlovian conditioning has focused on the behavior of individual organisms in socially isolated laboratory settings.

Biological theories are concerned with the costs and benefits of group living, from ecological and evolutionary perspectives. An important assumption of the biological approach has been that animals engage in social interactions because such interactions bring them ecological and genetic benefits. What might be the proximate mechanisms that shape social behavior in accordance with cost/benefit considerations? We suggest that control systems theory can be used to answer that question. Control systems theory is concerned with the analysis of how machines are designed to achieve a particular goal or purpose. A particularly effective way to reduce errors in the operation of a system involves detecting the errors and then using that information to adjust the future operations of the system. However, time lags in feedback mechanisms can seriously compromise the functioning of the system. Such time lags are especially likely in biological or behavioral systems. We will describe how Pavlovian feed-forward mechanisms can facilitate efficient performance by reducing time lags in biobehavioral systems.

Pavlovian conditioning is concerned with the formation of associations. The concept of associations has been for psychology what the concept of gravity has been for physics. It is the glue that holds experience together, helping to organize sequences of behavior. Although the concept of associations dates back to at least Aristotle, the modern era in the study of associations began with Ebbinghaus, Thorndike, and Pavlov, who first investigated the characteristics of associations using empirical methods. In contrast to Pavlov's early emphasis on the conditioning of glandular physiological responses, more recent studies have extended the applicability of Pavlovian conditioning to skeletal response systems (e.g., Hearst & Jenkins 1974; Holland 1984; Timberlake et al. 1982; Tomie et al. 1989). Pavlovian concepts can be further extended to the analysis of social behavior. We will illustrate this by describing how Pavlovian mechanisms are involved in a number of prominent forms of social behavior (agonistic behavior, sexual behavior, lactation and nursing, play behavior, and social grooming) and how these Pavlovian mechanisms may facilitate efficient performance.

2. Biological approaches to social behavior

Animal social behavior traditionally has been studied within the context of ecological and biological perspectives. These analyses have focused on the environmental and/or genetic factors associated with the formation and behavior of animal groups. Wilson (1975) defined an animal group as a "set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics" (p. 585). Some defining characteristics of animal groups are limited membership, intragroup communication, enduring relationships and cooperation between group members, and periods of synchronous activity (Daeg 1980). A fundamental assumption has been that for groups to form, the current and/or historical benefits of social living have to exceed its costs or disadvantages.

2.1. Theories of group formation

Theoretical approaches to animal social behavior can be arranged into three broad, nonmutually exclusive categories (Slobodchikoff & Shields 1988). Ecologically based theories focus on the impact of environmental challenges on the development and maintenance of social groupings (Crook 1964; 1966; 1970; Lack 1968). Genetically based theories use concepts such as indirect selection and inclusive fitness to explain how social living can be adaptive (Hamilton 1964; Trivers 1985). Finally, phylogenetic hypotheses suggest that explanations of social behavior should consider the natural history of a species, because the conditions that historically promoted group living may not be operating currently (Wilson 1975).

2.1.1. Ecological theories. Traditionally, ecologically based considerations of animal social behavior have used the comparative method to evaluate and make predictions about which types of environmental pressures favor animal groupings. This theoretical perspective suggests that the forces of natural selection have endowed animals with the ability to adapt to changes in the ecological landscape (Wrangham & Rubenstein 1986). Thus, animal groups occur because they allow individuals to better utilize or acquire certain essential or centralized resources (Alexander 1974; Crook 1972; Slobodchikoff 1984; Wittenberger & Hunt 1985).

The benefits most often associated with group living are increased foraging efficiency and improved predator defense and avoidance (Alexander 1974). Additional benefits that may accrue to group-living individuals include access to a greater array of reproductive options (Alexander 1974), protection from aggressive conspecifics (Wrangham & Rubenstein 1986), and improved thermoregulation (Wittenberger 1981). For social groups to be adaptive, these advantages must outweigh the costs associated with group living (Alexander 1974; Wrangham & Rubenstein 1986).

Although the benefits that result from living in groups vary across and within species, Alexander (1974, p. 328) described the costs of sociality as "automatic and universal." Invariably, group living increases exposure to parasites and disease and heightens competition for mates and survival needs such as food and shelter (Alexander 1974). Less common costs include greater conspicuousness to prey, a higher risk of inbreeding, and the potential for misdirected parental care (Alexander 1974; Grier & Burk 1992).

Once animal groupings occur, the overall social organization is heavily influenced by intraspecific variables (e.g., sex and age) that affect the degree to which individuals can compete for available resources (Wrangham & Rubenstein 1986). In larger groups, this competition often results in a stratification of the group, with some animals coming to hold more favored positions while others are relegated to less privileged roles. As a result, the costs and benefits associated with social living tend to vary between individuals and/or subsets of individuals (Alexander 1974; Dunbar 1988; Rubenstein 1975; Wrangham & Rubenstein 1986). For some group members, the costs will be higher and may include ultimate costs such as fewer or no opportunities for reproduction. For other animals, benefits will be enhanced and may include, for example, assistance in territory and/or nest defense and the rearing of young. Thus, in addition to considering the factors that bring animals together, it is important to consider how sociality is experienced at the level of the individual, as well as the means by which individuals can reduce the ratio of costs to benefits inherent to group living.

2.1.2. Genetically based theories. Genetically based theories also examine the evolution of social behavior from a cost/benefit perspective. However, in genetic analyses, the costs and benefits of social behavior are measured in terms of an individual's total genetic contribution to the next generation. This total contribution includes shared genes supplied by kin. From the perspective of the group-living individual, costly forms of social behavior are those that tend to decrease the number or likelihood of personal reproductive opportunities.

A cost/benefit approach was used by Hamilton (1964) to describe the four possible outcomes of animal interaction: *cooperation* (when both animals benefit as a direct result of the interaction); *altruism* (when the animal performing the behavior loses so that the other may gain); *selfishness* (when an animal benefits from an altruistic act); and *spite* (when both animals incur a net loss). Darwin was the first of many evolutionary theorists to recognize the challenge posed by examples of cooperative and altruistic behavior (Darwin 1859). Altruistic behavior seems paradoxical from a genetic perspective because the genes of selfish individuals should proliferate at the expense of less selfish individuals. As a result, genetically based considerations of social behavior have often sought to explain how selection processes can favor the evolution of cooperative and unselfish forms of behavior.

A prominent explanation, provided by Hamilton (1964), suggested that animals are more likely to participate in costly forms of social behavior if those activities result in fitness benefits for themselves or a related individual. According to this view, there are two distinct evolutionary processes: direct and indirect selection (Brown 1987; Brown & Brown 1981). Direct selection operates on the variability between individuals in terms of offspring production and survival. Indirect selection operates on the variability between individuals with regard to the reproductive success of relatives. Because related individuals possess common genes, unselfish and cooperative behaviors that serve to enhance a relative's reproductive success increase the unselfish individual's genetic representation in the next generation. Hamilton (1964) coined the term "inclusive fitness" to describe the additive effect of these two processes on an animal's genetic representation in the next generation. Thus, the most successful animals in terms of inclusive fitness leave many offspring and/or assist relatives and their offspring. However, because assistance provided to relatives often comes at the expense of personal reproductive pursuits, measures of inclusive fitness for some social animals are dominated by the indirect selection component.

Hamilton (1964) drew upon these concepts to develop a formula that has come to be known as "Hamilton's rule." Hamilton's formula is used to compare the effects of altruistic versus selfish behavioral strategies on an individual's inclusive fitness. The evolution of altruism will be favored in situations where altruistic strategies produce higher inclusive fitness values. This general idea has been used to explain seemingly altruistic behaviors such as helping behavior in pied kingfishers (Reyer 1984), alarm-calling in Belding's ground squirrels (Sherman 1977; 1985), and the sterile worker castes of eusocial insects (Hamilton 1964).

In more cognitively advanced species, altruistic forms of behavior may also be maintained by "reciprocal altruism" (Trivers 1971). Reciprocal altruism is essentially a delayed form of cooperation. It occurs when one animal assists another in one context and is then assisted by the same individual at a later time. Reciprocal altruism does not work in evolutionary terms if there are numerous cheaters. However, as suggested by Axelrod and Hamilton (1981), in long-lived animals that possess a memory for prior social encounters and outcomes, the advantages gained from isolated cheating episodes may be outweighed by the fitness costs accumulated during a lifetime of social interactions. Although reports of reciprocal altruism are rare, on a number of occasions Packer (1977) observed male olive baboons forming cooperative pairs to displace a dominant male. Reciprocity is possible in this species because baboons can recognize individuals and are capable of associating acts with outcomes.

2.1.3. Phylogenetic theories. Phylogenetic hypotheses focus on the evolutionary history of social species or groups. Phylogenetic hypotheses are considered when ecological and genetic cost/benefit considerations fail to provide a satisfactory explanation for a particular group structure (Slobodchikoff & Shields 1988) and/or when the focus of interest is on the historical factors or evolutionary origins of particular forms of social behavior. According to this view, a species' current social schema may no longer be adaptive but simply a remnant of past evolutionary pressures (Wilson 1975).

2.2. The experience of individuals in a social context

Most biological treatments of animal social behavior have focused on the conditions that promote or maintain group living, without devoting much attention to the social experience of the individual. At some point, however, all analyses of social behavior must consider the consequences of a social lifestyle for the individual participants. The account developed in this article focuses on the day-to-day social experience of group-living individuals as they encounter, assist, and compete with various group members. Fundamental to this approach is the idea that Pavlovian processes can provide a mechanism that adds predictability to an animal's social experience.

An individual's social experience is determined, in part, by the types of relationships it establishes with other group members. Social relationships, by definition, are associated with predictable behavioral exchanges (Scott 1977). The costs associated with social interaction decline as the participants become more familiar with each other. As Dunbar (1988) noted, an individual's social behavior is "a consequence both of behavioral strategies learned by experience and of the extent to which its cognitive capacities allow it to hypothesize and extrapolate about the future behavior of the world in which it lives" (p. 183). Pavlovian conditioning allows animals to anticipate how social encounters and outcomes will unfold, and thereby contributes to the predictability of social interactions. Anticipating the outcome is especially important when the interaction is with dominant or territory-holding individuals. Because the fitness costs of social behavior can be severe in these cases, the ability to predict the outcome of the interaction should be especially helpful.

In general, a major cost of social living for individuals is increased competition for mates and resources such as food, water, and territories. Some individuals are more successful in competing for resources than others. Thus, the social pressures, opportunities, and rewards associated with group living will tend to vary between individuals and result in a social milieu unique to each group member (Alexander 1974; Dunbar 1988; Rubenstein 1975; Wrangham & Rubenstein 1986). Animals relegated to lesser social positions are forced to make the best of a bad situation. Animals of higher status reap more of the benefits inherent to group living. However, regardless of an animal's social status or role, all animals approach social competition with the same mandate, to minimize costs relative to benefits.

3. Control systems theory and Pavlovian feed-forward mechanisms

As we have seen, biological theories have traditionally emphasized the ultimate evolutionary factors that encourage group living. The theories have had less to say about the proximate environmental factors that are responsible for the shape and form of a particular individual's social responses. Inanimate stimuli and stimuli provided by another animal elicit social responses and enable experienced animals to predict the occurrence, and in some cases the outcome, of impending social encounters. This ability to predict is invaluable because it enables anticipatory reactions and helps to fine tune and increase the efficiency of social interactions.

Living organisms, however, are not the only systems that benefit from foreknowledge. Engineers have long recognized that predictive functions are often necessary components in the design and proper functioning of mechanistic systems. Powerful methods have been developed in engineering for the analysis of how predictive functions facilitate system performance. In this section we review relevant aspects of systems theory and describe how those concepts, together with Pavlovian feed-forward mechanisms, can be used to analyze how predictive functions enable animals to utilize environmental resources more efficiently. The resulting model incorporates both evolutionary and environmental factors in the shaping of animal social behavior.

Systems engineering originally developed as a specialty in electrical engineering. Since then, similarities have been recognized between biological and electronic control systems, and this has led to explorations of the relationships between engineering and biology (Rosenblueth et al. 1943). The application of control theory to biological problems is based on the assumption that useful analogies can be drawn between the mechanisms of living and nonliving systems (McFarland 1971). Engineering applications of control theory are used to improve the operation of a machine that has been created to accomplish a specific purpose. Control system analysis is most useful when the machine under investigation consists of a complex interaction of multiple components and when these components have a propensity to vary under changing environmental conditions. Social interactions also involve multiple components that vary with changing circumstances. This parallel encouraged us to explore the application of control systems theory to the analysis of social behavior.

In engineering, a system is considered to be a collection of interacting components that provides a specified system response (Dorf 1992). The system's activities are determined by the characteristics of the individual components and by the machinery that connects those components (Vaidhyanathan 1993). Control mechanisms are necessary when a system's output varies outside acceptable operating levels. While some behavioral variability in living systems is inevitable (and probably advantageous), excessive variability can reduce the efficiency with which animals utilize important resources in their environment. Behavioral variability is especially likely when two or more organisms interact. Therefore, biological control mechanisms that monitor and control behavioral responses may be especially important in a social context. Functionally, such control mechanisms would reduce unnecessary energy expenditure and increase the probability that an animal engages in social behaviors previously found to improve the utilization of environmental resources.

3.1. Closed-loop feedback control

Two fundamental types of control systems have been identified: closed-loop systems that contain feedback mechanisms and open-loop systems that operate without feedback. Open-loop systems cannot adjust their mode of operation. This lack of adjustment capacity prohibits open-loop systems from compensating for errors that may occur during system functioning. Closed-loop systems, in contrast, are more effective in producing a specified output. System regulation is accomplished by tracking the output of the system and using that information to change how the system responds to future inputs (Dunderstadt et al. 1982).

Four essential components are needed to accomplish feedback regulation in nonliving systems: a transducer or controller, a monitor, a comparator, and a set of instructions that represent the appropriate or desired system performance. (Note that these are functional components. In actual control systems, many physical elements are typically required to accomplish each of these separate tasks.) The transducer is responsible for receiving the system's input and transforming that input into the system's output. Transducers, however, are susceptible to errors. Thus, the remaining components are needed to properly execute the transduction process. The monitor tracks the system's output and sends this information to the comparator. The comparator then measures the actual output against a desired output value. Changes to the transducer are then undertaken to compensate for any discrepancies between the two. In this way, feedback regulation provides error control and enables the system to maintain desired operating levels.

3.2. Time lags and instability

Delays invariably occur between the output of a system and subsequent adjustments. Such time lags in feedback regulation can substantially reduce the effectiveness of the control mechanism and under extreme conditions may actually cause the system to malfunction. The destabilizing effects of a time lag depend on the duration of the lag and the strength or intensity of the feedback control correction (Dworkin 1993).

Consider, for example, the effects of a delay in the operation of a simple thermostat that regulates room temperature by turning on either a heating unit or a cooling unit. If the thermostat operates with a substantial time lag, it will permit the room to get too hot before activating the cooling unit. Likewise, it will permit the room to get too cold before activating the heating unit. Thus, time lags will cause increased oscillations in room temperature. Oscillation problems become especially troublesome if the feedback correction is particularly strong, for instance, if very hot air is introduced to correct for a drop in temperature and very cold air is introduced to correct for a rise in temperature. Under these conditions, delayed feedback will exacerbate the destabilizing effects of temperature fluctuations. As this example illustrates, time lags can seriously compromise the effectiveness of feedback regulation (Kalmus 1966).

3.3. Feed-forward mechanisms as solutions to time lags

Effective mechanisms have been developed to overcome the destabilizing effects that time lags have on feedback control. Engineers have found that oscillation problems are reduced when systems contain mechanisms capable of predicting their own output errors. Such mechanisms provide regulatory systems with *feed-forward control* (Box & Jenkins 1970).

Accurate prediction of a future event can only be based on how similar events took place in the past. For example, a weather forecaster predicts rain not on the basis of clairvoyance but on the basis of patterns of prior meteorological events. Thus, accurate prediction or feed-forward mechanisms are possible only with the existence of some kind of memory. Memory allows feed-forward mechanisms to anticipate output errors that have occurred in the past under similar circumstances. Through feed-forward mechanisms, a system can be "corrected" before an output error actually occurs. In principle, feed-forward mechanisms are more useful than feedback mechanisms because they can reduce the destabilizing effects of time lags in feedback regulation and because they can adjust system functioning to prevent error.

3.4. Biological control mechanisms

Feedback and feed-forward control have been used in explanations of a variety of different biological functions. One early application concerned the control of body movements in the fly. Von Holst and Mittelstaedt (1950; see also Mittelstaedt 1954, cited in Kalmus 1966) proposed a model of movement control in which sensory feedback from efferent organs was compared with a template of the intended movement. From this comparison, new efferent signals could be adjusted to correct for previous inaccuracies. In humans, the cerebellum appears to be involved in processing teleceptive and proprioceptive feedback in the feed-forward control of muscle activation, motor learning, and posture (Smith 1996). Other recent examples of motor control systems include a neural network model with feed-forward and feedback loops for the neuromuscular control of human arm movements (Stroeve 1997) and a neural network model of locomotor control in the lamprey (Jung et al. 1996; see also Jordan 1996).

Feedback control was also an integral part of Sokolov's (1963) theory of habituation and was applied by Baerends (1970) to explain incubation behavior in birds. In incubation, sensory feedback from sitting on a clutch of eggs is compared with an internal target value, and this comparison is then used to increase or decrease future incubation responses. Feedback and feed-forward regulation has also been frequently used in analyses of feeding and drinking. The traditional view explained feeding and drinking in terms of feedback mechanisms that tracked fluctuations in physiological parameters that were considered indices of nutritional status (McFarland 1971). However, more recently investigators have become convinced that feed-forward mechanisms based on learning are more important and more useful in the control of feeding and drinking than feedback mechanisms (e.g., Ramsay et al. 1996).

The recent popularity of research utilizing simulated neural networks has encouraged a resurgent interest in systems theory and the concepts of feed-forward and feedback control. For instance, Berger, Bassett, and Orr (1991) proposed a multilayered neural network that describes the modulatory connections among hippocampus, basal ganglia, and cerebellum involved in the modification of learned behavior. Schmajuk and DiCarlo (1992; see also Schmajuk & Moore 1988) proposed a real-time multilayered neural network of Pavlovian conditioning. Computer simulations of the model correctly predict the effects of cortical and hippocampal lesions. They also predict hippocampal and medial septal activity during classical conditioning paradigms, including acquisition of delay and trace conditioning, extinction, blocking, discrimination acquisition, discrimination reversal, and generalization. Errors in the network's output are fed back to a hidden unit layer via a biologically plausible backpropagation procedure (see also Gluck & Meyers 1993; Schmajuk 1997).

3.4.1. Distinctive features of biological control systems. Although there are many functional similarities between the feedback control observed in living and nonliving systems, there are some important differences as well. For example, unlike nonliving systems, the control mechanisms of living systems must perform in the context of physiological constraints and other limiting metabolic factors. While nonliving systems function regardless of mechanistic redundancy or cumbersome system components, living systems are forced to accomplish feedback regulation using biological mechanisms pruned by environmental adaptations.

Living and nonliving control systems also differ with respect to the nature of the instructional component that dictates desired system performance. In a nonliving system, the instructions regulating the system's output are designed by the system's engineer to fit the demands of a specific task or environment. In contrast, the "instructions" that regulate a living system's "output" are shaped by the forces of natural selection (Rosen 1967). In this way, biological instructional codes actually evolve in response to the specific environmental demands living systems encounter. In nonliving systems, the system's instructions are designed to fit the environment. In living systems, specific environmental demands dictate the "design" of the instructions.

What might be the nature of the evolved instructional codes with respect to social interactions? As we have seen, traditional theories of social behavior have in common the assumption that there are specific costs and benefits associated with each particular social response. If this is true, natural selection should favor organisms that possess the biological mechanisms necessary to (a) calculate the cost/benefit ratio associated with a given social response, and (b) evaluate the calculated ratio to ensure that it is as low as possible under the extant environmental conditions. In essence, natural selection is presumed to favor individuals who are behaviorally predisposed to minimize the costs and maximize the benefits of group living. The instructional code for the regulation of social responses, therefore, should contain information necessary for organisms to seek lower cost/benefit ratios.

3.4.2. The feedback control of behavior. How the concept of feedback control may be applied to the regulation of behavior is illustrated in Figure 1. Each square in the figure represents a separate system component, and the solid arrows indicate how the components are functionally connected. Inputs and outputs are depicted without squares, and open arrows show the input and output projections. Biologically important sensory input (an unconditioned stimulus or US) is initially relayed to a stimulus/response actuator. Here sensory input gives rise to behavioral output (the unconditioned response or UR). The monitor component tracks the system's output and calculates the cost/benefit (C/B) ratio associated with the current output response. The calculated cost/benefit ratio is then sent to the comparator, which also receives input from the ratio instructions component. Here the calculated ratio from the monitor is evaluated with respect to the system's instructional code, which, as outlined above, specifies the attainment of the lowest possible cost/benefit ratio. Based on this analysis, necessary and appropriate changes to the stimulus/response actuator are undertaken so that subsequent output responses result in lower cost/benefit ratios. The extent to which the transducer needs adjustment is a function of how much the calculated cost/benefit ratio can be improved (lowered) under the extant environmental conditions.

3.4.3. The feed-forward control of behavior. As we have seen, a time lag between system output and subsequent transduction adjustments is detrimental to the functioning of nonliving feedback control mechanisms. Time lags are no less troublesome with respect to the feedback regulation of biological control systems, especially biological systems whose reaction speed is restricted by physiological constraints (Vaidhyanathan 1993). Furthermore, speeding up biological feedback mechanisms may require evolutionary adaptations that are too complicated or metabolically too costly to develop. Thus, like mechanistic control systems, living organisms rely on the feed-forward control provided by memory processes.

Figure 2 shows a feed-forward mechanism added to the feedback control system depicted in Figure 1. The modified system contains a memory component that receives sensory input as well as input from the monitor and comparator components. This enables the system to remember previously encountered stimuli, the calculated cost/benefit ratio associated with the behavioral responses to those stimuli, and any compensatory adjustments that may have been made.

Incoming stimuli can now activate information previously logged in memory. Activated memories are compared to the ratio instructions, and the outcome of that comparison is used to undertake anticipatory adjustments that modify imminent behavioral outputs. Thus, memories are used to anticipate the behavioral output so that adjustments to the stimulus/response actuator are made before mistakes occur – before unconditioned responses susceptible to

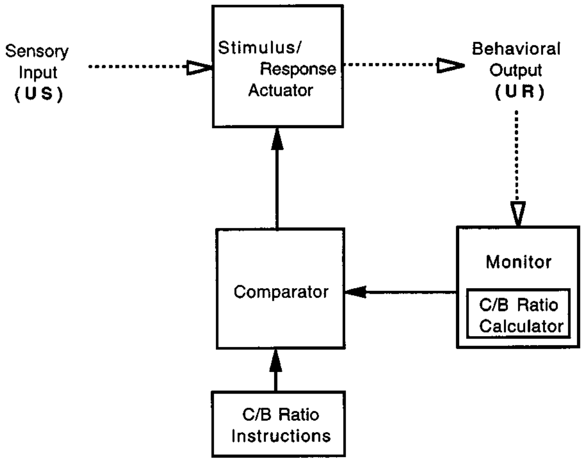

Figure 1. A closed-loop feedback control system for the regulation of behavior. Each square represents a separate system component, and the solid arrows indicate how the components are functionally connected. System input and output is depicted without squares. Open arrows show the input and output projections. The stimulus/response actuator translates sensory input (unconditioned stimuli [US]) into behavioral output (unconditioned responses [UR]). The remaining components provide feedback control. They enable the system to track and evaluate the cost/benefit ratio associated with the current output response. This information is then used to adjust the stimulus/response actuator so that future behavioral outputs result in lower cost/benefit ratios.

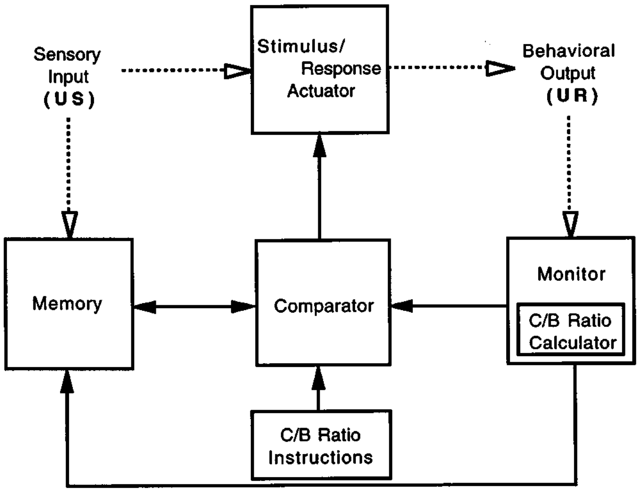

Figure 2. A control system for the regulation of behavior that includes a feed-forward mechanism to reduce the adverse effects of time lags in feedback regulation. Feed-forward control is gained with the addition of a memory module that stores previously experienced sensory input as well as previous comparisons and adjustments made through feedback control. The system is able to anticipate imminent behavioral output so that adjustments to the stimulus/response actuator can be undertaken before behavioral mistakes are made. This allows the system to operate more efficiently and effectively under the extant environmental conditions.

time lag errors are performed. The anticipatory adjustments permit more efficient and effective changes in the stimulus/response actuator than would normally occur without feed-forward control.

3.4.4. Pavlovian conditioning and feed-forward control. One of the most versatile and ubiquitous biological feed-forward mechanisms is Pavlovian conditioning (Hershberger 1990; Hollis 1997; Turkkan 1989). Pavlovian conditioning provides a way for animals to track the causal textures of their environments. It enables organisms to form representations of contingent relations between the events they encounter and to respond in anticipation of biologically important stimuli.

Pavlovian conditioning can result in either excitatory or inhibitory learning (Rescorla 1969). However, for the sake of simplicity, we will focus primarily on conditioned excitation. The feed-forward character of conditioned excitation is obvious when a dog salivates in response to a conditioned stimulus that usually precedes the presentation of meat powder (Pavlov 1927). The adaptive value of this type of anticipatory conditioned responding was recognized from the outset of studies of Pavlovian conditioning. Culler (1938) expressed the idea eloquently when he noted that without anticipatory conditioned responding, an organism would

> be forced to wait in every case for the [unconditioned] stimulus to arrive before beginning to meet it. The veil of the future would hang just before his eyes. Nature began long ago to push back the veil. Foresight proved to possess high survival value, and conditioning is the means by which foresight is achieved. (p. 136).

More recently, Hollis (1982; 1997) suggested that the feed-forward control made possible by Pavlovian conditioning is the primary basis for the adaptive value of excitatory conditioned responding. According to Hollis (1982), "the biological function of classically conditioned responding . . . is to enable the animal to optimize interaction with the forthcoming biologically important event [the unconditioned stimulus]" (p. 3). By being able to anticipate an unconditioned stimulus, the animal is better able to respond to it in a highly beneficial fashion.

Feed-forward Pavlovian control has been investigated extensively in physiological systems, the traditional domain of Pavlovian conditioning. A major reason for invoking Pavlovian conditioning here was to reduce time lags in feedback regulation. Dworkin (1993), for example, argued that "the conditioned reflex can be a powerful mechanism for eliminating intrinsic lags" (p. 48) and augmenting the effectiveness of a physiological feedback loop. Others have suggested that Pavlovian feed-forward mechanisms effectively reduce the need for feedback regulation (Ramsay et al. 1996; Seeley et al. 1997). According to the latter perspective, it is maladaptive to rely on feedback mechanisms when feed-forward mechanisms eliminate, or at least substantially reduce, the chances of errors occurring in the first place.

Figure 3 shows how the ability to form associations augments feed-forward control. The addition of Pavlovian conditioning to the control system is accomplished by supplementing the memory component depicted in Figure 2 with an associator component. The associator receives sensory input from both a conditioned stimulus (CS) and an unconditioned stimulus (US) and forms an association between them. The resulting CS–US association enables subsequent CS encounters to activate a representation of the US. The conditioned properties of the CS are retained in memory and also can be activated in the future through the presentation of the CS by itself.

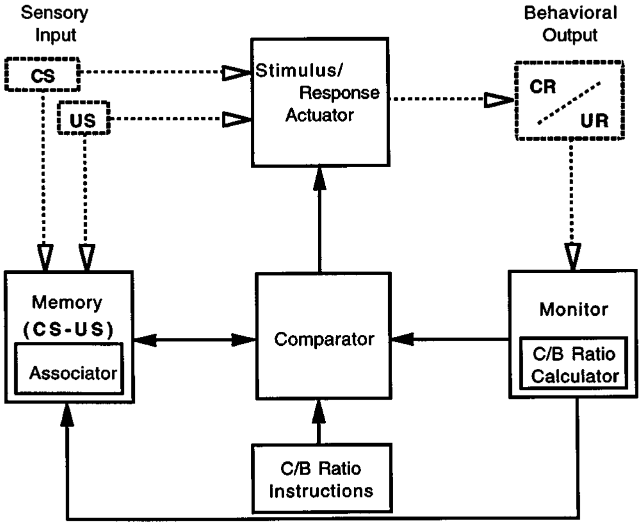

Figure 3. A behavioral control system that includes a Pavlovian feed-forward mechanism. An associator (located inside the memory component) receives sensory input in the form of conditioned and unconditioned stimuli (CS, US) and establishes an association between them. The memory component retains a representation of the association (CS–US) so that future CS presentations can activate feed-forward adjustments to the system in anticipation of the forthcoming US.

In excitatory conditioning situations, the CS typically occurs before the US. Therefore, once the CS has become conditioned and capable of activating the memory component, feed-forward control begins when the animal first perceives the CS. Thus, feed-forward control begins prior to presentation of the US. Once conditioned and registered in memory, CSs (and the US memories they activate) provide a means of anticipating necessary adjustments to the stimulus/response actuator. These "conditioned anticipatory adjustments" serve to prime the system in preparation for the forthcoming US.

4. Pavlovian feed-forward mechanisms in social behavior

Pavlovian conditioning involves the establishment of an association between a conditioned and an unconditioned stimulus. Pavlovian conditioning readily occurs in situations where a CS reliably precedes a US. Rabbits come to blink in response to a tone that precedes mild irritation of the eye (Gormezano 1966), rats become fearful of a tone that precedes foot-shock (Kamin 1965), and hungry pigeons come to approach and peck a spot of light that reliably precedes access to grain (Brown & Jenkins 1968). Thus, Pavlovian conditioning occurs in situations where two events are experienced in a predictable order.

Social situations also may be viewed as involving predictable event sequences. A social sequence begins with the fairly innocuous stimuli experienced when two animals are at a distance and just starting to take notice of one another and ends when they are close together and engaged in vigorous behavioral exchange. As an animal experiences the stimulus sequence on a number of occasions, it may learn to anticipate the terminal behavioral exchange on the basis of early cues that are predictive of the social encounter. Each participant in a recurrent social interaction can learn to predict how the interaction is likely to play out. For the sake of simplicity, we will focus on one participant at a time.

We assume that the stimuli encountered during the vigorous social exchange at the end of a social sequence are potential USs. The stimuli encountered at the beginning of the social sequence are potential CSs. The CSs may be physical or behavioral cues provided by the other animal at a distance or environmental cues correlated with the appearance of a conspecific. As Demarest (1992) has noted, "learning about cues in the environment that predict the location of another animal is important because it may provide a mechanism for enhancing social behavior" (p. 150).

The concepts of Pavlovian conditioning may be applied to a variety of different forms of social behavior. In this section we discuss how Pavlovian concepts may be applied to the analysis of agonistic behavior, sexual behavior, suckling and lactation, play behavior, and social grooming. In some of these cases, considerable evidence has already been obtained on the role of Pavlovian conditioning. In other cases, the evidence is less extensive and our discussion is more speculative.

4.1. Agonistic behavior

Agonistic behavior is a form of social behavior that results from intraspecific competition for desired resources such as food items, living space, nesting sites, status positions, and sexual partners (Poole 1985). Agonistic behavior is also exhibited by territorial species as a means of defending one or more of these resources from neighboring territory holders or other intruders. By definition a territory is "any defended area" (Noble 1939). This defense is accomplished by display, threat, or attack (Brown 1975). Territoriality is very common among bird species, and to a lesser degree is also seen in fish and mammals (Brown 1975). Territories are classified as serving mating, nesting, or more general purposes (Brown 1975; Daeg 1980).

For those territorial species in which successful territory and nest defense is highly correlated with reproductive success (Brown 1975), the ability to predict and prepare for combat should pay fitness benefits. Animals that can predict when a conspecific will invade their territory on the basis of an antecedent environmental cue should be more successful in warding off the invasion with an effective defensive display or fighting posture than animals that encounter an intruder unexpectedly. Thus, Pavlovian feedforward mechanisms should enhance the effectiveness of territorial defense.

The conditioning of agonistic behavior has been explored in two species of Anabantid fish, the blue gourami (*Trichogaster trichopterus*) and the Siamese fighting fish (*Betta splendens*), and in the three-spined stickleback (*Gasterosteus aculeatus*). Despite some species differences, these fish exhibit a similar form of territorial and reproductive behavior. In general, males establish and defend territories during the breeding season before the arrival of females. Females choose one or more males and lay caches of eggs in nests the males have built. The territory-holding males then fertilize the eggs and defend the nest. Reproductive success is thus highly dependent on the ability of males to acquire a nest site and then defend it from satellite males in search of a territory or a cache of eggs to fertilize. When the territory boundary is breached, males confront the invader with species-typical aggressive displays and threats. If the intruder does not withdraw, a fight ensues. The fight generally comes to a quick conclusion when one of the combatants adopts a submissive posture and flees.

In studies of the conditioning of agonistic behavior, the unconditioned stimulus has been an encounter with an intruding male. Studies with Siamese fighting fish have used the presentation of the male subject's mirror image to simulate an intruder (Thompson & Sturm 1965). Studies with the three-spined stickleback and blue gourami have used visual access to another male as the US (Hollis 1990; Jenkins & Rowland 1996). In the native environment of the fish, the CS for agonistic conditioning may be provided by cues of the intruder at a distance or inanimate environmental events correlated with the intruder's appearance. In the first laboratory study of agonistic conditioning, a brief electric shock was used as the CS (Adler & Hogan 1963). In subsequent experiments, visual and spatial cues served as conditioned stimuli.

Thompson and Sturm (1965) reported successful conditioning of four components of the aggressive display of Siamese fighting fish to a red or a green light CS. The conditioned responses included fin erection, undulating movements, gill cover erection, and frontal approach to the CS. Thompson and Sturm used a standard classical conditioning method in which the CS shortly preceded the US and conditioning trials were administered according to a preset schedule regardless of the subjects' behavior. However, they only tested four subjects.

Subsequent experiments with *Betta splendens* focused on the frontal approach response and included larger numbers of participants. In addition, a new method was developed in which the fish encountered the CS and US by swimming into one of two tunnels (Bronstein 1986a; 1986b). With this procedure, exposures to the CS and US were determined by the behavior of the subjects. Perhaps because of the lack of experimental control over CS and US presentations, the procedure has yielded inconsistent results (Bronstein 1986a; 1986b; 1988; Demarest 1992).

Studies in which the US was visual access to a potential intruder rather than a mirror-image stimulation have provided more consistent results. Jenkins and Rowland (1996) recently demonstrated the conditioning of both approach and zigzag movements in male sticklebacks. Sticklebacks have been noted to attack intruders on the basis of the red coloration of rival males (Tinbergen 1951). To see if this predisposition would influence the course of Pavlovian conditioning, Jenkins and Rowland compared red and green lights as cues in the conditioning of two groups of male sticklebacks. For one group, presentations of the red light (CS+) were paired with visual access to a "rival" male, and presentations of the green light (CS−) occurred without the US; for the other group, the green light served as the CS+ and the red light served as the CS−. The CS+ came to elicit significantly more approach and zig-zag movements than the CS− in each group. The conditioned agonistic behavior was robust and slow to extinguish. Furthermore, there was no difference in conditioned responding as a function of which colored light served as the CS+. Thus, despite their biological predisposition, stickleback males are not constrained to respond only to red as a predictor of potential conflict. These results are especially noteworthy because early ethologists believed that the aggressive displays of sticklebacks were primarily unconditioned and independent of experiential influences (Tinbergen 1951).

The classical conditioning of agonistic behavior has been investigated most extensively in studies with the blue gourami (Hollis 1984; 1990). In this research, males were first socially isolated and permitted to establish a territory. One group of subjects then received 15 conditioning trials per day for 24 days, in which a 10-second red light CS was followed by 15 seconds of visual access to a rival male. A control group received the CS and US in an unpaired fashion. Males in the paired group came to show a defensive frontal display to the red light in anticipation of viewing the potential rival. Thus, the red-light CS acquired stimulus control over the species-typical aggressive posture previously elicited only by the rival male. This opportunity to anticipate the rival male also resulted in better resource defense during a postconditioning test trial in which exposure to the CS was followed by removal of the barrier that separated the subject's territory from the territory of the adjacent male. During the test trial, subjects in the paired group delivered more bites and tail-beatings to the adjacent male than subjects in the control group. Thus, Pavlovian conditioning acted as a feed-forward mechanism that increased defensive behavior.

The relative inefficiency of the males in the control group to mount a successful defense suggests a potential conditioned inhibition effect. Just as the light cue predicted the presence of competition for the paired males, the same cue may have predicted "no competition" for the males in the unpaired group. Consistent with this interpretation, inhibitory conditioning of aggression was confirmed in a subsequent experiment by Hollis et al. (1984).

The opportunity to anticipate the presentation of a rival allows male gouramis to meet the competition more effectively. A CS associated with a territorial intruder increases the aggressive tendencies of males and enables them to exhibit the frontal display response more quickly. Even if the rapid recruitment of the display does not ensure triumph, it may provide a preliminary advantage in territorial defense. Evidence suggests that early success in aggressive encounters can have long-term beneficial consequences. Hollis et al. (1995) tested blue gourami males twice, once right after Pavlovian conditioning and again three days later. During the first test, a majority of the males that were conditioned to anticipate the presentation of a rival successfully defended their territory, as in previous studies. Interestingly, however, the males that won their first contest were also more likely to win their second contest. This outcome was particularly noteworthy because the second contest involved a different rival male and was unsignalled for both combatants. Thus, there was a significant positive carryover effect between the two contests. Changes in androgen levels as a result of victory may have contributed to this carryover effect (Hollis et al. 1995).

4.2. Sexual behavior

Sexual behavior contributes directly to reproductive fitness but is fraught with risks and uncertainty. Successful sexual interaction involves a delicate interplay between a male and a female in which the actions of one participant have to be carefully coordinated with the actions of its partner. An incorrect move can result in an aggressive reaction from either the potential sexual partner or another conspecific in the area. Given the sensitive and risky nature of sexual behavior, this is an area in which Pavlovian feed-forward mechanisms may be especially useful. Pavlovian mechanisms have been examined in several species, and evidence of the functional utility of such learning has been obtained as well.

4.2.1. Sexual conditioning in the domesticated quail. Sexual Pavlovian conditioning has been investigated most extensively in male domesticated quail (*Coturnix japonica*). In the first such study, Farris (1967) reported that male Japanese quail come to perform a courtship response (strut and toe-walking) to an auditory conditioned stimulus that signals the opportunity to copulate with a female. More extensive observations in subsequent studies with visual conditioned stimuli failed to replicate this result (e.g., Domjan et al. 1986) but showed that male quail come to approach and remain near the CS. This conditioned approach response is similar to the phenomenon of sign tracking that has been extensively documented in studies with laboratory rats and pigeons conditioned with food (Hearst & Jenkins 1974; Tomie et al. 1989). Just as animals come to approach and manipulate a localized CS that is paired with food, male quail come to approach (and sometimes manipulate) a CS paired with copulatory opportunity. The approach behavior is acquired even if a control procedure is used in which the US is omitted on trials when the response occurs (Crawford & Domjan 1993). This finding indicates that the approach behavior is a Pavlovian conditioned response and does not have to be instrumentally reinforced by access to the female. Another important feature of the response is that it is directed at the CS rather than the US. The conditioned approach response occurs even if the CS is presented nearly one meter away from where the female is released on the conditioning trials, and moving the CS to different locations after training does not disrupt the CS tracking behavior (Burns & Domjan 1996).

Because the sexual conditioned approach response is acquired quickly and reliably, it has enabled the exploration of numerous learning phenomena in the sexual behavior system. Phenomena that have been demonstrated include acquisition and extinction (Domjan et al. 1986; Holloway & Domjan 1993a), stimulus discrimination learning (Domjan et al. 1988), blocking (Köksal et al. 1994), second-order conditioning (Crawford & Domjan 1995), trace conditioning (Akins & Domjan 1996; Burns & Domjan 1996), conditioned inhibition (Crawford & Domjan 1996), and the effects of US devaluation (Hilliard & Domjan 1995; Holloway & Domjan 1993b).

Approach to a brief stimulus that signals copulatory opportunity is analogous to focal search behavior in foraging for food – search behavior limited to a specific area where the US is likely to be found. This type of conditioned response is observed when the CS–US interval used during the conditioning trials is of moderate duration. If the CS–US interval is increased substantially (e.g., from 1 min to 20 min), nondirected locomotion rather than focal search develops as the conditioned response (Akins et al. 1994). This nondirected locomotor behavior is analogous to general search behavior in foraging for food. General search behavior tends to predominate when the US is expected but not imminently (Timberlake & Lucas 1989).

Under other circumstances, the sexual conditioned response may include attempts to copulate with the conditioned stimulus. This occurs if a very short CS–US interval is used and the CS is an object that male quail can grab, mount, and contact with their cloaca. The conditioning of copulatory behavior is also facilitated by incorporating into the CS some of the species-typical features of a female quail. This can be done, for example, by adding a taxidermically prepared head and some of the plumage of a female to the CS object (Cusato & Domjan 1998; Domjan et al. 1992b).

Contextual cues can also serve as conditioned stimuli in Pavlovian sexual conditioning. However, the mode of action of conditioned contextual cues differs a bit from the mode of action of discrete, localizable stimuli. As has been found in more conventional learning paradigms (e.g., Bouton & Swartzentruber 1986; Grahame et al. 1990), contextual cues can "set the occasion" for the signal value of discrete conditioned stimuli (Domjan et al. 1992a). Conditioned contextual cues also increase the responsiveness of males to female cues. Males spend more time near a window through which they can see females if they are tested in a sexually conditioned context rather than a nonsexual context (Domjan et al. 1992a). They are also more likely to approach and copulate with a terrycloth object that includes a taxidermically prepared head and neck of a female in a context that has become associated with copulatory opportunity (Domjan et al. 1989). Such context-induced responsivity to female cues is particularly interesting because it is evident after a single conditioning trial (Hilliard et al. 1997).

4.2.2. Sexual conditioning in the fruit fly. A sexual learning effect that appears to involve Pavlovian conditioning has also been observed in the fruit fly (*Drosophila melanogaster*). However, in this case the phenomenon results in the suppression rather than facilitation of male courtship behavior. Recently mated female drosophila secrete a pheromone that acts as an unconditioned stimulus that inhibits male courtship behavior (Tompkins & Hall 1981; Tompkins et al. 1983). Experience of the inhibitory pheromone in connection with other features of a female fly results in suppression of courtship directed at virgin females (Siegel & Hall 1979). The conditioned stimulus can also be provided by a mutant male. Presentation of the inhibitory pheromone in combination with exposure to mutant males results in suppression of courtship directed at mutant males (Tompkins et al. 1983). For the conditioning effect to occur, the CS and US have to be presented at the same time. Following one with the other does not produce the effect. Exposure to the inhibitory pheromone by itself (a US-alone control procedure) or exposure to a virgin female without the pheromone (a CS-alone control procedure) also fails to result in courtship suppression (Tompkins et al. 1983).

4.2.3. Sexual conditioning in fish. Sexual conditioning has also been investigated in two fish species, the blue gourami (*Trichogaster trichopterus*) (Hollis et al. 1989) and the three-spined stickleback (*Gasterosteus aculeatus*) (Jenkins 1997). In the study with the blue gourami, for example, the conditioned stimulus was the presentation of a red light, and the unconditioned stimulus was visual access to a female. For one group of males, each presentation of the CS was followed immediately by the US. For another group, the CS and US presentations occurred unpaired. As training progressed, subjects in the paired group came to perform an anticipatory frontal display when the CS was presented and showed significantly more courtship appeasement responses when they were given access to a female.

4.2.4. Sexual conditioning in small mammals. A sexual conditioning effect has been identified in the house mouse that involves ultrasound vocalizations in males in response to the odor of female urine (Dizinno et al. 1978). Female urine appears to have two components (Sipos et al. 1992). One is an unstable volatile substance that elicits ultrasound vocalizations in male mice as an unconditioned response. This volatile component quickly becomes degraded after the urine is voided and loses its effectiveness. The second component of female urine is stable over a longer period and is less volatile, but it does not elicit male ultrasound vocalizations unconditionally. Rather, the stable component of the urine comes to elicit vocalizations by virtue of being associated with the unstable component.

Conditioning of male ultrasound vocalizations typically has been accomplished by having males copulate with a female and thereby encounter both the CS and US features of the female urine (Dizinno et al. 1978). Studies with females that presumably provided different scents (hypophysectomized females vs. normal females) have indicated that the learning can be specific to the odor that is encountered during copulatory experience (Maggio et al. 1983). Evidence indicating that conditioned vocalizations can come to be elicited to some extent by arbitrary odors encountered during copulation is also available (Nyby et al. 1978).

Sexual conditioning has been investigated in laboratory rats by placing males in a distinctive plastic tub for 10 minutes before moving them to a copulation arena in which they encountered a sexually receptive female (Zamble et al. 1985). After as few as eight conditioning trials, exposure to the conditioned stimulus reduces the latency of males to ejaculate when they are allowed to copulate with a female. Zamble and his associates have demonstrated numerous conditioning phenomena in this paradigm, including acquisition, extinction, latent inhibition, and second-order conditioning (Zamble et al. 1985; 1986; see also Cutmore & Zamble 1988).

Sexual conditioning effects have also been demonstrated in male Mongolian gerbils (*Meriones unguiculatus*) that have established a pair-bond. In these studies a compound olfactory/spatial cue served as the CS. The CS was paired with access to the subject's pair-mate during the postpartum estrus period of the female (Villarreal & Domjan 1997). Pavlovian conditioning decreased the latency to approach the CS and increased time spent near it.

4.2.5. Sexual conditioning of females. Much less evidence is available on the sexual conditioning of females than males. Hollis et al. (1989) observed conditioned frontal displays in both male and female gourami. However, only the conditioned males showed increased courtship appeasement responses during a mating test conducted after the conditioning trials. In studies with Japanese quail, Gutiérrez and Domjan (1997) found that females are much less likely than males to approach and remain near a CS that is paired with the presentation of a sexual partner. In contrast to this result, both female and male Mongolian gerbils have been found to approach and remain near a sexually conditioned olfactory/spatial CS (Villarreal & Domjan 1997). The comparable results obtained with male and female gerbils may be related to the fact that unlike Japanese quail, gerbils form pair bonds. However, other alternatives also require careful consideration (see Villarreal & Domjan, 1997, for a more detailed discussion).

Sexual experience has also been found to influence the sexual behavior of female rats and mice. Oldenburger, Everitt, and de Jonge (1992) found that female rats develop a preference for a distinctive compartment in which they previously copulated with males. Caroum and Bronson (1971) reported that the preference of female mice for male preputial gland extract is increased by copulatory experience with males.

4.2.6. The feed-forward character of sexual conditioning. If Pavlovian sexual conditioning acts as a feed-forward mechanism to optimize responses to the unconditioned stimulus, then conditioning should facilitate copulatory interactions between males and females. Several different lines of evidence support this prediction. As was noted above, Zamble et al. (1985; see also Zamble et al. 1986) reported that male rats achieve ejaculation faster when given a chance to copulate with a female after exposure to a sexually conditioned stimulus. In related observations, Domjan et al. (1986) reported that sexually conditioned male quail initiated copulation faster after exposure to the CS than subjects in a control group for whom the CS was not predictive of copulatory opportunity.

Sexual conditioning can also facilitate how females interact with males. A prominent aspect of sexual receptivity in female quail is squatting in response to the presence of a male (Noble 1972). Gutiérrez and Domjan (1997) found that the presentation of a sexual CS increases this squatting behavior when a male appears. This outcome demonstrates that, as with males, a Pavlovian sexual CS facilitates the sexual behavior of female quail.

A sexually conditioned stimulus can also influence the outcome of sexual competition. Gutiérrez and Domjan (1996) tested pairs of male quail in a 72 square meter outdoor aviary. A female was released at one end of the aviary after presentation of a localized auditory cue. The auditory cue was a sexually conditioned stimulus for one of the males but not the other. The point of interest was whether the male that copulated with the female first was the one that received the sexual CS on that trial. The results indicated that this was indeed the case. In 15 of 17 competition trials, the winner was the male that could anticipate release of the female because of the sexually conditioned CS.

In studies with blue gourami fish, Hollis et al. (1989) found that exposure to a conditioned sexual stimulus reduces aggressive displays and facilitates the emergence of courtship behavior when the male is permitted to interact with a female. The facilitation of courtship and sexual behavior is highly persistent and is manifest in decreased aggression, increased nest building, decreased latency to spawn, and increased clasping (Hollis et al. 1997). In addition, and most importantly, following exposure to a sexually conditioned stimulus, gouramis produce far more offspring than they do if their sexual interactions are not signaled by a CS (Hollis et al. 1997).

Other evidence indicates that exposure to a sexually conditioned stimulus can facilitate physiological reflexes related to reproduction. Graham and Desjardins (1980) demonstrated that a sexually conditioned stimulus triggers the release of leuteinizing hormone and testosterone in rats. Exposure to a sexually conditioned stimulus has also been observed to stimulate the release of sperm in quail (Domjan et al. 1998). Male quail that were exposed to a sexually conditioned stimulus released greater volumes of semen and greater numbers of spermatozoa than control subjects. However, conditioning did not alter other aspects of the sperm, such as their motility, concentration, and viability.

4.3. Conditioned maternal and infant behavior

Variations in infant survival are directly related to maternal responsiveness (Fleming et al. 1996), which is often a function of experience. For example, exposure to pup cues increases the maternal responsiveness of female mice (Noirot 1972). In addition, maternal experience has been shown to improve pup retrieval behavior (Carlier & Noirot 1965; Fleming & Rosenblatt 1974).

4.3.1. Conditioning of maternal behavior. The conditioning of maternal behavior has been explored extensively in sheep and rats. Parental behavior in sheep involves special problems because adult females and their suckling young form flocks in which newborn lambs can easily come in contact with nursing females that are not their mother. Nursing females that accept alien young might not have sufficient milk for their own offspring, thus reducing their reproductive fitness (Holmes 1990). Females rapidly learn the unique olfactory features of their own offspring. The learning appears to take place during parturition and is facilitated by the mother moving away from the herd just before a lamb is born.

The mother is highly responsive to the amniotic fluid that is ejected during the birth process, continually sniffing and licking it, as well as the ground with which the fluid comes in contact. When the lamb is born, the mother vigorously licks the lamb until it is clean of amniotic fluid. This seems to be critical to accepting the lamb for nursing. Washing neonates (which presumably reduces the odor of the amniotic fluid) reduces maternal licking behavior and maternal acceptance (Levy & Poindron 1987). On the other hand, maternal responsiveness can be induced by covering lambs in jackets soaked with amniotic fluid (Basiouni & Gonyou 1988).

Once maternal responsiveness has been established through contact with amniotic fluid, maternal acceptance comes to be elicited by the unique olfactory cues of only that mother's lamb (Poindron et al. 1993), presumably because these cues have become associated with the amniotic fluid. Studies attempting to identify the exact source and composition of these olfactory cues (Alexander 1978; Alexander & Stevens 1982) and attempts to disrupt the development of responsiveness to a lamb's unique scent by introducing artificial odors during the learning phase (Levy et al. 1996) have not been successful. Nevertheless, the available evidence is consistent with the suggestion that individual lamb odors serve as conditioned stimuli that quickly become associated with amniotic fluid, a biologically significant stimulus inherently meaningful to parturient ewes. The individual lamb odors then control maternal acceptance. However, additional studies employing unpaired controls need to be undertaken to substantiate this interpretation.

Olfactory associative learning has also been implicated in the maternal behavior of rats. Bauer (1993) investigated the malleability of preferences for nest and pup odors in first-time mothers. Rat mothers were capable of learning a novel nest odor (CS) if that odor was paired with normal odors from the mother's original bedding (US). This novel odor was then shown to facilitate the identification of the nest, as well as pups that had been placed in the nest (see also Beach & Jaynes 1956). Further, the mothers retained the conditioned preferences through their second litter. These results clearly show that associative learning helps dams identify their nests and their offspring – abilities that are highly correlated with reproductive fitness.

4.3.2. Conditioning of maternal neuroendocrine responses. Maternal lactation involves milk let-down and milk ejection. Both are mediated by neuroendocrine mechanisms triggered unconditionally by suckling of the nipple (McNeilly & McNeilly 1978). Suckling causes the release of oxytocin (OT) from the posterior pituitary gland. OT then travels through the bloodstream to the breast and facilitates the movement of milk into larger mammary ducts, causing milk let-down. The milk ejection reflex, on the other hand, is controlled by prolactin release from the anterior pituitary. Evidence from sheep, rats, and humans suggests that the milk let-down reflex and the milk ejection reflex are both susceptible to Pavlovian conditioning.

Fuchs et al. (1987) measured fluctuations in plasma OT levels in ewes and found that external cues provided by lambs came to elicit OT release as a result of the association of these cues with suckling. Lambs were separated from their mothers after birth, except for periodic feedings. OT concentrations rose significantly due to actual suckling 86% of the time, indicating a clear unconditioned response. After 2 days of testing, OT concentrations also rose significantly from baseline levels when a lamb was introduced into its mother's pen. The fact that OT levels increased in response to placing the lamb in the mother's pen only after the external cues of the lamb had been paired with suckling suggests that this increase was a conditioned response. However, this Pavlovian interpretation must await further testing because the external lamb cues were never presented in an unpaired fashion with suckling bouts.

Exteroceptive stimuli have been found to affect prolactin release as well in a number of species (mice, rats, goats, cows, pigeons, doves). Investigations have explored the role of external pup cues in eliciting and maintaining lactation in rat mothers during different stages of nursing (see Grosvenor & Mena, 1974, for a review). During the first 7 days postpartum, prolactin is released primarily as an unconditioned response to suckling. However, by day 14 postpartum, prolactin release also comes to be stimulated by the visual, olfactory, and auditory cues provided by the pups that reliably precede suckling. Continued nursing from day 14 to day 21 results in broad stimulus generalization of this effect. By day 21, increases in prolactin are elicited not only by the dam's own pups but also by cues from other lactating mother-pup pairs and general contextual cues from the animal room environment (Grosvenor & Mena 1972). In addition, a new inhibitory response to pup cues develops as the pups reach the age of weaning. By day 21, the pups have an inhibitory influence upon the action of prolactin in stimulating milk secretion (Grosvenor et al. 1977; Grosvenor & Mena 1974). Pup cues still elicit prolactin release but they also come to activate an inhibitory process that reduces the effectiveness of prolactin in stimulating milk secretion.

4.3.3. Conditioning of lactation in humans. Learning mechanisms also contribute to the regulation of human maternal feeding responses. Psychological factors related to the maternal milk ejection reflex were first reported by Waller (1938), who documented that milk ejection can be inhibited by embarrassment or elicited by the mother simply thinking of feeding (Jelliffe 1978). Evidence suggestive of conditioned oxytocin release was obtained by McNeilly et al. (1983), who measured oxytocin release during early and later stages of lactation (within 1 week postpartum and 4–11 weeks postpartum, respectively). OT samples were obtained from mothers in the presence of their own babies 15 minutes before suckling started, and at 1-minute intervals during the subsequent feeding. OT levels increased in all participants as a result of infant suckling. Half of the mothers also showed OT increases upon hearing their babies cry before the start of suckling. The remaining mothers showed OT increases either while preparing to feed or after seeing the baby become restless in expectation of feeding. Consistent with a conditioning interpretation, these effects were most consistent 4 to 11 weeks postpartum, after numerous pairings of prefeeding cues with suckling.

Caldeyro-Barcia (1969) was able to study conditioned milk-ejection by measuring intramammary pressure. Polyethylene tubes connected to pressure transducers were surgically implanted into the mammary ducts of lactating women. The milk-ejection reflex was then quantitatively measured in the breast opposite the one being suckled. By far the most effective means of eliciting the reflex was suckling by the infant. However, intramammary pressure also increased in response to seeing the baby or hearing the baby cry in an adjacent room (Caldeyro-Barcia 1969). This conditioned intramammary pressure response was nearly as intense as the response to actual suckling.

Further evidence that mothers can be conditioned to respond to cry stimuli was obtained by measuring changes in mammary skin temperature in response to hearing the recorded cries of a baby (Lind et al. 1971). After the cry stimulus was perceived, 85% of the lactating mothers showed significant increases in mammary skin temperature. No thermal increases were recorded in a control group of nursing mothers that were tested in the absence of the cry stimulus.

4.3.4. Conditioning of nursing in neonates. Learning mechanisms are also involved in regulating the nursing responses of neonates. Rat mothers elicit nipple attachment by placing amniotic fluid on their nipples (Teicher & Blass 1977; Blass 1990). Newborn pups locate the nipple by tracking the odor of the amniotic fluid. This mechanism shows considerable plasticity. Penderson and Blass (1982) injected either an artificial scent or saline into the amniotic sacs of 19-day-old rat fetuses and delivered the neonates surgically on day 21 of gestation. They then tested for nipple attachment following angiogenital stimulation of the pups in the presence of the artificial scent. Rat pups were given a choice of nipples treated or untreated with the artificial odor. Only those pups that were exposed to the artificial scent before and after parturition successfully attached to the nipples treated with this odor. Thus, nipple attachment was determined by the artificial olfactory manipulation (Fillion & Blass 1986a). The artificial scent also affected later sexual behavior. The presence of the odor on a sexually receptive female decreased the ejaculation latencies of male rats that developed a preference for the artificial scent as neonates (Fillion & Blass 1986b).

Evidence of learning in the control of suckling behavior is also evident from studies of human infants. Human infants are differentially responsive to their own mother's odors. Specific odor cues of the mother may facilitate early mother-infant attachment (Porter et al. 1988) or may help the infants locate the nipple for feeding (Blass & Teicher 1980). Human neonates that have been breast-fed differentially prefer the odors of their own mothers compared with the odors of unfamiliar lactating females. Bottle-fed neonates do not show such a discrimination (Cernoch & Porter 1985). Preferences for these odors likely develop as a result of the odors being paired with the unconditioned stimuli provided by suckling.

Nursing responses can also become conditioned to tactile and auditory cues. Using a sucrose solution in the mouth as the US, head-mouth orientation was successfully conditioned in infants to a number of artificial CSs including stroking of the forehead and the clicking of castanets (Blass 1990; see also Blass et al. 1984). Presenting the CS without the US after CS–US pairings resulted in crying in six out of eight infant participants. This type of frustration response is similar to the distress vocalizations of rat pups when their reward expectancy has been violated (Amsel et al. 1977; Blass 1990).

4.4. Play behavior

In contrast to the forms of social behavior reviewed in the above sections, explicit studies of Pavlovian conditioning have not been carried out with play behavior. However, the available evidence is consistent with the suggestion that Pavlovian feed-forward processes may also facilitate playful interactions.

By definition, the word "play" suggests behavior performed for reasons other than necessity. Play behavior typically occurs in preadults, presumably for self-stimulation or amusement. However, many examples of play behavior mimic in some way responses needed for survival. If nothing else, an animal's play behavior increases motor activity, facilitating muscle development and coordination.

While play behavior has been documented in a variety of vertebrate species, including birds (Ortega & Bekoff 1987), it is perhaps most common in mammals, especially canids and primates (Poole 1985). The earliest forms of play are characterized by exploration and self-discovery as the young animal begins to stray from the mother and interact with the environment (Harlow & Harlow 1965). If there is a peer base, the opportunity for interaction with conspecifics becomes available to the developing animal, and this provides the opportunity for playful interactions (Poole 1985). Harlow and Harlow (1965) described the development of a "peer affectional" system in young primates that includes a stage of interactive play, followed by a stage of more aggressive play in which the juvenile learns its place in the social order.

The ubiquitous nature of play behavior among mammals suggests that it had adaptive value during the course of mammalian evolution (Poirier & Smith 1974). Baldwin and Baldwin (1977) identified at least 30 possible functions for play and exploratory behavior. Common to many of these are learning opportunities that arise from environmental and peer interactions. For instance, it has been proposed that play provides reinforcement in the form of sensory stimulation as animals seek to obtain optimum levels of arousal (Baldwin & Baldwin 1977). Consistent with this hypothesis, the opportunity to engage in social play has been successfully used as a reinforcer for maze learning in rats (Humphreys & Einon 1981), and chimps will manipulate a lever for access to a human play partner (Mason et al. 1962).

If the opportunity for social contact and play can serve as a reinforcer, then the social play partner, for our purposes, can be considered an unconditioned stimulus. This social US occurs in a specific context and in association with environmental and behavioral signals. These contextual and behavioral signals, through their association with the US, may acquire predictive value and come to control conditioned responses relevant to play behavior. Consistent with this scenario, social play becomes more efficient with practice (Poole 1985). In addition, Poirier and Smith (1974) noted that mammalian species with the greatest capacity for learning also show the greatest propensity for play behavior.

Juveniles may acquire preferred play partners through associative processes. Positive and negative reinforcement will become differentially associated with various peers through repeated social contact. The contextual and behavioral signals that occur in conjunction with these bouts of peer contact could become associated with the reinforcement that follows the signal. Bekoff (1974; 1975) has identified such behavioral signals in the playful interactions of canids. For instance, coyotes (*Canis latrans*) attempting to solicit a playful interaction often adopt a "play bow" posture, crouching on their forelegs while elevating their hindlegs. In laboratory tests, 90% of successful playful interactions were preceded by such play signals. A high correlation was also found between those signals that were successful in eliciting playful interactions and those that were actually used (Bekoff 1974). Play signals have also been shown to clarify playful intentions when the behavioral intention of the soliciting partner is relatively ambiguous (Bekoff 1995). Other signals found to be temporally correlated with play behavior include the "play pounce" and "play face" in canids (Bekoff 1975; Fox 1970) and the primate "play face" (Chevalier-Skolnikoff 1974; van Hooff 1967).

Even if playfully intended, some play behaviors have the potential of inflicting injury on the unwitting playmate (Poole 1985). Signals that precede a playful interaction may acquire predictive value and assist animals in approaching positive play experiences and avoiding negative ones with animals that are likely to respond too aggressively. Learning to predict the form of the forthcoming play episode (wrestling, chasing, pouncing, biting) may also allow young animals to better prepare for the impending interaction and engage in more complex and satisfying forms of play. Thus, learning may decrease the potential costs of finding willing and compatible play partners and increase the effectiveness of the play behavior.

4.5. Social grooming

Another form of social behavior prominent in various species is grooming. When grooming behavior occurs in a social context it is termed mutual grooming, allogrooming, or social grooming. Social grooming is the act of cleaning a conspecific's fur, pelage, or skin. In birds a functionally similar form of this behavior is called social preening. However, grooming as a form of social behavior has been best documented in primates (Sparks 1967; see also Bernstein & Mason 1963; Lindburg 1973; Oki & Maeda 1973; Rosenblum et al. 1966; Sade 1965; Yerkes 1933), and is believed to serve various social and group functions (Carpenter 1942; Lindburg 1973; Sade 1965; Terry 1970; Washburn & DeVore 1961; Yerkes 1933). The importance of social grooming for some primate societies is evident in the amount of time spent in daily allogrooming activities (Bernstein & Mason 1963; Lindburg 1973; Southwick 1967). The act of grooming and being groomed may have reward properties for the participants (Lindburg 1973; Marler 1965; Yerkes 1933). If social grooming is a rewarding activity, then grooming partners can be characterized as social contact USs that are potentially available for Pavlovian conditioning. In this way social grooming is similar to social play.

In Lindburg's (1973) observations of Rhesus macaques, bouts of social grooming were among the first and last activities of the day when the groups' food or sleep needs had been satisfied. This suggests that the environmental context in which social grooming is most commonly displayed is predictable. The predictability of social grooming suggests that it should be amenable to Pavlovian conditioning. As a regular occurrence in a common context, grooming bouts with another individual may constitute discrete learning trials. These learning episodes may promote the formation of associations between environmental stimuli and preferred grooming partners.

Allogrooming may be most rewarding when the participants can anticipate the outcome and nature of the imminent interaction. Inherent to the act of being groomed is a relaxed posture and weakened defense that, in the wrong context or with the wrong conspecific, could have negative or injurious consequences. Presumably, a certain level of confidence between grooming partners must develop before grooming can acquire the properties that make it reinforcing. Because social contact is risky when the results of close proximity are unpredictable, social animals should come equipped to associate contextual and behavioral cues with both pleasant and aversive social outcomes. These associations would serve to increase the frequency of pleasant social experiences and decrease the frequency of unpleasant ones. In this way animals can gain greater control over the costs and benefits of social interactions such as grooming. Thus, predictability would appear to be important in the formation of stable grooming relationships, and Pavlovian associations are likely to be the means by which these relationships can acquire predictive properties. Or, as Lindburg (1973) put it, "Though it has not been experimentally tested, conditioning and learning might be essential in making the grooming preferences among group members specific" (p. 143).

The degree and rate of social grooming within a primate group varies intraspecifically according to the age, status, and sex of an individual (Lindburg 1973; Oki & Maeda 1973). These individual attributes probably serve as biological constraints that, in part, determine which group members can establish amicable grooming relationships. Not every group member is considered a potential grooming partner. For instance, in matriarchal primate societies same-sex allogrooming relationships are generally the domain of adult females (Lindburg 1973; Oki & Maeda 1973). The unrelated adult males in these societies may not be capable of perceiving other males as anything other than potential aggressors because the behavioral costs of doing so are too great. Thus, individual differences, when coupled with the contextual constraints discussed above, effectively limit the range of potential CSs available for association with the act of allogrooming. This enhanced specificity increases the likelihood that for any one animal only a few select individuals, or class of individuals, will serve as USs for association with the behavioral and environmental cues available to signal satisfactory grooming interactions.

5. Conclusion

Animal social behavior has been analyzed traditionally within the context of biological perspectives that emphasize ecological and genetic benefits. Presumably, evolutionary processes have shaped social behavior so as to increase its benefits relative to costs. However, the proximate mechanisms that increase the utility of social behavior have not been specified. How systems function to achieve a particular goal or purpose has been analyzed within the context of control systems theory. Those considerations have indicated that feed-forward mechanisms can significantly improve system functioning. In behavioral systems, a prominent feed-forward mechanism is Pavlovian conditioning. We accordingly explored the role of Pavlovian conditioning in several forms of social behavior.

Pavlovian conditioning of social behavior has been investigated most extensively in studies of sexual behavior, maternal lactation, and infant suckling. However, clear demonstrations of Pavlovian conditioning are also available for agonistic behavior, and Pavlovian processes may be similarly involved in social play and social grooming. In addition, several lines of evidence indicate that associative learning can increase the efficiency and effectiveness of these social interactions. Pavlovian conditioning has been shown to improve defensive behavior in the blue gourami, an Anabantid fish. It also has been shown to facilitate courtship and reproductive behavior in the blue gourami. Other evidence indicates Pavlovian conditioning can decrease the latency of copulation and stimulate the release of sex hormones in male rats. In quail, Pavlovian conditioning has been shown to increase the sexual receptivity of both males and females, increase the success of males in sexual competition, and facilitate the release of sperm. Pavlovian conditioning also has been shown to facilitate maternal neurohormonal responses involved in milk let-down and milk secretion and improve the efficiency of infant suckling in humans. Associative processes also have been implicated in mother-infant attachment in sheep.

The available evidence encourages us to propose that all social interactions can be profitably analyzed from the perspective of Pavlovian conditioning. It is our contention that Pavlovian feed-forward mechanisms can contribute significantly to the efficiency of social behavior. We further contend that this contribution is best understood from a perspective that integrates Pavlovian processes, biological theory, and concepts from control systems theory. Based on these assumptions, we predict that all social behavior will be more efficient and effective in situations where animals are able to use cues provided by the inanimate and social environment to predict how a social interaction will unfold. Conversely, social behavior will be less effective in situations that lack relevant social conditioned stimuli.

In principle our predictions are not tautological. Pavlovian conditioning need not occur in all social situations, and the presence of a Pavlovian CS need not increase the efficiency and efficacy of all social interactions. We are not aware of data inconsistent with our predictions. However, given the diversity of animal species and the diversity of forms of animal social behavior, the available evidence of Pavlovian control of social behavior is severely limited. Much work remains to extend this approach to other species and response systems.

The extension of Pavlovian concepts to the analysis of social behavior provides a number of advantages. First, the Pavlovian perspective provides a framework for the study of proximate mechanisms of social behavior by focusing on the stimuli that predictably occur in sequential social interactions. This emphasis on proximate mechanisms complements biological perspectives that have focused on ultimate factors that shape social behavior. Second, our extension of Pavlovian concepts helps integrate biological and learning approaches with the analysis of social behavior. This integration is achieved by using control systems theory to show that Pavlovian feed-forward mechanisms can increase the benefits of social behavior relative to its costs. Third, the use of control systems theory in combination with Pavlovian conditioning shows how memory mechanisms are involved in the shaping of effective social behavior. Fourth, the Pavlovian approach makes clear predictions about circumstances in which the efficiency and effectiveness of social behavior will be enhanced, as well as circumstances in which such effects will not be observed. Fifth, our analysis serves to extend Pavlovian concepts beyond the traditional domain of discrete secretory and other physiological reflexes to complex real-world behavioral interactions. This helps apply abstract laboratory analyses of the mechanisms of associative learning to the daily challenges animals face as they interact with one another in their natural environment.

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Let's go all the way – and include operant and observational learning

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Abstract: If biologists are going to incorporate learning into theories of animal behavior, why not go all the way and incorporate the enormous literatures on Pavlovian conditioning, plus those on operant and observational learning?

Domjan et al. have done an outstanding job of extending biological theories to include Pavlovian conditioning. As they point out in the second paragraph of section 1 (Introduction), "The biological approach . . . has largely ignored the role of learning or learned associations." Fortunately, comparative psychologists have known for decades that learning plays important roles in animal behavior (Greenberg & Haraway 1998), and they continue to amass expertise in dealing with it) – (as clearly seen in such journals as *Learning and Motivation, Animal Learning and Behavior,* and *The Journal of Experimental Psychology: Learning, Memory and Cognition.*

My main suggestion is this: If biologists are going to incorporate learning into theories of animal behavior, why not go all the way? Why not incorporate the enormous literature on Pavlovian conditioning plus those on operant and observational learning? Pavlovian conditioning is only an aspect of learning.

Domjan et al.'s model of control systems can deal not only with feed-forward mechanisms such as Pavlovian conditioning, it can also deal with feedback mechanisms such as *operant conditioning.* When primates approach each other for grooming, they often give facial and/or vocal signals that are CSs associated with friendly behavior – valuable feed-forward information. If the animals can groom successfully together, they experience the US of gentle tactile stimulation, a primary reinforcer that makes grooming rewarding. In fact, the reinforcer of tactile stimulation is feedback that the interaction was carried out successfully. Some individuals cannot groom successfully because one is hyperactive or aggressive; these individuals cannot receive prolonged positive reinforcement of tactile stimulation until they learn to inhibit the behaviors that interfere with grooming.

Operant and Pavlovian conditioning are often intertwined in complex and dynamic manners, as control theory would suggest, because both feed-forward and feedback are essential components of any complete model of control systems. Let me demonstrate this by expanding on the research presented in section 4.3.4. Consider a human mother who breast-feeds her baby each day. When she notices the infant pulling at her blouse, she sees stimuli that precede and predict that the baby will soon be sucking on her nipple, providing the US that causes the milk ejection reflex. Thus the baby's approach becomes a CS that triggers feed-forward mechanisms – eliciting pleasurable sensations and hastening the onset of the milk release reflex even before the US comes. Next are the feedback processes of operant conditioning. However, if the mother performs the operant behavior of holding her baby in a good position for successful nursing, she experiences a prolonged period of reward, since the USs of nipple stimulation and milk release are primary reinforcers. If she holds the baby in inappropriate ways and the baby cannot nurse, she does not receive the reinforcers. The mother's behavior is molded by *different reinforcement.* She receives reinforcing feedback for holding the infant in appropriate positions, and using awkward positions leads to few rewards or even punishment from an agitated infant. This operant example is completely compatible with Domjan et al.'s views that conditioning can facilitate social interactions.

Very often the US that is the cause of Pavlovian conditioning is also a primary reinforcer or punisher that increases or decreases the probability of the operant behaviors that precede it. Once CSs are established through Pavlovian conditioning, they can serve as secondary reinforcers and punishers. Money is a secondary reinforcer because it is associated with many different kinds of primary rewards.

In addition, many species are capable of *observational learning* – sometimes called imitative learning. Observational learning has been studied extensively in humans (Bandura 1977), and it fits with feed-forward models of learning. When one person, called a model, demonstrates an operant behavior, observers may gain useful information about the behavior. If the model is punished for the behavior, observers may abstain from imitating. On the other hand, when a model's actions lead to rewarding consequences, observers receive feed-forward information that they might also be rewarded for similar behavior. Naturally, all sorts of contextual and behavioral cues are part of the feed-forward loops. Research shows that people tend to imitate individuals whom they like, who appear to be happy, and who are not too different from them. In essence, models who are most likely to be imitated have some positive cues associated with them that serve as CSs for positive emotions in the observer. Most people do not imitate sad and unsuccessful individuals. Numerous CSs established by Pavlovian conditioning give us feed-forward cues that imitating one person may be more rewarding than imitating another individual.

After sociobiology became popular in the 1970s, comparative psychologists recognized that it failed to incorporate Pavlovian and operant conditioning, observational learning, and other important proximal causes of behavior (Baldwin & Baldwin 1981). In order to build more "balanced biosocial theories" of animal and human behavior, we need to counterbalance genetic and evolutionary theories with appropriate mixes of data about all forms of learning and other proximal causes (such as diet, health, and injury).

Domjan et al. have presented a very logical and carefully argued approach for including Pavlovian conditioning into biological models of behavior. Why not go all the way and incorporate all other proximal causes of behavior in an empirically defensible balance? An easy way to become sensitive to the multiple forms of learning seen in humans – and the ways these interact with each other – is to examine learning processes in our own daily lives (Baldwin & Baldwin 1998).

Social play is more than a Pavlovian romp

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Abstract: Some aspects of play may be explained by Pavlovian learning processes, but others are not so easily handled. Especially when there is a chance that specific actions can be misinterpreted; animals alter their behavior to reduce the likelihood that this will occur. The flexibility and fine-tuning of play make it an ideal candidate for comparative and evolutionary cognitive studies.

Domjan, Cusato & Villarreal are consistently cautious when discussing the use of Pavlovian feed-forward mechanisms in the control of social behavior, making it difficult to find any definitive statements with which to disagree strongly. Nowhere is this more obvious than in their brief section on social play (hereafter "play"). Nevertheless, ignoring their hedging, here we try to rescue some aspects of play from Pavlov's grip.

The nub of Domjan et al.'s views are expressed in the following statements (sect. 4.4; bracketed numbers and letters inserted for later reference).

(1) "If [a] the opportunity for social contact and play can serve as a reinforcer, then [b] the social play partner, for our purposes, can be considered an unconditioned stimulus" (para. 5).

(2) "Contextual and behavioral signals, through their association with the US, may acquire predictive value and come to control conditioned responses relevant to play behavior" (para. 5).

(3) "Juveniles may acquire preferred play partners through associative processes" (para. 6).

(4) "The contextual and behavioral signals that occur in conjunction with these bouts of peer contact could become associated with the reinforcement that follows the signal" (para. 6).

(1) Part [a] of the conditional is supported by the studies cited by Domjan et al. that use opportunity to play as a reinforcer. Granting that the antecedent of the conditional is true, the question is whether its consequent, [b], is true and if so, whether it follows from [a]. Is [b] true? Play partners do not reliably elicit play simply by their presence. Many animals spend more time engaged in other activities with their social partners. Of course no US produces its effects all the time; even the sight of food does not always produce salivation in a dog. But even if we factor in an internal motivational state for play, it is not true that a motivated animal will automatically start playing in the presence of a potential partner. Rather, from a very young age, an individual will usually perform play solicitation behaviors before engaging in play. So, if the presence of a play partner is a US for anything, it is for play signals rather than play itself. Thus we doubt [b] is true in the way it is intended, and the question of whether it follows from [a] is moot.

(2) and (4) Setting aside the tentative way in which (2) ("may acquire") and (4) ("could become associated") are expressed, making them effectively unassailable, we see problems with the likelihood of the expressed possibilities being true. Our skepticism about (1)[b] suggests an obvious problem, namely, if we are correct about play-soliciting signals being provoked in an unconditioned way by the presence of a play partner (under the proper motivational conditions), then many of the behavioral signals mentioned in (2) and (4) are not learned by association, but are more likely to be part of an innate system for the production of play (Bekoff 1977). In many species, there has been selection for various mechanisms for initiating and maintaining play. These include using specific play signals, varying the ways (for example, frequency, form, duration) that individual actions are performed, altering sequences of behavior, self-handicapping, and role reversing. Various signals and tactics may be used singly or in combination with one another (Bekoff 1977; 1995; 1999; Bekoff & Byers 1981; 1998). The highly stereotyped nature of these signals is an indication that they are not acquired merely by associative learning, although it is probably true that associative learning plays some role in fine-tuning the use of signals as play experience is gained.

Turning to (3), it is technically unassailable that juveniles "may acquire" play partners by any number of mechanisms, including associative learning. But we wonder if there is anything surprising in the claim that individuals play more with those with whom they enjoy playing. Perhaps we have missed something here, or are illegally smuggling something in by speaking of "enjoyment" rather than positive reinforcement. But without the technical dressing of S-R (stimulus-response) psychology, we wonder whether there is much more than a simple homily here.

Indeed, we find it rather striking that Domjan et al. report at length on Bekoff's discussion of the role of intention in play signals. This suggests to us that a cognitive ethological approach is more useful than theirs if one wishes to gain an understanding of social play (Allen & Bekoff 1997; Bekoff & Allen 1998). This includes postulating that individuals know they are playing because the actions performed differ when used during play when compared with other contexts (Hill & Bekoff 1977), because the order in which motor patterns are performed differs from, and might be more variable than the order in which they are performed during the performance of, for example, serious aggression or serious predation (Bekoff & Byers 1981), or because certain behavior patterns do not occur during play or serve to terminate ongoing play (e.g., submission, threat). The cognitive approach also involves treating play signals as semantically interpreted gestures that are used to change the meaning of actions that can be misinterpreted (e.g., vigorous biting accompanied by rapid side-to-side head shaking; Bekoff 1995). In some canids, play bows are used most often when an action preceding or following the bow might be misinterpreted.

As Domjan et al. note, it is unlikely that Pavlovian conditioning can explain all aspects of play (or other social interactions). Here, we provide an example of when these sorts of explanations do not account for available data. Specifically, Domjan et al. do not take into account the flexibility of the play and the fine-tuning that occurs, especially when there is a high probability that a play encounter may escalate into aggressive interaction. Much about play resists Pavlovian pigeonholing.

More comparative data are needed to gain a better understanding of the evolution of social play, of its cognitive dimensions, and its possible neurobiological bases (Bekoff & Byers 1998). Although not all individuals always display behavior patterns best explained by appeals to intentionality, we argue that play is one domain where such approaches are fruitful. Studies of animal play are so interesting and challenging because deciding when mechanistic explanations are more appropriate than cognitive explanations (and vice versa) will not only provide data that help us to understand play, but also cognitive processes in general.

Ecological heuristics for learning

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Abstract: Domjan, Cusato & Villarreal's target article is reviewed in the context of historical difficulty for learning studies in discriminating between learned and unlearned components of behavior. The research surveyed in the target article meets the criterion of differentiating between some learned and the unlearned aspects of social behavior, with Pavlovian conditioning shown repeatedly as a route by which reproductive and aggressive behavior is modulated.

The comedian Buddy Hackett is said to have reacted to some psychoanalytic writing by saying, "That Freud, he had some good stories, but he didn't know how to tell them."

By 1970 or thereabouts psychologists interested in animal learning had to cope with variations on the foregoing wisecrack that could be seriously applied to their own subject matter. Many behavioral bits and pieces had been revealed, but no coherent, provable account of life histories had emerged. Moreover, research was revealing that, although associative learning certainly occurred, the quality of associations would depend dramatically on the ecological problems that were naturally encountered by the subjects, with these problems represented by the specific apparatuses, stimuli, and responses used in laboratory studies (see Blanchard et al. 1989; Bouton & Fanselow 1997; Braveman & Bronstein 1985; Hinde & Stevenson-Hinde 1973; and Seligman & Hager 1972 for overviews.)

Furthermore, some of the most well-cited examples of associative learning were turning out, upon expanded and ethologically oriented observation, to include unlearned behavior that had been ignored, distorted, and mislabeled in order to remain consistent with the experimental goals of identifying and analyzing learning. Thus, rats' avoidance of painful footshock was reconceptualized as an unlearned antipredator reaction that sometimes could be modified by experience (Bolles 1970). Also, many attempts at positive reinforcement were rendered ambiguous and limited in scope once the existence of animals' unlearned species-typical behavior, and their shifts in attention, were appreciated (Breland & Breland 1961; Bronstein 1981; 1986a; Collier 1982; Collier et al. 1972; Moore & Stuttard 1979; Staddon & Simmelhag 1971). In sum, many of the best known assays of learning were inadequately sensitive, that is, not adequate for differentiating learned and unlearned components of behavior. Their external validity also had been called into question.

In part as a result of this increased and complicating understanding, Revusky (1975) noted the absence of any single, coherent domain that might be called "learning." Furthermore, Lockhard (1971), taking one of the more extreme positions, concluded that psychologists interested in animals had to conceive of themselves as studying a branch of zoology – in effect investigating largely unlearned, molar acts, as opposed to seeking out molecular responses and learned associations.

In short, by the early 1970s there was considerable recognition that the formation of highly general concepts about how learning occurred – an all-purpose reinforcement process and the equipotentiality of associations – sometimes were examples of extreme overreaching. Similar errors of thought had occurred in other scientific domains, and were described in the seventeenth century by Sir Francis Bacon as one of his Idols of the Theater: extremely sweeping and misorienting pronouncements made on the basis of very limited empiricism (see Bacon 1955; Zagorin 1998).

In reacting to the uncertain and shifting foundation for studies of learning, Domjan and his colleagues have attempted to integrate two important themes. First, there is a modified general-process assumption that, despite some practical and theoretical overreaching, associative processes (as revealed by Pavlovian procedures) play a measurable role, and probably an important one, in animals' social lives. This first assumption, the main point of Domjan et al.'s target article, receives overwhelming support. Pavlovian conditioning has been shown to modify several categories of social behavior in a proactive (feed-forward) manner. Furthermore, by assessing learning in the context of molar and functional acts, such studies help construct useful chunks of animals' life histories. This research strategy also prevents animal-learning techniques from confusing learned and unlearned components of behavior. Learning is seen as functioning to fine-tune unlearned, species-typical activities.

Second, since many species- and task-specific variations in learning have been revealed, Domjan et al. use the working hypothesis that the most prepared associations are likely to be those that alter behavior in the direction of increasingly efficient reproduction. (Shifts toward inefficiency, whether learned or unlearned, are tacitly assumed to have been selected against, that is, subjected to negative feedback over evolutionary time.) This second assumption is a reasonable, adaptationist heuristic that goes largely untested. However, it will be hard to gather evidence about whether imprecise or unstable social learning is associated with declining reproductive success – especially with wild-living animals, the most relevant case.

Is the avoiding of operant theory a Pavlovian conditioned response?

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Abstract: The proposed heavy dependence on Pavlovian conditioning to account for social behavior confounds phylogenically and ontogenically selected behavior patterns and ignores the extension of the principle of selection by consequences from biological to learning theory. Instead of acknowledging operant relations, Domjan et al. construct vaguely specified mechanisms based upon anticipatory cost-benefit considerations that are not supported by the Pavlovian conditioning literature.

Many of the things that animals do produce environmental effects, including effects on the behavior of other organisms, with subsequent actions similar in kind becoming more or less likely. This results in a three-term specification of the action – antecedent or discriminative stimulus, topographically or functionally defined response, and consequence – and cannot be captured by a two-term Pavlovian relation. Recognizing this, Domjan et al. introduce "memory" and "feed-forward" processes, greatly complicating an account under the guise of interdisciplinary inclusiveness, apparently in order to maintain a strictly Pavlovian perspective.

Three-term relations have been addressed much more directly as operant behavior, generated and maintained through a type of selection by consequences. Operant relations have been efficiently systematized and studied, with the resulting interpretive system validated both through its internal coherence (Catania 1998; Skinner 1953, see also 71 volumes of the *Journal of the Experimental Analysis of Behavior*) and through applications in the domain of human and nonhuman, as well as social and nonsocial behavior (Andronis et al. 1997; Daniels 1994; Epstein et al. 1980; Guerin 1994; Johnson & Layng 1992; Kulik et al. 1979).

Besides ignoring the extensive conceptual and empirical literature on operant selection per se, Domjan et al. overlook contemporary relationships between psychology and biology – not only in behavioral neuroscience but also in decades of fruitful exchange between behavior analysts and evolutionary biologists. The latter have been documented even in this journal (e.g., Fantino & Abarca 1985). Moreover, by sharing with biology common (selectionist) interpretive principles rather than by appealing exclusively to reductionistic mediational mechanisms (e.g., Smith 1986), one can effectively consider behavioral/psychological processes as extended in time, at multiple time scales (Glenn 1991). Pavlovian processes are best understood within this selectionist system, as phylogenically selected patterns of behavioral control by environmental stimuli, without conceding the privileged status that the target article grants to "proximate" (implicitly if not explicitly molecular) causative interpretations.

Surely, Pavlovian relations occur within social behavior, yet the authors never provide an explicit definition of "social behavior" and make only vague reference to "groups." The target article implies that complex human social behavior is within Domjan et al.'s purview, although illustrative examples are drawn mainly from experiments on species-specific, stereotyped, and rigid behavior patterns. Ignoring this and accepting the authors' "proximate focus," their interpretations are still flawed. For example, when the authors refer to "shaping effective social behaviors" within the context of their model (sect. 5, para. 5), they borrow terminology that was coined in dealing with selection of operant behavior via response-reinforcer contingencies; these are not covered by the relations that define Pavlovian conditioning. Pavlovian conditioning – poetically characterized in the article as generating "the glue that holds experience together" (sect. 1, para. 4) – encompasses only stimulus-stimulus relations. A conditioned stimulus, through its contingent relation with the unconditioned stimulus, modulates the occurrence of already existing response patterns (Rescorla 1988). In contrast, a "discriminated operant involves a response *selected* by the experimenter through shaping" (Jenkins 1973, pp. 189–90) – a response that would not result from mere temporal pairing of the discriminative stimulus with the reinforcer. "The [Pavlovian] conditioned response is a natural consequence of the stimulus-reinforcer pairing and is in that sense [ontogenically] *unselected*" (Jenkins 1973, p. 190, original emphasis).

Throughout the target article, the authors seem unconcerned about distinguishing between Pavlovian, operant, and other behavioral processes, whereas a significant body of research has shown that operant and Pavlovian relations are not reducible to one another and may only be dissociated by arranging explicit experimental procedures (e.g., Brown et al. 1982; Marcucella 1981). Jenkins (1977) showed that even the pigeon's key peck, which in its autoshaped form is considered a prototypical Pavlovian conditioned response, could not be reduced to either stimulus-reinforcer (S-S*) or response-reinforcer (R-S*) relations. He concluded that "the three-termed relation [S(R-S*)] identified by Skinner is alive and well and is not reducible to a pair of correlations" (p. 60). Gormezano and Kehoe (1975) further pointed out that many classical conditioning preparations violated Pavlov's stricture of administering the US independent of the subject's behavior. In those cases, selection by consequences invariably operates upon the behavior "necessary for the *receipt* of the US" (p. 151). These considerations make untenable many instances of the authors' interpretation, which indiscriminately apply principles of Pavlovian conditioning to situations most likely involving operant, three-term relations.

Domjan et al. attempt to compensate for this limited sway of Pavlovian relations by appealing to an implicit rationality of unspecified decision processes operating upon the metaphor of memory storage via "feed-forward processes." They assert that this assemblage of processes prevents "behavioral mistakes" by anticipating "imminent behavioral output" and modifying it according to a precalculated cost-benefit ratio. Their account relies on the predictive utility of Pavlovian relations challenged by findings such as those of Brady et al. (1969), in which two simultaneous, conventional measures of Pavlovian conditioning (conditioned suppression of lever pressing and blood pressure changes) rendered independent patterns of conditioning and subsequent extinction; each was sometimes present without the other. Moreover, Hearst and Jenkins's (1974) "long box" experiment showed that Pavlovian responding persisted even when it prevented consumption of the US; their subjects pursued the "sign" although this resulted in obviously lower "cost-benefit" ratios (see also omission studies, e.g., Williams & Williams 1969). Domjan et al.'s interpretation would further predict a correlation between conditioned response magnitude and the intensity of an unconditioned stimulus, a relation that could not be shown (Furedy 1970; Furedy & Doob 1971; cited in Gormezano & Kehoe 1975). In sum, many of the behaviors for which the authors invoke these implicitly rational decision processes and "feed-forward theories," said to operate upon loosely specified memory processes, will be predictable only post hoc, if at all. The behavior of concern has been addressed far more directly as behavior sensitive to its consequences, as operant behavior.

A final observation occasions the title of our commentary. Discussing play behavior, Domjan et al. allude to operant reinforcement relations as providing a basis for Pavlovian conditioning, whereby a play partner, by virtue of accompanying reinforcement, "for our purposes, can be considered an unconditioned stimulus" (sect. 4.4, para. 5). Remarkably, this statement identifies operant relations as the bases for unconditional stimulus properties, thus suggesting Pavlovian relations depend upon operant ones. If so, it is even less clear why the operant relations were not invoked directly to account for social behavior selected by its consequences. Furthermore, taking the statement at face value and extrapolating, it would appear that, to a Pavlovian theorist, operant relations function as aversive events feeding forward into the avoidance of acknowledging selection by consequences as fundamental behavioral process.

Adaptiveness, law-of-effect theory, and control-system theory

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Abstract: It is suggested that the control-system theory of Domjan et al. restates in engineering vocabulary the primary thesis of law-of-effect theories: namely, that classical-conditioning arrangements may involve CR-contingent reinforcement. The research cited by Domjan et al. is relevant to the idea that classical conditioning is an adaptive process, but is irrelevant to their control-system theory.

An enlargement of the domain of classical conditioning since the mid-1960s has reversed the long-standing view that, in comparison to instrumental/operant conditioning, classical conditioning is a restricted and minor contributor to organismic economy (e.g., Skinner 1953). Much of this enhanced importance of classical conditioning stems from experimental arrangements embodying a *loose* specification of classical conditioning through an experimenter-arranged CS-US relationship, without direct measurement of CRs in the motor system of the UR (cf. Gormezano & Kehoe 1975, pp. 148–54). By contrast, a *narrow* specification of classical conditioning requires direct measurement of CR. (Both require demonstration of learning via suitable control groups.)

Theorists who suspect that there are numerous stimulus-reinforcer (or cue-releaser) regularities in the complex natural environments of freely moving animals have found the loose definition congenial. Freed, thereby, from the traditional and technically challenging requirement of demonstrating a measured CR-UR relationship, they can arguably maintain that classical conditioning processes play an adaptive role in natural settings, including those that involve social interaction. Because the target article advances that argument, it is a contribution to what some hail as a new hegemony of classical conditioning (Turkkan 1989).

The idea that classical conditioning has an adaptive function has long been an appealing notion, underwritten by an evolutionary metaphysics embraced by researchers in conditioning and in animal psychology generally. In the first chapter of his *Conditioned Reflexes,* Pavlov (1927) casually ascribed adaptive functions to conditioned salivation and other putative instances of signalization learning. American researchers of a Functionalist stripe (e.g., Culler 1938) claimed that learning to anticipate biologically important events provides the organism with (unspecified) advantages of preparing for the event. The reader is directed to section 3.4.4 of the target article for more of the same line of thought.

This appealing notion has occasionally been put to the test in the course of evolution of "law-of-effect" theory (Coleman & Gormezano 1979): Specific, measurable, and testable adaptive functions of CRs were suggested by the idea that classical-conditioning preparations (may) involve CR-contingent (i.e., instrumental) reinforcement stemming from the way the CR alters the sensory value of the US (e.g., Perkins 1968; Schlosberg 1937; cf. Martin & Levey 1969). Prokasy (1965) suggested that CRs typically undergo "response shaping" of intensive, temporal, or other measurable qualities of the CR as it becomes more adaptive during conditioning. A dependence upon the narrow definition of conditioning is evident; indeed, the human eyelid-conditioning preparation was extensively used in developing this theory.

The control-system theory of the target article – or at least an ontogenetic portion of it, as we note below – appears to be very closely related to law-of-effect theory, although the abstract notion of "cost/benefit ratio" obscures the kinship. Figures 1 and 2 involve what would be called, in law-of-effect language, experience-mediated shaping of the UR (e.g., Martin & Levey 1969). In Figure 3, CRs are brought into the picture and, because the same "actuator" controls CR and UR expression, are apparently assigned a function like that of URs. The authors' theory proposes that the adaptiveness of the CR in preparing for the US is enhanced during learning by control-system devices that monitor experienced outcomes (i.e., indicators of costs and indicators of benefits for the organism) of the CR (and UR). Organismic machinery calculates the ratio of these experienced values and compares it to a preset cost/benefit ratio serving as a goal state. Changes in the CR are made so that the ratio comes to be "as low as possible under the extant environmental conditions" (sect. 3.4.1). (We decline to comment on the phylogenetic application of the theory through CR-mediated costs and benefits to one's genetically related descendants.)

Having identified a kinship of theories, we note that laboratory evidence (gathered under the narrow specification) testing the law-of-effect theory is therefore also pertinent to the control-system model; the evidence is either largely negative or problematic (see Coleman & Gormezano 1979). Rather than take note of such pertinent but unfavorable evidence, the authors seek support from research that uses the loose specification of classical conditioning: In naturalistic settings, freely moving organisms are given opportunities to emit instinctual behaviors, and usually – but not invariably – conditioning is measured indirectly through change in some behavior that is not unequivocally a CR.

Such procedural features create problems for the authors. As a research preparation departs more and more from the constraints ("limitations," "restrictions") of the narrow specification, the investigator's ability to identify a behavioral sequence as "classical," "instrumental," or (perhaps) "instinctive" is increasingly compromised. Unrestricted behavior in seminatural settings is a complex mix of several behavioral categories. Thus, only a portion of the cited research permits the authors to claim that the adaptiveness of classical conditioning has been demonstrated, rather than instrumental or instinctive or some other behavior category. In a couple of instances (e.g., Hollis et al. 1995), there is a demonstration that cue-stimuli ("CSs") enhance some social (agonistic) performance for organisms that have such prior cue-learning. However, none of the cited research *requires* the control-system model of cost-benefit calculations; and the cited research demonstrates neither that there is an improvement in the features of the CR (or UR) during conditioning nor that the CR features are essential to attainment of the benefit, as the control-system theory clearly implies.

Domjan et al.'s interpretations of less rigorously identified or measured phenomena in the heterogeneous arena of social conduct (play, grooming, etc.), although suggestive, do not constitute *evidence* for the model. We have to conclude that the control-system model is irrelevant to the research that is cited.

The "benefit" of Pavlovian conditioning – performance models, hidden costs, and innovation

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Abstract: A proper evaluation of the biological significance of Pavlovian conditioning requires consideration of performance mechanisms. Domjan et al.'s definition of net benefit is simplistic, and their model promotes convergence in behaviour, ignoring the possibility of *innovation.*

In this commentary, we wish to draw attention to three issues: (1) that the biological significance of Pavlovian conditioning can be properly evaluated only when performance mechanisms are considered, (2) that the net benefit in an encounter that is bestowed by Pavlovian conditioning cannot be defined as easily as Domjan et al. suggest, and that (3) their model would foster convergence in behaviour, when divergence might as easily be adaptive.

First, Domjan et al. argue that it is the predictive value of Pavlovian conditioning that endows the animal with a biological advantage. However, it is clear that an abstract quality such as "predictive significance" cannot be isolated as an attribute that can be selected for: It has to be associated with specific behavioural traits (Plotkin 1983). This is where an understanding of performance mechanisms (how the predictive significance of a CS is translated into conditioned responding) becomes critically important. Most contemporary performance models of Pavlovian conditioning adopt a behaviour systems analysis of conditioned performance (e.g., Davey 1989; Timberlake 1983) suggesting that what an animal does during a CS is a function of its motivational state (e.g., hunger), the structure of the behaviour system that underlies this motivational state (e.g., the organism's species-specific feeding behaviour system), and the presence of any stimuli that might release components of that behaviour system (e.g., food search or consummatory behaviours).

An understanding of these performance mechanisms is important in discussing the function of Pavlovian feed-forward mechanisms because they do not always generate adaptive behaviours. For example, for a wide range of species, a localisable CS for food that is distal to the food site will often generate performance that is adaptively inferior to unsignaled performance (e.g., Hearst & Jenkins 1974), and the predictive significance of a Pavlovian cue can – and often does – entirely disrupt the performance of an instrumental response required to obtain or consume the UCS (Boakes et al 1978; Breland & Breland 1966).

So, although predictive significance can be viewed as a beneficial adaptive characteristic, it is not always so, and can only be fully understood in the context of how the predictive significance of the CS is translated into behaviour. This omission seems to be a weak link in Domjan et al.'s control systems model. For example, it is not at all clear how the adjustments to the system in anticipation of a forthcoming UCS will interact with performance mechanisms to enhance biological benefit.

Even assuming that performance models of behaviour can be overlooked, much of Domjan et al.'s model is supported by evidence that ignores (1) the hidden costs of behaviour, and (2) the dynamic nature of social interaction. The authors assume that the net benefit to an animal can easily be defined by a direct behavioural outcome. For example, it seems intuitively appealing that, ceteris paribus, learning to initiate copulation or accelerated ejaculation latency (see sect. 4.2.6) benefits an animal (especially considering the risks from predators during mating). However, the net benefit of, say, approaching a mate more quickly must depend on that mate reacting favourably to this advance. At the time of "conditioning" the system cannot predict the mate's response and so cannot evaluate the net benefit of learning a particular behaviour. So, Hollis's (1984) blue gourami fish (sect. 4.1) may have enjoyed a defensive advantage over their intruders only because those intruders were actively prevented from learning a signal that predicted a rival.

A related point is the notion of hidden costs. For example, we know that hungry rats can consume significantly more food than controls when it is predicted by a reliable CS (Zamble 1973; Zamble et al. 1980). Prima facie, this seems like adaptive behaviour; however, Pavlovian CSs that predict food also increase energy-expending activity (see Davey 1989). As such, the initial benefit of conditioning may be counteracted by the hidden cost of learning. The benefit bestowed by Pavlovian conditioning hence cannot be defined as easily as Domjan et al. suggest; instead, net gain should be considered within the context of a dynamic system, with due consideration to hidden costs of learning.

Finally, according to the model, memory is used to anticipate behaviour and prevent mistakes. This is to assume that successful past behaviours will be repeated in favour of unsuccessful or unknown ones. Memory will therefore act as a behavioural *limiter* in that novel or innovative behaviours will never be tried; the result is convergence in the behavioural repertoire (especially for prewired behaviours such as imprinting; Lorenz 1935). The "monitor" in the model acts to evaluate a behavioural outcome in terms of its net benefit. An accurate evaluation requires detailed knowledge of the relative benefit of a particular behaviour over another. In a system in which convergence occurs, the relative benefit of a specific behaviour is obscured: The net benefit of the behaviour might be poor compared with another "innovative" behaviour that memory prevents the animal from trying. Convergence may seem adaptive – innovative behaviours *could* be catastrophic – but only so long as all members of all species have restricted and predictable interactions. If this were true, however, being able to disrupt these predictable patterns of interaction through innovative behaviour could endow the innovator with a considerable net gain in inclusive fitness. For their model to work, Domjan et al. need to demonstrate that natural selection would favour predictability over innovation.

In summary, we hope to have drawn attention to several points. First, the "monitor" in the model may not have accurate insight into the net benefit of a behaviour because of hidden costs, the dynamic nature of social interactions, and the restrictive behavioural repertoire allowed by the model. The system proposed is somewhat static; to become more fluid, it needs (1) a mechanism for encompassing the dynamic nature of interactions and (2) an explanation of how performance mechanisms interact with learning process to produce adaptive behaviour.

Fish displaying and infants sucking: The operant side of the social behavior coin

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Abstract: We applaud Domjan et al. for providing an elegant account of Pavlovian feed-forward mechanisms in social behavior that eschews the pitfall of purposivism. However, they seem to imply that they have provided a complete account without provision for operant conditioning. We argue that operant conditioning plays a central role in social behavior, giving examples from fish and infant behavior.

Domjan et al. make an impressive case for the role of "Pavlovian feed-forward mechanisms" in the control of a wide range of social behaviors. We comment briefly on a particular strength and a potential limitation of their provocative account.

The usefulness of "forward-looking" perspectives of behavior is sometimes compromised by purposive or teleological baggage. Not so the present effort. The authors clearly provide a mechanistic account of the feed-forward process that is grounded in past events (and "memory"). In doing so, the account harks back to the tactics employed by two of the most influential views of learned behavior in the past century, those of Hull and of Skinner. As discussed by Fantino and Logan (1979, Ch. 2) these great theorists explained ostensibly purposive behavior in terms of selection by consequences. As Skinner noted, "Instead of saying that a man behaves because of the consequences which are to follow his behavior, we simply say that he behaves because of the consequences which have followed similar behavior in the past (Skinner 1953, p. 87). Thus, consequences become antecedents, and the forward-looking becomes amenable to a scientific analysis. The target article employs a comparable approach as it assigns a central role to Pavlovian feed-forward mechanisms in the analysis of social behavior.

There is a difference, of course. And that difference leads us to an issue that we believe requires expansion of the authors' model.

Whereas Hull and Skinner were very much concerned with instrumental or operant behavior, the present model addresses Pavlovian mechanisms exclusively. We find this odd. Surely there are Pavlovian underpinnings of much social behavior. But to explain social behavior without explicit acknowledgment of operant contributions is to offer a necessarily impoverished account. Some examples are offered.

Domjan et al. note "that the stimuli encountered during the vigorous social exchange at the end of a social sequence are potential USs. The stimuli encountered at the beginning of the social sequence are potential CSs" (sect. 4, para. 3). While this is certainly true, an equally plausible assumption would replace "USs" with "reinforcing stimuli" and "CSs" with "discriminative stimuli," in a comparable operant account. Indeed we do not see how it would be possible (or desirable) to try to force social interactions into an exclusively Pavlovian *or* operant framework. Very likely that was not the authors' intent; however, the article gives the impression that the Pavlovian framework is sufficient.

We will restrict our examples to the worlds of fish and humans. Much has been written about Pavlovian involvement in the social behavior of the Siamese fighting fish (*Betta splendens*). This research is reviewed in the target article. But Fantino et al. (1972) also implicated operant processes in their three experiments on aggressive display in that redoubtable fish. We allowed fish to swim through either of two apertures. In one experiment, swimming through one aperture produced a mirror image and swimming through the other produced food. While the fish chose the mirror image more frequently at moderate levels of deprivation (48 hours and 120 hours) for both rewards, each of the four subjects reversed his preference at the highest level of deprivation employed (240 hours). In subsequent experiments, we showed that fish preferred the opportunity to display when the choice response did not also produce electric shock and that contingent but not noncontingent electric shock suppressed aggressive display. All of these findings are compatible with the notion that the opportunity to display serves as an instrumental reward.

The role of operant processes in the social behavior of infants and children is probably even more apparent than in nonhuman organisms. For example, Siqueland (1968) showed that neonates could learn to increase or decrease their rate of head turning when doing so was reinforced by the opportunity to suck on a pacifier. Sucking can also serve as an instrumental response. DeCasper and Spence (1986) demonstrated that 2- to 3-day old infants who had been exposed repeatedly in utero to a passage from *The cat in the hat,* a story by Dr. Seuss, learned to increase or decrease their rate of sucking in order to hear the familiar passage.

Clearly then, a complete account of social behavior in human and nonhuman organisms cannot ignore operant conditioning. Operant and Pavlovian processes play complementary roles in most behavior. The target article gives a lucid account of the role played by Pavlovian mechanisms. In doing so, it makes a valuable and interesting contribution.

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Extending the model: Pavlovian social learning

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Abstract: Domjan et al.'s model of how Pavlovian processes regulate social interaction can be extended to social learning, where an individual learns about the value of events, objects, or actions from information provided by another. The conditioned properties of a particular social partner, following from a history of interactions with that partner, can modulate the efficiency and specificity of social learning.

Domjan et al. consider the "feed-forward" modulation of social interactions through Pavlovian conditioning processes. A related domain, social learning, can also be usefully conceptualized in terms of Pavlovian processes (see also Fragaszy & Visalberghi, submitted). Social learning is learning about the value of events, objects (including locations), and/or actions from public information provided to the learner by another individual (Giraldeau 1997). Any process that affects an individual's responsiveness to publicly provided information will affect the efficiency or specificity of social learning.

Social learning can be extremely rapid and long-lasting, as when an individual learns to fear something when it observes another behaving fearfully toward that object (Curio 1988; Mineka & Cook 1988). It can also be highly variable across individuals and across partners, so that social learning occurs most effectively within specific social dyads (e.g., parent and offspring) or among members of a particular class (e.g., among age peers) (Coussi-Korbel & Fragaszy 1995, Laland et al. 1993). Models of social learning must address how exposure to public information can be so effective in promoting learning (with obvious biological utility), and at the same time how susceptibility to social learning can vary so widely across context and individual.

Conditioned modulatory influences that reflect individual histories of social interaction could impact social learning. First, salience of information provided by social partner(s) may be enhanced through *emotional contagion.* Emotional contagion is a family of psychophysiological, behavioral, and social phenomena that result in a pervasive tendency in one person to mimic and synchronize expressions, vocalizations, postures, and movements with another person, rapidly, automatically, unintentionally, and out of awareness (Hatfield et al. 1994). The properties of the social companion that elicit contagion appear to act like unconditioned stimuli, and the effects of emotional contagion appear to be unconditioned responses. Functionally, emotional contagion leads to a convergence of emotions among the interactants, and to attentional synchrony. The hypothesized Pavlovian aspect of emotional contagion with respect to social learning is that the unconditioned response to the social partner's expressed affect can be associated with the immediately antecedent or concurrent events or stimuli: The learner "catches" the other's affect *and* the "target" of that affect, when one is evident. Thus, to the extent that an observer experiences emotional contagion, it can potentially form Pavlovian associations between the new affective state and salient contextual variables. Mineka and Cook's (1988) work with rhesus monkeys (*Macaca mulatta*) serves as an example of emotional contagion contributing to rapid and long-lasting social learning: Monkeys acquired a strong and long-lasting fearful response to a previously neutral stimulus from a single, very brief (15 seconds or less) exposure to another monkey behaving fearfully in the presence of this stimulus. Suboski (1990) presents a similar model of observational conditioning.

The second way in which Pavlovian conditioning can enhance social learning is through "occasion setting" (reviewed in Holland 1992). Occasion setting is a modulatory function in which one CS (conditioned stimulus) modifies the efficacy of Pavlovian associations between other cues and the US (unconditioned stimulus).

This modulatory function has been shown by Peter Holland and colleagues to be distinct from the familiar elicitation functions of CSs.

A paradigmatic example of occasion-setting is provided by an experiment conducted by Ross and Holland (1981). The experiment involved training food-deprived rats in an appetitive situation. Rats that heard a tone and then received food consistently spontaneously tossed their heads (called a "head jerk") during the interval between the tone cue and food delivery. Rats that saw a light and then received food consistently spontaneously reared on their hind legs during the interval between light cue and food delivery. When the rats experienced both cues in sequence (e.g., saw a light come on briefly, a few seconds later heard a tone, and then a few seconds later received food), they consistently reared on their hind legs after the light came on, and jerked their heads after the tone came on. In the occasion-setting situation, after the CR to the tone alone was extinguished (i.e., head jerk did not occur), the rats again experienced the compound presentation of light-pause-tone-pause-food delivery. In this circumstance, the rats jerked their heads when the tone came on in the compound stimulus condition, but when the tone came on without the light preceding it, they did not jerk their heads. In Holland's terminology, the first CS, the feature cue (light, in this example) "sets the occasion" for the conditioned response to the second CS, the target cue (tone) in the compound CS. Occasion setting is a robust phenomenon, appearing over a broad range of timing intervals between feature and target cues, so long as the feature cue (that sets the occasion) occurs before the target cue (that immediately precedes the US) and the feature cue is a better predictor of the US than is the target.

Finding a likely example of occasion-setting where a social partner serves as the feature cue, and some other stimulus (e.g., a predictor of food) as a target cue, is easy. For example, a young black rat, with its mother while she processes whole pine cones, is able to obtain and eat some pine nuts; a young black rat, alone with the same cones, is not able to obtain nuts (Terkel 1996). For the young black rat, the mother in this situation is the probable occasion setter; and the presence of the unopened pine cone is the probable target cue, preceding appearance of the US in one case but not the other. The mother's presence and actions support the young rat's conditioned responsiveness to pine cones, as it learns to open the cones itself.

It seems a short step, conceptually, to link modulatory processes in conditioning that affect learning with the affective-regulating properties of social companions to construct a Pavlovian model of social learning. In general, those individuals eliciting the strongest emotional contagion and those conditions in which the social partner's behavior is a better predictor of important outcome than any particular other cue (supporting the social partner serving as an occasion setter) will be associated with the most effective social learning.

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Feeding forward versus feeding backward

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Abstract: The Domjan et al. target article is a valuable summary of a vital field of conditioning and learning. It lists, thumbnails, and organizes classical and recent findings into a useful and familiar structure. Perhaps it is time to consider modern developments in ethology, experimental psychology, and computer science that supersede the traditional structure.

Practical considerations. Despite the forward sounding title, the heart of Domjan et al.'s target article is a traditional mechanism that feeds backward by consulting a hypothetical memory bank that stores positive and negative consequences of past actions. Backward acting mechanisms of this kind necessarily increase time lags and oscillations. They are also highly vulnerable to rapid changes in a dynamic environment, because they must accumulate enough fresh data to average out old data before they can recognize changes. This is impractical for industrial systems and living systems that must respond to new conditions as soon as possible (R. Gardner & Gardner 1992).

Arbitrary learning in a single trial is common in ethology. Von Frisch (1950, pp. 6–8) showed how bees under field conditions learn to return to an arbitrary color after a single experience of food and color. Tinbergen (1951, pp. 97–100) showed that wasps in the field use arbitrary landmarks to return to nests and feed their larvae. Extensive research documents the memory of birds for specific caches of food. Birds recover a high proportion of food that they cached themselves and a low proportion of food cached by other birds of the same species, indicating that they cache their food in arbitrary locations. Birds remember a staggering number of different caches, far beyond any feats of memory ever demonstrated in the operant conditioning chamber (Vander Wall 1990, pp. 158–69). They must remember each location after a single experience and consume all the food in each cache on the first return visit.

Under natural conditions a living animal must learn to avoid further pain and injury after a single experience. Systems that must calculate contingencies after repeated painful and safe experience (e.g., Rescorla 1967; 1968) would surely fail in a natural world of danger, poison, and predation. The traditional temporal parameters of conditioning set down by Pavlov are largely artifacts of many repeated trials. A different picture that is more relevant to the natural world emerges from modern studies using a single trial, or a very few trials of conditioning (Ayres et al. 1985; 1987; Brower 1958; Garcia et al. 1966; Heth 1976; Keith-Lucas & Guttman 1975; Spetch et al. 1981; Van Willigen et al. 1987). The memory bank required by models of learning that feed backward is an impractical and unlikely mechanism for the survival of living systems (see R. Gardner & Gardner 1998, pp. 76–87).

Consequences and conditioning. Traditionally, the defining characteristic of classical conditioning is conditioning that is independent of positive or negative consequences. Omission procedures demonstrate robust conditioning by contiguity in spite of negative consequences (R. Gardner & Gardner 1998, pp. 76–87, 153–54; Sheffield 1965; Williams & Williams 1969). Contiguity is a sufficient and powerful basis for classical conditioning. Nevertheless, the target article attributes classical conditioning to positive and negative consequences of conditioned responses feeding backward to reinforce conditioning, even though the title promises a mechanism that feeds forward.

Domjan et al. repeatedly propose the possibility of benign evolutionary consequences of conditioning. Yet, anyone old enough to read this article has probably acquired a long list of bad habits. The baggage of maladaptive habits that most adult human beings carry with them is quite as well learned as their adaptive habits, and often maddeningly better learned. Other animals also acquire maladaptive habits both in the laboratory and under natural conditions. Clearly, conditioning fails to protect us from acquiring maladaptive habits. Someone who wants a young child or a captive animal to acquire good habits rather than bad habits needs something more practical than benign assurance that the net effect of conditioning is usually favorable for the species.

Human behavior includes dramatic examples of persistent responses with obviously negative consequences. Maladaptive habits, often socially maladaptive habits, persist in spite of repeated negative consequences. When the negative consequences are serious, some even recommend psychotherapy. Classic symptoms of anxiety resemble conditioned defensive behavior that is evoked in anticipation of impending painful experience. Eating and drinking disorders resemble conditioned consumatory behavior. Powerful maladaptive consequences of conditioning are a vital link between disparate fields of psychology (Liddell 1956). Truly useful systems of conditioning must deal with maladaptive as well as adaptive conditioning.

Comparators versus fuzzy controllers. The target article leans heavily on the venerable concept of homeostasis proposed by Cannon (1932) and the set points and comparators popularized in vintage World War II technology by Norbert Wiener (1948). A thermostatic comparator, for example, responds to a temperature sensor by heating up the system when temperature falls below a set point or cooling it down when temperature rises above another set point. Set points and comparators are unlikely models for living animals because they depend on outside supplies of vital resources. The thermostat in a home works well, but only so long as someone pays for unlimited amounts of energy from external suppliers. When the price of energy rises, many home owners allow the temperature to fall or rise to uncomfortable levels in preference to uncomfortably empty refrigerators or idle automobiles. Set points fail in artificial systems when critical needs compete for limited resources.

The traditional analogy between home thermostats and body temperature fails because living systems must balance conflicting needs, or die. Body temperature drops when perspiration evaporates on the body surface, but this cooling device is strictly limited. Perspiration leads to dehydration, and dehydration leads to death. A live animal must replace the water lost in perspiration fairly soon. Seeking water demands movement, energy expenditure, and further increases in temperature. Seeking water often brings risk of death from predators that wait for prey at watering places. Autonomous systems must resolve conflicts.

The nineteenth century view of motivation and drive concerned the mobilization of energy as in a steam engine. The modern view concerns the allocation of energy and time within a complex matrix of conflicting motives in a dynamically shifting environment. Modern industrial systems also require controllers that are much more sophisticated than comparators. Fuzzy controllers (Kosko 1993; Zadeh & Kacprzyk 1992) are simple, effective, and economical systems currently in use under exacting industrial conditions. Fuzzy controllers can balance multiple conflicting demands in situations of flux and change that resemble the problems of living animals under natural conditions. R. Gardner and Gardner (1998, pp. 194–203) describe, in enough detail to be intelligible to nonspecialists, a 1995 case history of an industrial problem solved by two computer scientists (Kipersztok & Patterson 1995) in the Research and Technology division of Boeing Aircraft Company. Boeing's problem was to allocate the resources of a massive parallel processing system to serve conflicting computational requirements of a huge industrial organization. Kipersztok and Patterson's fuzzy controller offers a practical model for analogous problems of conflict faced by living animals (see Fig. 1).

Fuzzy systems find good working solutions to practical problems without striving for optimality. Fuzzy controllers are cheap and easy to design and also cheap and easy to adjust to changing demands, which makes them even more appropriate as models of evolutionary adaptation. Designers have tested fuzzy systems by deliberately introducing defective elements or removing some elements entirely. The controllers continue to function, although they limp along less efficiently (Kosko 1993, pp. 339–61). This flexibility of fuzzy systems allows computer scientists to improve on their first approximations and to modify each part of a system easily and quickly as conditions change. Crude but powerful fuzzy systems are promising models for rapid adaptation to dynamically changing natural ecosystems. Fuzzy systems, like living systems, survive without achieving optimal solutions to unique and often transient ecological situations.

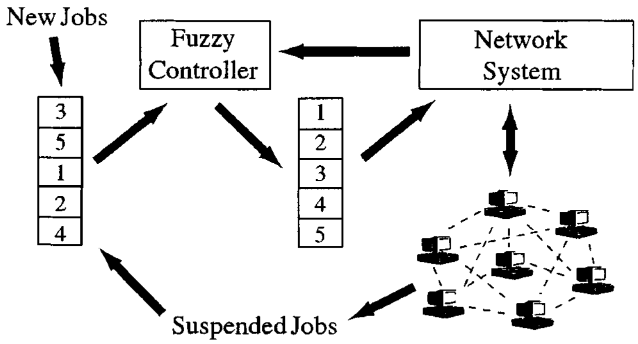

Figure 1 (Gardner). Diagram of an intelligent fuzzy controller for network queuing. From Kipersztok and Patterson (1995). Copyright 1998 by R. Allen Gardner.

The breadth-depth tradeoff: Gains and losses as the unidirectional shift in Pavlovian conditioning continues

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Abstract: Domjan et al. continue a consistent trend in Pavlovian conditioning, that of accounting for more behaviors while sacrificing specificity of predictions. Despite the sacrifice, their model provides a valuable framework within which social behavioral research may operate. It may also allow ethologists and evolutionary psychologists to pursue questions about which feed-forward systems should produce which behaviors in social settings.

Domjan et al.'s claim that "all social interactions can be profitably analyzed from the perspective of Pavlovian conditioning" (sect. 5), which is remarkably bold on its face, is made all the more bold by certain other considerations. First is the fact that "most of the research on Pavlovian conditioning has focused on the behavior of individual organisms in socially isolated laboratory settings" (sect. 1). The interaction of two or more behaving organisms marks a significant expansion of the universe of Pavlovian phenomena. Second, the conditioned stimuli used in most Pavlovian research are simple and readily defined in terms of their physical dimensions, whereas the stimuli involved in social behavior are anatomical, physiognomic, and behavioral characteristics of conspecifics, which are generally complex and unfixed, and must be defined in functional terms. Third, the conditioned responses studied in Pavlovian conditioning are often glandular or reflexive, and although they have broadened in recent years to include skeletal and functionally defined responses, they are seldom as complex or as adaptable as those involved in social interactions.

Conceptions of Pavlovian conditioning have changed throughout this century to account for more behavior systems, to allow for more varied behavior within a system, and, perhaps inevitably, to provide less guidance regarding the form of the conditioned response. Domjan et al.'s article represents a further step in all these linked trends.

As students of introductory psychology are taught the world over, Pavlov (1927) trained dogs in his original conditioning experiments to salivate in the presence of stimuli to which they did not previously salivate. He accomplished this by pairing the initially neutral stimuli with meat powder, to which dogs salivate unconditionally. The program was built upon a single behavioral system (digestion), studied learning predicated on a single unlearned reflex (salivation), and the conditioned response was identical to – and therefore trivially predictable from – the unconditioned response.

Quite a bit later, using different behavioral systems, conditioned responses were observed that were the *opposite* of the unconditioned responses on which training was based, principally in responses to stimuli that predicted the administration of various drugs (Guha et al. 1974; Obal 1966). For example, although morphine elicits reduced sensitivity to pain, stimuli associated with morphine create increased pain sensitivity (Siegel 1977). When studying the conditioning of a response that has not been studied previously, there are thus at least two conditioned responses that may be observed: the unconditioned response and its opposite. It is generally presumed that conditioned responses are not arbitrary, but rather serve adaptive purposes that may themselves be predicted, or at least subjected to post hoc analysis. Conditioned responses that are the opposite of their unconditioned counterparts are typically called "compensatory" responses, suggesting, for example, that prolonged exposure to morphine may cause maladaptively low sensitivity for pain, which may be compensated for by conditioned responding of an opposing nature.

It appears that anticipatory salivating may serve an adaptive purpose as well, in allowing the initial digestion that is performed by saliva to proceed more efficiently once food is delivered. Because there are thus at least two possible conditioned responses associated with each unconditioned response, and because predictions derived from ecological considerations of adaptiveness are not foolproof, one may be unable to predict the conditioned response when Pavlovian conditioning is engaged in a new behavioral system.

The same trends were continued with the discovery of autoshaping (Brown & Jenkins 1968) and other forms of sign tracking (Hearst & Jenkins 1974). These extend the domain of Pavlovian conditioning from autonomic responding to skeletal responses, and also provide an example of a case in Pavlovian conditioning where responses must be functionally defined in relation to the sign that is tracked.

Domjan et al. extend these frontiers further with their treatment of social phenomena as cases of Pavlovian conditioning (sect. 4). They deal with autonomic responses such as aggressive displays, courtship displays, and infrahuman and human lactation; and with skeletal but physically defined responses such as biting and tail beating, courtship struts, and conditioned copulation. But other responses demand functional definitions and are considerably more complex than what is often approached for explanation in Pavlovian terms, including maternal acceptance, social grooming, and play. Approach is also defined in terms of the object of approach, and is not a newcomer to the Pavlovian domain, but is less complex than the others. In addition to involving conditioned responses that are less readily defined in physical terms, these systems also produce conditioned responses with less clear relationships with their associated, unconditioned responses. CRs are no longer the same as URs, nor their opposites, but such unpredictable and seemingly unrelated responses as, for example, the "play face" (Fox 1970) in canids, which has no physical relationship to play itself, except that both occur in a reliable temporal order after conditioning has taken place.

This declining specificity of prediction may be an inevitable price to pay as Pavlovian conditioning is extended to ever more complex domains, and may indeed be a measure of the complexity of those domains, and thereby of the ambitiousness of applying Pavlovian conditioning to them. And while the specificity of predictions is less than what is customary in other Pavlovian paradigms, it may be equal or superior to that provided by other approaches to social phenomena. The feed-forward mechanism specified by Control Systems Theory and embedded in Pavlovian conditioning can provide a productive framework for explaining social phenomena, and the problem of identifying and predicting conditioned responses from an adaptive perspective is a fertile field where evolutionary psychologists, control systems theorists, and ethologists might converge with social psychologists and learning theorists.

Strategies for integrating biological theory, control systems theory, and Pavlovian conditioning

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Abstract: To make possible the integration proposed by Domjan et al., psychologists first need to close the research gap between behavioral ecology and the study of Pavlovian conditioning. I suggest two strategies, namely, to adopt more behavioral ecological approaches to social behavior or to co-opt problems already addressed by behavioral ecologists that are especially well suited to the study of Pavlovian conditioning.

One would expect the study of Pavlovian conditioning to appeal to many animal behavior researchers. Not only is it a ubiquitous phenomenon in vertebrates (Macphail 1982; 1993), as well as a growing number of invertebrates (Byrne 1990; Mcphail 1993), but as Domjan et al. demonstrate in their review of conditioned social behavior, Pavlovian conditioning also affects a wide variety of behavioral functions throughout animals' lives. Paradoxically, however, in the animal behavior literature, conditioning is a marginal phenomenon at best. For example, in the broad surveys provided by animal behavior texts, conditioning is rarely if ever mentioned outside a highly circumscribed chapter on learning. That is, despite the fact that behavioral ecologists readily acknowledge that the behavior they study in the wild often reflects the impact of learning, the study of conditioning per se has been a hard sell to the very audience that many of us have sought to reach.

The target article describes a new approach to this impasse. The authors detail a thoughtful and highly original framework for integrating the study of Pavlovian conditioning within behavioral ecology and control systems theory. The real innovation, to my way of thinking, is that the proposed synthesis finds a common denominator in cost/benefit analysis, a critical concept to both control systems theory and behavioral ecology. But will this approach spark the kind of interdisciplinary bridge building that, thus far, remains elusive? It certainly should capture the attention of control systems theorists. As Domjan et al. make clear (sect. 3.4), many already are attracted to the study of conditioning. Thus, in this target article, they will find a ready-made and very interesting new problem. Their task will be to explicate Figure 3 (sect. 3.4.4), the authors' sketch of a behavioral control system. That is, they will need to determine how the various components actually interact with one another. However, doing so requires that they understand a bit more about a critical component, namely the cost/benefit ratio instructions.

Ay, there's the rub! That exercise requires the cooperation of behavioral ecologists, those who have been at work delineating the costs and benefits of social behavior. However, to attract a critical mass of behavioral ecologists to the study of learning – the paradox I describe above makes clear how unsuccessful previous attempts have been – psychologists need to narrow the research gap.

By "research gap," I mean that the questions psychologists ask of conditioned behavior do not map readily onto those asked by behavioral ecologists. Moreover, from the perspective of their discipline, the way in which the study of conditioned social behavior makes contact with behavioral ecology is to provide little more than a label, namely "Pavlovian conditioning," for what already is recognized as learned behavior. Heresy, you say? I think not (and describe why below), but in any case I will argue that if real integration is the goal, then we psychologists need to begin bridging that gap.

An example will help illustrate my point. Behavioral ecologists have demonstrated that, in territorial species, "experience" enables males to maintain a territory more effectively than males without "experience." For example, in red-winged blackbirds, as well as in many territorial species, the tendency of males to return to the same territory year after year, called *site fidelity*, is thought to reflect their ability to learn about the predictable locations of food, rivals, and predators (e.g., Beletsky & Orians 1987). Research on conditioned aggressive behavior (sect. 4.1, para. 8–10), which has demonstrated that Pavlovian signaling of a rival enhances the effectiveness of territorial defense (e.g., Hollis et al. 1995), potentially has identified one source of that "experience." Although I do not denigrate the importance of these findings – after all, they have enabled us to pursue other proximate questions about behavior – they do not tell behavioral ecologists much more than they already know. And thus, if the goal is to integrate evolutionary theory and the study of conditioned aggressive behavior, then we need to address more directly the questions posed by those who already study evolutionary theory in that context. For example, to what extent does the advantage of signaling account for the fact that territorial owners are much more likely to win an encounter than are territorial intruders? To what extent does site fidelity reflect Pavlovian associations between geographical cues and the appearance of food, rivals, predators, and mates?

The problem does not lie in this area of conditioned social behavior alone. As careful perusal of the target article will reveal, the research gap between psychologists' study of Pavlovian conditioning and the study of behavioral ecology is symptomatic. What is gained by relabeling maternal "experience" as "associative learning" (sect. 4.3.1)? To what extent do Pavlovian phenomena like blocking, extinction, stimulus discrimination learning, second-order conditioning, and the effects of US devaluation (sect. 4.2.1, para. 2) affect the behavior of male quail in the wild? In other words, until those of us who purport to study conditioning of social behavior begin to address questions asked by behavioral ecologists, I am not optimistic that it is possible to achieve the kind of integration that the target article proposes. I hope I am wrong, but I doubt it.

Recognizing that we psychologists are not likely to don Wellington boots and head for the field, I suggest an alternative approach, namely that we co-opt problems already addressed by behavioral ecologists, problems that are especially well suited to the laboratory study of Pavlovian conditioning. For example, every day at dusk, convict cichlid fish retrieve their young by taking them into their mouths and spitting them into a pit they have dug. Although some recent research (Reebs 1994) suggests these fish somehow are able to anticipate night onset, the possible contribution of Pavlovian conditioning remains to be discovered. This particular example, and many others like it, provide excellent opportunities, not only for revealing the operation of associative learning, but also for examining the way in which Pavlovian phenomena like blocking, extinction, and second-order conditioning help to refine animals' abilities to solve the ecological problems they face.

Recently, a behavioral ecologist friend of mine asked, "Why do you insist on calling what you study 'Pavlovian conditioning'; after all, it's just another label, isn't it?" I take that comment as a wake-up call – and Domjan et al.'s proposal offers an exciting new approach, but only if we are willing to heed that call.

Boxing Day

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Abstract: A convincing case is made for the importance of conditioning in social interaction, but more than Pavlovian conditioning is involved: UR (unconditioned response) modification, imprinting, Skinnerian conditioning, and other forms of behavior modification are adduced as Pavlovian. Beyond its value as an icon, control theory is not brought to bear in an informative fashion on these phenomena.

The game of life, like that of science, is one of prediction and control. Knowledge is power because it reduces entropy; that differential can be exploited in the creation of new potential energy – acquiring food – and in the conservation of old energy – finding shelter from storms and predators. Feed-forward is prediction in the service of control. It is an excellent model for conditioning, but in the target article by Domjan et al. it is exploited only in name. There is little new in what the authors offer: Powers (1978) promulgated a hierarchical control theory of behavior, and the authors' review of social control is, well, a review. Their juxtaposition, however, makes control theory available for its own round of prediction and control in the realm of behavior analysis, and that is the signal contribution of the target article.

Reflexes are open-loop. An unconditioned reflex (UR) must be quick, and to achieve this speed it is usually open-loop. Blow on a subject's eye, shout in his ear, remove his support, put a nail underfoot, and there is no time for cost/benefit analyses; the reaction is knee-jerk. The only way Figure 1 in the target article can be correct is for the C/B Ratio Calculator to be a fixed threshold, and the C/B Ratio Instructions to be a hard-wired "Go." Graded effects are closely tied to stimulus intensity – the well-known "stimulus-intensity dynamism effect." Reflexes can be potentiated by a succession of weaker stimuli and inhibited by precisely timed subthreshold stimuli (Hoffman & Ison 1980), but such sensitization and habituation can be dealt with by less complex cognitive mechanisms than those boxed in Figure 1.

Boxed in. Figure 3 does not specify what kind(s) of adjustments the memory module makes on the comparator (and vice versa). The effect may be either to trigger a version of the UR or to trigger a compensatory reaction (Siegel & Allan 1996). This fundamental difference deserves more explanation than "provide a means of anticipating necessary adjustments to the stimulus/response actuator" (sect. 3.4.4), for within this box lies all of contemporary association theory, and more.

In many of the examples given, the conditioning effect is a *modification of the UR* rather than the generation of a CR. In others (e.g., the identity learning of sect. 4.3.1), it is an *imprinting* of individual scent (*identiscent*) as a sign-stimulus when that stimulus is paired with the odor/taste of amniotic fluid, of mother's milk, and so on. Thereafter the identiscent becomes a releaser for other species-specific behaviors. (Predator-learning provides additional examples: Prey learn to avoid pike based on either the scent of its recent diet [Chivers et al. 1996] or on the actions of other prey previously exposed to the scent chemicals [Mathis et al. 1996]. This learning is interspecific, both in terms of the species of prey-scent emanating from the pike and of the species showing fright responses.)

Preference for an identiscent (sect. 4.3.4) is also packed into the box of Pavlovian conditioning. A good case could be made that the conditioned reinforcing value of a stimulus is based on simple pairing, but "based on" does not mean "tantamount to Pavlovian conditioning." This is yet another extension of what is meant by classical conditioning. Such fiat breeds hegemonies (Turkkan 1989).

In the analysis of *play behavior* we get a boxed set, Skinner and Pavlov, for the price of Pavlov alone. All examples in section 4.4 involve *operant conditioning*, often initiated by a US (invitation to play). Play involves learning what responses are effective in interacting with others, which conspecifics to challenge and which to defer to; learning about timing and surprise, fainting, and bluffing. These are all based on consequences of actions: feedback. Pure Skinner. Where's the Pavlov?

Domjan et al. conclude "that all social interactions can be profitably analyzed from the perspective of Pavlovian conditioning" (sect. 4.5). Well, I have always liked the perspective that operant conditioning is just Pavlovian conditioning of approach to the responses that predict a US/reinforcer. The best way to see my hand pressing a lever is to learn how to get it to press a lever. With that qualification we can relabel instrumental learning as Pavlovian, and with other shoehorns bring all forms of conditioning under the Russian rubric. That would be worthwhile if doing so increased, rather than decreased, our ability to predict and control behavior. But does it?

Cartoon cartons. What does control theory predict about these natural histories, now all mustered into a Pavlov Box? Not much. Feed-forward reduces the deleterious effects of lag in control systems: If I can learn what to fear and what to love, I am better able to avoid the former and approach the latter before it is too late. Very important; not new. The boxy figures are mere cartoons, as none of the machinery of control theory is brought to bear on learning. There is much more that could have been said: Underdamped systems are fast but unstable; they should be seen where speed is essential, as in the escape from novel stimuli, followed by decaying oscillation (a return for inspection to establish mate or food potential). Overdamped systems are slow but stable; they should occur when time allows, as in maternal imprinting, with a leisurely postpartum cleaning that establishes an enduring bond. There are integro-differential control systems, and adaptive control systems and hierarchies of control systems, each with special properties that could correspond with the demands of different niches.

The authors have overextended the control-system cartoon to interacting control systems, where other nonlinear models might be more useful. Organisms routinely shape other organisms' structures and behaviors, the latter in ways behaviorists could admire. For example, Axen, Leimar, and Hoffman (1996) showed that lycaenid butterfly larvae signal their protecting ants that food is available by waving tentacles. They apparently shape ants' attendance by a high rate of signaling and feeding on first contact, after absence, and after attacks; at other times they thin out the schedule of reinforcement by decreasing the frequency of signaling.

Signs, cosigns, and tangents. Sometimes it is to the individual's advantage to "tell the truth" in social interaction (e.g., Furlow 1997), sometimes to lie (Semple & McComb 1996), and sometimes not to know its own mind (Dawkins & Krebs 1978). Sometimes signaling is useful, even in fights (Hurd 1997), and sometimes it is fatal, even in cooperation (Killeen & Snowberry 1982). These nuances of social behavior – signs given and cosigns returned – lie far beyond the simple control-system metaphor. Unfortunately, so also do many of the simpler interactions cited. The natural history is good, but the feed-forward metaphor is tangential, touching the data only in the initial segment of description – anticipating the future – and extrapolating linearly beyond the data, which gyre and gimble in the most nonlinear, interactive, and counter-controlled fashion.

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On levels of analysis and theoretical integration: Models of social behavior

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Abstract: Evolutionary theory supplies a framework for integrative models of social behavior. In addition to those that include conditioning, evolutionary theory is equipped to explain the acquisition of structures designed to enable individuals to learn by observing others, create mental models of the environment, and coordinate social interactions by taking the perspectives of others.

Domjan et al.'s target article takes some steps toward integrating biological, mechanical, and psychological explanations of social behavior. My goal in this commentary will be to outline a framework that advances this integrative endeavor, paving the way for the inclusion of other, more cognitive, approaches.

Like the authors, I believe that an integrative theory of social behavior must rest on a platform derived from, or at least consistent with, evolutionary theory. The three biological approaches outlined by the authors are based on the following essential assumption. Genes (selected in ancestral environments) produce structures (in current environments) that dispose individuals to emit social behaviors that fostered the inclusive fitness of those who possessed the structures in ancestral environments. But natural selection is a post hoc sort of process. When environments change, so also may the adaptiveness of behaviors mediated by structures selected in ancestral environments. One way of combating this problem is to design flexible structures capable of adjusting their mechanisms in response to environmental inputs. Structures may be preprogrammed to develop in different ways in different environments, or to produce different behaviors in different circumstances. The mating behavior of male scorpion flies is an often-cited example.

Structures that mediate operant conditioning are flexible structures that adjust their output in response to contingencies in current environments. These structures are programmed to induce individuals to emit operant responses, then adjust the probability of repeating the response in accordance with its consequences – a feedback system. Compared to fixed action patterns, operant conditioning, or trial and error learning, is a pretty good (adaptive) system, but it is limited in at least one important respect: The initial response the organism emits could be maladaptive. Clearly, it would be more adaptive to be able to predict in advance the consequence of making a response, and this is where the feed-forward mechanisms of classical conditioning (which also could be interpreted as discrimination learning in operant conditioning) come in.

Unconditioned responses (UCRs) to unconditioned stimuli (UCSs) are responses that enabled organisms to satisfy basic physiological needs such as hunger and sex in ancestral environments. Most UCS-UCR associations also are adaptive in current environments, but, as the authors point out, the adaptiveness of making an UCR varies with parameters of the environment. Through classical conditioning, animals are able to refine their survival and reproductive response systems in ways that increase their efficiency, which enables them to coordinate with environments their ancestors never experienced. (No ancestral dog ever salivated to a bell.)

Note that structures mediating classical conditioning are not general purpose structures designed to treat all CSs equally. As revealed by the research of Breland and Breland (1961) and Garcia and Rusiniak (1980), these structures were designed by natural selection to favor CSs that reliably predicted adaptive responses in ancestral environments. Because the sexes differ in their reproductive strategies, the CS that enhance the adaptiveness of males' sexual responses may not enhance the adaptiveness of the sexual behavior of females (cf. sect. 4.2.5).

Thinking about evolved structures of learning in this way makes it clear that classical conditioning also is limited to the extent that it is based in UCS-UCR associations that could be maladaptive in current environments. For example, unconstrained responses to sexual stimuli that enhanced our ancestors' inclusive fitness may land people in jail today. To flesh out an integrative model of social behavior, we need to extend the analysis of structures that enable individuals to adapt to their current environments without making potentially maladaptive responses. Structures that enable people to learn by observing what happens to others – through vicarious conditioning and modeling – play an important role in social behavior (Bandura 1986). So also do structures that enable individuals to create mental models of the environment, and, in effect, anticipate and predict the consequences of their behaviors in their heads before performing them. As the psychologist Aronfreed (1976) demonstrated three decades ago, thoughts and intentions can serve as CSs that, when paired with UCSs, may acquire the power to regulate social behavior.

Domjan et al. tend to focus on only one party in social exchanges. A complete account will need to attend more fully to the interactional nature of social behavior, that is, the ways in which each party influences the behavior of the other. Successful social behavior requires coordination of two or more parties with potentially conflicting interests, each evolved to enhance his or her own inclusive fitness. Certainly the CSs that each party emits help regulate the behavior of the other. But to fully account for social coordination, in humans at least, we need to attend to people's ability to create representational models of their partner's minds, models that enable people to anticipate and predict what others want, need, are up to, and how others will react to their behavior. Such structures have evolved in the human species, giving rise to abilities labeled variously as empathy, role taking, perspective taking, and mind reading. They are amazing in their complexity – for example, enabling people to understand what their partners are thinking they are thinking their partners are thinking – and in their social significance, as antidotes to egoism (Krebs & Van Hesteren 1994). In effect, people incorporate others into themselves. In the context of this commentary, these structures are important because they enable people to predict in advance the social consequences of emitting social behaviors, that is to say, they enable them to predict the reactions of their social partners, and to coordinate their exchanges in ways that maximize their mutual benefits.

It is time to inhibit Pavlovian conditioning

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Abstract: Despite a promising introduction, Domjan et al.'s target article fails to capitalize on the concept of information intrinsic to control theory. The authors limit their application of feed-forward models to simple nondynamic cases. Their applications to social behavior are stimulus-occasioned responses. Agents might as well be dogfood! The notion of "conditioning" is generalized without warrant to explain virtually any acquired predictive capability.

On first glance, this appeared to be an interesting and potentially significant target article. Domjan et al. suggest analyzing social behaviors using a synthesis of evolutionary theory, control theory (CT), and Pavlovian conditioning. They provide an informative review of recent research into Pavlovian processes in relatively natural settings – with much of that work carried out by the authors. Surely social/sexual behavior is fundamental to any understanding of behavior. Moreover, learning and control systems have an obvious connection. And, God knows, it is time for an integrated framework that unites the various fragments of psychological inquiry scattered over dozens of journals. Unfortunately, this initial promise was not fulfilled.

Control theory and psychology. Concepts of CT are hardly new to psychology. Pavlov himself seems to have understood well the role of feedback in maintaining equilibrium, for example, in selecting just the right mixture of salivary secretions for a given substance introduced into the mouth. Pavlov also – no surprise – saw how a conditioned stimulus might adaptively signal the appropriate mixture for a given substance based on prior experience. Nor did he limit such preparatory signals to food availability.

Many psychological conceptions over the years implicitly employed CT concepts, as Miller, Galanter, and Pribram (1960) pointed out in their seminal book, *Plans and the structure of behavior.* Domjan et al. claim that CT has not been "extended to social behavior" (sect. 1, para. 2). This ignores Bowlby's (1969) widely cited analysis of maternal attachment in terms of CT (see also McPhail & Tucker 1990).

Prior uses of CT concepts would not concern us if the authors had taken hold of these ideas and made full use of them. However, I did not find the expected discussion of information, models of interactive anticipatory social processes, and control – particularly in light of recent behavioral and physiological interpretations of Pavlovian conditioning in terms of information (e.g., Kamin 1968; Kim et al. 1998). The virtue of an explicit CT framework is that it offers an explanatory vocabulary for purposive behavior that transcends diverse methodologies, specific neurophysiological implementations, and parochial terminology.

Feed-forward "working models" of social behavior. The target article presents a rather simplistic application of feed-forward models, particularly in connection with social behavior. Where is the dynamic element? What can it mean to say, "in principle feed-forward mechanisms are more useful than feedback mechanisms" (sect. 3.3)? Are reflexes really more "useful" than learning? Even Pavlov saw conditioned reflexes as just one of several mechanisms, including inhibition, that regulate behavior. Milk leaking from a mother's breast at the thought of feeding is no more or less "useful" than inhibition of lactation by embarrassment. It is the overall adaptive balance of the behavioral system that is important.

Did the authors oversimplify "social" behavior in order to save the concept of conditioned reflexology? Or were they tacitly denying the necessity of treating social "objects" as agents despite their CT framework? Agency requires feed-forward models of behavior of considerable computational complexity, involving a hierarchy of goals, intentionality, and possibly a "theory of mind." Maybe this would be a bit much for Pavlovian conditioning? Perhaps I am asking more from the article than is being offered?

Nevertheless, everyone agrees that feed-forward models are necessary for complex interactive behaviors. These "working models," as Bowlby called them, must be adequate for the tasks at hand and indeed in practice reflect the interactive complexities of those tasks. For example, speaking requires a compression of a multilevel hierarchy into a stream of speech in which movements several hundreds of milliseconds in the future must be anticipated by the model. Conversation requires that this speaking system be embedded within another control system. Consideration of such movement problems led Nikolai Bernstein (1967) and Karl Lashley (1951) to their notorious criticism of the reflexology of Soviet and American behaviorism.

So what does the article offer? As far as I can tell, its feed-forward models are little more than a "black box" list of conditioned reflexes. Now this might work for those elements of social behaviors that are not intrinsically social, that is, behaviors that are directed toward objects that just happen to be agents. What about most interactive mammalian social behaviors, including reciprocity, mating, communication, social learning, and parenting? What do the Pavlovian feed-forward models for these activities look like?

What is "Pavlovian conditioning" anyway? At one time, American psychologists struggled to shoehorn all learning, regardless of species or behavior, into some sort of conditioning model. The subsequent "cognitive revolution" was as much a revulsion at the vague overgeneralizing of conditioning paradigms as anything. Yet Domjan et al. continually talk about "Pavlovian mechanisms" as if these were a known causal quantity. There may be a place for the expression "Pavlovian conditioning" in the twenty-first century: perhaps as a method for studying types of associative learning – maybe a physiologically unique subset of associative mechanisms? Certainly it must be something other than a synonym for predictive association.

Pavlovian perceptions and primate realities

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Abstract: The extent to which Pavlovian feed-forward mechanisms operate in primates is debatable. Monkeys and apes are long-lived, usually gregarious, and intelligent animals reliant on learned behavior. Learning occurs during play, mother-infant interactions, and grooming. We address these situations, and are hesitant to accept Domjan et al.'s reliance on Pavlovian conditioning as a major operant in primates.

Domjan et al. intend to demonstrate a middle range theory of proximate mechanisms for social behavior. They propose a model integrating biological theory, control systems theory, and Pavlovian conditioning. Their use of Pavlovian conditioning in explaining physiologically based social behaviors, for example, sexual and agonistic behaviors, appears plausible. Their integrated model and utilization of Pavlovian conditioning in particular fails to adequately address play behavior, social grooming, and learning among primates. They fail to address the evolutionary significance of primate gregariousness and its implications.

Primates thrive in social groups. Their large brains and prolonged immaturity are tied to learning behavioral and social skills, and, depending on species and sex, life in rather stable, complex, and bisexual social groups. For intelligent, gregarious primates, the social group ensures continuity of social traditions because its members benefit from lessons learned generations before their birth.

Domjan et al. cite increased resource competition as a cost of social living. However, more resources are potentially located by acting in concert than by acting alone. With chimpanzees exploiting figs that are seasonally clustered in widely scattered trees, the more eyes (noses, ears), the greater the chance of locating food. Rather than keeping the resource secret, the location is advertised and food is shared with other members of the regional population (Sugiyama 1972).

The opportunities and rewards of social living vary according to one's family group. Behavioral patterns can be unique to individual families within the social group. Primates manifest group-specific and family-specific behaviors (Poirier 1992).

When a Japanese macaque troop grows beyond a stable number, when troop members cannot predict how individuals will act or cannot recognize one another, tension and aggression rise, and the troop splits along matrilineal lines (Itani et al. 1963; Kawamura 1968). Among humans, too, when predictability vanishes so does the comfort level needed for efficient functioning. Predictability is the cement of social communication and social living.

We have researched primate maternal/infant dyads, play behavior, and grooming – arenas where Domjan et al. located Pavlovian feed-forward mechanisms. Maternal responsiveness to an infant is influenced by the infant's sex, birth order, and age; the number and sex of siblings and other (especially female) relatives within the social group; the habitat; maternal experience; the mother's dominance status; and the length of the mother's nipples (associated with parity; Poirier 1973).

A mother might consume amniotic fluid, placenta, and parts of the umbilical cord for many reasons. Removing physical and olfactory evidence of birth byproducts protects the newborn and mother from predation at their most vulnerable time.

If rat males decrease ejaculation latencies in the presence of recognizable odors, do they mate more frequently with female sibs because of their attraction to a shared odor? If this occurs, it runs counter to the trend in mammals to avoid mating with close relatives. Do male rats attempt frequent mating with their similarly-scented mothers, or do mothers show greater and earlier rejection of male pups to "condition" males against trying to mate with her? Why do human neonates prefer nursing from a female with a recognizable odor (their mother, presumably)? A mother benefits because she is not suckling (investing in) another's offspring. However, an infant might gain if it nursed randomly from any female. An orphaned youngster might benefit if it did not discriminate among lactating females in its nursing behavior. Mother and infant may not always share the same benefits. A possible adaptive consequence of neonates nursing from females with a recognizable odor is immune system compatibility and increased immune system function gained from nursing from an individual with whom you share considerable genetic material.

The bigger the brain, the longer the life span, the more the need for social living, the more complex the environment (including the social environment), the greater the importance of play. Long-lived, intelligent social animals learn many things in play, including the proper sequencing in the communication matrix. Play is a social cement; animals that play together stay together. Canid and primate literature is replete with examples of the need for and value of play for proper social, physical, emotional, and intellectual development. Play becomes more efficient with practice, related partly to an individual acquiring predictability in the communication system (Poirier & Smith 1974). Increased sensory input has been associated with increased synaptic development in young animals. Play behavior could be associated with increased complexity in parts of the brain associated with the development of social behavior.

Domjan et al. refer to the use of a play partner as an unconditioned stimulus (or reinforcer). They fail to address why there is a decline and often a total loss of play behavior among adults of many species. They also fail to discuss situations where a play partner is a punisher rather than a reinforcer.

Domjan et al. assume that age, status, and sex are biological constraints that determine which group members can be grooming partners. However, status is a special case because it is not only ascribed, it can also be achieved. Although much primate social grooming is tied to cleaning a conspecific's or one's own hair, social grooming more importantly maintains social ties. Among social primates, sociality is reinforced and maintained by intense tactile relationships. High frequencies of social grooming maintain and cement social bonds. For many primate species, grooming – like play – maintains kinship bonds. High grooming counts indicate close kinship bonds (or, with some baboons, close friendships). This is especially true for female kin. Close kin (especially female kin) have high mutual grooming scores. Not infrequently, a frightened, submissive animal seeks tactile contact with its tormentor. Such contact relaxes the frightened subordinate. Social grooming is a rewarding activity, a fact emphasized by the amount of time invested in this behavior by primates and by facial and body expressions maintained by animals involved in grooming. Domjan et al. fail to adequately note that habitat, sex of the participants, and kinship affect social grooming.

Pavlovian conditioning as a product of selection

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Abstract: Biologists recognize Pavlovian conditioning as a mechanism by which individuals can adaptively modify their social and nonsocial behavior quickly to relevant features of the natural environment. This commentary supports Domjan et al.'s point that psychologists could gain important insights by broadening the range of species and behaviors they study and by continuing to adopt a functional perspective to investigate Pavlovian conditioning and other forms of learning.

Domjan et al. emphasize the need for psychologists to maintain a functional perspective in the study of Pavlovian conditioning.

They do this by focusing on its role in the social behavior of animals, a topic typically considered the domain of ethologists, sociobiologists, and behavioral ecologists. Biologists have for a long time based their approach to understanding behavior in terms of its consequences for fitness, and they continue to do so. When ethologists consider Pavlovian conditioning, they usually focus on its functional significance for the animal and view it as a widely occurring mechanism by which behavior could be adaptively modified (e.g., Lorenz 1965; Tinbergen 1965). Psychologists focused on other issues, leading Lorenz (1981, p. 260) to remark that "investigators of learning processes have apparently failed to notice that an *explanation* is needed for the indubitable fact that learning practically always results in an improvement of the teleonomic function of behavior." In the 1960s and 1970s, however, psychologists began to focus explicitly on learning as an adaptive specialization (e.g., Hinde & Stevenson-Hinde 1973; Seligman & Hager 1972; Shettleworth 1972), but this approach seemed to lose steam after several years, or at least maintained a lower profile. Domjan et al. and other proponents (e.g., Domjan & Hollis 1988; Hollis 1997; Shettleworth 1998; Timberlake 1990) make the case why psychologists should continue to adopt this functional perspective in their studies of animal learning.

Biological systems are opportunistic. A trait or mechanism that provides overall fitness advantage to its bearer and has some genetic basis is likely to spread in the population. Pavlovian conditioning is such a mechanism; it enables an animal to associate a formerly neutral stimulus, such as the movement of a leaf, with an unconditioned stimulus, such as a prey item, so that the animal can, for example, predict the imminent appearance of the prey, prepare and position itself to capture it, and thereby enhance its foraging efficiency. Domjan et al. discuss examples that suggest that this is no less true for traits that function in social interactions. Moreover, a mechanism that benefits an animal in one context, for example, feeding, can also be enlisted in another context, for example, to predict and prepare for the impending arrival of a prospective mate or rival. The latter effect would provide additional benefit to the animal, as well as subject the mechanism to additional selection pressures imposed by the new context. Selection acts on the whole organism, and traits may be selected for their function(s) in a broad range of contexts. Hence, Pavlovian conditioning, like any trait, learned or otherwise, will not be adaptive in all contexts; it is often seen to misfire, especially when tested in the laboratory or under other unnatural conditions in which it did not evolve.

Sensory systems provide an example of how traits established through selection in one context may subsequently be adopted for use in another; they typically come to subserve several functional categories of behavior in a variety of contexts. The same eyes that enable an animal to detect enemies, food, or shelter may also be used to detect and evaluate mates, rivals, and offspring. Thus, each organism is the result of evolutionary compromise but the range of adaptations that selection can produce in a given species is both limited and biased by its phylogenetic heritage and past history. There has recently been intense interest among biologists to understand how the design constraints of an animal's sensory system evolved under a given selection regime may bias the evolution of subsequent traits in the animal. It has been suggested, for example, that properties of a species' sensory system selected for one function, such as detecting prey, may drive in its descendants the evolution of signaling systems used in mate choice and other social behavior (e.g., Baerends 1971; Endler 1992; Ryan et al. 1992). We would expect the mechanisms mediating Pavlovian conditioning and other forms of learning to be shaped similarly by evolution, and the predispositions and constraints in learning that different species show support this (Hinde & Stevenson-Hinde 1973; Seligman & Hager 1972; Shettleworth 1972).

Although evolutionary biologists emphasize that the mechanisms mediating Pavlovian conditioning evolved because they give the animal an overall fitness advantage, psychologists, too, have recognized the "highly adaptive" nature of this process (e.g., Moore 1973). Moore (p. 183) points out that Pavlovian conditioning is important in most natural situations because it "would cause the animal to return to places, or objects, or substances, or organisms in the presence of which it was likely to encounter the sorts of unconditioned stimuli which elicit approach reactions."

Domjan et al. go further in the present article. They argue for the application of a control systems approach in the study of Pavlovian conditioning and draw on evidence from a range of species (from fruit flies to mammals, including humans) and social behavior (from mating and fighting to play and grooming) to reinforce the important point that Pavlovian mechanisms not only facilitate an animal's contact with the unconditioned stimulus, but that the "feed-forward" effects of the conditioned stimulus act to prepare the animal to respond to the unconditioned stimulus quicker and in an appropriate (i.e., adaptive) manner. Each of these effects – that is, facilitating encounters between the animal and a given unconditioned stimulus and preparing the animal to respond appropriately to that stimulus – would select for Pavlovian mechanisms in social as well as in nonsocial contexts, a point that will be apparent to those who recognize that learning mechanisms, like other traits, are shaped by natural selection.

How useful is an individual perspective for explaining the control of social behavior?

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Abstract: Pavlovian feed-forward mechanisms represent an individual perspective that ignores how repeated interactions between the same individuals lead to social relationships. These can determine social cues, coordinated behaviors, asymmetries between partners, and physiological and emotional states associated with social interaction.

Domjan et al.'s target article offers a strong case for going beyond a theoretical perspective based on fitness, outcomes, and evolution to include the behavioral mechanisms underlying social behaviors. They propose that an important component in the *control* of social behaviors is generated by Pavlovian "feed-forward" mechanisms in which the CS is the appearance of another individual and/or contextual cue and the UCS is whatever happens when they meet. The conditioning would be adaptive by generating anticipatory responses prior to biologically important encounters that influence their outcomes in ways that will be beneficial to the individuals.

This commentary addresses certain limitations in the extent to which Pavlovian anticipatory responses can contribute to our understanding of how animals engage in social behaviors. Although the target article is successful in calling attention to Pavlovian mechanisms that *influence* social behavior, conditioning is often limited to dimensions such as likelihood, latency, amplitude, and physiological concomitants without explaining how the behaviors arise in the first place. There are some examples of directed responses, for example, search or attack behaviors, but it is not clear how these are explained only by Pavlovian associations. One problem is that the target article does not consider the important distinction between S-S and S-R associations, and the possibility that they have distinctly different impacts on social interaction. For example, whereas the examples of endocrine secretions can be explained as S-R conditioning, CS-UCS associations would evoke a mental representation of an anticipated social interaction with a familiar individual that ought to influence how an individual selects among behavioral options. This, however, would still leave unexplained what actually determines the behaviors used during such interactions.

The fact that social interaction can involve familiarity points to an aspect of social behavior that can be influential in controlling how animals interact: the social relationships that arise from repeated interactions between the same individuals (Hinde 1979). Social relationships are ignored in the target article. Instead, the analysis remains firmly within the tradition of classical learning theory by relying entirely on learning processes at the *level of the individual.* In this case, the process is acquiring associations between sequential events during past social encounters that influence how an individual will behave during future encounters. Skinner (1953) made an analogous claim when talking about learned cooperation:

> Social behavior may be defined as the behavior of two or more people with respect to one another or in concert with respect to a common environment. It is often argued that this is different from individual behavior. . . . But a "social law" must be generated by the behavior of individuals. It is always an individual who behaves, and he behaves with the same body and according to the same processes as in a non-social situation. . . . The individual behavior explains the group phenomenon." (pp. 297–98)

Adopting an individual perspective has implications for the kinds of experimental analyses we use with respect to both stimuli and behavior. For example, Skinner's approach to modeling cooperation was based entirely on individual behavior-reinforcement sequences by minimizing or eliminating social interaction and the development of any possible relationship between the "partners." Typically, two animals are isolated in adjacent chambers and separately reinforced for temporal synchrony between individual acts such as bar pressing or key pecking. Under these conditions, it makes no difference whether timing is based on using social or nonsocial cues. Comparable levels of coordination are obtainable with partners separated by either transparent or opaque partitions, as long as the latter condition includes nonsocial stimuli such as lights or sounds presented to one partner following a correct response by the other (Hake & Vukelich 1972). The target article similarly pays little attention to whether the stimuli involved in conditioning are social or nonsocial, and whether this would make any difference on responding.

On the response side, Domjan et al. fail to consider how repeated social interactions between the *same* individuals lead to a social relationship that can be influential in determining states and behaviors during social encounters (Hinde 1979; Schuster et al. 1993). For example, the target article briefly mentions how play behaviors "become more efficient" with practice (sect. 4.4, para. 5). What is the significance of "more efficient?" Is aggressiveness reduced? Do other behaviors become preferred options? Are emotional ties strengthened?

There are in fact many situations in which two or more individuals join forces by developing highly coordinated strategies for achieving outcomes that are shared, for example, cooperation in group hunting, reproductive pair bonds, predator detection, challenge rituals between territorial neighbors, intergroup defense, and intergroup aggression (Dugatkin 1997). Such phenomena suggest that the control of social behaviors often involves processes that extend beyond the conditioning of individual responses. As examples of instrumental conditioning, they represent behavior-outcome sequences that involve not one but two (or more) individuals that not only develop coordinated strategies for achieving shared goals but are free to interact in other ways (Schuster et al. 1993). Coordinated actions are therefore likely to be embedded in more complex relationships that incorporate a number of asymmetries between partners. These include differences in initiating social actions, sharing jointly acquired outcomes, and using each other to coordinate actions in time and space (Chalmeau & Gallo, 1996; Schuster et al. 1993). Sometimes coordination can also include participants that have learned to adopt complementary roles (Boesch & Boesch 1989; Stander 1992). It is by no means clear whether the "laws of learning" that govern individual action can be assumed to apply when individuals act in concert. For example, are the effects of partial reinforcement or extinction insensitive to whether one or two individuals are involved? We do not know.

It is likely that the development of such relationships includes Pavlovian feed-forward processes, as suggested by Domjan et al. But these would be influenced not only by event sequences experienced by individuals, but by social relationships that will also exert strong influence on the behaviors adopted during social encounters and the emotional and physiological states conditioned by such encounters. By focusing on processes and outcomes at the individual level (e.g., Stephens & Anderson 1997), we risk ignoring the consequences that such relationships exert on the control of social behavior and the value that each participant places on engaging in social behavior.

It still takes at least two to tango

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Abstract: The target article provides a useful investigative model for studying social behaviors, but it falls short of establishing a more comprehensive conceptual framework for understanding complex social interactions. Social behaviors such as play involve a dynamic and complex interplay between two or more organisms. Even when feed-forward mechanisms are taken into account and the model is anchored to evolutionary theory, the utility of this model is still limited by the conspicuous absence of neurobiological theory and data.

Since the beginnings of behaviorism in the early part of this century, organisms have been largely viewed as behaving within a social vacuum. As Domjan, Cusato & Villarreal clearly point out, the social reality in which most organisms live has largely been ignored by this tradition in the behavioral sciences. Although it was refreshing to see a behavioristic attempt at understanding the social lives of animals, it was still disappointing to see the authors limit their discussion to a traditional and mechanistic explanation of behavior. The empirical approaches favored by the authors will no doubt be invaluable in deciphering the underlying mechanisms of social behaviors, but failing to appreciate the true complexity associated with social interactions and the extent to which specific neural circuits are involved in these complex interactions could stifle that quest.

Domjan et al. suggest that play behavior may take advantage of feed-forward mechanisms, and the data seems to support this. Play is a good example of a complex social interaction that can be readily studied by looking at the relatively simplistic play of young rats. Play in this species is almost exclusively comprised of rough-and-tumble wrestling, with each rat of a play dyad (rats most often play in pairs) vigorously attempting to gain access with their snout to the nape of their partner. When the nape of a suitably receptive play partner is contacted, that rat will most often respond by rolling onto its back, although other responses have been observed (e.g., Pellis & Pellis 1998). This body posture, known as a pin (e.g., Panksepp et al. 1984), will normally occur only within the confines of a playful encounter and is the direct result of sensory stimulation of the nape (Siviy & Panksepp 1987).

For playful encounters to occur in the first place and continue once they have been set in motion, the intent of each partner must be clearly communicated (Bekoff 1995; Pellis & Pellis 1996). This type of communication is often referred to as "metacommunication," because it tells the recipient how to interpret future communications. A rat allowing itself to be pinned could be thought of as a metacommunicative response, as it appears to signal that rat's intent to continue the bout. More to the point of the target article is the extent to which a conditioned anticipatory response prior to a playful encounter could be present and whether such a response could have metacommunicative value. In an initial experiment done in my lab to address this question, rats were allowed to play in a distinctive two-chambered apparatus, and their behavior prior to that play opportunity was assessed. As testing progressed over a period of days, those rats allowed to play in that chamber showed progressively higher levels of activity than did rats who played in a different chamber (Siviy 1998). These data suggest that juvenile rats were exhibiting an anticipatory increase in activity when placed in a situation previously associated with play. However, this anticipatory "eagerness" did not appear to be a directed response or to signal any playful intent. In other words, it probably did not have any metacommunicative value. The same type of nondirected energized behavior can also be observed if a rat is expecting an opportunity to drink a sweetened solution or is about to receive some other positive reinforcer (reviewed by Blackburn et al. 1992).

Anticipatory responses that are more specific and directed to an opportunity for play can apparently be conditioned as well. A recent study by Knutson, Burgdorf, and Panksepp (1998) reported that juvenile rats will emit 55 kHz ultrasonic vocalization both during play bouts and when placed alone in a testing chamber where they have previously been allowed to play. These vocalizations appear to represent an anticipatory response by the rat. In a recent attempt to establish this phenomenon in my lab, we have also found a very robust increase in 55 kHz vocalizations during a 2-minute period that followed a discrete CS (20 seconds of auditory clicks repeating at 4 Hz) and preceded a 5-minute opportunity to play. Since these vocalizations are emitted before and during a play bout, they may carry some metacommunicative value. An important point about these data, however, is that the anticipatory response (vocalizations) continues throughout the play encounter. This would appear to suggest that playful intent is continually being evaluated, and the roles of "sender" and "receiver" of these behavioral signals are constantly shifting back and forth between the participants.

These data are consistent with Domjan et al.'s suggestion that feed-forward mechanisms are present in the playful interactions of many mammals. However, I would contend that there is more going on than certain signals (e.g., play bows in canids, play faces in primates, ultrasonic vocalizations in rats) becoming associated with reinforcing, playful interactions. In all of these instances where specific types of behavioral signals occur during play, an advantage is gained not only by the animal emitting the anticipatory response. The animal to which the signal is directed also gains an advantage, because it learns that what is to follow is playful and could be responded to as such. Of course, a distinguishing feature of playful encounters is that the relative roles between the two playing partners rapidly, and constantly, shift during the course of the encounter. The rat who initiates a playful encounter by chasing its partner and making a nape contact may, in the next moment, be the one that is chased. I am convinced that the mechanistic model provided by the authors can handle this complex interplay of activity.

I would also argue that the types of behavioral signals and responses observed in complex social interactions such as play are not learned by young animals, but rather are the result of activating innate neural circuitry that, in turn, modulates anticipatory responses to both social and nonsocial behaviors. For example, cues that predict food tend to increase activity in mesolimbic dopamine systems (e.g., Blackburn et al. 1989), just as cues that predict an encounter with a receptive female also increase mesolimbic dopamine activity in male rats (Damsma et al. 1992). Although we have yet to measure mesolimbic dopamine activity in young rats presented with cues that predict play, administration of the dopamine antagonist haloperidol attenuates the conditioned anticipatory increase in activity prior to play (Siviy 1998).

Just as behaviors do not occur in a social vacuum, social behaviors do not occur in an affectively neutral arena. Understanding the affective sequelae associated with these behaviors and how these are represented in the brain is crucial to fully understand the nature of social behaviors. I would argue that stimuli, which have come to be associated with and predict playful encounters, will set up a central affective state in the brain that presumably involves mesolimbic dopamine circuitry. Activation of this affective neural system would result in both a generalized excitatory state (anticipatory eagerness) and an anticipatory response that is more specific to the particular behavior in which the animal is about to be engaged (e.g., ultrasonic vocalizations prior to play). As suggested by Domjan et al. and evident from the above-mentioned examples, Pavlovian conditioning and the concept of feed-forward mechanisms can provide indispensable investigatory tools for pursuing these avenues of inquiry. While biological theory provides the authors' model with a necessary evolutionary anchor, the conceptual framework they seek to provide cannot be complete without the inclusion of both neurobiological theory and data.

Feed-forward and the evolution of social behavior

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Abstract: Feed-forward Pavlovian conditioning can serve as a proximate mechanism for the evolution of social behavior. Feed-forward can provide the impetus for animals to associate other individuals' presence, and cooperation with them, with the acquisition of resources, whether or not the animals are genetically related. Other social behaviors such as play and grooming may develop as conditioned stimuli in feed-forward social systems.

Feed-forward Pavlovian conditioning can function as a proximate mechanism for the evolution of social behavior. As Domjan et al. note, three types of hypotheses have been suggested for the evolution of social behavior (Slobodchikoff & Shields 1988): genetic, ecological, and phylogenetic. Of these, the phylogenetic one is the default hypothesis, invoked when we cannot come up with a plausible explanation for why social behavior evolved within a social group (Slobodchikoff 1988). The other two hypotheses offer more possibilities for explanation: The genetic one suggests that animals cooperate because of close relatedness and the genetically beneficial effects of helping relatives (Hamilton 1964), whereas the ecological hypothesis suggests that animals cooperate because of the benefits obtained from cooperative resource extraction (Slobodchikoff & Schulz 1988). In their present form, neither of the latter two hypotheses offers any mechanism for how animals would develop such cooperative behavior, either toward relatives or other individuals who can help with resource extraction and utilization. Feed-forward conditioning can provide such a mechanism.

Many animals living in a social group can make a choice: Stay in the social group, or leave the group and live as solitary individuals. Except for the eusocial insects with their sterile castes, such choices can be seen in the form of the flexible social systems found in a variety of different animals (Lott 1991). One approach to the matter of choice is to list the costs and benefits of social behavior (Alexander 1974) and make the assumption that animals are assessing these costs and benefits and making a decision on the basis of the cost/benefit ratio of staying in the social group (Wilson 1975). However, exactly how animals might be able to make this cost/benefit ratio assessment is not discussed.

Feed-forward conditioning offers a simple mechanism for explaining how social groups can become established. Let us suppose that two animals coexist spatially and temporally, either because they are related (i.e., the genetic hypothesis) or because they have been attracted to the same habitat for the purposes of resource extraction or utilization (i.e., the ecological hypothesis). In these circumstances, the two animals can respond to each other aggressively, with one animal chasing away the other, or they can respond neutrally, by ignoring each other, or they can respond cooperatively, by helping each other to construct a shelter or by sharing food or the location of food sources.

Decisions about sharing or cooperation appear to be made on the basis of ecological factors, such as the availability and abundance of resources, even among relatives. As Slobodchikoff (1984) has pointed out, a relatively small proportion of *Hymenoptera* (bees and wasps) is social, probably because of the availability of resources, although all species of *Hymenoptera* have the haplodiploid system of sex-determination that led Hamilton (1964) to speculate about the benefits of inclusive fitness in the evolution of sociality. Resources can be food, shelter, or the availability of other animals to serve an antipredatory function, such as that found among cooperative mammals such as meerkats (*Suricata suricatta;* Blumstein 1999; Clutton-Brock et al. 1999).

If the animals respond to each other cooperatively, then feed-forward can become an important proximate mechanism for strengthening the cooperative response. Here the reinforcer might be access to a resource (e.g., food). Each of the animals can then function as a CS, and the feed-forward mechanism leads to the procurement of more resources. This in turn can lead to behaviors that we see within social groups, such as play and social grooming. In this context, these behaviors can be viewed as CS byproducts of the feed-forward mechanism. The learned system of cooperation can then be transmitted culturally to subsequent generations, and if it increases the fitness of the members of the social group, it can serve as the basis for natural selection for behaviors that increase the strength of the cooperation.

Such feed-forward mechanisms can also serve as the initial impetus for the evolution of sterile castes among the eusocial animals. As pointed out by Slobodchikoff (1984) and Slobodchikoff and Schulz (1988), if an animal is going to have an expectation of zero fitness as a solitary individual, and an extremely small but greater than zero average fitness expectation as a member of a social group, the animal in an evolutionary sense should choose to be in the social group. Among the social insects, workers are functionally sterile, but the fitness expectation for any individual is not zero. In most social insects, whether an individual egg develops into a sterile worker or a reproductive adult is determined by dietary considerations and the needs of the colony (Michener 1974; Slobodchikoff & Schulz 1988; Wilson 1971). Thus, each egg has a small chance of becoming a reproductive adult, in which case that individual acquires an extremely high fitness. If an individual insect cannot survive as a solitary individual but can survive as part of a group, then evolution would favor the development of sociality, as long as each individual in the group had an average reproductive expectation that was greater than zero. Feed-forward conditioning can serve as the initial mechanism by which the group forms, and the resource requirements and availability can then determine how many individuals can reproduce (see Slobodchikoff & Schulz 1988).

Bottoms-up! A refreshing change in models

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Abstract: Top-down models typically used to explain social behavior involve specific adaptations and higher level cognition. The Pavlovian conditioning model proposed can be extended to explain formation of dominance hierarchies and group structure, can replace a pheromonal model of reproductive suppression, and can be applied to language learning. This bottom-up approach based on general learning principles is a refreshing alternative to top-down models.

During the past 25 years the study of behavior has been marked by top-down cognitive or sociobiological explanations with little attention to mechanisms. General process theories of learning have been disparaged and displaced with "biological constraints." The "adapted mind," with innate, species-typical modules, has replaced the "plastic brain" that can be shaped by conditioning and reinforcement. In this context Domjan et al. provide a refreshing change. Complex social behavior can emerge through a bottom-up process of associative learning. This model of Pavlovian feed-forward mechanisms can be applied in several other domains.

Dominance hierarchies found in many species have been thought to be characteristic of the species displaying the hierarchy and to result from individual variation in the predisposition to become dominant. However, the emergence of hierarchies might come through a series of interactions between initially equal individuals. Chase et al. (1994) find that winners tend to win subsequent interactions and losers to lose subsequent interactions. Thus a chance result from a single interaction can lead to a cascade of winner and loser effects among a group of socially interacting individuals, leading to the emergence of a dominance hierarchy through a series of chance interactions reinforced by the individual's prior history of winning and losing. The "winner" and "loser" effects must be indicative of a conditioning process that affects subsequent competitive performance. If winning and losing also become associated with some characteristics of the individuals encountered (voice, looks, or smell), then a hierarchy might be maintained with little additional fighting.

Hemelrijk (1996) not only describes the formation of dominance hierarchies as a bottom-up process but provides plausible bottom-up explanations for group structure and reciprocal altruism that do not require cognitive or species-specific processes. She cites modeling work by Hogeweg and Hesper (1983) that uses completely identical individuals initially that through chance and self-reinforcing interactions leads to the complex social structures through a process similar to the Pavlovian processes of Domjan et al. High-level cognitive processes need not be invoked to explain the formation and maintenance of social structure.

Another example emerges from work we have done on cooperatively breeding cotton-top tamarins. In captivity, we find that there is only a single reproductive female in a group, and all other group females are reproductively suppressed to the extreme of never ovulating. Our initial thinking was that the reproductive female exerted suppression through either behavior or chemical signals. However, we found no evidence of high levels of aggression between reproductive and nonreproductive females (Snowdon et al. 1993) and no evidence of elevated cortisol levels that might suppress reproductive hormones (Ziegler et al. 1995). However, transfers of scent marks from reproductive females continued to suppress ovulation in nonreproductive females who moved to new social groups, suggesting a contraceptive pheromone (Savage et al. 1988). Although we started searching for the contraceptive components of scent marks, additional results suggested that odors could not be the sole mechanism. In fact, females housed away from olfactory stimuli from the reproductive female, but with their brothers, failed to ovulate until they encountered a novel male. Thus, the scent marks of the reproductive female were not necessary or sufficient to maintain inhibition of ovulation.

Based on convergence between captive and field data, we have suggested that subordinate females are restraining their own reproduction until appropriate mates and environmental conditions are available (Snowdon 1996). However, the self-restraint model fails to provide a mechanism for reproductive inhibition by scent marks. Pavlovian conditioning provides an appropriate mechanism. Scent marks provide information for cotton-top tamarins to discriminate between familiar and unfamiliar females and between reproductively cycling versus noncycling unfamiliar females (Washabaugh & Snowdon 1998). Thus, a subordinate female can associate an odor from a familiar reproductive female with prior experience (such as rare aggressive or other behavioral events) that limits breeding opportunities. Generalization from the odor cues of a familiar cycling female allows a female to evaluate the reproductive state of novel females and thus to determine whether it is prudent to invest in reproduction or to maintain her nonreproductive state. Instead of hypothesizing that odors contain specific compounds that block reproduction, I find it more fruitful to think of the odors as cues used in associative learning that influence a female's reproduction.

We can also see associative learning providing feed-forward mechanisms in language acquisition, the prototypical area of the "adapted mind." Saffran et al. (1996) have presented 8-month-old human infants with two-minute sequences of nonsense syllables. Within these sequences are triads of syllables that occur together 50% or 70% of the time. After the exposure phase infants show greater habituation to the triads of syllables that occurred together, than to triads of syllables that had rarely been presented together. This experiment provides a rapid associative process for an infant to be able to extract words from a speech string. However, it is not clear what the unconditioned stimulus would be in this study, so it may not fit a strict Pavlovian interpretation. Nonetheless, in a real world interaction with caretakers, one can imagine that an infant's response to words might lead to increased attention or caregiving.

In summary, Domjan et al. provide us with plausible mechanisms for explaining complex social behavior in terms of general associative conditioning processes. Although the model does not mean that there are no innate modules for controlling social behavior or that organisms are not capable of higher cognitive processes, the prudent scientist will evaluate these general bottom-up processes before assuming that modularity or cognitive processes are necessary to explain social behavior.

How is the feed-forward Pavlovian control system instantiated in neurobiology?

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Abstract: While feed-forward mechanisms may be ubiquitous in biological systems that form the substrates of Pavlovian conditioning, the control system proposed by Domjan, Cusato & Villarreal seems too elaborate for Pavlovian conditioning of simple skeletal muscle responses. We discuss here how the known neural substrates of classical eyeblink conditioning can be described in feed-forward terms, but argue that the monitor/comparator part of the system is not necessary and perhaps could even be detrimental to simple, nonsocial forms of Pavlovian conditioning.

Domjan, Cusato & Villarreal discuss how feed-forward mechanisms, specifically those of Pavlovian conditioning, provide benefits to organisms engaging in social interactions. The authors provide clear examples of how associative learning can increase the effectiveness of social behavior in various species of animals. Clearly, the effects of experience acquired from associating environmental stimuli on subsequent behavior have been well established in the learning literature. However, in focusing on Pavlovian conditioning, the authors ignore the enormous contribution of operant learning to social interactions, which may be far too complex to be properly analyzed solely with Pavlovian principles. This issue aside, there is an obvious appeal in the use of biological and control systems theory for understanding of social learning. However, a major deficiency in the authors' approach lies in the use of hypothetical "boxes," depicted in various figures, to represent elements in the proposed behavioral control system. It seems possible that with the existing knowledge about the neurobiology of learning and memory, these elements can be represented by brain structures that make up existing biological models of learning.

When one looks at data concerning known neural correlates of Pavlovian conditioning, a case can be made that not all portions of Domjan et al.'s proposed control system are needed during some forms of Pavlovian conditioning. Thus the author's system design may not be universal for all Pavlovian conditioning situations, but rather specific to more complex social learning situations. More specifically, although feed-forward mechanisms may be important for all forms of Pavlovian conditioning, it seems unlikely that all of the components of the behavioral control system depicted in Figure 3 of the target article are necessary for the conditioning of skeletal muscle responses. In fact, a case could be made that including a monitor and comparator in this system could slow down response execution to the point that CRs would not be observed. We use classical eyeblink conditioning as an example. In this procedure, several pairings of a tone CS and an air puff US eventually produce eyeblink CRs to presentations of the tone. The effective CS-US interval for this type of Pavlovian conditioning ranges from about 100 msec to 3–4 sec. In part due to its simplicity, we know a great deal about the neural circuitry that is critical for encoding this simple learning procedure (e.g., Steinmetz 1998). This system therefore should be useful for instantiating the authors' control system idea into the known neurobiological correlates of at least one type of Pavlovian conditioning.

The CS and US pathways for classical eyeblink conditioning have been delineated so we can trace sensory inputs into the system (Sears & Steinmetz 1991; Steinmetz 1990). The stimulus/response actuator can be identified as the accessory abducens and facial nuclei, as these are the cranial nerve nuclei known to be responsible for generating the CR and UR (Cegavske et al. 1976). Presentations of both the tone CS and air puff US are known to activate neurons in these brain stem nuclei before paired training is initiated. We have hypothesized that the CS-US associator and memory reside in the cerebellum (cortex and deep nuclei), because this structure is critical for acquisition and retention of the classically conditioned eyeblink response (e.g., Steinmetz 1998). Compatible with the idea that feed-forward mechanisms are involved in this system, it appears that once the associator and memory in the cerebellum are activated by the CS (i.e., after learning), the cerebellum can act rather *directly* on the stimulus/response actuator (the abducens and facial nuclei) to produce a behavioral output (the CR). Interesting to note, paired CS-US presentations are known to alter properties of the UR in addition to establishing the CR (e.g., Canli et al. 1992). In addition, the learned response is incredibly well timed and it has been suggested that this timing is due to *feedback* interactions that occur within this basic conditioning circuitry, especially feedback involving cerebellar output back onto the US input to the cerebellum (e.g., Sears & Steinmetz 1991). Thus feedback control, in addition to feed-forward control, may be very important in determining the final CR that is generated.

The portion of Domjan et al.'s proposed behavioral control system that is difficult to account for by the known neural circuitry of eyeblink conditioning is the monitor and comparator portion of the control system. First, it is difficult to conceive why this circuitry would be necessary for classical eyeblink conditioning, because the calculation of cost/benefit ratios would not seem to be important for the generation of learned skeletal muscle responses. Second, given that eyeblink CRs can be established and executed with CS-US intervals as short as 100 msec, it seems likely that recruiting this extra circuitry could actually interfere with the execution of the quick response that is required in this situation. We would therefore like to suggest that, while a feed-forward mechanism is actually engaged during classical eyeblink conditioning, input concerning cost/benefit information is not important for this type of Pavlovian conditioning and this part of the control system is not used. This is not to say that other forms of Pavlovian conditioning do not use this portion of the control system and, in fact, there are some variations of classical eyeblink conditioning where one can speculate that this part of the control system is very important (e.g., contextual conditioning, conditioned inhibition, etc.). Moreover, the hippocampus, neostriatum, and amygdala all seem to be ideal candidate structures for encoding the monitor/comparator portion of the authors' proposed behavioral control system. This hypothesis is certainly testable.

An integrative approach to the modeling of behavior

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Abstract: Theorists of learning, regulation, and evolution explain behavior using remarkably different concepts because of pressures toward specialization, a focus on testing simple causal theories that underconceptualize the contributions of the organism and its environment, and the absence of a working model capable of surviving in a complex environment. We add suggestions for the development and testing of such a model.

Behavior is explained by learning theorists as a product of association, by regulatory theorists as the result of control through feedback, and by biological theorists as due to evolution. Each discipline focuses on a subset of behavioral determinants without acknowledging that an organism based on their theory alone, if it lived at all, would be an awkward clanking beast bound for disaster. Domjan et al. attempt to make up for the delayed adjustments allowed by evolution and control theory by emphasizing the role of learning in producing more rapid, anticipatory (feed-forward) adjustments. But even learning can be slow, costly, and incomplete (Johnston 1982). Imagine an organism learning to find food, regulate intake, avoid predators, and reproduce in the absence of extensive perceptual-motor organization tuned to the social environment and interrelated regulatory processes allowing search and survival. As Domjan et al. point out, the key to a proper theory of an organism is the integration of evolution, regulation, and experience. So why has such a synthesis been so slow to develop?

Three issues seem important. The first is the continual pressure toward specialization in training and research. In terms of training, the time required to master the concepts, literature, and procedures of an area (while competing for publications, positions, and grants) leaves little time for exploring even closely related approaches. In terms of research, scientists must acquire the common vocabulary and procedures before they can get an audience for their results.

A second issue is the tendency to relate experimental outcomes only to the experimenter's manipulation without acknowledging the particular animals' contribution, a contribution that is typically embedded in the design of the apparatus and procedures but not conceptualized. For example, in the study of learning, attention is focused on the relation imposed by the experimenter between the predictive stimulus and the reward. Many contributions of regulation and evolution are built into the apparatus and procedures. Regulatory issues are handled by daily feedings and control of environmental cues. Evolutionary issues are handled by inbreeding animals and by designing the experimental apparatus and procedures to engage desired aspects of the animal's repertoire. Lest it seem that only learning theorists share this problem, consider drawing conclusions about the foraging of a species based on the effect of infusing glucose into the bloodstream of tethered rats. The contribution of learning and digestive regulation are not dealt with, nor are evolutionary issues ranging from dietary requirements to foraging specializations. The results, though not wrong, are incomplete and may be misleading.

The third issue is the absence of testable working models that tie together evolution, regulation, and learning. We think Domjan et al. are on the right track by trying to integrate evolution, control theory, and learning, and their review of learning in social behavior goes a long way toward documenting its complex regulatory, evolutionary context. However, we would like to see them go even further. In addition to organizing their review by functional systems of behavior (reproduction, aggression), they could have attempted to specify the contribution of the perceptual-motor organization and multiple regulatory structures and processes each species brings to the experimental situation. This would provide a more concrete foundation for integrating evolution, regulation, and learning. As further encouragement, we offer the following observations:

1. Learning is not the only type of anticipatory mechanism. Evolution can be thought of as a feed-forward mechanism that results in individuals with the ability to avoid negative circumstances before there is danger of disequilibrium (e.g., the humidity-related kinesis of wood mites). Specific motor control mechanisms often include appropriate predictive biases (like the aiming bias built into the predatory strike of a praying mantis).

2. Learned feed-forward processes improve regulation only in some circumstances. In other circumstances they interfere. For example, misbehavior (Breland & Breland 1961) appears to reflect the intrusion of anticipatory responding based on preorganized perceptual-motor mechanisms related to foraging. Similarly, adjunctive drinking seems based on anticipatory processes related to meal termination that markedly interfere with water regulation under conditions of spaced food presentation.

3. Regulation by a simple set point is probably rare in biological phenomena. Dual thresholds appear in temperature regulation. Reliable baselines of responding that produce regulatory behavior under constraint often are best viewed as resulting from a competitive balance between multiple regulated behaviors (Timberlake 1984). Also there is strong evidence for multiple regulatory tendencies in behavior like copulation in male rats and mobbing in chaffinches.

4. It seems preferable to treat Pavlovian conditioning as a procedure than as a simple basic process of association between the CS and US. Behaviorally, the basic process view does not acknowledge the role of the CS-US interval and CS and US type in producing different forms and levels of conditioned behavior (Timberlake 1994). Neurophysiologically, it is not clear yet if there is a single unitary mechanism of Pavlovian conditioning at a subcellular level, but evidence so far speaks of different brain locations and neural configurations as a product of the CS type, US system, and timing involved.

5. The memory concept introduce by Domjan et al. seemed essential but perhaps overworked and underspecified. It includes both previously experienced sensory input, previous comparisons and adjustments, and a choice standard. The concept needs to be unpacked.

6. Finally, as a concrete check on the viability of any model, it seems worthwhile at present to combine development of a systems model of behavior with an attempt to construct from it a real or virtual robot. The contribution of a robot is that it cannot survive on words, at least not outside a very peculiar environment. It is not enough to show experimentally what variables can determine responding, it is necessary to find out what and how they contribute to survival.

Authors' Response

Extensions, elaborations, and explanations of the role of evolution and learning in the control of social behavior

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Abstract: Reactions to the target article included requests for extensions and elaborations of the schema we proposed and discussions of apparent shortcomings of our approach. In general, we welcome suggestions for extension of the schema to additional kinds of social behavior and to forms of learning other than Pavlovian conditioning. Many of the requested elaborations of the schema are consistent with our approach, but some may limit its generality. Many of the apparent shortcomings that commentators discussed do not seem problematic. Our schema encourages a broad view of the behavioral consequences of Pavlovian conditioning – including learned modifications of responding to the unconditioned stimulus. Costs and benefits addressed by our schema are the long-range reproductive consequences of learning – not the immediate reinforcing consequences of particular conditioned responses. Our approach allows the evolution of learning to yield maladaptive behavior and can be extended to characterize dynamic social interactions. We clarify that ours is not a homeostatic model involving ideal set points, and we clarify and defend our application of Pavlovian concepts to the analysis of social play.

The purpose of our target article was to provide a new perspective on social behavior by using concepts from control theory to integrate common biological approaches to social behavior with concepts from learning theory, especially Pavlovian conditioning. As **Slobodchikoff** pointed out, our account provides proximate mechanisms for the evolution of social behavior. Such proximate mechanisms are lacking in genetic, ecological, and phylogenetic explanations of social behavior but are essential for a complete theory of an organism (**Timberlake et al.**).

We did not presume to be original in our treatment of evolutionary theory or control theory. However, we considered the integration of these ideas with Pavlovian conditioning to be innovative, and we were gratified that others (e.g., **Hollis, Killeen**) also recognized the novelty of this contribution.

As **Rowland** noted, the social behavior of nonhuman animals has been primarily of concern to ethologists, sociobiologists, and behavioral ecologists (see also **Hollis**). Roland went on to point out that our contribution was to bring social behavior into the domain of investigators of learning. This integration of studies of learning and social behavior can contribute to each area of inquiry. **Goodie** pointed out that our approach extends the analysis of Pavlovian conditioning to complex natural stimuli and complex social behavior, and **Schuster** noted that the learning mechanisms we discussed extend the analysis of social behavior beyond a theoretical perspective based on fitness, outcomes, and evolution. Another important benefit of the integration, noted by **Snowdon,** is that it allows for complex social behavior to emerge through a bottom-up process of associative learning. Snowdon characterized this as a "refreshing change" from more common top-down cognitive and sociobiological accounts of social behavior.

As is typical of theoretical proposals, our ideas have antecedents in previous theoretical and empirical efforts. **Limber** and **Killeen** pointed out that control concepts have been previously used in analyses of social and other forms of behavior by Miller et al. (1960), Powers (1978), Bowlby (1969), and others. **Rowland** and **Bronstein** focused on antecedents to our proposal in studies of learning. They noted that our concerns can be traced to discussions in the 1960s and 1970s concerning the shortcomings of general process learning theory in explaining apparent adaptive specializations and biological constraints on learning (e.g., Hinde & Stevenson-Hinde 1973; Seligman & Hager 1972). Those discussions emphasized that a complete account of learning has to consider how the behavior and learning of organisms have been shaped by evolution. Our approach likewise recognizes that learning has to be considered in an evolutionary framework. However, instead of focusing on how evolution has constrained the operation of learning processes, our emphasis is on how learning can contribute to adaptive behavior patterns. As Bronstein correctly observed, we see learning as functioning to fine tune unlearned, species-typical activities.

R1. Extensions of the schema

Many of the commentators took us to task because our schema did not provide a complete account of social behavior or a complete account of the ways in which learning may be involved in determining the nature of social responses. We have no quarrel with these types of comments. Our schema was not intended to be a complete account of either social behavior or of learning mechanisms involved in social behavior. We also did not intend explain complex human social behavior, contrary to the impressions of **Cardinal et al.** As the commentators pointed out, there are various factors that influence social activities in addition to learning, and Pavlovian conditioning is not the only form of learning that is involved in social interactions.

R1.1. Other social factors and forms of social behavior.

According to **Poirier & Field,** we did not consider that primate maternal responses are a function of the infant's sex, birth order, age, number and sex of siblings, habitat, maternal experience, mother's dominance status, and length of the mother's nipples. They also noted that we did not take age into account in our treatment of play behavior or discuss the role of habitats, sex, and kinship relations in our discussion of social grooming. Some of these factors (maternal experience and dominance status) may be mediated by the kind of learning mechanisms we described (see **Snowdon**). Other factors mentioned by Poirier and Field can be incorporated into the schema we proposed by considering them as limitations on the circumstances under which a particular event can serve as an effective unconditioned (or conditioned) stimulus. However, we did not consider these details because they would have added considerable complexity to the schema we proposed and would have obscured commonalities across the forms of social behavior that we described.

Several commentators suggested that our schema could incorporate forms of social behavior that we had not considered. **Snowdon** suggested that our schema could be extended to include dominance hierarchies, reproductive suppression in female tamarins, and perhaps language acquisition. **Fragaszy** suggested that we extend the schema to include emotional contagion and social learning effects.

Schuster was less sanguine about possible extensions of our schema. He expressed concern that our schema did not consider cooperation and coordinated group behavior, such as group hunting and group predator detection. He also expressed concern that we did not consider the role of social relationships in our account of social behavior.

We applaud suggestions to extend the schema to other forms of social behavior. In addressing a limited set of phenomena, our intent was not to limit discourse but to get the discussion started. Some of the additional phenomena suggested will be easier to incorporate into the schema than others. Phenomena such as cooperative hunting may be so strongly determined by instrumental contingencies (see sect. R1.2) that it cannot be incorporated into the kind of Pavlovian schema we proposed. However, our schema can be readily extended to incorporate the effects of social relationships. Some social relationships depend on individual recognition, which appears to have a Pavlovian component (Riters & Balthazart 1998). Other effects of social relationships may be incorporated into our schema by assuming that the nature of the social US that one organism provides another depends on the relationship that exists between them. An individual of high dominance status, for example, provides very different types of stimulation than one of low status. Therefore, experience with high status individuals should produce different types of learned behavioral adjustments.

R1.2. Other forms of learning. We emphasized Pavlovian conditioning in our schema for a number of reasons. First, Pavlovian conditioning is the most obvious type of learning that comes to mind when one considers difficulties that result from the delays in the operation of feedback control mechanisms (see sects. 3.2 and 3.3). Second, Pavlovian conditioning has not been prominently recognized as a process relevant to social behavior. Hence, an emphasis on Pavlovian mechanisms is more newsworthy than an analysis based on instrumental conditioning. Third, our perspective on Pavlovian conditioning makes laboratory studies employing a Pavlovian paradigm more easily generalized to an animal's natural environment (see Domjan 1998). We will have more to say about this issue in section 2.3.2. Suffice it to say here that, as **Hollis** commented, the relevance of laboratory learning phenomena to the "real world" is a matter of considerable importance to behavioral ecologists. Finally, we have to admit that our emphasis on Pavlovian conditioning was also encouraged by the fact that much of our own empirical work has been based on that paradigm. However, our choice of the Pavlovian paradigm in our own research was not arbitrary but motivated by some of the other reasons cited above.

Commentators suggested that we should have considered other forms of learning as well. **Krebs** and **Baldwin,** for example, recommended that we include observational learning and imitation learning. Many others (**Baldwin, Cardinal et al., Fantino & Stolarz-Fantino, Killeen,** and **Steinmetz et al.**) expressed concern that we did not include instrumental conditioning as a learning mechanisms that governs social behavior. In general, our reaction to these suggestions is similar to our reaction to having omitted certain forms of social behavior. We did not intend to suggest that Pavlovian conditioning is the only type of learning that is involved in social behavior, and we applaud efforts to extend the schema to incorporate other forms of learning.

To incorporate other forms of learning, the sensory inputs and the behavioral outputs represented in our schema would have to be modified. Changes also would have to be made in the learning process represented in the memory module. Thus, how learning changes behavioral output and the kind of behavioral output the system monitors would have to be specified differently. However, the ways in which the system monitors and responds to the relative costs and benefits of the learned behavior could be retained in the schema.

R1.2.1. The special problem of instrumental conditioning. Some of the comments concerning the role of instrumental conditioning were rather vociferous. Contrary to the implications of **Cardinal et al.,** we are certainly familiar with, and respectful of, instrumental conditioning. In fact, Crawford et al. (1993) reviewed research on the instrumental conditioning of sexual behavior in one of the 71 volumes of the *Journal of the Experimental Analysis of Behavior* that Cardinal et al. cited in their commentary. We also discussed instrumental conditioning of sexual behavior in Domjan and Holloway (1998) and in Domjan and Crawford (1998).

Some of the commentators were puzzled why we would suggest that something like play behavior might be under Pavlovian control when an instrumental interpretation would seem to be more obvious. **Killeen,** for example, claimed (without documentation) that play involves learning what responses are effective in interaction with others, which conspecifics to challenge and which to defer to – all based on the consequences of actions. "Pure Skinner. Where's the Pavlov?" as Killeen put it. We will have more to say about play in section R3.7. In the present context, however, we suggested that claims about instrumental control should be put to empirical test rather than accepted on the basis of descriptive evidence and plausibility arguments. (Of course, claims about Pavlovian control have to stand up to similar experimental scrutiny.)

The learning literature has numerous examples of behavior that initially seemed "obviously" instrumental that turned out to be strongly under Pavlovian control when the proper experiments were conducted. Perhaps the most prominent of these is the pigeon's key-peck response. For many years, Skinner and his students considered the key-peck response of pigeons reinforced with food to be "obviously" governed by response-reinforcer contingencies. However, Brown and Jenkins (1968) demonstrated a strong Pavlovian component in the control of key pecking.

Another example comes from research on sexual conditioning. As we noted in section 4.2.1, male quail will approach a CS paired with access to a sexually receptive female when the CS is presented near the door to the female's cage. This certainly looks like an instrumental situation. The approach response is necessary to get access to the female and therefore may develop through instrumental reinforcement. However, the conditioned approach behavior develops even if an omission control procedure is instituted in which approaching the CS results in cancellation of access to the female (Crawford & Domjan 1993). This outcome is similar to the results of studies of omission training of the pigeon's key peck response (Williams & Williams 1969). Mail quail also approach the CS if the CS is placed far away from the female's door (Burns & Domjan 1996), as in Jenkins's "long-box" experiment (see Hearst & Jenkins 1974). The long-box procedure also involves a negative contingency between approaching the CS and sexual reinforcement and therefore should suppress responding if the behavior is under instrumental control. This kind of evidence gives us confidence to suggest that Pavlovian control may be operative even in situations that on the face of it appear to be "obviously" instrumental.

Some of the commentators (e.g., **Baldwin, Fantino & Stolarz-Fantino,** and **Steinmetz et al.**) argued that we should include instrumental conditioning as a learning process governing social behavior for the sake of completeness. We have no quarrel with that suggestion. Our emphasis on Pavlovian mechanisms was not intended to rule out other types of learning as well. However, we take exception to the claim that little insight into social behavior can be gained from focusing only on Pavlovian conditioning.

Cardinal et al., for example, argued that social behavior is best characterized by a three-term contingency involving the cues (S) in the presence of which social behavior occurs, the social response (R), and the positive or negative reinforcing consequence (S*) of that response. A corollary to this argument is that behavior governed by a S-R-S* three-term contingency cannot be broken down into Pavlovian (S-S*) and instrumental (R-S*) components. According to this argument, a focus on just Pavlovian mechanisms is bound to be useless. We reject this conclusion for two reasons. First, even in cases where a three-term contingency is operative, that does not mean that Pavlovian S-S* associations do not have any role in the control of the behavior. S-S* associations may still make a significant contribution to the resultant responding. Second, the mere claim that something can be conceptualized in terms of a three-term contingency is not proof that such a contingency is actually operative. As with claims of "obvious" instrumental contingencies discussed in the preceding paragraph, these interpretations have to be empirically verified.

R2. Elaborations of the schema

In describing any schema or model, decisions have to be made about what to include and what to leave out. No matter what level of description is selected, some people are apt to ask for more detail and others for less. **Steinmetz et al.** expressed the opinion that our schema was unnecessarily complicated to characterize simple eyeblink conditioning. In contrast, many other commentators requested elaborations of various aspects of the schema.

Timberlake et al. suggested that in discussing learning effects we consider in greater detail the pre-existing perceptual-motor organization of the organism and the multiple regulatory structures and processes that organisms bring to a learning situation. **Cardinal et al., Killeen,** and **Timberlake et al.** requested that we provide more details about the memory module. **Steinmetz et al.** and **Siviy** suggested that we discuss how various components of the schema may be instantiated in the nervous system. Others requested elaborations of the concepts we borrowed from biological theory, control theory, and learning.

Many of these requests for elaboration are compatible with our schema, and we welcome them. We omitted details at this stage because we wanted to focus on connecting different areas of discourse rather than describing each area in a comprehensive fashion. In addition, we wanted to focus on features that various forms of social behavior have in common rather than on features specific to particular social situations. The neural instantiation of our schema, for example, is likely to differ depending on the form of social behavior that is involved. Therefore, we are skeptical that a general model of the learning in social situations can be developed at the level of specific neural loci and neural connections.

R2.1. Elaboration of cost/benefit calculations. Our schema included an assessment of the costs and benefits of social Pavlovian conditioning because cost/benefit calculations are an essential component of biological approaches to social behavior. The costs and benefits that are of ultimate interest are those that contribute to reproductive fitness. A number of commentators emphasized that these costs and benefits have to be considered in greater detail and in the broad context of the entire organism.

Rowland noted that reproductive fitness involves the whole organism, and **Limber** pointed out that in considering the costs and benefits of learning it is important to consider the overall adaptive balance of the organism rather than the apparent function of a single conditioned response. **Davey & Field** also advocated this point of view and went on to caution that any calculation of costs and benefits should also consider possible hidden costs of learning. We agree with all of these comments. We did not intend to suggest that the costs and benefits of a particular instance of Pavlovian conditioning can or should be calculated in isolation. We recognize that evolution operates on the net result of the organism's total activities. We also recognize (contrary to Davey & Field's impression) that evolution selects for outcomes rather than processes. That is why the cost/benefit calculations in our schema are performed as a part of a module that monitors behavioral output, not as a part of a module that represents learning processes.

Given that cost/benefit calculations have to be made in the context of the entire organism, such calculations are rather difficult to carry out. As **Hollis** pointed out, behavioral ecologists rather than learning psychologists are probably best equipped to accomplish this task. We admit that we took a rather informal approach to cost/benefit calculations when we assumed that increases in the efficiency of social behavior brought about by Pavlovian conditioning are of adaptive significance. However, evidence directly linking Pavlovian conditioned behavior to increased gamete release and fecundity is starting to be obtained (Domjan et al. 1998; Hollis et al. 1997). Furthermore, as **Bronstein** noted, it is reasonable to assume that increasing the efficiency of critical social activities such as sexual behavior and maternal care will have significant fitness benefits. However, we fully agree that claims of adaptive significance are best justified by empirical data rather than plausibility arguments.

R2.2. Elaboration of control concepts. A few commentators expressed concern that we underutilized concepts from control systems theory. **Limber,** for example, was disappointed that we did not use the specific vocabulary of control theory that "transcends diverse methodologies." **Killeen** pointed out that there are numerous different types of control systems (damped, undamped, overdamped, integro-differential, adaptive, and hierarchical), each with its own special properties that could be put in correspondence with the demands of different ecological niches. **Gardner** suggested that we incorporate fuzzy controllers into our schema. We agree that control theory has much more to offer for analyses of animal social interactions than we explicitly specified, and we welcome elaborations of control systems concepts within the context of the schema we presented. It was not our intention to exhaust the potentially limitless applications of control theory to animal social behavior. Rather, we wanted to use control theory only as a tool – a means by which to integrate Pavlovian concepts with ecological and genetic theories of social behavior.

As we discussed in section 2, traditional analyses of animal social behavior have focused on the conditions that promote or maintain group living. Implicit in these theories is the notion that social animals are behaviorally predisposed to minimize the costs and maximize the benefits of group living. Thus, any plausible system intended to represent the nature of an individual animal's social responses has to include components that carry out and evaluate cost/benefit calculations. Biological theories of social behavior have had little to say about the proximate mechanisms that allow individual animals to fine-tune and predict how their day-to-day social interactions will unfold. Few biological theorists, however, would deny that such fine tuning and prediction reduces the cost/benefit ratio. Since Pavlovian mechanisms are a means by which such fine tuning and prediction can take place, we proposed that associator and memory components be included in analyses of social behavior. Control concepts were used to describe how these multiple components fit together to modulate individual social responses. Although limited, our use of control concepts enabled us to bring together in a unique way the proximate and evolutionary factors that determine the nature of social interactions.

R2.3. Elaboration of learning mechanisms. The most frequent requests for elaboration of our schema concerned learning mechanisms. Many commentators suggested specific learning issues that should be addressed. Others complained that the term "Pavlovian" is little more than a label and does not provide any significant insight into learning. Another aspect of this line of criticism was the claim that schemas like ours are not likely to integrate biological and learning approaches to the study of behavior until Pavlovian conditioning is shown to be responsible for naturally occurring behavior.

R2.3.1. Pavlovian conditioning – not just a label. Several commentators (e.g., **Bekoff & Allen, Killeen, Limber**) complained that our claim that Pavlovian conditioning is involved in social behavior is little more than a label. We beg to differ. The term Pavlovian carries with it a great many commitments. It implies that there is an unconditioned stimulus that activates major components of the behavior of interest. It also implies that there is at least one conditioned stimulus that becomes associated with the US. The resultant association enables the CS to activate anticipatory conditioned responses and/or adjustments to how the organism reacts to future signaled presentations of the US. The term also commits us to numerous factors that presumably govern the vigor and expression of these behavioral effects (blocking, overshadowing, latent inhibition, reminder effects, extinction, CS-US interval effects, CS and US intensity effects, etc.). Finally, the term distinguishes this type of learning from other important mechanisms of behavior change, such as habituation, sensitization, and instrumental conditioning. Indeed, were it not for the restrictive implications of the term Pavlovian conditioning, we doubt that so many commentators would have requested that we expand our schema to include instrumental and other learning mechanisms (see sect. R1.2).

We hasten to recognize, however, that in most of the areas of research that we reviewed, the full implications of a Pavlovian interpretation have not been empirically documented. As we pointed out in section 4.2.1, numerous features of Pavlovian conditioning (e.g., acquisition, extinction, discrimination learning, second-order conditioning, blocking, trace conditioning, conditioned inhibition, context conditioning, US devaluation effects, and resistance to omission training) have been demonstrated in the sexual conditioning of male quail. However, such a broad examination of Pavlovian mechanisms has not been carried out in the other areas of research we reviewed. This kind of work is needed to fully justify a Pavlovian interpretation in those other cases.

R2.3.2. Pavlovian conditioning – not just a laboratory phenomenon. It was suggested by **Hollis** that the integration of biological and learning approaches to social behavior we advocated is not likely to have much of an impact across disciplines unless examples of Pavlovian learning are demonstrated in the natural life circumstances of animals. That is, research on Pavlovian conditioning needs to move farther from the sterile controlled environment of common laboratory paradigms and closer to the uncontrolled and complex environments in which nonlaboratory animals live. We certainly agree that it is important to document the relevance of laboratory paradigms to behavior as it occurs in the wild. But, how far should research move toward naturalistic studies of learning, and what is far enough? Hollis expressed the opinion that we have not gone far enough. In contrast, **Coleman** was of the opinion that we already went too far to be able to examine Pavlovian mechanisms carefully.

Our personal view is that research should move as far as possible towards studying Pavlovian conditioning in the natural environment of animals. However, there are some conceptual limitations to a truly naturalistic study of learning mechanisms. The term "learning" or "Pavlovian conditioning" implies that specific causal factors are responsible for the behavior under scrutiny. To identifying or demonstrate the existence of those causal factors, experimental manipulations have to be carried out. Such experimental manipulations inevitably disturb or violate the natural environment of the organism, and that makes it impossible to investigate learning in a purely natural environment. Therefore, the best that can be accomplished is to study learning in "semi-natural" environments.

How close did the research we reviewed come to that goal? **Coleman** characterized all of the social situations that we described as "semi-natural," although we suspect that behavioral ecologists would consider that characterization too generous. Nevertheless, some aspects of the social situations we described make generalization to the natural environment of the animals a reasonable extrapolation.

All of the unconditioned stimuli that were involved in the experiments we described are events that are likely to occur in natural environments. Some of the studies also involved conditioned stimuli that are likely to occur in nature. For example, in the work of Dizinno et al. (1978, described in sect. 4.2.4), the conditioned stimulus was an olfactory component of the urine of female mice. In the work of Caroum and Bronson (1971, described in sect. 4.2.5), the CS was the odor of the preputial gland of male mice. In other research (e.g., Cusato & Domjan 1998; Köksal et al. 1994), the conditioned stimulus for a male quail was provided by species typical visual features of a female. Finally, a number of the examples we described involved CS-US sequences that very likely also occur in nature. This was the case, for example, for the development of olfactory vocalizations to the odor of female urine that Dizinno et al. (1978) observed after allowing male mice to copulate with a female (see sect. 4.2.4). The preference for male odor that Caroum and Bronson (1971) observed after allowing female mice to copulate with males also involved stimulus sequences that occur in nature. Numerous other clear examples of naturally occurring CS-US sequences were described in research on the conditioning of maternal behavior (sect. 4.3). Given all of these examples, we are a bit more optimistic than **Hollis** that the conditioning effects we described actually occur in the natural ecology of organisms.

R2.3.3. Requested elaborations of Pavlovian conditioning. A number of commentators would have liked to see us provide more details in our treatment of Pavlovian conditioning. **Fragaszy,** for example, suggested that we include occasion setting in our schema. **Davey & Field** requested that we spell out how learning mechanisms generate performance. **Schuster** requested that we distinguish S-S from S-R learning mechanisms in our analysis. In principle we welcome these suggestions and look forward to extensions of our schema to include these factors.

R3. Explanation of apparent shortcomings of the schema

A number of commentators discussed what they considered to be shortcomings of the schema we presented. In this last section we address the most frequently mentioned shortcomings and argue that they are not as problematic as the commentators suggested.

R3.1. Problems with specification of the conditioned response. As **Davey & Field** pointed out, how learning is manifest in the behavior of the organism is a critical issue because it is behavioral output that is selected through evolution rather than the underlying learning process. The common assumption is that Pavlovian conditioning results in the acquisition of a conditioned response (CR) to the CS. **Goodie** briefly reviewed the history of research on the nature of conditioned responses and pointed out (along with **Coleman**) that in more traditional examples of Pavlovian conditioning, the CR is always closely related to the unconditioned response or UR. In analyses of social behavior, however, the CR may not have a clear relation to the UR. In fact, as **Killeen** pointed out, a conventionally recognized anticipatory CR was not always evident in some of the examples we described. Does this present a problem for a Pavlovian analysis of social behavior? Coleman suggested that it does. We suggest that it does not.

We adopted what **Coleman** characterized as a loose specification of Pavlovian conditioning. In this specification, Pavlovian conditioning is identified solely by demonstrating that the behavior change of interest is produced by having a CS paired with a US. As Coleman noted, critical to this approach is that a comparable behavioral effect does not occur in appropriately arranged control groups. But that is the only requirement. The approach does not hinge, for example, on the conditioning procedure producing a CR that is similar to the unconditioned response.

Given this perspective, it is not problematic if the conditioning procedure produces changes in how the organism responds to the US. In fact, we would suggest that conditioned modifications of the responding to the US may be more ecologically relevant than the acquisition of a conditioned response to the CS. A conditioned response to the CS is an unproductive "false start" unless the US actually occurs. Ultimately, the ecological significance of conditioned behavior comes from responding more effectively to unconditioned stimuli. Thus, from an evolutionary perspective, much of the importance of Pavlovian conditioning may involve changes of how the organism responds to unconditioned stimuli rather than conditioned stimuli. As **Bronstein** put it, in our schema "learning is seen as functioning to fine tune unlearned, species-typical responses."

R3.2. Control of Pavlovian conditioned behavior by its consequences. Several commentators suggested that our feed-forward Pavlovian mechanisms are in fact feedback mechanisms in which future actions are controlled by the outcomes such responses had in the past (**Coleman, Gardner**). Coleman went on to characterize our view of the adaptive significance of Pavlovian CRs as being in the tradition of law of effect accounts of Pavlovian conditioning. We do not consider this to be a correct interpretation because it ignores major differences in the time scale of law of effect mechanisms as compared with the cost/benefit calculations in our schema. As **Cardinal et al.** pointed out, "one can effectively consider behavioral/psychological process as extended in time, at multiple time scales." However, we admit that the target article was not as clear on this point as it might have been.

According to the law of effect account of Pavlovian conditioning, conditioned responding develops in a Pavlovian procedure because the CR changes the US to make it more desirable or reinforcing. This reinforcing consequence of the CR is presumed to occur soon (if not immediately) after the CR. As **Coleman** pointed out, such law of effect accounts of Pavlovian conditioning have not held up under experimental scrutiny. We are well aware of that literature and have contributed to it (Crawford & Domjan 1993). However, we do not accept Coleman's conclusion that evidence from empirical tests of the law of effect account of Pavlovian conditioning refutes our schema.

Our treatment of the consequences of Pavlovian conditioning differ from the law of effect account in three important ways. First, the consequence whose benefit is assessed in our schema is not a change in the unconditioned stimulus. Rather, we are concerned primarily with changes in how the organism responds to the US. We are concerned with changes in behavior, not change in a stimulus. Second, the consequence that is important in our schema is not something that makes the US more desirable or reinforcing in the instrumental sense. Rather, it is something that makes responses to the US more adaptive. The benefit of Pavlovian conditioning that we are dealing with is its contribution to reproductive fitness. Costs and benefits are calculated in relation to reproductive fitness, not instrumental reinforcer efficacy (see also sect. R2.1). Finally, the assessment of the cost/benefit ratio occurs over a much longer time scale than the time scale for the delivery of a reinforcer following an instrumental response in the law of effect. Assessments of reproductive fitness cannot occur over the range of seconds or minutes required for the operation of the law of effect. This difference in time scales is critical.

R3.3. Maladaptive learned behavior. A number of commentators (**Cardinal et al., Davey & Field, Gardner,** and **Timberlake et al.**) questioned our claim that Pavlovian conditioning results in adaptive behavioral outcomes by citing examples of apparent maladaptive behavior produced by learning procedures. Two types of evidence were cited. One involved the work of Breland and Breland (1961) who reported on their efforts to condition a variety of unusual instrumental responses in chickens, raccoons, pigs, and other animals for entertaining displays. To be entertaining, the behavioral tasks chosen had to be unusual for the species involved (chickens "playing" baseball, pigs putting coins in a piggy bank, etc.). The second line of evidence commonly cited was Jenkins's "long-box" experiment (see Hearst & Jenkins 1974) in which a small key light that served as a CS for pigeons was placed about 90 cm away from the location of the food hopper. Pairings of the keylight with food resulted in the pigeons approaching and pecking the key light rather than going to the food hopper to eat. Because of the long distance between the CS and the food hopper, the pigeons often missed getting to the food before the end of the trial.

We do not find such examples of maladaptive behavior problematic for our claim that Pavlovian feed-forward mechanisms contribute to reproductive fitness. Any behavioral tendency that evolved in a particular set of circumstances or ecological niche can appear to be maladaptive if the organism is tested in a sufficiently different or evolutionarily foreign environment. As **Rowland** put it, "Pavlovian conditioning, like any trait, learned or otherwise, will not be adaptive in all contexts; it is often seen to misfire, especially when tested in the laboratory or under other unnatural conditions in which it did not evolve." The stimulus arrangements and response requirements used by Breland and Breland (1961) were rather unusual for the species they tested. The same can be said of the Jenkins "long-box" experiment. We are not aware of any circumstances in the natural history of pigeons where a signal for food might be located nearly a meter away from the food source. The examples of maladaptive behavior cited by the commentators say more about the maladaptive nature of the procedures used in those experiments than the maladaptive nature of Pavlovian conditioned behavior.

R3.4. Characterizing dynamic social interactions. A number of commentators complained that the system we proposed failed to capture the dynamic nature of social interactions. **Krebs,** for example, noted that a more comprehensive conceptual framework was needed to fully account for the interactive nature of social behavior and that our system fell short of representing "the ways in which each party influences the behavior of the other" during social exchanges. **Limber** suggested that we limited our application of feed-forward control to "simple, nondynamic cases" of social behavior.

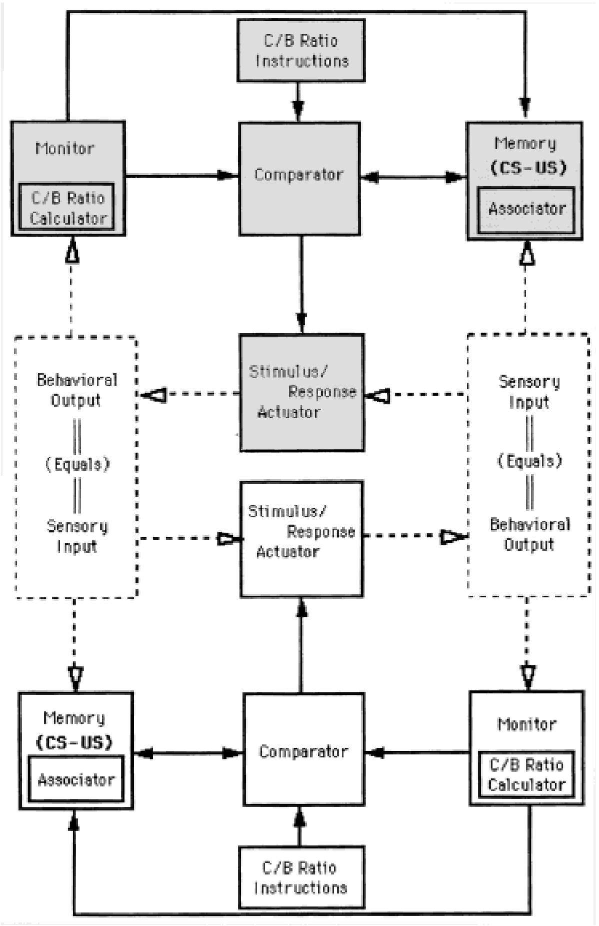

Figure R1. A schematic diagram that illustrates the dynamic nature of social interactions. As in the target article figures, each square represents a separate system component; now, open and shaded boxes are used to represent systems involving different social partners. Individual components and their functional connections are as in the previous figures. Boxes with dotted lines represent information shared by both systems (sensory input and behavioral output). The conditioned and unconditioned response output of one system functions as the conditioned and unconditioned stimulus input of another system consisting of a mirror set of components. In this way, the original schema can be extended to include two or more participants engaged in social exchange.

As **Krebs** and **Schuster** noted, our schema was designed to account for the social responses of only one participant at a time. We focused on the individual in a social context for the sake of simplicity and because evolutionary selection operates at the level of the individual. Any schema designed to account for behavior in an evolutionary context, whether that behavior be social or non-social, must ultimately be stated in terms of individual organismic variables.

Although we focused on one individual at a time, our schema was deliberately set up so that either participant in a social exchange could be the focus of the analysis. Because of that, our approach can be readily extended by applying the schema to two (or more) interacting parties at the same time. The interactive nature of social exchanges would emerge from such simultaneous application of the schema to both participants.

In a dynamic social interaction, the responses of one individual become part of the stimulus complex that motivates the behavior of the other participant. In a nursing interaction, for example, the suckling responses of the infant provide the sensory stimulation that activates the milk let-down response of the mother. That maternal response in turn provides the stimulation that maintains further suckling by the infant. Our schema can be extended to include both participants in a social exchange by considering the conditioned and unconditioned response output of one system as the conditioned and unconditioned stimulus *input* of a separate system consisting of a mirror set of components. How this interaction unfolds is depicted in Figure R1.

As in Figures 1–3 of the target article, each square in Figure R1 represents a separate system component, only now we use open and shaded boxes to depict separate systems for each social partner. The components of each individual system and how they are functionally connected remains unaltered from our original diagrams. Boxes with dotted lines represent information that is shared by both systems, and open arrows indicate the projections of this shared information. During initial social encounters, each partner responds to the other with relatively innate forms of social behavior. One system's behavioral output in the form of unconditioned responses serves as unconditioned stimuli or sensory input for the other system. With repeated interactions between the individuals, each can use specific aspects of the other's social responses as conditioned stimuli to help predict how the impending social interaction will unfold. In this way, the shared relationship between the two social partners becomes both unique and dynamic. Thus, the basic components of our original system design can be adapted to account for what **Siviy** characterized as rapidly and constantly shifting roles between social partners during complex social interactions.

R3.5. Possible unique forms of learning in social situations. Concern was expressed **Schuster** that "it is by no means clear whether the "laws of learning" that govern individual action can be assumed to apply when individuals act in concert." We acknowledge that some unique forms of learning may be discovered in social situations that were not recognized in studies of individual organisms. However, we do not believe that such an undemonstrated possibility should squelch efforts to exploit the considerable body of available evidence on Pavlovian conditioning. It is more prudent to base future research on a firm empirical foundation than it is to assume that previously established principles of Pavlovian conditioning will not hold up when the paradigm is extended to social situations. The rule of parsimony also supports proceeding from the assumption that previously established principles will continue to operate in new situations.

R3.6. Living organisms do not rely on ideal set-points. We share **Timberlake et al.**'s assertion that, "regulation by a simple set point is probably rare in biological phenomena," and that the regulation of behavior is "best viewed as resulting from a competitive balance between multiple regulated behaviors." The concept of multiple regulation was also suggested by **Gardner** in his discussion of "fuzzy systems" as an alternative to set-points and/or optimality in the control of system functioning. However, both Gardner and Timberlake et al. appeared to have overlooked the fact that the schema we proposed regulates its output *without* simple set-point comparison. We admit that the design of our system borrows much from vintage control systems theory (Dworkin 1993; McFarland 1971). However, we departed from these traditional conceptions in a number of important ways, especially with respect to set-points and comparison with an optimal set point.

In traditional nonliving control systems, the comparator receives information about the system's current output from the monitor and then compares this output value to an ideal set-point value located in the instructions component. Adjustments in the system's performance are then undertaken to reduce any discrepancies between the actual and ideal system output. Our schema differs from such a homeostatic system in several major respects. First, the monitor component in our schema tracks not just the system's behavioral output, but also the costs and benefits associated with this behavioral output (see Figs. 1–3). Second, unlike the moment-by-moment assessment of system performance characteristic of the comparator component in classic nonliving control systems, the comparison process in our schema occurs over a much longer time scale since it involves assessment of the organism's overall reproductive fitness (see sects. 3.4.1 and R2.1). Third, the instructional code in our system (the C/B Ratio Instructions) does not contain a preset ideal value or desired set point, just as there is no ideal value or set point for evolution. System operations change through evolution to achieve greater reproductive fitness, but there is no "optimal" level of reproductive fitness. The operation of the system we proposed will change to reduce the cost/benefit ratio associated with responding to an unconditioned stimulus, but we do not assume the existence of an "optimal" cost/benefit ratio that is defended as a homeostatic level.

R3.7. The special case of social play. Our suggestion that Pavlovian processes are involved in social play attracted the attention of several commentators. **Bekoff & Allen,** for example, noted that the highly stereotyped nature of play signals suggests that play signals do not acquire their properties through associative processes. The implication is that play behavior is largely unconditioned species typical behavior. However, that is not problematic for our schema. As **Bronstein** commented (see also sect. R3.1), our approach emphasizes how learning serves to modify unlearned species typical behavior patterns and does not require the learning of new responses. Bekoff & Allen admitted that learning may play "some role in fine-tuning the use of signals as play experience is gained." We consider that type of "fine-tuning" to be very important.

Bekoff & Allen questioned our characterization of the unconditioned stimulus for social play. We admit that we were too simplistic when we said that the presence of a social play partner serves as the US. We should have been more clear to point out that it is only under conditions conductive to play behavior that the social partner serves as an effective US.

Our suggestion that individuals may acquire preferred play partners through associative processes was dismissed by **Bekoff & Allen** as a "simple homily." But that ignores the critical issue of how play partner preferences develop. Calling something a "simple homily" does not inform us about its underlying mechanisms. Our suggestions were focused on what those underlying mechanisms might be, and as we pointed out in section R2.3.1, the claim of Pavlovian learning is not vacuous.

Bekoff & Allen also commented that the most fruitful approach to play research is based on concepts that attribute animals with a considerable degree of cognitive prowess. We suggest, in the spirit of **Snowdon**'s commentary advocating a "bottom-up approach," that simpler explanations for complex behaviors should be considered before animals are characterized as having such cognitive abilities as self awareness and intentionality. In particular, it is ironic to see strong appeals to intentionality in the explanation of animal play behavior when intentionality and volition are being seriously questioned as significant contributors to the control of human behavior (Bargh & Chartrand 1999; Wegner & Wheatley 1999).

Siviy described play as a form of "meta-communication" and suggested that the dynamic nature of play indicates that there is more than just learning involved. It was never our intent to imply that Pavlovian conditioning can completely explain social play (or any other social behavior). Our goal was to propose a schema that would lead to the consideration of learning processes in play behavior. The usefulness of such a schema is evident in descriptions of Siviy's own experiments. In these experiments, cues associated with the opportunity to engage in play behavior produced anticipatory increases in activity and caused rats to emit ultrasound vocalizations in anticipation of (and throughout) play episodes. These findings are in accord with a behavior systems approach to learning and are also illustrative of how feed-forward mechanisms can be involved in play behavior. Future experiments should focus on how the efficiency of play interactions between partners is improved by the availability of cues previously associated with play bouts.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively

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