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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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13 Cognition and Emotion in Concert in Human and Nonhuman Animals

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A major question in our research program is how in human and nonhuman animals the balance between positive (“reward”) and negative experiences (“punishment,” “stress”) affects the efficiency of long-term behavior—defined as choosing strategies with the most profitable cost–benefit outcomes—in a “complex” (multiple-choice) environment. The balance between positive and negative experiences results from the continuous integration of such experiences. At least in humans it has been shown that failure of such an integration leads to inefficient long-term behavior in a complex (social) environment (Damasio 1996). In order to address this question, we place experiences in a neurobehavioral model, show how they can be made accessible for experimentation—especially in nonhuman animals—and briefly discuss a method for studying long-term behavioral efficiency.

Motivational Systems and Neurobiology

Emotion and Cognition

The relationships between internal physiological changes on the one hand and behavioral changes on the other in relation to the availability of different commodities in living organisms are described as motivational systems. Commodities are items in the environment that are potentially important to the animal’s fitness. Motivational states such as hunger, thirst, and libido arise because of a difference between actual and reference values in an animal’s physiological systems, and subsequent behavior—appetitive and consummatory (Craig 1918)—is directed at eliminating this difference.

As reviewed elsewhere, two features of commodities are relevant for an animal’s behavior (Spruijt et al. 2001): knowledge of when and where a commodity is available (cognition) and assessment of the incentive or rewarding value

of a commodity before and after consumption (emotion).

The “when” component of cognition deals with an animal’s capacity to associate stimuli with the arrival of commodities. These mechanisms have been studied in Pavlovian conditioning experiments. The cognitive load increases as the interval between the offset of the cue (conditioned stimulus, CS) and the onset of the arrival of the commodity (unconditioned stimulus, US) increases from zero (delay conditioning) to several seconds or minutes (trace conditioning; Lieberman 2000; Clark and Squire 1998; Wallenstein et al. 1998). The trace-conditioning paradigm measures what others have referred to as beliefs in the context of intentional action or goal-directed behavior (Heyes and Dickinson 1990). The “where” component of cognition deals with an animal’s capacity to assess the stimuli that indicate where commodities may be found. These mechanisms have been studied in a number of spatial tasks such as the Olton radial maze and the Morris water maze (Kalat 1998). The cognitive load increases as the stimuli that indicate the commodity’s position are progressively less directly “attached” to the commodity itself [the shift from proximal (direct) to distal (configurations of) stimuli (Wallenstein et al. 1998)]. Behavior based on these configurations of stimuli may be conceived of as belief-based behavior, as mentioned earlier.

Incentive value is dependent on an animal’s current internal state (the more the animal has been deprived of the commodity, the higher the commodity’s incentive value), prior experience with the commodity, and its general properties (for food as a commodity, see Grill and Berridge 1985). Thus incentive value may differ among different commodities and over time for the same commodity.

Berridge and colleagues (Berridge 1996; Berridge and Robinson 1998) have convincingly

argued that the system mediating incentive value has two different components with separable functions: the affective component (“liking”) and the appetitive component or the disposition to consume the commodity (“wanting”). Both “liking” and “wanting” are theoretical constructs referring to different internal (neuronal or psychological) evaluation processes in the valuation of and behavior toward commodities. “Liking” refers to the immediate appraisal of commodities as pleasurable or not pleasurable (after consumption); “wanting” refers to the disposition to act upon this appraisal on future or new occasions, or in other words, on the activated representation of “the liked” (prior to consumption; see also Spruijt et al. 2001). “Liking” and “wanting” are conceptually similar to what has been described elsewhere as “emotion” and “desire” in the context of intentional action or goal-directed behavior (Heyes and Dickinson 1990; cf. van den Bos 2000).

We (Spruijt et al. 2001) have suggested elsewhere that the role of the system mediating the incentive value may lie in guiding the organism in “doing the best thing,” which is captured in Cabanac’s maxim: pleasant is useful (Cabanac 1971). In other words, what is good for the individual’s fitness in the long run (functional level of analysis of behavior) is directed by an immediate sense of “good” or “bad” (causal level of analysis of behavior). We (Spruijt et al. 2001) have argued that different motivational systems share this reward-mediating system so that conflicts between motivational systems can be settled by using a common currency.

For instance, when selecting whether to eat or to drink, levels of physiological factors representing the metabolic state cannot be directly compared with levels of physiological factors representing the state of bodily fluids. However, if both systems also measure the degree of pleasure they provide, a comparison based on a common currency may be carried out by a structure that is connected to both motivational systems.

We propose that to make this comparison (in fact a comparison of apples and oranges), it is sufficient to compare the degree to which the difference between an actual and a reference value can be reduced, irrespective of the nature of the difference, by a commodity with a specific incentive value. The common currency could be the physiological representation of the reduction, for each motivational system, of the difference between actual and reference values. The system that produces the largest reduction (i.e., the highest concentration of a physiological measure) related to the reward will allow control over behavior to be initiated [this concept is captured in Cabanac’s maxim: pleasure is the common currency (Cabanac 1992)]. Thus each motivational system has specific physiological consequences for initiating and terminating activities aimed at a specific goal. Apart from those specific consequences, there are also common consequences that allow a comparison between motivational systems. This comparison can only be made when the level that deals with common consequences has a supervisory position in the hierarchical organization of various motivational systems.

Neurobiology

This hierarchical organization of motivational systems has its counterpart in the organization of the central nervous system. The central nervous system may be conceptualized as a hierarchically organized series of negative feedback loops in which stimuli are processed at different levels and in which each level adds its specific component or programming rule to behavior (see Cools 1985; van den Bos 1997; Powers 1973).

At the lowest levels, the processing of stimuli is more directly related to the physical aspects of the stimuli. The processing is rapid, so that immediate responses are elicited, whereas at increasingly higher levels the processing becomes progressively less directly related to the physical

aspects of the stimuli (i.e., more abstract) and less rapid, so that more delayed responses are elicited and facilitated. In other words, the higher levels deal with more general aspects of the programming of behavior whereas the lower levels deal with more concrete aspects. Each level in the hierarchy controls its own aspect in the programming of behavior (Powers 1973).

Motivational systems show such a hierarchical neuronal organization. At lower levels in the central nervous system, specific motor patterns directed at consuming a commodity are regulated, whereas at higher levels, more general aspects of obtaining a commodity and assessing its value are regulated. [See e.g., Grill and Berridge (1985) and the next section for food items; see Spruijt et al. (2001) for a general discussion.] As discussed by Berridge and colleagues, “liking” is mediated by the opioid endorphin (forebrain) system, whereas “wanting” is mediated by the dopamine (forebrain) system (Berridge and Robinson 1998). These systems interact in (inter alia) the ventral tegmental area (VTA). The VTA contains the dopaminergic projections to the ventral striatum, prefrontal cortex, and amygdala, which are activated by the endorphin system (see Spruijt et al. 2001 for a review). This leads to the prediction that “liking” affects “wanting” and not the other way round. The belief cognitive component is at least dependent on the hippocampus for its expression (Clark and Squire 1998; Wallenstein et al. 1998). The hippocampus is an integrating high-level center in the central nervous system (see Spruijt et al. 2001 for a review).

Measuring Emotion, Cognition, and Their Relationship

In order to study the relationship between “liking,” “wanting,” and “beliefs,” independent measures are needed that can be (cor)related at the level of individuals.

Measuring “Liking”

Although the following method concentrates on “liking” in the context of food items, it may be applied to other commodities as well. In the context of food items, “liking” is conceived of as perceived palatability (Berridge and Robinson 1998). Palatability is not a measure of taste quality or intensity, but is a complex central evaluation (Grill and Berridge 1985). In humans, changes in palatability are often measured through verbal reports and are scored on a one-dimensional scale ranging from pleasant to unpleasant (Cabanac 1971), whereas in animals such changes are measured by changes in species-specific behavioral patterns in response to food, so-called “taste reactivity patterns” (TRPs; for a review see Berridge 2000). In general, two kinds of TRPs can be distinguished: ingestive or hedonic patterns and aversive patterns. They have been described in many species, including rats (*Rattus norvegicus*) and various primate species and humans (Berridge 1996, 2000; Grill and Berridge 1985). We have recently described TRPs in domestic cats (*Felis silvestris catus*; van den Bos et al. 2000).

These hedonic and aversive TRPs occur in relation to two different classes of food stimuli or solutions, sweet (glucose being the prime example) and bitter (quinine being the prime example), respectively. They are present early during ontogeny (see Berridge 2000; Grill and Norgren 1978; Grill and Berridge 1985) and do not appear to require structures above the midbrain for their expression (see Grill and Norgren 1978). As such, they appear to represent an immediate and unconditional response to a stimulus (level 0 as defined by Grill and Berridge 1985). Given the appearance of these TRPs as described in different papers (in cats, lip licking as a hedonic pattern; in rats, head shaking as an aversive pattern), it may be argued that they are the product of natural selection operating over many gen-

erations either to facilitate the ingestion of food items with a high nutritional value as much as possible or to remove food items with a potentially high mortality risk from the oral cavity or area as much as possible.

The fact that the balance between hedonic and aversive TRPs in response to stimuli may be changed according to the internal state of the organism or previous experiences (for reviews see Berridge 1996, 2000; Berridge and Robinson 1998; Grill and Berridge 1985) shows that these behavioral patterns are also under the control of higher levels in the central nervous system and that these stimuli are also processed at higher levels (levels 1, 2, and 3 according to Grill and Berridge 1985). As such, “palatability” is hierarchically organized.

It is likely that the internal processing at progressively higher levels becomes more unitary, so that at the highest level only a single continuum exists (liking: pleasant-unpleasant) on which the organism will base its behavior (or which feeds into the next system, such as the system dealing with “wanting”), while the direct food-related response at the lowest levels is expressed along two different dimensions. In humans this single continuum is what is experienced and verbally or otherwise reported.

The question now is whether it is possible to take these two different low-level dimensions and integrate them into one high-level dimension. We have reduced these two behavioral dimensions to one hypothetical internal (psychological) dimension by subtracting the sum of the mean durations of the aversive patterns from the sum of the mean durations of the hedonic patterns and labeled this the composite palatability score (CPS; Meijer et al. submitted). We have subsequently explored the use of the CPS in order to measure “liking” in cats. Our results thus far show that the CPS is potentially a valid measure to assess “liking” based on these TRPs.

This procedure leads to the following prediction: There may be individuals in which the im-

mediate responses to food items as reflected by hedonic and aversive TRPs are present (they are directed at ingesting or removing as much of the food as possible) but “liking” as measured by CPS (the internal evaluation of the food’s incentive value as reflected by the strength of the hedonic and aversive TRPs) is not; and there may be individuals in which both exist. This refers to the ontogeny of these levels in individuals of the same species or to the phylogeny of these levels between individuals of different species. What is needed therefore is to show that “liking” has consequences for future behavior, and that these consequences may be manipulated independently of the immediate occurrence of the TRPs themselves. As argued earlier, “liking” affects “wanting.” By delineating an independent measure for “wanting” and by showing that “liking” (CPS) directly affects “wanting” (measured in whichever way), one step is taken to show ontogenetic and/or phylogenetic processes.

Measuring “Wanting”

If “wanting” reflects the activation of the “liked,” then it follows that the more a commodity is liked, the more an individual is willing to work for that commodity, or the more the animal will look forward to the commodity’s arrival when it is reliably announced. The former may be measured by operant conditioning using a progressive ratio paradigm, the latter by Pavlovian conditioning, testing during the extinction phase or by using an interval between conditioned and unconditioned stimulus (Spruijt et al. 2001). Combinations of these exist as well (see Wyvell and Berridge 2000). Up to now we have employed mainly the Pavlovian conditioning procedure, although we will apply all three methods in the near future.

In our Pavlovian paradigm, a conditioned stimulus is paired with a commodity (unconditioned stimulus) in which the interval between

the CS and US is gradually increased from zero to even 20 minutes in rats, cats, and minks (van den Berg et al. 1999; van den Bos et al., in preparation; von Frijtag et al. 2000; Spruijt et al. 2001). A relatively long interval between CS and US has been used to allow the extensive occurrence of anticipatory behavior. The hypothesis is that the anticipatory behavior seen with different kinds of reward (food, receptive female) has general characteristics in common. We have observed an increase in the number of behavioral transitions (hyperactivity) in the CS-US interval in rats in experiments involving these different rewards (Spruijt et al. 2001). It seems that the major characteristic of this commodity-aspecific anticipatory behavior is the increased frequency of exploratory behavioral patterns, as if short abrupt fragments of these behavioral elements are displayed.

Anticipation is not expressed in the same way in different species under similar conditions because we have recently observed that in cats anticipation is not expressed as an increase in activity in a Pavlovian conditioning procedure, but rather as a decrease using the same paradigm as in rats (van den Bos et al., in preparation; cf. Timberlake and Silva 1995).

“Liking” and “Wanting”

Up to now we have only fully combined these approaches in a Pavlovian paradigm using domestic cats, measuring “liking” by the occurrence of TRPs and “wanting” by the number of behavioral transitions. The data thus far suggest that, as predicted, the more an item is “liked” as measured by the CPS, the more it is “wanted” as measured by the number of behavioral transitions. Owing to the more complex analysis of “food liking” in rats (see Berridge 1996, 2000) we have not managed to fully combine these approaches in rats. However, it was shown recently in rats that, as we predicted, pharmacologically enhancing “wanting” did not increase

“liking” (Wyvell and Berridge 2000). Furthermore, Dickinson and colleagues have shown that rats change their “wanting and belief behavior” (measured by pressing levers in an operant task) according to changes in “liking” (the incentive value of food items) in setups that indicate that they behave by combining these different mental representations (see van den Bos 1997 for a review).

Now the question arises of how we can show that this system affects long-term efficiency in behavior. To show how this might be approached, in the next two sections we discuss an experimental method to change the system’s sensitivity (the consequence of social stress in adult rats) and an experimental setup to show how multiple choices may be measured and manipulated (a closed-economy system).

Changing the Sensitivity of the Incentive Value System by Social Stress

In a recent series of experiments we submitted rats (*Rattus norvegicus*) to a social stress paradigm (von Frijtag et al. 2000). Using the Pavlovian conditioning paradigm, it turned out that stressed rats, in contrast to control rats, did not show hyperactive behavior in the interval between the CS and US (5 percent glucose solution; “wanting”), whereas their consumption of the glucose solution (“liking”) appeared normal. Accordingly, it would appear that the rats are able to assess the immediate value of glucose—although it should be mentioned that we did not measure TRPs in this study and intake is not a reliable indicator of “liking” (Berridge 1996)—but they are not able to integrate its incentive value in their future behavior because they are not able to recall its value prior to presentation. The effect of stress on anticipatory behavior could be reversed by long-term treatment with the antidepressant drug imipramine (von Frijtag et al., submitted).

Given these results, it is now possible to study these rats in more detail in different kinds of environments that put different loads on their ability to assess the costs and benefits of different strategies. It may be predicted that the more complex the environment is in terms of the number of different choices an animal has to make, the more an animal will fail to behave efficiently. Such a test is described in the next section.

Multiple-Choice Environment: A Closed-Economy System

One approach to measuring long-term behavioral efficiency and the role of cognition and emotion in it in different species is the closed-economy approach that Mason and colleagues (Cooper and Mason 2000; Mason et al. 2001) have used for their studies in mink (*Mustela vison*). In this setup, the animals live for long periods of time in an environment in which they can visit several compartments containing various commodities. Costs can be imposed upon the entrance to these compartments by, for example, attaching weights to entrance doors, and benefits can be increased or decreased by changing the commodity's value. In general, animals will prioritize activities according to the cost–benefit ratios they attach to different commodities (Mason et al. 2001). Thus this system allows the assessment of various features of their behavior toward commodities; for example, whether they differentially appreciate the consumption of commodities (“liking”; cf. method above), whether they look forward to consuming commodities or are willing to work for commodities (“wanting”), and whether they are able to learn the location of and the relationship between cues and the arrival of commodities (cognition). It may be expected that when the “incentive value system” is not functioning properly (e.g., owing to chronic stress), is not yet developed (ontogeny), or is not present (phylogeny), the affected animals will show different priorities in their

behavior than animals in which this system is present and functioning optimally.

Conclusion

Human and nonhuman animals behave efficiently in changing environments. This efficiency of behavior requires that (1) they have knowledge of spatial and temporal relationships in their environment (cognition); (2) they are able to measure and predict the success of the outcome of their actions (emotion); and (3) emotion and cognition are tightly connected. The approach presented here allows us to carefully delineate the system mediating the incentive value in different species and thereby understand its role in long-term efficient behavior. The integration of methods and concepts from neuroscience, psychology, and ethology has led to a fuller understanding of the relationship between an animal and its environment.

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