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Research Report

Dopaminergic and non-dopaminergic value systems in conditioning and outcome-specific revaluation

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ABSTRACT

Animals are motivated to choose environmental options that can best satisfy current needs. To explain such choices, this paper introduces the MOTIVATOR (**M**atching **O**bjects **T**o **I**nternal **VA**lues **T**riggers **O**ption **R**evaluations) neural model. MOTIVATOR describes cognitive–emotional interactions between higher-order sensory cortices and an evaluative neuraxis composed of the hypothalamus, amygdala, and orbitofrontal cortex. Given a conditioned stimulus (CS), the model amygdala and lateral hypothalamus interact to calculate the expected current value of the subjective outcome that the CS predicts, constrained by the current state of deprivation or satiation. The amygdala relays the expected value information to orbitofrontal cells that receive inputs from anterior inferotemporal cells, and medial orbitofrontal cells that receive inputs from rhinal cortex. The activations of these orbitofrontal cells code the subjective values of objects. These values guide behavioral choices. The model basal ganglia detect errors in CS-specific predictions of the value and timing of rewards. Excitatory inputs from the pedunculopontine nucleus interact with timed inhibitory inputs from model striosomes in the ventral striatum to regulate dopamine burst and dip responses from cells in the substantia nigra pars compacta and ventral tegmental area. Learning in cortical and striatal regions is strongly modulated by dopamine. The model is used to address tasks that examine food-specific satiety, Pavlovian conditioning, reinforcer devaluation, and simultaneous visual discrimination. Model simulations successfully reproduce discharge dynamics of known cell types, including signals that predict saccadic reaction times and CS-dependent changes in systolic blood pressure.

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Abbreviations: AMYG, Amygdala; BG, Basal ganglia; BP, Systolic blood pressure; CS, Conditioned stimulus; DA, Dopamine; FEF, Frontal eye fields; FSS, Food-specific satiety; GUS, Gustatory inputs; ITA, Anterior inferotemporal cortex; LDT, Laterodorsal tegmental nuclei; LH, Lateral hypothalamus; LH_gus, Gustatory-receptive lateral hypothalamic cells; LH_in, Drive input receptive lateral hypothalamic cells; LH_out, Lateral hypothalamic output cells; LTM, Long term memory; MORB, Medial orbitofrontal cortex; MTM, Medium term memory; ORB, Orbitofrontal cortex; PIT, Posterior inferotemporal cortex; PPTN, Pedunculopontine nucleus; RHIN, Rhinal cortex; RT, Reaction time; SD, Striosomal delay cells in the ventral striatum; SNc, Substantia nigra pars compacta; STM, Short term memory; SVD, Simultaneous visual discrimination; TD, Temporal difference; US, Unconditioned stimulus; VIS, Visual inputs; VP, Ventral pallidum; VS, Ventral striatum; VTA, Ventral tegmental area

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1. Introduction

Animal behavior is fundamentally opportunistic. Animals choose actions whose consummatory responses serve their basic biological needs, such as avoidance of damage, regulation of body temperature, and replenishment of energy stores. Many of these needs vary over life cycles, seasons, and days, as do the environmental opportunities for making appropriate consummatory responses. Choosing options that can best satisfy currently pressing needs often requires temporarily ignoring options that, under different subjective conditions, would be evaluated as highly attractive. This may require temporarily ignoring some current needs that would be strong enough to dominate behavioral choices if the animal were relocated to an environment that supported consummatory responses matched to those needs.

What brain processes allow an animal to use cues to quickly assess the options in its environment and estimate their values relative to the animal's current needs? How are strong needs ignored when the environment affords no opportunity for their satisfaction? How are normally attractive and highly available options ignored for a time after the needs that they consummate have been satisfied? To address such questions, a neural model is proposed and simulated to explain laboratory phenomena such as: the conditioning of cues that predict specific outcomes in a task setting, the automatic revaluation of conditioned stimuli (conditioned reinforcers) following food-specific satiety, and motivational and emotive influences on decision processes, reaction time, response vigor, and blood pressure. The phenomenon of automatic revaluation has only recently been thoroughly investigated and requires additional explanation (Dickinson and Balleine, 2001; Corbit and Balleine, 2005). Revaluation refers to the observation that motivational shifts can alter the vigor of conditioned responses.

Outcome-specific revaluation occurs when shifts in motivation alter conditioned responding in a manner that respects the different reward associations of these responses and how this motivational shift differentially impacts the consumption value of these outcomes (Corbit and Balleine, 2005). Normally, changes in conditioned responding follow the law of effect, and the value of a CS only reflects the experienced value of its associated food reward. However, for first-order and second-order conditioned stimuli, revaluation automatically occurs in an outcome-specific fashion (Corbit and Balleine, 2003, 2005; Hall 2001). The effect is automatic in that changes in the value of rewards impact the vigor of conditioned responding without new CS–US pairings. In contrast, motivational shifts alter the vigor of higher-order conditioned responses in an outcome-specific fashion only after additional training trials have taken place during which the reward is experienced in the new motivational state (Balleine et al., 1995).

Key aspects of these phenomena are explained within a neural circuit that integrates homeostatic, hedonic and emotional information to calculate the current value of conditioned and unconditioned cues. The model serves to detail, contrast, and elaborate the roles of dopaminergic and non-dopaminergic value systems and mechanisms that are engaged by most evaluative tasks, including Pavlovian and operant conditioning (Berridge, 2001; Berridge and Robinson, 1998). These results were reported in preliminary form in Dranias et al. (2006, 2007a, 2007b).

The MOTIVATOR (**M**atching **O**bjects **T**o **I**nternal **VA**lues **T**riggers **O**ption **R**evaluations) model focuses on cognitive–emotional processing wherein sensory and cognitive neocortex interacts with an evaluative neuraxis composed of the hypothalamus, amygdala, orbitofrontal cortex, and basal ganglia. An overview of the model, which has been specified as a real-time dynamical system and simulated in Matlab, is shown in Fig. 1. This model unifies and further develops the Cognitive–Emotional–Motor, or CogEM, model of cognitive-emotional learning and performance (Grossberg, 1971, 1972a, 1972b, 1975, 1984; 2000a, 2000b; Grossberg and Gutowski, 1987; Grossberg and Levine, 1987; Grossberg et al. 1987; Grossberg and Merrill, 1992; Grossberg and Schmajuk, 1987) and the TELOS model of how an animal learns to balance reactive vs. planned behaviors through learning based on reward expectation and its disconfirmation (Brown et al., 1999, 2004). The CogEM model focused on how affective brain regions, such as the lateral hypothalamus and amygdala, interact with sensory and cognitive areas, such as inferotemporal cortex and orbitofrontal cortex. The TELOS model focused on how the basal ganglia regulate attention and reinforcement-based learning in thalamocortical systems. The current model proposes how both amygdala and basal ganglia processes interact to control reward-based processes.

In the MOTIVATOR model, visual inputs activate view-invariant representations of visual objects in the anterior inferotemporal cortex (ITA). Gustatory cortex relays the taste properties salty, sweet, umami, and fatty to rhinal cortex (RHIN) and to gustatory-responsive lateral hypothalamic cells (LH_gus). RHIN cells also receive ITA inputs, and can thereby code gustatory-visual properties of food rewards. Endogenous drive and arousal inputs project to lateral hypothalamic input cells (LH_in). LH_in cells represent the homeostatic state of the animal by reporting fat, salt, amino acid, and sugar levels. LH_gus cells correlate gustatory tastes with corresponding homeostatic features and excite lateral hypothalamic output cells (LH_out), which project to amygdala (AMYG) cells that categorize LH_out states. The LH-AMYG network computes the net subjective outcome associated with a consummatory act. It thereby defines a neural representation of US (unconditioned stimulus) reward value. Because the AMYG also receives conditionable CS-activated signals from ITA and RHIN, it can mediate CS–US learning. Given a CS, the AMYG and LH interact to calculate the expected current value of the subjective outcome that the CS predicts, given the current state of deprivation or satiation for that outcome. The AMYG relays the expected value information to ITA-recipient orbitofrontal (ORB) and RHIN-recipient medial orbitofrontal (MORB) cells, whose activations code the relative subjective values of objects. These values guide behavioral choices.

The model basal ganglia (BG) detect errors in CS-specific predictions of the value and timing of rewards. Striosomes (SD) of the ventral striatum (VS) prevent predicted rewards from generating SNc/VTA responses by inhibiting dopamine cells in the SNc/VTA with adaptively timed signals (Fig. 1). Inputs from the LH_gus and the ventral striatum (VS) excite the pedunculopontine nucleus (PPTN/LDT) whenever a