COGNITIVE DECISION PROCESSES AND FUNCTIONAL CHARACTERISTICS OF THE BASAL GANGLIA REWARD SYSTEM

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1. INTRODUCTION

Cognitive behavior of individuals is generally described in terms of reactions to rewards or to predictions concerning future rewards. Physiological systems that are involved in reward mechanism might thus be correlated with various cognitive effects. Such basal ganglia systems include the midbrain dopaminergic system (Schultz 1998), and the striatal tonically active neurons - TANs (Aosaki et al. 1995, Raz et al. 1996). In this chapter we propose that both midbrain dopaminergic and striatal cholinergic interneurons (TANs) continuously emit a complex tri-phasic neural message (neural signature of reward) which is modulated by the fitness of the environment to the animal predictions.

A major field of cognitive psychology research is Decision Theory, which describes decision processes and anomalies. A key finding in Decision Theory (Kahneman and Tversky, 1979) is that the behavior of an individual is shifting from risk-aversion (when possible gains are predicted) to risk seeking (when possible losses are predicted). The second section of the current chapter presents an analysis of this effect from the basal ganglia point of view, and offers insights for the origin of the behavioral asymmetry.

It was found (e.g., Schultz, 1998), that dopamine neurons tend not to respond to stimuli which predict future aversive rewards. The third section of this chapter proposes an evolutionary explanation to the asymmetrical nature of the basal ganglia reward system. We propose that responses to aversive stimuli are not handled by the basal ganglia system, since this system is devoted for the more complex control of sequential behavior. Other more primitive systems, based on pattern detection algorithms, are called into action following aversive stimuli.

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2. DECISION THEORY AND PHYSIOLOGICAL REWARD SYSTEMS

2.1 Review of Major Cognitive Psychology Findings

In classical decision theory (Von Neuman and Morgenstern, 1953) it was an established axiom that decision-makers are risk averse, i.e. when facing two alternatives having the same expectancy, they will choose the one with the lower variance. Nevertheless, the pioneering work of Kahneman and Tversky in the field of cognitive psychology (1979, 1982) have severely undermined such classical paradigms.

In particular, Kahneman and Tversky (1982) have conducted several experiments to test decision making under uncertainty (see fig. 1). They showed that when potential profits are concerned, decision-makers are indeed risk averse, but when potential losses are concerned, subjects become risk seeking. This dichotomy in the attitude towards risk is in contradiction with classical paradigms, which assume that decision makers should always be risk averse, both when a potential profit and when a possible loss are predicted.

In Experiment #1 subjects are asked to choose between two alternatives which contained a (hypothetical) potential to gain money. Most subjects prefer alternative (A) to (B), thus showing risk aversion (preferring low variance to a slightly higher expectancy), in accordance with the "rationality paradigm". Nevertheless, when asked to choose between alternatives which refer to a possible loss (Experiment #2), most subjects prefer alternative (B*), which contains higher variance and higher risk. The subjects become risk seeking when losses were concerned.

Tversky and Kahneman concluded that the attitude towards risk is determined according to a "reference point", which is the basis for evaluating possible outcomes of the decision: When future rewards are perceived as profits compared to the current reference point, a risk aversion behavior is observed. When future rewards are perceived as losses, a risk-seeking behavior emerges. These observations were termed "Prospect Theory."

2.2 Main Functional Characteristics of the Basal Ganglia Reward System

The main functional characteristics of the basal ganglia reward systems can be summarised as follows (based on Schultz 1998):

i) The dopaminergic system codes the error between the prediction about the reward and the actual reward. That is - if the reward is stronger or sooner than expected, the dopamine neurons' activity rises. If the reward is weaker than expected, the dopamine neurons'

Experiment #1
The subject has to choose between:
(A) A sure gain of $80.
(B) 85% chance of winning $100 and 15% of winning nothing.

Experiment #2
The subject has to choose between:
(A*) A sure loss of $80
(B*) 85% chance of losing $100 and 15% chance of losing nothing.

Figure 1. Typical Risk Aversion / Risk Seeking experiments (After Kahneman & Tversky, 1982)

activity declines. Finally, the continuos background dopaminergic activity signals that the environment is as good as predicted.

ii) The dopaminergic system hardly responds to predictions about aversive rewards.

A simple heuristics that connects physiological signals with decision making would therefore be (Schultz et al., 1997): An organism should take actions correlated with increased reward-signal activity and avoid actions correlated with decreases in the rate of the neuronal reward-signal.

The responses of striatal cholinergic tonically active neurons (TANs) are very similar to the dopaminergic responses, yet with an opposite polarity, e.g., the main response of TANs to an unpredicted rewarding event is a depression (pause) of their background tonic activity (Aosaki et al. 1995, Raz et al. 1996). An exciting observation is that in both cases, the main response (the dopaminergic burst or the pause of the TANs) is flanked with activity of opposite polarity. Thus, excitatory bursts flank the pause of the TANs (figure 2) and short pauses can be seen preceding and following the burst of dopaminergic neurons (see for example, fig. 3, in Schultz et al., 1993 and figs. 1,2 in Mirenowicz and Schultz, 1994).

A recent review (Redgrave et al., 1999) indicated that the short-latency dopamine response might be too short (50-110 ms) to signal reward error, and suggested that the dopaminergic burst participates in the process of switching attentional and behavioral resources to unexpected, behaviorally important stimuli. Previous studies of TAN activity also reported very short (68±21 ms) latency responses in line with the early reports of the dopaminergic activity. Still, more recent studies indicated much longer latency for both the dopaminergic neurons (151±3 ms, mean±SEM, Mirenowicz and Schultz, 1994) and TANs (119±33 ms, 150±78 ms depending on the behavioral mode, Apicella 1997). Similarly, our studies of TAN responses revealed a stereotypical response with mean latency to reward around 200 ms from the reward-cue onset (figure 2).

Another support for the role of dopaminergic system in switching behavior (Redgrave et al., 1999) is the contradiction between the studies of the electrical activity of dopaminergic neurons and the neuro-chemical studies of striatal dopamine level in response to aversive events. While the electro-physiological studies indicate that the dopaminergic neurons are insensitive to aversive events, many neurochemical studies (see review in Redgrave et al., 1999) have indicated that aversive stimuli can increase the release of dopamine in the stria-

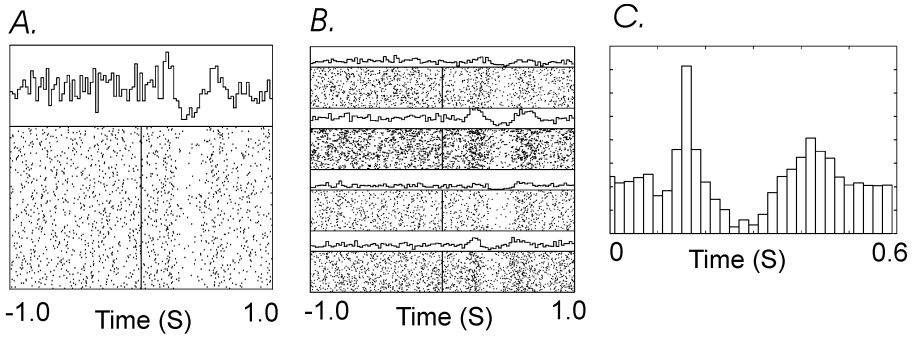

Figure 2. Responses of striatal TANs to reward-cue. A. Raster display (126 trials, below) and Peri-stimulus histogram (above) of a single TAN (HN07, unit 8). B. Raster displays (135 trials) and PSTHs of four simultaneously recorded TANs (HN06, units 2,8,15&13). C. Average PSTH of the reward responses of 23 TANs recorded on different recording sessions. Bin size =20 ms in all PSTHs.

tum, and that dopamine depletion impair the behavior that is elicited by these stressful events. Our recent preliminary studies of TANs' activity might resolve this contradiction. Using a multi-neuronal rate template we found that the characteristic response of TANs to reward (burst, pause, burst) is a collaborative phenomenon, that can be spotted in all behavioral epochs, and not only in time locking with the reward cue. The rate of this "neuronal reward signal" increases following the reward cue in correct trials, and drops below the background level following behavioral errors. We therefore suggest that the actual signal emitted by the striatal cholinergic or mid-brain dopaminergic neurons is not simply the number of spikes or the amount of released neurotransmitters. Rather, both basal ganglia reward systems elicit a continuos background level of complex tri-phasic neuronal signal. The rate of this neuronal reward signal is (up or down) modulated by the fitness between the animal prediction for future reward and the actual environmental events.

2.3 Physiological Basis of Decision Theory

Tversky, Kahneman and their successors concentrated primarily on the cognitive aspects of decision making. A basal-ganglia model can explain their findings in a broader perspective. We assume that although the basal ganglia reward systems were mainly studied with basic stimuli such as food or drink, it also respond to money stimuli, even if they are of a less "physical" nature. We shall therefore refer to money gains and losses as appetitive and aversive stimuli respectively, and analyze the cognitive experiments in the physiological framework.

Experiment 1: Profits
A = { ($80, p=1.) }
B = { ($100 , p=0.85) , ($0, p=0.15) }

Reference point (P=$80) is positive, therefore the dopaminergic system (D) is active.

Choose (A) → R=P → D unchanged (No error in prediction)
Choose (B) →
If R=$100 → R>P → D increased
If R=$0 → R<P → D decreased

Experiment 2: Losses
A* = { (-$80, p=1) }
B* = { (-$100 , p=0.85) , ($0, p=0.15) }

Reference point is negative (P*= -$80), therefore the dopaminergic system is not active.

Choose (A*) → R=P* → D still not active
Choose (B*) →
If R= - $100 → R<P* → D unchanged (still not active)
If R=$0 → R>P* → D increased (Unexpected reward)

Figure 3. Physiological analysis of Prospect Theory

2.3.1 Analysis of Experiment (1) - Risk Aversion in Profits

To recall, the subjects have to choose between a sure gain of $80 (alternative A) and a gamble (alternative B) between a gain of $100 (probability 0.85) and a gain of $0 (probability 0.15). The basal ganglia reward systems code errors in predictions (characteristic (i) above). Therefore, a reference point P (i.e. a prediction) is needed so that the reward systems could properly respond to the actual reward R. Since the two alternatives are both circa $80, which is the assured gain, this value makes the best candidate for becoming a reference point in this case.

When a subject chooses alternative (A), the actual reward will be $80. In this case the actual reward and the prediction (reference point) are identical, so there is no change in the neuronal activity level (see fig. 3). If a subject chooses alternative (B), the reward could either be $100 (which implies an increase in the neural activity, since Reward > Prediction) or $0 (which implies a decrease in the neural activity level). Kahneman and Tversky (1982) have shown that most subjects prefer alternative (A), where there is no change in the neural activity to alternative (B), where there could be an increase or a decrease in the activity level.

If one assumes a ternary model of the dopaminergic neurons, the above physiological analysis of Tversky and Kahneman's results could imply the following amendment to Schultz et al 's (1997) heuristics cited above:

1. Take actions correlated with increased reward signal activity and avoid actions that are correlated with decreases in basal ganglionic reward activity.
2. It is more important to avoid actions that lead to decreases in reward activity than to take actions that tend to increase basal ganglionic reward activity.

If we assume a continuous model of the dopaminergic and striatal cholinergic neurones, the cognitive results can be analyzed as stemming from a weighted average index for the possible increases and decreases in the reward system's activity for alternative (B). Under this assumption, the index calculated for alternative (B) must be lower than the index calculated for (A) in order for the subjects to prefer alternative (A).

2.3.2 Analysis of Experiment (2) - Risk Seeking in Losses

In this experiment, the two alternatives involve possible losses: either a sure loss of $80 (alternative (A*)), or a gamble between a loss of $100 (with probability 0.85) and $0 (with probability 0.15). The reference point in this case could be P= -$80, since this is the "sure loss", based on which the gamble is measured. The key element in the analysis of experiment #2 is property (ii) above, which asserts that the dopaminergic system does not respond to aversive stimuli. A loss of money is considered as an aversive stimulus. When a subject chooses alternative (A*), he receives a reward R= -$80. Analyzing the case similarly to Experiment 1 above (see figure 3), we would have concluded that since the reward R is equal to the predictions or since there is no coding of aversive cases (losses), there is no change in the dopaminergic level. An analysis of the choice of alternative (B*) is a little different. If the reward R is -$100, there is no response of the basal ganglia reward system, since the reward system does not code the aversive stimuli. However, if R=$0, the reward is referred to as an "appetitive surprise", since the reference point is P= -$80. In this case the reward systems will increase their activity.

The analysis for both a ternary and a continuous model will be as follows: When choosing (A*), no increase in the reinforcement activity will have a chance to occur. Choosing (B*) may lead to such an increase, but it will not lead to any decrease in the activity level. Therefore, a subject who is driven by basal ganglionic reinforcement impulses will be inclined to choose (B*), similar to Tversky and Kahneman's findings.

The shift from risk aversion to risk seeking can thus be explained using the asymmetrical nature of the basal ganglia systems (property (ii)). Moreover, the characteristics of basal ganglia neurons can also give insights for the emergence of a reference point in cognitive decision processes, as is described above.

3. THE ASYMETRICAL NATURE OF THE BASAL GANGLIA REWARD SYSTEM

It has been shown that the dopaminergic neurons respond preferably to appetitive stimuli (Schultz et al., 1997, Schultz, 1998). When considering the physiological reward systems in the context of cognitive decision making, the underrating of the information carried by aversive stimuli may have negative implications on the organism's survival, since aversive stimuli can help the organism avoid future hazards.

The underreaction of the reward system to aversive stimuli can be given a physiological explanation. A dopaminergic neuron's base firing level is 4-10 spikes per second (Schultz 1998). When an unpredicted appetitive stimulus occurs, the neuron's activity can easily go up to a higher level. Nevertheless, when an unpredicted aversive or disappointing event occurs, the firing rate can only go a few spikes per second down (since the base level is very close to 0). This means that even if dopaminergic neurons were responding equally to aversive and appetitive stimuli, they could not present a significant decrease in their activity. The average frequency of the tri-phasic TAN's signature of reward is even lower than the frequency of the background firing of the dopaminergic and cholinergic neurons. Therefore the possible modulations of this signal are also truncated by the zero level, and are naturally asymmetric.

The asymmetrical nature of the reward systems can also be given a functional explanation. While lower organisms primarily exhibit pattern recognition behavior (e.g., when receiving an air puff from the left, the organism will move to the right), higher organisms in the phylogenetic tree also apply sequential decision processes. A pattern recognition process will be most suitable for a "fight or flight" situation, where a quick decision is required. Sequential decision processes may produce better decisions, but they are harder to realise using neural networks, considering the parallel nature of such processes and the amount of calculations needed (see Beiser, & Houk, 1998 for the role of basal ganglia networks in sequential behavior).

Sequential decision processes may be thus preferable to pattern recognition when speed of decision making is of less importance. The plausibility of an immediate hazard could therefore serve as a rough indicator for the shifts between sequential and pattern-recognition decision making. When considering a possible source for this dichotomy, one may notice the growth of the basal ganglia over the phylogenetic tree (Marin et al. 1998). Basal ganglia play an important role in sequential processes (Aldridge and Berridge, 1998, Graybiel 1998) and are controlled by the midbrain dopaminergic and striatal cholinergic system.

It may thus be that the basal ganglia reward system is used to maintain sequential decision processes, while pattern-recognition faster, simpler neural networks maintain behavior. We can therefore hypothesise that the basal ganglia reward system does not have to respond to aversive stimuli, since they are already handled by other sub-systems that exhibit a pattern-recognition behavior. A possible sub-system, which performs this task, may be located in the cholinergic Nucleus Basalis (NB). The NB receives inputs from the limbic and the paralimbic structures, and sends projections to the entire cortex. Kilgard and Merzenich (1998) have shown that the NB can signify the behavioral importance of different stimuli. They propose that the NB may enable the cortex to ignore irrelevant stimuli, while focusing on other stimuli. The Nucleus Basalis might therefore constitute a good candidate for a complementary system that resolves the asymmetry nature of the basal ganglia reward system.

4. CONCLUSIONS

Cognitive behavior of individuals is generally described in terms of reactions to rewards or to predictions concerning future rewards. The neural activity of the dopaminergic and cholinergic systems of the basal ganglia may thus be correlated with various cognitive effects.

We presented some striking similarities between cognitive decision processes and functional characteristics of the basal ganglia reward system. In particular, Tversky and Kahneman's Prospect Theory (describing cognitive decision processes) was analyzed in terms of the functional characteristics of midbrain dopaminergic and striatal cholinergic interneurons. We propose that the dichotomy between risk aversion and risk seeking modes of behavior is dependent upon the asymmetrical nature of these neuronal systems. Moreover, we propose that the emergence of sequential behavior (as opposed to pattern-detection behavior) comparatively late in the process of evolution has led to the asymmetrical nature of the basal ganglia system.

The correlations between cognitive descriptions of decision making and physiological features of the basal ganglia are still mostly obscure. We do not claim to have considered the whole picture in this chapter, but we do think we presented a promising track for future research. The comparison of the two levels of research, physiological and psychological, may give insights for further experiments in both disciplines. We believe that further study of the basal ganglia using gradient of aversive and appetite stimuli will help us shed light on the critical role of these neuronal networks in normal and pathological behavior.

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6. REFERENCES

Aldridge, J.W. and Berridge, K.C. Coding of serial order by neostriatal neurons: a "natural action" approach to movement sequence. J. Neurosci. 18: 2777-2787, (1998).

Aosaki, T., Kimura, M., and Graybiel, A.M., Temporal and spatial characteristics of tonically active neurons of the primate's striatum, J. Neurophysiol. 73: 1234-1252 (1995).

Apicella, P., Legallet, E., and Trouche, E., Responses of tonically discharging neurons in the monkey striatum to primary rewards delivered during different behavior states, Exp. Brain Res. 116: 456-466 (1997).

Beiser, D.G. and Houk, J.C. Model of cortical-basal ganglionic processing: encoding the serial order of sensory events. J. Neurophysiol. 79: 3168-3188 (1998).

Graybiel, A.M. The basal ganglia and chunking of action repertoires. Neurobiol. Learn. Mem. 70: 119-136, (1998).

Hollerman, J.R., Schultz, W., Dopamine neurones report an error in the temporal prediction of reward during learning, Nature Neurosci. 1: 304-309 (1998).

Kahneman, D. & Tversky, A., Prospect theory - an analysis of decision under risk, Econometrica 47:263-291, (1979).

Kahneman, D., & Tversky, A., The psychology of preferences, Sci. Am. 246:136-142 (1982).

Kilgard, M.P., & Merzenich, M.M., Cortical map reorganization enabled by Nucleus Basalis activity, Science 279: 1714-1718 (1998).

Marin, O., Smeets, W. J. A. J. & Gonzalez, A., Evolution of the basal ganglia in tetrapods: A New Perspective Based on Recent Studies in Amphibians, TINS, 21, 487-495 (1998).

Mirenowicz J. and Schultz W., Importance of unpredictability for reward response in primate dopamine neurons. J. Neurophysiol. 72: 1024-1027 (1994)

Raz, A., Feingold, A., Zelanskaya, V., and Bergman, H., Neuronal synchronization of tonically active neurons in the striatum of normal and Parkinsonian primates. J. Neurophysiol. 76: 2083-2088 (1996).

Redgrave P., Prescott, T.J, and Gurney K. Is the short latency dopamine response too short to signal reward error? TINS, 22: 146-151 (1999).

Robbins, T.W., Everitt, B.J., Neurobehavioral mechanisms of reward and motivation, Current opinion in Neurobiology 6, 228-236 (1996).

Schultz, W., Apicella P., and Ljungberg T. Responses of monkey dopamine neurons to reward and conditioned stimuli during successive steps of learning a delayed response task. J. Neurosci. 13: 900-913 (1993).

Schultz, W., Dayan, P., and Montague, P.R. , A Neural substrate of prediction and reward, Science 275, 1593-1599 (1997).

Schultz, W., Predictive reward signal of Dopamine neurons,. J. Neurophysiol. 80:1-27 (1998).

Von Neuman, J. and Morgenstern, O., Theory of Games and Economic Behavior, Princeton University Press, 3rd edition (1953).