Published in final edited form as:
Curr Top Behav Neurosci. 2016 ; 27: 1–12. doi:10.1007/7854_2015_402.

The Behavioral Neuroscience of Motivation: An Overview of Concepts, Measures, and Translational Applications

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Abstract

Motivation, defined as the energizing of behavior in pursuit of a goal, is a fundamental element of our interaction with the world and with each other. All animals share motivation to obtain their basic needs, including food, water, sex and social interaction. Meeting these needs is a requirement for survival, but in all cases the goals must be met in appropriate quantities and at appropriate times. Therefore motivational drive must be modulated as a function of both internal states as well as external environmental conditions. The regulation of motivated behaviors is achieved by the coordinated action of molecules (peptides, hormones, neurotransmitters etc), acting within specific circuits that integrate multiple signals in order for complex decisions to be made. In the past few decades, there has been a great deal of research on the biology and psychology of motivation. This work includes the investigation of specific aspects of motived behavior using multiple levels of analyses, which allows for the identification of the underpinning neurobiological mechanisms that support relevant psychological processes. In this chapter we provide an overview to the volume "The Behavioural Neuroscience of Motivation". The volume includes succinct summaries of; The neurobiology of components of healthy motivational drive, neural measures and correlates of motivation in humans and other animals as well as information on disorders in which abnormal motivation plays a major role. Deficits in motivation occur in a number of psychiatric disorders, affecting a large population, and severe disturbance of motivation can be devastating. Therefore, we also include a section on the development of treatments for disorders of motivation. It is hoped that the collection of reviews in the volume will expose scientists to a breadth of ideas from several different subdisciplines, thereby inspiring new directions of research that may increase our understanding of motivational regulation and bring us closer to effective treatments for disorders of motivation.

Keywords

Motivation; Cost-benefit analysis; Addiction; Apathy; Translational research

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1 Why Motivation Is Important to Understand

Understanding what drives motivated behavior in humans is a truly fascinating endeavor. But as important as our curiosity for knowing what drives us as individuals, and what supports individual differences in levels of motivation among our friends and colleagues, is the critical question; why do motivational processes get disrupted when the clinical and personal consequences can be so devastating? As we will see across this volume, motivated behaviors involve biological and psychological processes that have undergone evolution at numerous levels, from individual molecules all the way to species-specific social organization. While motivational processes represent heritable traits of fitness, humans suffer from a number of disorders of motivation that can be organized into two distinct categories. The first category is composed of the apathy and pathological deficits in motivation commonly seen in patients with schizophrenia and affective disorders. The second category involves problematic excesses in behavior including addictions, the pathological misdirection of motivation. Developing treatments for disorders of motivation requires a detailed understanding of how motivated behavior occurs, how it is dynamically regulated under normal conditions, and how it is disrupted in disease. This volume provides reviews of recent research in each of these areas.

2 What We Mean by the Word Motivation

The concept of motivation is a useful summary concept for how an individual's past history and current state interact to modulate goal-directed activity. In this book, the authors examine the motivation to pursue many different goals. One general aspect of motivated behaviors is that they lead to a goal and obtaining the goal is rewarding. Thus, motivation, defined as the energizing of behavior in pursuit of a goal, is a fundamental property of all deliberative behaviors. One of the earliest psychological theories of motivation, Hull's drive theory, posited that behaviors occur to reduce biological needs, thereby optimizing the organism's potential for survival (Hull 1943). However in Hull's theory, motivational drive functioned solely to energize responding, drive was not responsible for initiating, or maintaining the direction of action. Later, motivation was conceptualized to consist of both a goal-directed, directional component and an arousal, activational component (Duffy 1957; Hebb 1955). This is the framework of motivation still in use, such that if motivation were a vector—its length would represent the amplitude, or intensity of pursuit, and the angle of the vector would represent its focus on a specific goal. In this analogy, a motivation vector affected by apathy might have a reduced length in all directions and a motivation vector affected by addiction might have an increased length and a less flexible direction. The chapters in this volume explicitly acknowledge that motivation affects which responses occur as well as the vigor of those responses. It appears that we are just beginning to understand that these two aspects of motivation have both common and distinctive neural underpinnings. For example, circadian factors may energize the general motive of seeking food or mate (Antle and Silver, this volume), but the specific actions that occur in pursuit of these goals are regulated by different substrates (see Caldwell and Alders, Woods and Begg, Magarinos and Pfaff, all in this volume). Similarly, local cues that signal food availability may energize many food seeking actions, signals for specific foods differentially energize actions associated with obtaining the specific outcome. Again, the neural substrates of the general and specific effects are somewhat distinctive. At each level, whole classes of specific actions are made more or less likely by these factors (Neuringer and Jensen 2010). We suggest that there is generally a hierarchical structure to motivation in the sense that general arousal factors such as sleep–wake cycles will affect many different motives, that activation of specific motives (e.g., hunger, thirst, social motives) can activate many specific actions that could lead to many specific outcomes within a general class of goals, and that more temporally and situationally specific factors determine the specific actions that occur in pursuit of that goal (Timberlake 2001). With this in mind, it is clear that disruptions in motivation can occur at multiple levels of control which suggests there may be multiple interacting ways to attempt to treat disruptions.

3 A Simplified Overview of How Motivation Might Work in the Brain

Many different factors influence motivation, including the organism's internal physiological states, the current environmental conditions, as well as the organism's past history and experiences. In order for all these factors to influence motivation, information about them must be processed in a number of ways; it must be evaluated and encoded, and unless the motives are novel, the valuation and encoding will be affected by learning and retrieval processes. A simplified overview of how such diversity of information must be processed and integrated to result in motivation (both response selection and action vigor) is shown in Fig. 1. Here, we organize the problem into a single, highest order concept that motivated behaviors represent the actions associated with the highest net value that results from a cost–benefit analysis that encompasses all of the potential influencing factors and processes.

4 Cost–Benefit Computation as the Arbiter of Motivated Behavior

The *costs* associated with behavioral action may include physical effort, mental effort, time, loss of potential opportunities, discomfort, and danger (the risk of pain and potential death). The *benefits* associated with behavioral action might include fulfilling physiological and psychological needs, obtaining reinforcement secondary to those needs, escaping from harm, or avoidance of some of the costs listed above. As mentioned above, information entering the cost–benefit computation for any specific motive will be processed in several ways. The value of every cost and every benefit must be calculated and encoded. The concept of encoding value and experimental methods for measuring encoded value are discussed in detail by Redish et al., in this volume. It is important to consider that value must be encoded when a goal is obtained and then stored for future retrieval when obtaining that goal again becomes relevant. When that happens in the current moment, the assessment of value must be conditioned both on this past experience as well as the current state and environmental conditions. Goals are likely to be obtained with some temporal distance from the initiation, or even conclusion of behavioral output. Single neuron activity in several brain regions including orbitofrontal cortex, anterior cingulate, and basolateral amygdala has been shown to correlate with reward prediction and this work is reviewed by Bissonette and Roesch in this volume. The encoded values of costs and benefits do not belong in absolute scales because the values of all costs and benefits are rendered relative to the animal's current physiological state as well as the current conditions of the surrounding environment.

Much has been learned about the role of dopamine in reinforcement learning, and its impact on motivated behavior from experimental manipulations of the dopamine system in rodents. This work is comprehensively reviewed by Salamone et al. in this volume. In addition to learning about the costs and benefits of a particular action, subjects also learn about specific signals that are associated with obtaining particular goals. Such signals can have an enormous influence on motivated behavior, and several chapters in this volume provide details of when and how environmental cues can influence response selection and response activation. These include Corbit and Balleine's chapter on learning and motivational processes contributing to Pavlovian–instrumental transfer and John O'Doherty's chapter on the neural substrates of motivational control in humans. Cue learning is also discussed in the context of motivational disorder, in the chapters by Meyer et al. and Barrus et al., that deal with substance abuse disorders and gambling.

Another aspect of the computation that energizes specific action has to do with signals that a particular goal is currently available. These signals occur on multiple timescales. Specific times of day can become associated with the opportunity to obtain specific goals, and discrete cues can signal the opportunity to achieve a goal as well as what specific ways there are to achieve it. For example, when meals occur at a regular time of day, there are behavioral, hormonal, and neural changes that occur in anticipation of a meal time that give rise to the motivation to seek food (Antle and Silver, in this volume). Encountering a restaurant can activate the specific behavioral sequences that lead to the ordering of food and the specific foods themselves can activate specific consummatory responses. All along this sequence of temporally organized behavior, there are concomitant changes in hormonal and neural states that energize and guide action (Woods and Begg in this volume).

After effective encoding of all the relevant costs and benefits, a computational process (the cost–benefit computation) is required to resolve the appropriate direction and vigor of action to be taken. This complex interplay of factors and processes is schematized in Fig. 1.

How conceptually the cost–benefit computation is made is currently unclear. It is still unknown whether the value of costs and benefits are calculated on the same scale or not, whether their weights are integrated or subtracted such that, for example, the amount of predicted effort reduces the value of the predicted reward. Or perhaps, there is a circuit component that acts as a comparator of these two component values. An additional complication is that for any given motive, there are often multiple types of costs and potentially multiple types of benefits involved because many different types of control systems and circuits are at play (e.g., neuroendocrine, circadian, Pavlovian). This leads to the question of how so much diversity of information can all be used to make an appropriate response selection and determine action vigor. Do all factors enter into a singular, highly complex equation, as our simplified diagram (Fig. 1) may seem to imply? Or do some systems continually run in parallel, with behavioral output as the result of a hierarchical switching from one system to another? Or perhaps there is fluctuation in the degree to which different factors influence the computation, e.g., the relative weights of physical and mental costs depend on the energy state of the organism.

Furthermore, it is possible that these alternative regulatory schemes are not mutually exclusive. For a detailed discussion on the potential mechanisms by which multiple deliberative processes that are running in parallel may each influence motivation (see Redish et al. in this volume). In the case of appetitive conditioning, there is evidence to suggest that animals can rapidly switch between responding that is driven by two different control systems, goal directed or habitual (Gremel and Costa 2013). Audiovisual cues can trigger the rapid switching, implying that these two alternate circuits are constantly online and available in parallel. On the other hand, instead of a multi-tiered, hierarchical, or switching system, other work suggests that all information enters a singular computation process, and the output of this meta-computation is what drives motivation. This concept is favored by Magarinos and Pfaff (this volume) whose work on the sexual motivation of female rodents may suggest that for this specific motive, at least some factors may be integrated into a single decision-making process.

Above we have described the complex situation of many different factors influencing a single motive. It must also be recognized that at any given time, there may be competition for multiple goals and that imbalances in the strength of the motivations for each goal can cause conflict and dysfunctional behavior. The chapter by Cornwell et al. describes how human well-being depends not only on satisfying specific motives, but also on ensuring that motives work together such that no individual motive is too weak or too strong. It is becoming clear that different motivational systems have control elements that are unique to each system but that there may also be common substrates, perhaps close to the final steps that determine behavioral output. This is well illustrated in the chapter on defensive motivation by Campese et al. and in the chapter on social motivation by Caldwell and Alders. Again, the neurobiological mechanism whereby different motive systems interact is an important but not yet well-understood problem. Of particular interest will be to understand how defensive motivations interact with appetitive ones. The vast majority of modern work on motivation concerns itself with the mechanisms of appetitive motivation. Campese et al. show how to leverage what is now known about fear learning to understand the neurobiological mechanisms of defensive motivations. In a similar vein, Cornwell et al. argue for the importance of understanding how promotion/prevention motives in humans is an important modulator of other motives. Hopefully, the future will include a greater focus on understanding defensive motivations.

5 Research Approaches to Understanding Motivation

To increase our understanding of motivation in the brain, there are numerous approaches that can be taken. In this volume, many different academic approaches are represented as the research reviewed includes clinical, experimental, and comparative psychology; and several neuroscience subfields including, cognitive, molecular, cellular, behavioral, and systems neuroscience. This means that specific questions or single hypotheses can be, and often are being, approached at multiple levels of analysis. Indeed, it is when research programs combine a number of techniques, or use information derived from a few different techniques to propose (and test) new hypotheses that the most compelling results are obtained. For example, the work described by O'Doherty in this volume includes the use of human fMRI studies to investigate potential action-value signals that have been proposed from rat electrophysiological recordings. The research described by Redish et al. considers computational models of decision making and tests these models by measuring neuronal activity during deliberative behavior. In the chapter by Ward, the approach to testing motivational deficits in mice has very much been informed by the data from molecular and clinical studies in humans. By phenocopying in mice the molecular changes that have been detected in patients using PET imaging techniques, the behavioral consequences can be probed under well-controlled conditions. In a similarly translational manner, the research described by Robinson et al. in this volume applies electrophysiological and optogenetic techniques in rodents to probe behaviors that are altered in people with addictions. In the chapter by Barrus et al., the authors discuss the development of rodent paradigms designed to test various psychological theories of substance use and gambling disorders.

6 Organismal Level Biology Is Critical to Understanding Motivation

When multiple levels of analyses are used to investigate motivational processes, a critically important concept becomes apparent. While the evolution of traits that support motivation occurs at the level of molecules, proteins, cells, and circuits, it is the entire organism, and its interaction with the environment that is selected. An example of this concept is easily seen in the research on circadian modulation of motivation (Antle and Silver) and in the work on motivation for eating (Woods and Begg). For example, in the case of feeding we know many of the molecules and circuits involved in both the intrinsic, homeostatic factors which drive the motivational to eat, such as hormones and peptides, and we also know the neuromodulators and circuits that are responsible for some of the extrinsic/environmental influences on eating such as predictive cues. We are beginning to understand how these signals are integrated in order for decisions to be made and behavioral responses to occur; though as described above, understanding the mechanism of integration is currently a critical area of research.

7 Motivation Gone Wrong

Patients with many different psychiatric diagnoses may experience deficits in motivation, including depression, schizophrenia, bipolar disorder, PTSD, and anxiety disorders. In this volume, we focus on the neurobiology of motivational deficits in depression and schizophrenia primarily because these are the two illnesses in which pathological deficits in motivation play a major role in patient functioning and clinical outcome (Barch et al. 2014; Strauss et al. 2013). As such, far more research has been done on motivation in depression and schizophrenia than any other illness. In the last few decades, it has been recognized that the motivational deficits in Schizophrenia and depression share similarities, but also distinct differences. These differences occur because as mentioned above, there are many components involved in motivated behavior and each of them represent potential vulnerabilities that may be involved in different pathophysiological mechanisms. An excellent review of the similarities and differences in mechanisms underlying motivational deficits in depression and schizophrenia is provided by Barch et al. in this volume. The central difference in these types of pathologies is that many depressed patients suffer from impairments of in-the-moment hedonic reaction. Such anhedonia can diminish an individual’s capacity for anticipation, learning, and effort. In contrast, patients with schizophrenia demonstrate relatively intact in-the-moment hedonic processing. Instead, patients suffer impairments in other components involved in translating reward experience to anticipation and action selection.

There are also separate chapters that go into more specific detail for each of these pathophysiological conditions. An update on candidate pathomechanisms for motivational deficits in depression is provided by Treadway’s chapter. This volume devotes two chapters to the topic of motivation deficit in schizophrenia because this area of research has been more active than it has been in depression. This is likely because antipsychotic medications that successfully ameliorate the positive symptoms of schizophrenia (delusions, hallucinations, etc.) have been available for some time, leaving patients with the residual negative symptoms, of which a motivation is the primary driver of poor outcome and low quality of life (Kiang et al. 2003).

Current concepts of motivation deficits and how motivation is assessed in patients with schizophrenia is reviewed by Reddy et al. Waltz and Gold extend these concepts into the exploration of the relationship between a motivation and the representation of expected value. The clinical research reviewed in the chapters that deal with apathy and motivation in humans is complimented by a chapter on methods for dissecting motivation and related psychological processes in rodents (Ward). Research using animal models is critical for several obvious reasons, including the availability of genetic manipulations, molecular modifications as well as invasive in vivo monitoring procedures that are not possible in human subjects. What hasn’t previously been obvious is how well we can use such animal models to investigate the various components of motivation that are particularly relevant to human disease. Ward describes such procedures and explains how best to leverage our current clinical knowledge using state-of-the-art mouse models.

On the flip side of apathy may be when motivation for a specific goal can come to dominate action in maladaptive ways as appears to be the case in addictions. Excessive behavior for many types of rewards including drugs, food, gambling, and sex can be problematic. In addiction, rapid and strong learning about what leads to reward, excesses in experiencing the hedonic value of rewards, exaggeration in representing those values, and dominance in being guided by those representations can all lead to significant narrowing in the diversity of motives. Several theories exist that attempt to explain the process of addiction in terms of disruption of motivational processes. Each theory differs in the emphasis on which specific aspects of motivation are primarily affected. The chapters by both Meyer et al. and Robinson et al. describe the motivational processes underlying substance abuse disorder. The chapter by Barrus et al. extends this discussion into the field of gambling. Barrus et al. suggest that many of the processes affected in gambling are the same as those affected in drug addiction, and therefore, the paradigms that have been successfully used to study drug addiction in animal models can be successfully modified to identify neurobiological mechanisms related to gambling. The central hypothesis in these analyses of addictions of drugs and gambling (as well as addiction to food and other things) is that an aberration in reward processing and/or in the control by cues associated with these rewards underlies the problematic nature of addictive behavior and its resistance to change.

8 Treatments

Given the modern emphasis on reward processes as a fundamental component of motivation, it is encouraging that modern cognitive/behavioral approaches to treating motivational disturbances focus on creating reward contingencies that modify deficits or excesses in behavior. Saperstein and Medalia describe how in schizophrenia patients motivation enhancing techniques are critical to treatment-related improvements within cognitive remediation therapy. In the case of addictions, Walter and Petry provide an overview of research indicating that contingency management is a demonstrably effective psychosocial treatment for substance use disorders. The central concept of contingency management is that extrinsic motivators are used to change patients' behaviors. Specifically, reinforcement is provided when patients demonstrate abstinence. In the descriptions of both treatment approaches, the chapters consider the important role that intrinsic motivation may play in clinical success.

We are hopeful that the great progress in understanding the neurobiology of motivation described in this book will influence new ideas that will lead to novel pharmacological, physiological and psychological/psychosocial approaches to treatments for disorders of motivation. The identification of novel pharmacological treatments is dependent on the ability of preclinical researchers to investigate potential targets and screen potential candidate compounds using truly meaningful endophenotypic assays. The chapters in this volume that describe clinical studies of patient with disorders of motivation describe how motivation has been dissected into a number of component processes and the specific processes that are selectively disrupted in disease have been identified (Reddy et al., Barch et al., Waltz and Gold). To identify drugs that will be effective for disorders of motivation, preclinical assays must focus on the same specific processes affected in humans (see Ward in this volume). A recent example of the development of the kind of research tools that are needed for the purpose of investigating potential treatment targets is the strategy of dissecting goal-directed action from arousal by modifying previously existing rodent behavioral tasks (Bailey et al. 2015a). These new tools can then be used to assay specific effects of drugs that affect novel treatment targets (Simpson et al. 2011) and Bailey et al. (2015b). This novel approach was directly inspired by the literature on the selectivity of processes disrupted in humans with disorders of motivation.

In addition to pharmacological treatments, there is also the possibility that electrophysiological treatments for disorders of motivation may be developed. Deep brain stimulation (DBS) is currently used to treat a number of neurological and psychiatric conditions (Kocabicak et al. 2015; Kringelbach et al. 2007; Udupa and Chen 2015). DBS has been used to treat essential tremor, Parkinson's disease, treatment refractory major depression, severe obsessive–compulsive disorder, and chronic pain for several years. Several other applications are in experimental stages, including clinical trials for pervasive addiction and symptoms of schizophrenia. Such an invasive procedure requires many successive small-scale clinical trials before optimal procedures can be successfully developed. A significantly less invasive procedure used to modulate brain activity is transcranial magnetic stimulation (TMS). While the mechanism(s) by which TMS alters neuronal function and network activity is not understood, due to its noninvasiveness, hundreds of clinical trials have been conducted for a long list of neuropsychiatric conditions, including schizophrenia, and craving/addiction. A comprehensive review of studies of repetitive TMS has recently been published (Lefaucheur et al. 2014).

Lastly, we are also hopeful that the emerging understanding that there are multiple systems driving motivation on an organismal level will lead to the development of treatment schemes that are more comprehensive than those that have been developed in the past. It may be that subtle adjustments in several of the factors that are involved in disorders of motivation (the endocrine system, circadian system, neurotransmitter function, etc.) can result in greater improvements and less side effects than treatments that focus on a single system.

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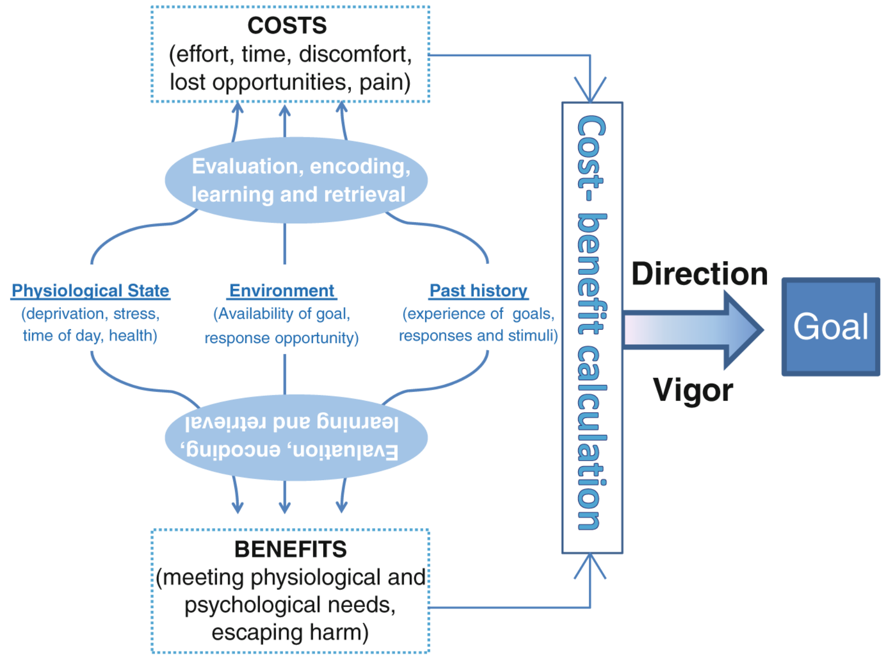

Fig. 1.

A simplified diagram of the influencing factors and processes that are involved in motivation. This framework of motivation places cost–benefit analysis central to the concept of motivation. Three major categories of factors are known to influence motivation: the individual's physiological state, the environment, and the individual's past history. Information about all 3 categories of factors will be subject to a number of processes (represented inside the blue oval), including evaluation and encoding. In almost all circumstances, the motive, environment, and physiological state will not be novel; therefore, information will also undergo learning and retrieval processes. All of the combined processes result in weighting of all the costs and benefits related to the motive, and the output of the cost–benefit calculation will impact upon the direction and vigor of action that the individual takes toward the motive goal