and Sherlock Holmes, although both human beings, thus currently differ in ontological status.

►Logical

Ontology

Definition

Ontology is the study of being or of what there is. Typically, ontologies of philosophers might comprise concrete objects like chairs or electrons, abstract objects like numbers or ►propositions, properties like the property of being a chair, facts like the fact that Paris is west of Warsaw, or events like the 2004 World Series.

►Epiphenomenalism

Opacity

Definition

Primarily a feature of certain sentences, e.g., of many ascriptions of propositional attitudes. The truth of such ascriptions does not systematically depend on the truth or falsity of the proposition involved. Consider the following two belief-ascriptions: "Mary believes that 1 + 1 = 2" and "Mary believes that 2756 + 488 = 3244." Even though both propositions ("1 + 1 = 2" and "2756 + 488 = 3244") are true, the two beliefascriptions can differ in truth-value. Whether it is true that Mary believes that 2756 + 488 = 3244 therefore does not systematically depend on the truth of "2756 + 488 = 3244."

►Representation (Mental)

Open Loop Behavior

Definition

Behavior that is executed without feedback control. This may, in nature, be due to completing a task before feedback is possible.

Open Reading Frame

Definition

The region of the gene between the start and stop codon that encodes for the protein.

Operant

Definition

Control by the consequences, i.e. by positive or negative reinforcement (=punishment) that is the result of a particular behavior and that shapes the future expression of that behavior.

Operant Conditioning

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O

Synonyms

Instrumental conditioning

Definition

Operant conditioning describes a class of experiments in which an animal (including humans) learns about the consequences of its behavior and uses this knowledge to control its environment.

Characteristics

Our life consists of a series of experiences in which we learn about our environment and how to handle it. Learning about the environment ("the plate is hot") and learning the skills to control it ("riding a bike") have been experimentally conceptualized as classical and operant conditioning, respectively. The two are so intertwined that a treatment of operant conditioning is impossible without reference to classical conditioning.

Operant Conditioning

Operant (instrumental) conditioning [1] is the process by which we learn about the consequences of our actions, e.g., not to touch a hot plate. The most famous operant conditioning experiment involves the "Skinner-Box" in which the psychologist B.F. Skinner trained rats to press a lever for a food reward. The animals were placed in the box and after some exploring would also press the lever, which would lead to food pellets being dispensed into the box. The animals quickly learned that they could control food delivery by pressing the lever. However, operant conditioning is not as simple as it first seems. For instance, when we touch a hot plate (or the rat the lever), we learn more about the hot plate than about our touch: we avoid contact of any body part with the plate, not only the hand that initially touched it. Obviously, we learned that the hot plate burns us. It is not only confusing that this type of environmental learning is usually called classical conditioning, we cannot even be sure that it is the only process taking place during conditioning.

Classical Conditioning

Classical (Pavlovian) conditioning [2] is the process by which we learn the relationship between events in our environment, e.g., that lightning always precedes thunder. The most famous classical conditioning experiment involves "Pavlov's dog": The physiologist I.P. Pavlov trained dogs to salivate in anticipation of food by repeatedly ringing a bell (conditioned stimulus, CS) before giving the animals food (unconditioned stimulus, US). Dogs naturally salivate to food. After a number of such presentations, the animals would salivate to the tone alone, indicating that they were expecting the food. The dog learns that the bell means food much as we learn that the plate is hot in the operant example above. Therefore, it is legitimate to ask if operant conditioning is in essence a classical process. Both operant and classical conditioning serve to be able to predict the occurrence of important events (such as food or danger). However, one of a number of important differences in particular suggests that completely different brain functions underlie the two processes. In classical conditioning, external stimuli control the behavior by triggering certain responses. In operant conditioning, the behavior controls the external events.

The Relationship Between Operant and Classical Conditioning

Ever since operant and classical conditioning were distinguished in 1928, their relationship has been under intense debate. The discussion has shifted among singular stimulus-response concepts, multiprocess views, and a variety of unified theories. Today, modern neuroscience distinguishes between procedural memories (skills and habits) and declarative memories (facts or events). The intensity and duration of the debate can in part be explained by the fact that most learning situations comprise operant and classical components to some extent: one or more initially neutral stimuli (CS), the animal's behavior (BH), and the ►reinforcer (US). The example above of learning to avoid touching a hot plate is very instructive. Extending the hand (BH) toward the round hotplate (CS) leads to the painful burn (US). In principle, our brain may store the situation as memory of the pain associated both with the hotplate (classical conditioning, CS-US) and with the extension of the hand (operant conditioning, BH-US) to predict the consequences of touching the plate at future encounters.

Habit Formation

A phenomenon called habit formation [3] confirms the tight interaction between operant and classical components in operant conditioning. In the early stages of an operant conditioning experiment (e.g., a rat pressing a lever for food in a Skinner box), the animal performs the lever presses spontaneously with the aim of obtaining the food (goal-directed actions). This can be shown by feeding the animals to satiety after training: they now press the lever less often when they are placed back in the box, because they are not hungry anymore. However, the same treatment fails to reduce lever pressing after the animals have been trained for an extended period. The behavior has now become habitual or compulsive; whenever the animals are placed now in the box, they frantically press the lever even if they are not hungry (or even if the food will make them sick). Although in the early stage of operant conditioning the behavior controls the environment (lever pressing to obtain food), habit formation effectively reverses the situation such that now the environment (box, lever) controls the behavior (lever pressing). One could say that overtraining an operant situation leads to a situation very similar to a classical one. Thus, operant conditioning consists not only of two components (operant and classical) but also of two phases (goal-directed and habitual behavior), with the relationship of the components changing with the progression from one phase to the next. Despite many decades of research filling bookshelves with psychological literature, our neurobiological understanding of the mechanisms underlying these processes is rather vague. What little is known comes from a number of different vertebrate and invertebrate model systems on various levels of operant conditioning. This essay is an attempt to integrate the neuroscience gained from many such disparate sources.

Neuroscientific Principles in Operant Conditioning

If there is a consensus for a critical early-stage process in operant conditioning, it is that of reafference. To detect the consequences of behavior, the brain has to compare its behavioral output with the incoming sensory stream and search for coincidences. The neurobiological concept behind this process is that of corollary discharges (or efference copies). These efference copies are "copies" of the motor command sent to sensory processing stages for comparison. Thus, neurobiologically, any convergence site of operant behavior and the US is very interesting with regard to potential plasticity mechanisms in operant conditioning. The efference copies serve to distinguish incoming sensory signals into self-caused (reafferent) and other, ex-afferent signals [4]. Modern theories of operant conditioning incorporate and expand this reafference principle into two modules: one is concerned with generating variable behavior and another predicts and evaluates the consequences of this behavior and feeds back onto the initiation stage [5]. Some evidence exists that the circuits mediating these functions are contained within the dorsal and ventral striatum of the vertebrate brain. We have only very poor mechanistic knowledge about the first module. Behavioral variability could be generated actively by dedicated circuits in the brain or simply arise as a by-product of accumulated errors in an imperfectly wired brain (neural noise). Despite recent evidence supporting the neural control of behavioral variability, the question remains controversial. Only little more is known about the neurobiology of the second module. Promising potential mechanisms have been reported recently from humans, rats, crickets, and the marine snail *Aplysia*. These studies describe conceptually similar neural pathways for reafferent evaluation of behavioral output (via efference copies) and potential cellular mechanisms for the storage of the results of such evaluations at the convergence site of operant behavior and US. However, to this date, a general unifying principle such as that of synaptic plasticity in classical conditioning is still lacking.

From a larger perspective, there is evidence suggesting that the traditional distinction of entire learning experiments into either operant or classical conditioning needs to be reconsidered. Rather, it appears that an experimental separation of classical and operant components is essential for the study of associative learning. As outlined above, most associative learning situations comprise components of both behavioral (operant) and sensory (classical) predictors. Vertebrate research had already shown that operant and classical processes are probably mediated by different brain areas. Research primarily from the fruit fly *Drosophila* and *Aplysia* has succeeded in eliminating much if not all of the classical components in "pure" operant conditioning experiments, a feat which has so far proven difficult to accomplish in any modern vertebrate preparation. This type of operant conditioning appears more akin to habit formation and lacks an extended goal-directed phase. These paradigms successfully reduce the complexity of operant conditioning by isolating its components and as such are vital for the progress in this research area. The new invertebrate studies revealed that pure operant conditioning differs from classical conditioning not only on the neural, but also on the molecular level. Apparently, the acquisition of skills and habits, such as writing, driving a car, tying laces, or our going to bed rituals is not only processed by different brain structures than our explicit memories, but also the neurons use different biochemical processes to store these memories.

The realization that most learning situations consist of separable skill-learning and fact-learning components opens the possibility to observe the interactions between them during operant conditioning. For instance, the early, goal-directed phase is dominated by fact learning, which is facilitated by allowing a behavior to control the stimuli about which the animal learns. Skill learning in this phase is suppressed by the fact-learning mechanism. This insight supports early hypotheses about dominant classical components in operant conditioning [6], but only for the early, goal-directed phase. If training is extended, this suppression can be overcome and a habit can be formed. Organizing these processes in such a hierarchical way safeguards the organism against premature stereotypization of its behavioral repertoire and allows such behavioral stereotypes only if they provide a significant advantage. These results have drastic implications for all learning experiments: as soon as the behavior of the experimental subject has an effect on its subsequent stimulus situation, different processes seem to be at work than in experiments where the animal's behavior has no such consequences, even if the subject in both cases is required to learn only about external stimuli. Conversely, apparently similar procedural tasks that differ only in the degree of predictive stimuli present may actually rely on completely different molecular pathways. The hierarchical organization of classical and operant processes also explains why we sometimes have to train so hard to master certain skills and why it sometimes helps to shut out dominant visual stimuli by closing our eyes when we learn them.

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Operant Conditioning

Definition

A Definition of operant conditioning, also called instrumental conditioning, requires a distinction between elicited and emitted behavior. Elicited behavior is a response that is associated with a biologically relevant stimulus. Pavlovian or classical conditioning is an example of elicited behavior since there is always a formal, temporal relationship between the conditional stimulus (for example, a bell) and the unconditional stimulus (for example, meat powder to the tongue which elicits salivation). After a number of pairings, the conditional signal is seen to elicit a response that is similar to that elicited by the unconditional stimulus. Emitted behavior is behavior, which is produced by the subject in order to obtain a desirable outcome (commonly called a reinforcer): such behavior is said to operate upon the environment to produce reinforcement. In typical studies of operant conditioning, the availability of the reinforcer is signaled by a cue of some sort. Thus, the relationship between elicited and emitted behavior is complex. However, any discussion of this issue goes well beyond the subject matter of this essay.

Operational Closure

Definition

Operational (or organizational) closure means that certain relations and processes define a system as a unity, in determining the dynamics of interaction and transformations that the system may undergo as such a unity (Maturana/Varela). Operationally closed systems are not causally closed, i.e. they may interact causally with the environment.

Operculum

Definition

Part of the posterior portion of the inferior frontal gyrus of the frontal lobe in the brain.

Ophiid (Type)

Definition

“Snake-like,” “snake-type.”

►Evolution of the Brain: At the Reptile-Bird Transition

Opioid

Definition

Any compound or substance that binds to the opioid receptor resulting in the activation of the receptor.

►Analgesia

Opioid Peptides

Definition

Opioid peptides are short sequences of amino acids which mimic the effect of opiates in the brain. Endogenous opioid peptides are derived from three gene families, β-endorphins, enkephalins and dynorphins. Three types of opioid receptors, μ, δ and κ receptors, are pharmacologically identified.

Opisthotonus

Definition

Arched back produced by tonic contractions of the back muscles, for example in ►tetanus.

►Tetanus (Pathological)

OPN4

►Melanopsin