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Operant Variability and the Evolution of Volition

Allen Neuringer
Reed College, USA

Volition has been debated for thousands of years: what is it, how is it possible for biophysical beings to behave in a voluntary manner, indeed, does volition exist? Evolution of volition has rarely been part of the discussion. In this paper, I argue that operant-conditioning studies provide evidence for evolved volition. Three attributes are common to operant and voluntary behaviors. One is that responses are goal-directed, purposeful, some say rational, or controlled by reinforcing consequences. A second is that the responses vary – from random-like to repetitive – with predictability (or unpredictability) depending upon contexts and consequences. A third attribute is that responses appear to be self-generated or, in operant terms, emitted. These attributes are found in many species, simple to complex, but species also differ in details. Taken together, the evidence supports an evolutionary basis of volition.

Volition has been the source of debate for more than 2000 years and the topic continues to be a focus in philosophy (Kane, 2002), physiology (Prochazka, Clarac, Loeb, Rothwell, & Wolpay, 2000) and psychology (Baer, Kaufman, & Baumeister, 2008). The evolution of volition has rarely been part of the discussion: most writers on the topic assume that it is unique to human beings. If volition, in fact, depends upon unique aspects of human brain, consciousness or language, it might be fruitless to seek its evolutionary heritage. My goal in the present paper is limited to one question: is the evidence consistent with the claim that volition has evolved? I cannot identify a common ancestor or multiple lineages. Rather, I will try to show that non-human animals, across many species, show the progenitors of voluntary behaviors (for ease of presentation referred to as 'volition'), and that species differ in levels or degrees of voluntary control.

Volition is an elusive concept and I therefore begin by discussing it from three points of view, those of layperson, philosopher, and operant researcher. Many disagreements exist, but I focus on three areas of agreement to facilitate an evaluation of volition's evolutionary roots.

The Layperson's View

i) Voluntary Acts Have a Purpose, Goal, Or Reason

Voluntary behaviors are explained by their purpose, intent, or goal, or as an attempt to acquire or accomplish some end. When asked, "Why did you do that?" the normal adult might reply, "I cooked because I was hungry and wanted to eat," or "I stopped the car because the traffic light turned red." Actions are explained by reasons and desired consequences. The purposeful or goal-oriented aspects of a voluntary act provide information that enables its prediction – whether the actor is oneself or another individual. This is

Please send correspondence to Allen Neuringer, Psychology Department, Reed College Portland, Oregon 97202. (Mailto: allen.neuringer@reed.edu)

especially true for habitual acts (e.g., what you do upon waking in the morning, the route you take when you walk from one often-visited place to another, the timing and sequencing of your working, eating, and relaxing activities, and so on). Thus, knowledge of goals and habits can lead to accurate predictions of voluntary behaviors.

ii) Voluntary Acts are Sometimes Unpredictable

At the same time, if an act is voluntary, it is assumed that it could be done differently or withheld completely. That is, a second characteristic of volition is demonstrated or potential unpredictability. Acting in an unexpected manner, playing a trick, and punning are examples of unpredictable (at least to some extent) behaviors. Many games involve intentional unpredictability (e.g., repeatedly hiding a penny in your left or right hand and presenting closed fists for a child to predict, or attempting to outwit an opponent in a competitive game or sport). In other cases, people hide their true goals and motivations and act deceptively, so as counter prediction. Even when the behavior is repetitive and habitual, it is assumed that the individual *could have* behaved unpredictably. That is, the potential to act in unusual and different ways – a characteristic of all voluntary behavior – trumps the goal-dependent predictability of many voluntary responses.

iii) Voluntary Acts are Freely Chosen

It is commonly believed that people initiate – decide, cause, choose – their voluntary actions. These behaviors are not compelled or pushed by outside forces, such as physical constraints or threats of harm, nor are they forced by internal compulsions due to addictions and physiological malfunctions. The choice and exact timing of an action are all 'up to' the actor – who is free to do what she or he wants. And just as self-initiation is an attribute of the voluntary act, so too is ability to inhibit – to choose *not* to behave in a given manner. Thus, *self-initiation* and *self-control* are commonly noted attributes of volition, with emphasis on self.

In brief, then, as commonly conceived, voluntary acts are goal-directed and therefore often times predictable but other times not, and self initiated. There are, of course, other attributes, such as intentionality and responsibility, but I will attempt to show that the three named will enable assessment of whether volition has evolved.

Philosophical Positions

Among the many explanations of volition offered by philosophers, three are related to the just discussed attributes and will be referred to under the headings of determinism, indeterminism and free will (Doyle, 2011; Kane, 2002).

i) Determinism

Some philosophers argue that all behaviors are determined. Humans are biological and physical beings, and responses are caused by biophysical events. The determinist assumes that reasons for actions – purposes, goals, desires to accomplish and the like – are caused by a combination of genetic variables, prior experiences, current conditions and other identifiable causes. If "I did it because I desired some outcome" was the reason given, then availability of external goods and prior experiences, in combination with my biology, determine my desires. Thus, the determinist posits causes for goals and purposes, and a causal flow from these to actions.

Determinist interpretations of volition have been traced back to Democritus in the 5th century BC and are a prevalent theme in western thought, gaining strength with the developments of Newtonian physics, the British Associationist philosophers, and in psychology, Freud, Pavlov and Watson. Today, most researchers in psychology assume that human actions can be explained (perhaps completely) by functional relationships between environmental or physiological variables and behavior. Behavioral, social and cognitive psychologists identify environmental events that accurately predict responses even when participants perceive the responses to be under their own voluntary control (e.g., Wegner, 2002). Physiological studies show that conscious thoughts and perception sometimes follow – not anticipate – the initiation of *voluntary* acts, and because consciousness is often posited as a prerequisite for volition, the very idea of *volitional* action has been questioned (Fried, Mukamel, & Kreiman, 2011). Much research is consistent with a deterministic interpretation and philosophers cite that research to support their position.

How, then, do determinists account for the belief in volition? Certainly they do not accept that volitions are uncaused but rather they describe different types of relationships. For example, if the child is held by her arm and forced to walk to the other side of the room, her actions would be referred to as involuntary. However, if the child sees a treat on the other side of the room and runs to it, her actions would be described as voluntary. The difference, according to the determinist, is in the type of causal relationship but in neither case can the action be attributed to an autonomous (independent of environmental influence) agent.

ii) Indeterminism

A competing position is that an internal source of randomness or indeterminacy frees the individual from environmental determination. This idea was first introduced by Epicurus in the 3rd century BC and more than 2000 years later both Gustav Fechner and William James hypothesized indeterminate contributions to human choice (see Doyle, 2011; Heidelberger, 2004). Developments in quantum physics are cited to support the indeterminist position.

iii) Free Will

A third philosophical position is that free will is a uniquely human capacity inherent in soul, mind, consciousness, or, most recently, central nervous system massive interconnectivity (Edelman, Gally, & Baars, 2011). When we act in a way that has no identifiable external cause, and do so under our own initiative; or when we deliberate –covertly talk to ourselves, and imagine – the resulting action is said to be due to our free will. Voluntary behaviors, according to this interpretation, are the external manifestations of the uniquely human capacity to act independently of environmental dictates, with freely willed actions initiated internally and not dependent upon (nor predictable from knowledge of) external causes.

Numerous philosophers have argued for and against each of these philosophical positions. Free will is said to be an *ad hoc* hypothesis that cannot be tested empirically. Additionally, the free-will position is increasingly hard to maintain as evidence accumulates concerning the environmental causes of (so-called) voluntary actions. Determinism and indeterminism are often contrasted, with evidence for one offered as proof against the other. According to some, determinism leaves no room for (truly) volitional behavior. If behavior is (completely) determined, then the belief in self-initiation and free-willed choice is a false belief. Indeterminists hypothesize control by random processes, but what, then, is the contribution of the actor? If responses are controlled by random events at the level of neural communications (for which there is increasing evidence, e.g., Glimcher, 2005), then the actor (or the *self*) has no independent control. Furthermore, random responses could lead to absurd acts and consequences that would maim the actor. Thus, supports for each of the described positions are offered and met with reasons to reject each. A contemporary philosopher puts the situation as follows:

> The problem of free will in its broadest outline is this. Free will seems to be incompatible with both determinism and indeterminism. Free will seems, therefore, to be impossible. But free will also seems to exist. The impossible therefore seems to exist. (Van Inwagen, 2000, p. 169)

My view is that there is value in each of the three positions. Voluntary behaviors are generally goal-oriented or purpose-guided (thereby sometimes providing a high degree of predictability); they are sometimes (truly) unpredictable, in part because of their probabilistic or stochastic – the two terms are used interchangeably – nature and in part because unpredictability is sometimes adaptive; and they appear to emanate *from within*. Operant-conditioning research and theory provide parallels to each of these.

Operant Conditioning

Instance, Class, and Contingency

It will be helpful first to distinguish among three usages of the term, *operant*. In one case, the term refers to an individual response, an instance, such as in “the rat’s response was reinforced,” with the response being a particular left-paw depression of the lever.

A second usage is operant as a *class,* comprised of individual responses, each of which results in a common reinforcer. Class is implied when it is said that an operant is learned or conditioned. For example, “The rat’s lever-press was conditioned” refers to the operant class that consists of the many ways that the rat depressed the lever (and was reinforced for so doing), including left and right paw pressing, jumping, biting, and the like. Skinner described the operant as a “generic” class that can include diverse structural or topographic characteristics (Skinner, 1935a). For example, reaching for a saltshaker and asking your partner to pass the salt might be members of a single operant class. In technical terms, the saltshaker serves as a discriminative stimulus and the different responses, both members of an operant class, are reinforced by access to salt. As will be seen in much that follows, the characterization of the operant as a class is important for an understanding of volition.

The third usage refers to a three-term contingency, this too described by Skinner. In the presence of a discriminative stimulus, if a response results in a reinforcer, then when that stimulus is again experienced, the response is likely (or more likely) to be emitted. Because both discriminative stimuli and reinforcing consequences influence the occurrence of members of an operant class, it can be said that ‘what is learned’ is the three-term contingency. The generic term, *operant behavior,* implies all three, namely an operant *response* (or instance), emitted as a member of an operant *class,* which is under the control of an operant *contingency*. I will now discuss operant parallels to the lay and philosopher characterizations of volition.

i) Operant Responses are Directed at and Controlled by Reinforcers

Skinner placed the *cause* of an operant response in the reinforcement contingency: reinforcers that are contingent upon them select and strengthen the responses. The relationship is bi-directional: a response produces the reinforcer and the reinforcer influences future occurrences of the response. Reinforcing consequences thus serve as a *cause* for future operant behavior and knowledge by an observer of the history of response-reinforcer relationships enables prediction of future actions. Stated in its extreme form, reinforcement contingencies *determine* operant behavior. Indeed, Skinner often took a determinist stance:

> We have moved forward by dispossessing autonomous man… This escape route is slowly closed as new evidences of the predictability of human behavior are discovered. (Skinner, 1971, p. 19-21)
>
> We cannot prove…that human behavior…is fully determined, but the proposition becomes more plausible as facts accumulate. (Skinner, 1974, p. 189)

Skinner's determinism is consistent with positions maintained across the different sub-fields of psychology

> Determinism makes free will possible. It also makes psychology possible. If psychological events were not determined – caused – by antecedent events, psychology could make no sense. (Baer, 2008, p. 309)
>
> If you want to be a scientist, you better be a determinist…It is a proper job for a scientist to find and document (via experimental studies) the cause-effect relations that form and guide human actions. Therefore, I am a determinist. (Howard, 2008, p. 261)

Most scientists, operant behaviorists included, argue that determinism must be assumed in order to maintain the search for causal relationships and for science to progress.

ii) Operant Responses are Unpredictable

While most behaviorists assume that behavior is determined, operant theory also posits an underlying unpredictability – or variability – of operant responses. As indicated above, when a rat is reinforced for pressing a lever, any action that depresses the lever suffices to produce a food pellet. Especially early in training, the rat may press in different ways, with some of these becoming members of the 'lever-press class' that continue throughout the remaining stages of conditioning. Skinner described the individual members of the class in terms of probabilities, with instances emerging probabilistically from within the class, i.e., they appear to be generated by a stochastic process.

> Suppose that we are studying the behavior of . . . a rat in pressing a lever. The number of distinguishable acts on the part of the rat which will give the required movement of the lever is indefinite and very large. . . They constitute a class, which is . . . defined by the phrase "pressing the lever." Now it may be shown that . . . the rate of (lever-press) responding . . . maintains itself or changes in lawful ways. But the responses which contribute to this total number-per-unit-time are not identical. *They are selected at random from the whole class* [emphasis added] – that is, by circumstances which are independent of the conditions determining the rate. (Skinner 1935a, pp. 44-45; see also Malone, 1987; Moxley, 1997, Skinner, 1938)

As will be described below, the variability of operant responses is not "random" in the sense of all responses having equal probabilities. Rather the probability distribution is precisely influenced by reinforcement contingencies.

iii) Operant Responses are Emitted

In the early days of behavioral experimentation, as exemplified by Thorndike, Hull, and many others, responses were thought to be elicited by prior stimuli. Skinner (1935b) held the same view in his earliest publications. Reinforcers served to establish (or stamp in) the power of particular stimuli – present when a response was reinforced – to elicit future responses. Skinner's later research took him in a different direction, in large part because when rats were free to respond at any time for food reinforcers – with external stimuli held constant – the behaviors could not be described in stimulus-response terms. Skinner (1974) said it this way:

> To distinguish an operant from an elicited reflex we say that the operant is 'emitted.' (It might be better to say simply that it appears, since emission may imply that behavior exists inside the organism and then comes out. But the word need not mean ejection; light is not in the hot filament before it is emitted). The principal feature is that *there seems to be no necessary prior causal event* [emphasis added]. (pp. 52-53)

The failure to identify eliciting causes led to the idea of the operant class – a grouping of responses – with individual instances 'emitted' from the class. One difference between Stimulus-Response and Emitted-Response analyses is that a *particular response* is predicted in the former case and a *distribution of possible responses*, each with some associated probability, in the latter.

Explaining Volition

What does it mean for an action to be *freely chosen* (in lay terms), or due to our *free will* (philosophers), or *emitted* (behaviorists)? Simply put, what does it mean for an action to be voluntary? Consider first unpredictability. Unpredictability is common in physics and biology, with examples provided by random emission of atomic particles and random assortment of genes during meiosis, and we generally do not attribute volition to those kinds of events. Moreover, as indicated above, random actions do not provide for 'personal control,' any more than do determined reactions. That is, random acts are not the kind of behavior we attribute (most of the time) to voluntary actors. Rather, voluntary behaviors are generally thought to be goal-directed, functional and (for some) rational. Thus, unpredictability alone cannot explain volition.

Consider reinforcement next. Reinforcement contributes importantly to the control of operant behavior but it, too, does not explain operant emission or volition. Selection by consequences, a phrase often used to describe reinforcement, occurs in many domains not normally characterized as voluntary, including development of the nervous system, generation of antibodies, and phylogenetic evolution. Even direct "operant reinforcement" is insufficient to indicate volition. An example is dopamine administration contingent upon firing of a single brain neuron leading to increased firing (Stein, Xue, & Belluzzi, 1994). Although the neuron may model some aspects of voluntary action, most of us would not attribute volition when the only indication is increased action-potential frequency, even when that depends upon contingent dopamine. Thus, neither reinforcement alone nor unpredictability alone explains volition.

I will argue in the remainder of the paper that control by reinforcement of both classes of responses and (un)predictability of responses explains the unique nature of emitted operant behavior and of voluntary action. The hypothesis in more detail is that, because of previous experiences with reinforcement contingencies, (i) a set of potential responses is activated by the current context; (ii) the context also controls the probabilities (or uncertainties) of the activated instances; and (iii) the resulting action therefore appears to have emanated from internal processes (from within). Because of the relationships of both type and (un)predictability of response to reinforcement contingencies, the voluntary operant is functional (or intended to be functional). Probabilistic emergence of functional instances from a class provides the unique attributes of emitted operant behaviors *and* the unique attributes of volition: controlled and functional actions whose (un)predictability is itself functional.

More than 80 years of operant-conditioning research shows that reinforcers control operant response topographies, frequencies, forces and the like, and that literature will not be reviewed. Until relatively recently, however, the variability of operant behavior was generally attributed to 'noise', to ignorance (of the observer), or to *induction* or *elicitation (*by such things as drugs, deprivation, or distance from reinforcement -- as will be discussed below). The next section describes evidence critical to the position taken in this paper, namely that reinforcers directly control response (un)predictability, a less widely acknowledged phenomenon.

Variability is Controlled by Reinforcement Contingencies

Variability is an operant dimension, controlled by reinforcement contingencies in ways similar to the other dimensions (reviewed in Neuringer, 2002; Neuringer & Jensen, 2012). Here is some of the evidence. (1) When variability is required for reinforcement, much higher levels are maintained than when variability is not a controlling dimension. For example, pigeons generated highly variable response sequences across two keys only when variability was explicitly reinforced. When food was provided independently of the variability, 'easy' sequences were repeated (Page & Neuringer, 1985). (2) Levels of variability are controlled by discriminative cues. For example, in the presence of one stimulus, pigeons learn to repeat a single sequence whereas given a different stimulus, they respond variably (Abreu-Rodrigues, Lattal, Santos, & Matos, 2005; Arantes, Berg, Le, & Grace, 2012; Souza & Abreu-Rodrigues, 2010; Ward, Kynaston, Bailey, & Odum, 2008). The same discriminative control is observed in rats (Abreu-Rodrigues et al., 2004; Denney & Neuringer, 1998). (3) When reinforcement is contingent upon a specific level of variability, from repetition to random-like, that level is produced (Grunow & Neuringer, 2002; Jensen, Miller & Neuringer, 2006; Page & Neuringer, 1985). (4) Reinforcement of variability has been demonstrated across many types of responses, including lever presses and button or key pushes, body movements, soccer kicks, block building, picture drawing, saccadic eye movements, animal vocalizations, and human language, among others (reviewed in Neuringer, 2002; see also Paeye & Madelain, 2011; Schusterman & Reichmuth, 2008). Taken together, the evidence strongly indicates that variability is a dimension of behavior that comes under the control of contingencies of reinforcement (see Barba, 2012a and 2012b for an opposing view).

Operant Classes

A set or class of responses is implied whenever variability is reinforced. This is true both formally (in terms of measurements and statistical evaluations) and empirically (in terms of reinforcement contingencies). Sometimes individual members of the class are explicitly specified, as when 16 different sequences of left and right responses define the class. Sometimes the class is more loosely defined, as when porpoises were reinforced for novel (never-before-emitted) response topographies (Pryor, Haag, & O'Reilly, 1969).

Operant classes differ from one another in many ways: in terms of the types or topographies of responses that comprise the class; the numbers of response instances in the class; the probability distributions of within-class instances; the ease with which new classes are established and modified, including segregation of one class into two or more and combinations of classes; and in the modifiability of dimensions of within-class instances, including force, duration, latency and topography. These differences can affect the predictability of response outputs. Thus, for example, if within-class instances are equally probable, then as class size increases, predictability decreases. If probabilities of within-class instances differ from one another, then prediction accuracy increases with increasing differences. Figure 1 provides cartoon depictions of four hypothetical operant classes. In each case, a class (indicated by a large circle) is activated by a discriminative stimulus (S^D). In A, the class is comprised of nine equiprobable (equal strength) response instances, as when an individual emits the digits 1 through 9 with equal probabilities and is reinforced (S^R) for so doing. In B, the class contains only two equiprobable response instances, as when an individual responds optimally in a matching pennies game. In C, the within-class response probabilities differ, indicated by the different sized circles. An example is provided by many competitive games, such as basketball, where probabilities of actions differ due to the particulars of the situation but still maintain high degrees of uncertainty. Lastly D represents the hierarchical nature of some operant classes, as when an individual is asked to name an animal and conjures up two types, farm animals and zoo animals, resulting in one class being activated and, in turn, an instance emerging.

Reinforcers play a dual role in that they specify both the types of responses that constitute a class and the predictability of instances that emerge from the class. Two examples will illustrate this point. In a chamber containing three keys and two levers, rats were reinforced for variable responding across the two levers but only one of the keys, i.e., three of the five operanda were active. The rats learned to distribute their responses variably on the three active operanda and rarely or never responded on the other two (Neuringer, Kornell & Olufs, 2001). In another experiment, rats were reinforced for varying sequences of four responses on two levers, L and R, and distributed their responses across the 16 possible sequences. When the reinforcement contingency changed so that a sequence was reinforced only if it began with LL, this resulted in increased probabilities of variations among only those sequences, e.g., LLRL, LLLR, LLLL. Thus the contingencies reinforced a combination of sequence types and variations (Mook, Jeffrey & Neuringer, 1993; see also Ross & Neuringer, 2002). More generally, when variable responses are reinforced, both “what to vary” and “how much to vary” are influenced by discriminative cues and reinforcing consequences.

Operant Responses and Voluntary Actions

What is true for operants is true as well for volitions: “what to do” and “how predictably to do it” are both influenced by contexts and consequences. For example, if a police officer demands your name, you are highly likely to provide your true name; but in a game of “fool the questioner,” you may be more likely to emit a name that would be difficult to predict (e.g., “I’m Frosty the Snowman”). In many competitive games, responses are sometimes highly predictable (when the soccer player kicks the ball towards the net) and sometimes unpredictable (the stops and turns as the player runs across mid-field). Variations in predictability are part of creative activities as well. For example, Leonard Bernstein described how classical composers establish expectations (with sequences of notes) and then provide surprising resolutions. And a translation of a Baudelaire poem, *Enivrez-vous*, contains the following line: “Get drunk, with wine, poetry, or virtue...” Virtue? Ah, yes.

Voluntary actions span the range of predictability, from expected to unexpected, predictable to unpredictable, random-like to repetitive, and do so (or are intended to do so) appropriately or functionally. Indeed, the ability to *vary levels of predictability* is a sign of volition. Just as high variability does not by itself indicate operant control, so, too, high variability (or apparent indeterminacy) is not sufficient to indicate voluntary control. The novice violinist may vary the sounds that emerge from the violin, but the result is uncontrolled noise. The accomplished violinist has exact control over those sounds, with an ability to play in a highly predictable fashion (a well-known piece of music) or to vary individual dimensions, including loudness, pitch, and timbre. The same can be said about more common voluntary actions (e.g., the difference between an infant's reach for an object and an adult's). The infant is uncontrollably variable whereas variability of an adult's reach is related to the momentary demands (e.g., pressing the doorbell versus playing with a puppy). Thus for both operant and volition, consequences control predictability (Vereijken, 2010). The parallel suggests that actions will appear to be voluntary when operant control of variability is observed, and I turn next to experimental evidence that supports this claim.

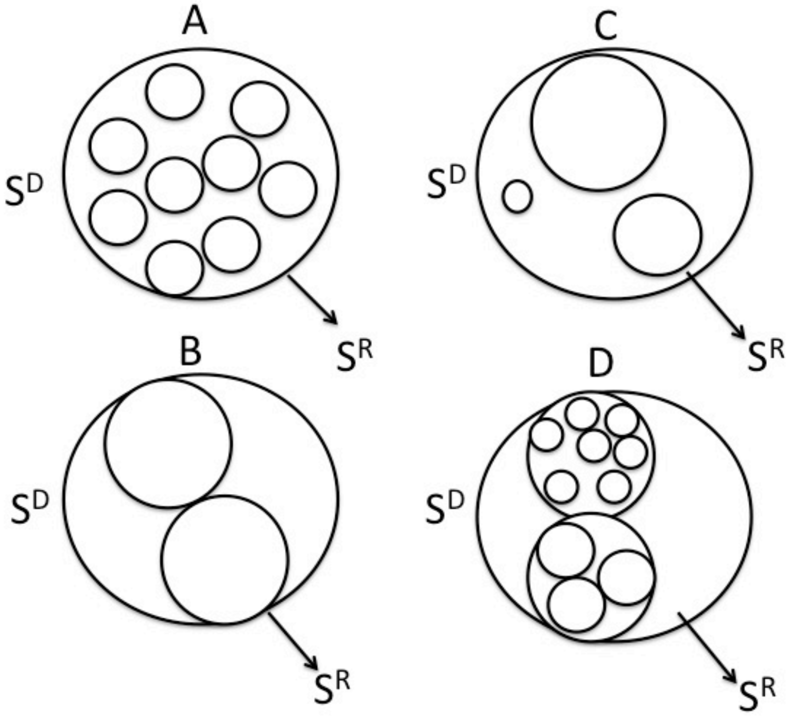

Figure 1. Conceptual cartoons of four operant response classes. The large circles represent four classes. The smaller circles represent individual response instances within each class. The sizes of the small circles represent their probabilities or strengths. A = class comprised of nine equiprobable instances. B = class comprised of two equiprobable instances. C = Class comprised of three instances with different probabilities or strengths. D = Hierarchical class comprised of two sub-classes, each of which is comprised of equiprobable instances, three in one case and seven in the other. S^D = discriminative stimulus that 'sets the occasion' for activation of a response class. S^R = reinforcement that is contingent upon emission of a within-class response.

Operant Variability and Voluntary Action: Experimental Evidence

According to the lay and philosophers' views discussed above, both unpredictability and consequence-directed predictability are signs of volition. Experimental evidence supports these views. For example, psychophysical experiments with human participants show that randomly moving objects appear more animate than repetitive and predictably moving ones (Pratt, Radulescu, Guo, & Abrams, 2010). Other experiments show that objects that produce reinforcement-like consequences appear more animate than objects for which outcomes are independent of actions (Tremoulet & Feldman, 2006). Each of these effects may contribute to attributions of volition but, as I argued above, neither alone suffices. To restate: highly variable behaviors *that are not functional* – as, for example, in ADHD – do not provide evidence for volition. Equally, reinforced predictable (or repeated) behaviors *that never vary* also provide insufficient evidence for volition – as seen in addictions and obsessive-compulsive behaviors. Rather, actors appear to behave voluntarily when both type and predictability of action are governed by reinforcing consequences.

To test this hypothesized relationship between volition and operants, Greg Jensen, Paul Piff, and I performed a series of psychophysical experiments in which a moving icon on the screen of a computer (a small dot) represented a virtual actor that chose repeatedly among three alternatives (the choices being represented by movements of the dot in three different directions) (Neuringer & Jensen, 2010; Neuringer, Jensen & Piff, 2007). Human participants observed as the actor's choices were occasionally reinforced (represented by a change in the dot's color) under concurrent schedules of reinforcement. Participants were asked to judge how well the actors' choices represented voluntary selections made by a real human player.

Highest estimates of volition were obtained when both choice distributions and choice predictability changed as functions of the reinforcement schedules. When only one or the other of these relationships was observed, volitional estimates decreased. Thus, for example, when choice distributions matched reinforcer distributions – thereby maximizing reinforcement under the experimental conditions – but individual choices could easily be predicted in all cases, assessment of volition was low. The results were consistent with the hypothesis that voluntary actions demonstrate functional *ways of responding* (in this case shown by response distributions) together with functional *levels of (un)predictability*. This conclusion indicates a way to study the evolution of volition, namely through cross-species comparisons of operant responses with emphasis on the control by reinforcers over both response classes and response (un)predictability. Before we turn to volition in non-human animals, I will describe how the present formulation differs from three related offerings.

What's New?

i) Skinnerian Operant Theory

The proposed relationship between volition and operants may seem like an old message to those familiar with Skinner's contributions and those of contemporary behavior analysts: he and others refer to the *voluntary operant*. The claim I make is similar – the operant is a model of voluntary action – but I attempt to explain *operant emission*, something generally ignored in the past. It is not probabilistic (and unpredictable) generation alone that accounts for the voluntary nature of the operant. Nor is the absence of prior eliciting stimuli sufficient, nor the contingent response-reinforcement relationship. Rather it is the fact that reinforcement contingencies influence not only the activated class of operant responses (types and properties of response), but also the within-class probabilities (or probability distributions), and these change moment-to-moment as the stimuli, context, and contingencies change moment-to-moment. Critical attributes of volition depend upon the sensitivity of *both* response class and probability to consequences. The dual sensitivity results in highly unpredictable behaviors *sometimes* and highly predictable behaviors at other times but functional (or intended to be functional) in all cases of voluntary action. The Skinnerian corpus suggests that responses become increasingly predictable with reinforcement experience, but that happens only *sometimes*, and the 'times' depend upon the contingencies. Thus operant classes do not always narrow and voluntary actions are not inexorable. To anticipate what follows, the malleability of operant classes is itself a variable and, consistent with the evolutionary roots of volition, it differs across species.

ii) Jamesian Two-Stage Free-Will Theories

Readers familiar with William James' writings on volition (James, 1884/1956) and more recent developments in philosophy (Dennett, 2003; Doyle, 2011; Kane, 1985), may also wonder about the originality of the present contribution. These *two-stage theories* argue that volition can be explained by a combination of random and determined components, thereby yielding both degrees of predictability and autonomy. There are two basic forms of two-stage theory. In one, options are randomly generated and followed by deterministic selection, e.g., while sitting at my desk, I might (randomly) think of activities for this evening, these options then considered rationally so that I deterministically select the best option. This form of theory might be referred to as random generation followed by determined selection. The second form of the theory reverses these: deterministically generated options are followed by random selection.

I see two problems with previous two-stage theories. First, they generally imply that *random selection* is a constant, with options being equally likely. A large body of experimental literature demonstrates that the equiprobability assumption is incorrect: choice probabilities are highly sensitive to reinforcement allocations and contingencies (Davison & McCarthy, 1988; Jensen & Neuringer, 2008). A second problem is that the set of options is *either* randomly generated (for some theories) *or* deterministically provided (for others). On the other side of the process, selection is *either* random (for some theories) *or* determined. The present formulation integrates the random and determined aspects in the following way. First, histories of reinforcement and other experiences establish responses that have different probabilities of (in the future) emerging from an activated class. Thus there are deterministic influences (e.g., reinforcement) with response *probabilities* (or response strengths) the result. Second, the current conditions, such as contexts, stimuli, and potential reinforcers probabilistically engender membership in the class (which responses are activated) as well as the distribution of the individual probabilities (strengths) of the members. Thus again we see deterministic and probabilistic influences combined. Instances are probabilistically selected (to become members of an operant class) and selectively probable (as to their emission from the class). Probability and selection are present at every stage of class formation and response emission. The difference between previous two-stage theories and the present one is that here the two stages are integrated.

iii) Brembs' Non-Linear Dynamical Model

Björn Brembs, a neuroscientist who focuses on invertebrate species, has suggested that voluntary behaviors (e.g., in fruit flies) can be explained by non-linear dynamical activity in the brain, activity that is more or less variable, depending upon circumstances, and is at least in part independent of environmental inputs (Brembs, 2011). Brembs provides evidence consistent with these claims. As in the present paper, Brembs emphasizes the controlled and adaptive nature of variability, but his examples indicate that the default state is one of variability and that responses become predictable when reinforced. Decreased variability with learning is commonly emphasized in most operant conditioning studies but low variability is not a necessary or general characteristic of operant behavior.

A second difference between Brembs' position and the present one is his emphasis on non-linear dynamical (chaos) models to account for variability versus the present emphasis on class-based stochastic models. Brembs argues that deterministic-type processes provide the internal control necessary for levels of variability to change adaptively. These non-linear models can indeed generate different levels of predictability, including random-like outputs, and therefore provide a possible basis for the variations that are a signature attribute of volition. However, it is not clear how non-linear models account for the class nature of operant responses, the malleability of classes, and within-class dynamics. The two models may underlie different aspects of volition. For example, dynamical processes might be responsible for "additive continua" (Stevens, 1957) such as the speed and force of repeated responses, whereas class-based stochastic processes might control "substitutive processes," such as choices among locations, actions, or goals (reinforcers). Lastly, Brembs presents the two-stage model that I critiqued in the previous section. In many ways, however, I agree with the overarching theory and applaud Brembs' research.

Interim Conclusion

The operant has characteristics commonly attributed to voluntary action. Operant responses are goal-directed and consequence-influenced. This describes not only the type or quality of the operant, but also the predictability of operant instances. Because predictability varies – from repetitions to random – and does so functionally, the operant appears to be internally controlled. It thus satisfies three criterial attributes of volition: appearance of control from within; goal-directedness; and more-or-less predictability, depending upon circumstances. I present an unusual view of the operant, unusual in that it highlights direct control of unpredictability by reinforcement contingencies. But viewing the operant in this light provides a way to assess volition across different species, to which I next turn.

Stasis and Diversity in the Evolution of Volition

When attempting to assess evolutionary history, one must examine characteristics that differ across species as well as common ones (Papini, 2002). The evolution of genes is a case in point, with many genes conserved while others differ. The following sections describe three characteristics of volitional action that have been highlighted throughout this paper: reinforcement, variability, and operant response emission. Each of these is seen across a wide spectrum of species, but differences also emerge.

i) Reinforcement

From planaria and aplysia, through fruit flies and honeybees, to fish, birds, rodents, monkeys and humans, when responses are reinforced, they increase in frequency (e.g., as seen in journals such as *Behavioural Processes; Journal of Experimental Psychology: Animal Behavior Processes; and Journal of the Experimental Analysis of Behavior;* see also Brembs, 2003, 2011; Giurfa, 2007). However, species differ in types (or topographies) of operant responses and in the number of different operants that have been conditioned. Thus, for example, rats, pigeons, dogs, horses, monkeys, elephants and many other vertebrate species have been trained to emit complex responses under control of discriminative stimuli and reinforcers (McGreevy & Boakes, 2011) but nothing approaching that has been reported (at least to this date) for invertebrate species. Species may also differ in sensitivity to conditioned reinforcers; to attributes of reinforcers, such as delay and magnitude; and in the sensitivity to reinforcement of response dimensions, such as latency, force, frequency, topography and variability. Consistent with an evolutionary hypothesis, sensitivity to reinforcement has been correlated with genetic differences (Ferguson, Cobey & Smith, 2001; Luman, Tripp & Scheres, 2010; Shabani et al., 2012).

ii) Induced Variability

Behavioral variability is observed across many species, from simple to complex, but most often reported is *induced* (or elicited) variability where specific stimuli elicit the same responses in all members of a species. The *E. coli* bacterium provides an example at the simple end of the evolutionary spectrum. *E. coli tumbles* randomly when its environment lacks nutrients, thereby moving unpredictably in space, but moves straight ahead when it comes upon a gradient of nutrients that improves in quality (Berg, 2000; Staddon, 2001). Driver and Humphries (1988) describe elicited *protean*, or random-like, behaviors in many other species. Threats of predation commonly elicit protean responses. For example, rabbits zig and zag, impala scatter unpredictably, many species of birds show erratic flight patterns, and fish demonstrate random swimming trajectories– all in response to the anticipation or appearance of a predator. Groups of animals sometimes respond randomly as a strategy to counter-attack a predator, e.g., when a hornbill (a tropical bird) is attacked by a snake, other hornbills will rush at the snake from unpredictable locations and in random order. In each of these cases, the behaviors are random but within functional constraints. The constraints are of two forms. First, the variable behaviors are elicited only by specific conditions (e.g., presence of a predator). Second, the responses increase the likelihood of escape, avoidance or protection, but the particulars differ, depending upon the individual species. Escape responses of cockroaches demonstrate the constrained nature of protean behaviors. When a threatening object approaches, e.g., a human hand, the cockroach moves in a direction away from the hand, but within that constraint, the particular angle of movements is random (Domenici, Booth, Blagbum & Bacon, 2008). Thus, protean behaviors demonstrate evolved classes of specific responses that occur in random-like fashion.

Elicited variability is also observed as a side effect of reinforcement schedules. For example, variability of operant responses increases when reinforcement frequencies decrease (see, e.g., Neuringer, Kornell, & Olufs, 2001; Stahlman & Blaisdell, 2011). This variability is not part of the reinforcement contingency – variability does not produce reinforcement – but occurs as an induced or elicited effect. Proximity to reinforcement – in time or space – also induces variability, with the greater the distance from reinforcement, the higher the variability, an effect observed whether or not variability is explicitly reinforced (Cherot, Jones, & Neuringer, 1996). A related finding is that small rewards induce higher levels of variability than larger (Doughty, Giorno, & Miller, 2013). The conclusion, from both observational (e.g., on protean responses) and experimental (e.g., on reinforced responses) research is that stimulus-elicited, unpredictable responding is common across many species, from simple to complex. But as is the case for reinforcement effects, characteristics of elicited variations – including number, type, and complexity of responses – differ across species. Also as with reinforcement, response variability has been related to genetic differences (Antonini, Narad, Langberg, & Epstein, 2013; Dingemanse, Both, Drent, Van Oers, & Noordwijk, 2002; Perry, Sagvolden, & Faraone, 2010; Schmitt & Hiemke, 1998).

iii) Operant Class and Voluntary Emission

The voluntary nature of operant responses derives from reinforcement of response classes (types, characteristics, topographies of class members) and within class probability distributions. To the best of my knowledge, there are few comparative studies of operant-class formation and dynamics, but informal observations suggest that species differ in a number of ways. To take an extreme comparison, the volitional competency of *E. coli* differs from the human artist because the number of response classes is extremely limited in the case of *E. coli* and approaches limitlessness for humans. Also differing in extreme ways are the abilities to vary levels of variability under influence of consequences. Whereas *E. coli* tumbles randomly or moves repetitively – two points along the variability continuum – for pigeons, rats, and humans reinforcement contingencies control precise levels of variability that span the continuum (Grunow & Neuringer, 2002; Jensen, Miller, & Neuringer,2006; Machado, 1989; Neuringer, 1992; Page & Neuringer, 1985).

A comparison of the tongue-like protrusions of aplysia and human language makes a similar point. Frequencies of protrusions change when food is contingent upon it (Nargeot, Petrissans, & Simmers, 2007). Random or rhythmic tongue protrusions may define the totality of the aplysia response class, one or the other. Humans, of course, demonstrate massively complex linguistic classes. At each point in the generation of verbal output, a class of possible next utterances is activated, in part by the previous utterances, in part by context, and in part by the overarching goal of the utterances. These same controlling variables influence within-class probabilities. Both verbal classes and within-class probability distributions are therefore readily manipulable. My point is that the complexity and dynamics of operant classes provide a continuum on which species differ, and volitional competency is indicated by that same continuum. Implied is that volition is not a dichotomy, e.g., not simply voluntary or involuntary. Individuals *within* a species also demonstrate different levels of volitional control and, for a given individual, volitional control varies as a function of the response domain. For example, if a professional violinist were compared to a professional tennis player, their voluntary controls would differ, depending upon the response class domain. In brief, levels of voluntary control are functions of operant response classes, between and within species, as well as within individual members of a species.

Operant variability provides a measure of operant class dynamics and therefore of voluntary control. To the extent that variability is *not* sensitive to control by reinforcers, volition would be counter-indicated. For example, Blough (1966) reinforced pigeons for emitting responses that approximated an atomic emitter with exponentially distributed times between responses (or interresponse times). The birds succeeded to a surprising extent, but very short interresponse times had to be omitted from the contingency and analysis – this because the short times were insensitive to the reinforcement contingencies. Thus, voluntary control over short interresponse times could not be attained. Morgan and Neuringer (1990) compared the effects of three different response topographies on rats' ability to vary when variability was reinforced. Although the contingencies were the same across the three cases, highest variability was generated when responses were on the levers, intermediate levels on keys, and lowest levels when pulls on overhead wires were the operants. According to the present analysis, voluntary control of lever presses exceeded that of wire pulls. The biasing effects of response topographies were also shown when different topographies were included in a single operant class (Jensen & Neuringer, 2009). A reasonable hypothesis is that, compared to non-human animals, human beings show a much greater ability to vary – and most importantly to vary levels of variability – across widely different response classes and topographies, e.g., whether the responses are verbal or motor, and do so under precise control by contexts and consequences. For example, songbirds sing highly variable songs with levels of variability controlled by contexts (Slater & Lachlan, 2003). However, a much greater level of controlled variability is provided by the large number of words contained in the vocabularies of adult speakers, e.g., of English (upwards of 20,000 word families, with a single family consisting of variants such as run, ran, and running) (Goulden, Nation, & Read, 1990), and the astoundingly large number of meaningful combinations. All animals demonstrate variable behaviors, but the ranges of variations differ across species, as does the ability to control specific levels. Consistent with an evolutionary thesis, heritable differences in reinforced variability are observed across rat strains (Mook, Jeffrey, & Neuringer, 1993).

Related Evidence: Categorization and Tool Use

Probabilistic emissions from classes of functional responses has been documented in other domains, and I will discuss two. Categories are analogous to operants in that both depend upon establishment of response classes, often by reinforcing consequences. In both, stimuli and contexts activate classes comprised of many instances. When asked to "Name a country," a person might respond with "France, England, Haiti," or many other names. Analogously, when "Play the piano" is requested of an accomplished pianist, any number of different key sequences might be pressed. Humans categorize innumerable stimuli, e.g., colors, animals, fruit (Murphy, 2002). Humans are also adept at creating novel categories at the moment of request (Barsalou, 1987). In one experiment, for example, college students generated high to low probability instances of such categories as "something to eat on a diet" and "a thing that might fall on your head" (Neuringer et al., 2007). A high probability example of "fall on your head" was "rain," an intermediate probability example was "leaf," and a low probability one was "airplane." Thus humans are effortlessly able to generate instances across the predictable-to-unpredictable dimension of verbal categories, much in the same way as described for motoric operants.

Non-human animals categorize (e.g., Loidolt, Aust, Meran, & Huber, 2003; Mackintosh, 2000; Smith, 2013; Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). Herrnstein (1984) wrote, "To categorize … must be so enormous an evolutionary advantage that it may well be universal among living organisms." (p. 257). But species differ in this competency (e.g., Mackintosh, 2000). For example, dividing categories into sub-categories, something humans do across many domains, appears difficult for the pigeon (Wasserman, Kiedinger, & Bhatt, 1988). Differences in animals' categorization capacities may provide important information about their volitional abilities.

Tool use provides another example of operant variability that could prove helpful in evaluating voluntary control. Corvids and non-human primates construct or locate novel instruments to gain access to food sources (e.g., Kenward, Rutz, Weir, & Kacelnik, 2006; Ottoni & Izar, 2008). In these species, when one way of confronting a problem is not successful, other responses are explored, thereby demonstrating sensitivity of response variations to consequences. Simpler forms of tool use have been reported in other species, including invertebrates (insects, sea urchins, crustaceans, arachnids, octopuses and gastropods), fish, amphibians, and reptiles (Shumaker, Walkup, & Beck, 2011). A recent example of the last is that alligators orient themselves so that twigs and branches are placed atop their snouts. They do this mainly when birds in their areas are building nests. When a bird attempts to retrieve the stick for its nest, it is captured and consumed (Dinets, Brueggen, & Brueggen, 2013). But alligator tool use differs from corvid and primate cases in terms of number and complexity of responses comprising the 'tool' class. Studies of tool use and, more broadly, problem solving, indicate the differential facilities of species to form functional classes and to modify within-class probability distributions, thereby providing a measure of volitional capacity. Heritability studies indicate a significant genetic contribution to tool use and, more generally, to innovative novel behavior (Reader, 2003).

Neural Complexity

Brain sizes (both absolute and relative to body size), proportions of brain devoted to cortex, and number of cortical neurons have been correlated with measures of animal intelligence (Jerison, 1985; Roth & Dicke, 2005). On the behavioral side of the intelligence correlation, competencies closely related to those discussed in this paper have been proposed. For example, "…comparative and evolutionary psychologists and cognitive ecologists have converged on the view that mental or behavior *flexibility* is a good measure of intelligence, resulting in the appearance of novel solutions that are not part of the animal's normal repertoire" (Roth & Dicke, 2005, p. 250). Jerison (1985) emphasizes that, across evolution, brain development (e.g., encephalization) provides for "an increase in information processing capacity" (p. 21). The behavioral analog of 'information processing' may be 'information generating' as seen in the establishment and modification of operant classes and within-class probability distributions. Thus, the relationship between brain and intelligence may also represent a relationship between brain and volition.

Conclusion

A main point of this paper is that individual operant responses emerge probabilistically from activated classes of potential responses (a position closely related to Skinner's 1935a original description of the operant). Reinforcing consequences control the individual probabilities (or variability, uncertainty, unpredictability, surprise value) of these within-class instances as well as their other characteristics – their types, topographies, intensities, sizes and the like. The control by reinforcers over both probabilities and characteristics helps to explain three attributes of voluntary behavior: functionality (actual or intended), unpredictability (to a greater or lesser degree, depending upon contexts and consequences), and emission (or within-organism origination).

Many species, from simple to complex, exhibit responses that are sensitive to reinforcing consequences. Species differ, however, in the number of operants in their repertoire, the ease with which new operant classes are created, and within-class dynamics. Human language demonstrates the most generative of complex operant classes. In language, classes are activated and modified moment-to-moment, including rapid changes in class membership and member probabilities. Similar dynamic modifications of response characteristics and variability can be readily observed in many aspects of daily life, including playing with a child, preparing a meal, fixing a piece of equipment, competing in games or sports, teaching, creating music or poetry, and conversing with friends. These are operant actions, shaped and influenced by reinforcers, and they provide evidence of voluntary control.

What about non-human animals? Responses by species from Aplysia and Drosophila to human can be operantly conditioned and systematic induction of high versus low levels of response variability has been documented. Direct reinforcement of variability has been less studied, but two species commonly used in behavioral research, rats and pigeons, are readily reinforced for responding predictably in one context (one set of discriminative stimuli) and unpredictably in a second and specific levels of variability are also under operant control (Neuringer, 2002). Reinforcement of specific responses as well as response unpredictability has been experimentally demonstrated in other animals as well, such as porpoises (Pryor, Haag, & O'Reilly (1969), walruses (Schusterman & Reichmuth, 2008), songbirds (Manabe, Staddon & Cleaveland, 1997) and fish (Roots, 2000). Do members of these species therefore exhibit voluntary behaviors? My answer is yes, to the extent that the characteristics and probabilities of their responses are sensitive to reinforcing consequences. However, non-human animals have not demonstrated similar-to-human numbers and complexity of operant classes, ability to modify classes moment-to-moment, or to create novel classes comprised of predictable to unpredictable responses. Thus, given current knowledge, it is likely that non-human species differ among themselves and from humans in terms of their *degree of evolved volition*.

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