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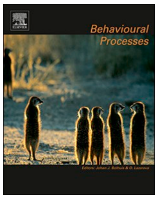

# Adaptive systems influence both learning and conscious attention

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ABSTRACT

The scientific study of animal behavior had its beginnings in two separate scientific traditions. *Adaptive explanations,* as expanded by ethological studies of natural behavior, emphasized that behavioral traits were guided by innately organized stimulus and response dispositions. *Associative explanations*, as expanded by conditioning studies, emphasized that behavior was shaped by learned connections formed between stimuli, responses, and motivational outcomes. When William Timberlake began his career as a learning psychologist, he adopted a *behavior systems* approach that helped to reconcile the different emphases of these two traditions. Behavior systems argued that pre-organized adaptive dispositions also contribute to learning. They bias what stimulus and response features are most likely to be engaged and influence patterns of behavioral expression during conditioning. The first half of this paper surveys Timberlake's early research and highlights some of his many explanations of conditioning outcomes using this approach. The second section of this paper describes my extension of this approach to reconcile differences between adaptive and associative accounts of consciousness. It argues that pre-organized biological dispositions for attention contribute to conscious awareness. These "attention systems" bias what topics are most likely to be noticed and influence the affective dispositions that are activated during conscious attention.

The scientific study of behavior had its beginnings in two largely separate traditions, nativism and empiricism. Natively formed traits were thought to result from the adaptive organization of the nervous system via natural selection. This emphasis grew largely from the writings of Charles Darwin (1871, 1872) on the formation of mental processes in animals and man, and on George Romanes' (1882, 1883) attempts to build a scale of mental functions based on Darwin's ideas. Romanes' extensions suffered from a lack of rigor and dependence on anecdotal reports. However, his work provided a framework for thinking about comparative differences in behavioral and mental traits. Subsequently, adaptive explanations became a topic of scientific study in the field of ethology based on work by Karl von Frish (1919, 1953), Konrad Lorenz (1937, 1970), and Niko Tinbergen (1942, 1951). The ethologists emphasized the ecological fit of an organism to its natural environment and argued that systems of adaptive traits were dependent on biologically prepared drives and stimulus-released action patterns.

Empirically formed traits were thought to result from the organization of the neural system via the formation of new associations. This associative emphasis began with the philosophical writings of John Locke (1690). Locke rejected the notion of innate ideas, instead arguing that all ideas were formed from connections among sensations. David Hartley (1749) gave associations a physiological basis arguing that they resulted from vibrations in the nerves. He proposed that separate vibrations were connected via contiguity during experience. James Mill (1829) expanded on Hartley's ideas, arguing that all associations formed due to synchronous or successive contiguity. His son, John Stuart Mill, ventured into the emergent nature of associations, proposing that they could be more than the sum of their parts (Mill, 1843/2011Mill, /, 2011Mill, /, 2011Mill, 1843/2011Mill, /, 2011Mill, /, 2011Mill, 1843/2011Mill, /, 2011Mill, 1843/2011). However, John Stuart Mill's associate, Alexander Bain, continued to link the association of ideas with physiological processes and surprisingly gave particular attention to reflexes (Bain, 1855, 1859).

Subsequently, the acquisition of associative explanations became a topic of scientific study in behavioral research with the work of researchers such as Ivan Pavlov, Edward Thorndike, and Burrhus Frederic Skinner. These researchers developed what came to be called "conditioning" models that emphasized the sequential stimulus and response conditions that led to associative connections. Beginning with reflexes, Pavlov (1904/1966Pavlov, /, 1966Pavlov, /, 1966Pavlov (1904/1966Pavlov, /, 1966Pavlov, /, 1966Pavlov (1904/1966Pavlov, /, 1966Pavlov (1904/1966, 1927), for example, showed that stimulus-stimulus contiguity could cause reflexive reactions to the second stimulus to be elicited by the first stimulus. Thorndike (1898, 1913), and later Skinner (1938, 1953), emphasized the importance of response pairings with significant stimulus outcomes. Thorndike noted that when an action was followed by a "satisfying state of affairs" it was

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strengthened, but when it was followed by an “annoying state of affairs” it was weakened. He called this *the law of effect.* Skinner later described events that strengthened response associations as *reinforcers*, and those that weakened them as *punishers.*

Based on their different origins, adaptive explanations were considered to describe the natural behavior of animals, and thus to be part of biology. In contrast, associative explanations were considered to follow from conditioning processes and to be part of psychology. Conditioning theorists argued that higher-order traits were acquired by learned associations and suggested that ethological traits were, at best, beginning points. Thus, biological components were generally dismissed as unimportant for associative explanations. To emphasize this point, conditioning theorists often used what they thought of as “arbitrary” cues and responses in their studies. The idea was that if they could show that learning routinely connected arbitrary cues and actions, then biological predispositions would be seen as less important.

It was in the context of these conflicting theoretical approaches that William Timberlake began his career as a learning psychologist at Indiana University in 1969. It is commonly claimed that creative minds think outside the box. However, it is my observation that the really inventive thinkers don’t just think outside the box; they often create whole new conceptual boxes. Timberlake was such a thinker. His ideas were inspired by his belief that because biological dispositions are built into animals, there is no way an organism could leave them behind during conditioning. Thus, his research emphasized the idea that biologically based stimulus and response dispositions must necessarily influence what is learned during conditioning studies. Following this logic, he gradually framed what he called a *behavior systems* model for thinking about how biological traits and conditioning mechanisms interact during learning. In the first section of this paper I highlight a number of examples of Timberlake’s work as he explored this behavior systems approach.

## 1. Behavior systems and learning

Although Timberlake’s research was guided by a behavior systems emphasis, his research ventured into many topic areas. Later in his career he occasionally opined that had he focused on fewer topics he might have had more impact. Other theorists who have adopted a behavior systems framework have largely focused on a particular behavior system. For example, Michael Domjan (1994; 1997) focused on the role that behavior systems played in organizing the sexual behaviors of Japanese quail. Alternately, Michael Fanselow (1989; Fanselow and Lester, 1988) focused on the role that behavior systems played in organizing fear-related behaviors in rodents. However, Timberlake recognized that the behavior systems for foraging should necessarily be engaged in many food-rewarded studies.

As a result of this interest, Timberlake looked for examples of how the behavior systems for foraging influenced behavioral expression in a range of traditional learning paradigms. Initially, this was not always well received by learning theorists, but this approach turned out to be a strength. It meant that behavior systems couldn’t be dismissed as an explanation that was only needed in special cases. Still, the broad range of conditioning topics that Timberlake addressed makes it more difficult to summarize his work. Therefore, my strategy will simply be to revisit some of his early work and show how Timberlake applied behavior systems explanations to performance and learning in a variety of conditioning paradigms.

### 1.1. Characterizing behavior systems

As noted, learning theorists suggested that the behaviors trained in conditioning studies began as largely arbitrary activities. B. F. Skinner, for example, claimed that "learned behavior is constructed by a continual process of differential reinforcement from undifferentiated behavior, just as the sculptor shapes his figure from a lump of clay" (Skinner, 1953, p. 92). In this view, animals were proposed to begin life largely as a tabula rasa that had to be trained to behave adaptively. However, a common problem with this argument is that there are many biologically important tasks that an animal must negotiate efficiently to survive. Examples include finding food and water, building nests or burrows, maintaining adequate body temperature, avoiding predators, procuring mates, and caring for new offspring. If the dispositions for all of these needs begin as little more than undifferentiated lumps of clay, it is unreasonable to assume that they would all be shaped into functionally successful behaviors quickly enough to ensure survival.

Ethologists, in contrast, proposed that animals inherited sensory and motor dispositions that were sufficiently adaptive to solve basic biological tasks without learning. Further, they noted that these dispositions often fit into sequences that served as multi-level strategies. Initially, an animal may not have access to food, but if it has dispositions for exploring, then it will search. If it has focal search strategies, then certain items are more likely to be investigated and manipulated making it more likely to find food. And, of course, when food is encountered consummatory activities would automatically be engaged. Ethologists didn’t deny that learning could occur in such sequences and make them more efficient, but they emphasized that the appetitive activities had been “shaped” by natural selection to ensure a high likelihood of success before learning occurred.

The behavior systems model assumes this ethological framework. One implication of this framework was that learning is likely to engage several aspects of an appetitive sequence, not just the actions that immediately precede reward. Thus, temporal patterns of search and investigation are likely to be activated even when reward is not contingent on their expression. Indeed, some of them might be engaged even if they delay access to reward. The point is that behavior systems involve pre-established appetitive dispositions, not just consummatory activities. As a result, the behaviors occurring in a conditioning procedure should be expected to engage a number of biologically prepared search and handling activities, not just contingently rewarded actions. Further, these appetitive dispositions would be hierarchically arranged so that they naturally flowed from general exploration to more specific modules of activity based on supporting cues.

Fig. 1 illustrates a subset of Timberlake’s proposed behavior systems for predation in the rat. Each behavioral module may involve one or more sensing-reacting units of activity. For example, locomotion could involve various forms of movement through physical space; socialization would involve attention to another rat, perhaps sniffing and grooming. The modules, in turn, fit within modal groups such as general search. Modules in each modal group tend to be energized

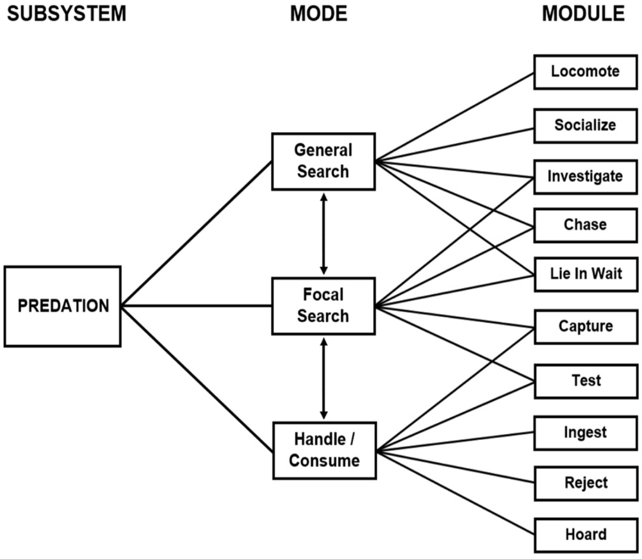

**Fig. 1.** A behavior systems diagram for elements of rat predation.

together. Thus, general search may involve the activation of locomotion, socialization, and investigation. Investigation, in turn, may serve as a branching point to a focal search mode. The idea is that the activities are flexible and opportunistically engaged by supporting cues. The modes, in turn, fit within a larger goal-directed subsystem resulting in a systematic hierarchy of activities for that goal. It is this hierarchy of sensing-reacting dispositions that the behavior systems model proposes an animal brings with it to a learning paradigm.

### 1.2. Alley and maze running

Given that the behavior systems model predicts that sensory and motor dispositions are structured prior to learning, it follows from the model that the more successful learning paradigms are likely to be effective because they specifically involve cues and activities that activate supporting predispositions. To make this point obvious, Timberlake began studying a commonly used experimental paradigm in rats, straight alley running. Most learning theorists assumed that alley running was largely arbitrary and that rats learned to run down an alley because they were rewarded. However, wild rats are known to follow above-ground trails and underground passages (Calhoun, 1962). Thus, Timberlake assumed that alley running was not arbitrary and instead that it likely engaged pre-established trail following dispositions.

To demonstrate this point, Timberlake (1983) showed that rats learned to run a straight alley, that is, they come to run faster and "goal-directed" errors were reduced, even if the rats were never rewarded. A standard argument against such findings was that alley running must have been rewarded in some way. To evaluate these arguments, Timberlake ran an extensive series of studies to seek out possible causes and to control for possible sources of reinforcement. He found that rats learned faster when they were accustomed to the alley, and thus less fearful. He found that adding a small object in the goal box, increased the rate at which they learned, presumably by increasing their interest in the goal box. He ruled out the idea that handling the rats, or removing rats from the goal box was a critical reward by varying those features. In general, he found that rats learned faster if they were deprived of food, and thus more motivated to explore, and if they were more curious and less fearful. However, he consistently found that they learned without any obvious reward.

In later work, Timberlake and Wesley White (1990) extended these findings by studying rats' exploration of a standard eight-arm maze. While rats learned to run an alley without reward, they found that undeprived and unrewarded rats did not choose novel arms on the maze at above chance levels, infrequently ran to the ends of arms, and failed to display a consistent search strategy. However, they found that food-deprived, yet unrewarded, rats entered significantly more novel arms in their first eight choices than expected by chance, generally ran to the ends of chosen arms, and increasingly chose adjacent arms. Further, these maze running dispositions improved over trials. In effect, they showed that rats didn't require reward to learn to explore a maze, but that rats did need to be food-deprived to explore systematically.

While most researchers were content simply using eight-arm mazes to tests rats' memory and foraging skills, Timberlake remained curious about why rats adapted to mazes so readily. The standard eight-arm maze is elevated about a meter off the floor to ensure that rats cannot easily change runways mid path. However, rats can leap when necessary, so it was always possible that they might jump from one alley to another. Usually, small side rails were placed on the runways to discourage jumping. However, jumping across paths was rarely a problem. It seemed the rats preferred foraging by following the runways. Thus, Timberlake wondered if there was something about the runways that engaged rats' natural foraging activities. To understand this question better, Timberlake disassembled the standard maze design, put the arms of the maze on the floor, and varied various features of the runway paths.

In one set of studies John Roche and Timberlake (1998) showed that rats predominantly follow maze arms even when they do not directly lead to food. In fact, they readily follow arms with zig-zag passages. In cases where the arms did not lead directly to food, the rats eventually varied from them at places to make their search more efficient, but their initial behavioral preference was to follow the arms. In another set of studies (Hoffman et al., 1999) the authors found that after some early exploration, rats traveled along arms to food, even when the resultant distance was up to three times the minimum distance. With no food present, rats also traveled along the arms. If the arms were removed the rats traveled along the enclosure walls as much as possible. This was similar to trail following in wild rats (Calhoun, 1962). In subsequent work, Timberlake et al. (1999) found that locomotion on the maze was influenced more by the sensory mechanisms of trail following, in particular, whisker contact with edges, than by a tendency to minimize travel distance or maintain a central-place search pattern.

Timberlake's studies of how alley and maze features interact with the rat's search behaviors are some of my favorites, because they highlight his persistence in seeking out natural exploratory dispositions. Few others would disassemble an elevated maze and place its parts on the floor, but for Timberlake this was not an unusual strategy. In general, these studies were never high-profile findings. Alley running and maze running studies continued to be used under the assumption that reward was generally essential for more successful performance. However, the assumption that alley and maze running activity was completely arbitrary was no longer promoted. Increasingly, researchers began to recognize that pre-organized appetitive sequences could not be dismissed in the analysis of conditioning. Eventually it was accepted that alley running and maze running paradigms work so well because they engaged natural behavior patterns.

### 1.3. What makes an event a reinforcer?

The behavior systems approach emphasizes the importance of making baseline observations to determine natural behavior patterns before imposing learning contingencies. This follows from the strategy in ethology of taking ethograms of natural behavior before doing formal studies. Baseline ethograms allow researchers to assess motivational patterns prior to experimental studies and to observe how behavior patterns change under various conditions. Observations in natural environments also provide insight into the function of specific behaviors. A driving idea behind adopting this strategy is that the more researchers know about an animal's natural behavior, the more likely it is that they will recognize how components of natural activities contribute to the results obtained in conditioning studies. This position is one of Timberlake's most enduring contributions to learning theory.

Although Timberlake formulated a behavior systems model for learning, he didn't begin his career with a fully formulated model. Much of his early work involved showing that baseline measures could provide insight into natural dispositions that might be engaged in learning studies. Conditioning studies emphasized that responses that were followed by rewarding situations would be strengthened. However, most learning theorists did not address why an event acted as a reward. They simply observed that some activities acted as reinforcers, and then used that observation circularly to explain why they worked as rewards. However, a prominent researcher, David Premack, was also interested in explaining what made some activities reinforcing. After a series of studies, Premack proposed that for an activity to be a reinforcer for another activity it must be a higher probability behavior in baseline measures (Premack, 1965). This idea came to be known as the *Premack principle*. The Premack principle was a first step in defining the properties of a reinforcer.

Still, Timberlake noted that it was common in learning studies to deprive subjects of food in order to make feeding an even higher probability activity. Further, he noted that response schedules introduced their own aspects of deprivation by limiting the amount of the rewarding activity available after a contingent activity was completed.

Based on these observations, Timberlake hypothesized that it was not merely a high baseline probability that made an activity rewarding, it was also the extent to which it was constrained from preferred baseline levels during a conditioning schedule.

Following this idea Timberlake went on to show that lower probability baseline activities could reinforce higher probability activities, if access to the lower probability activity was deprived more than access to the higher probability activity during a schedule (Timberlake and Allison, 1974). This explanation came to be known as the *response deprivation* model. Following this logic, Timberlake and Mark Wozny (1979) showed that wheel running could be rewarded by eating, when eating was proportionally more deprived. However, eating could be rewarded by opportunities for wheel running, when wheel running was proportionally more deprived. Gawley et al. (1986) even found evidence that rats were shifting from running-to-drink to drinking-to-run during a long session, apparently because they became satiated for drinking faster than they became satiated for running.

Response deprivation was a critical addition to reinforcement theory. It meant that reinforcers were not unique categories of behavior. They were simply activities that were more deprived than the activity they were rewarding. Subsequently, theorists (Allison, 1983; Hursh, 1984; Lea, 1981) expanded the response deprivation logic to link it with economic models of supply and demand. Increase the demand for B, by restricting its availability more than the availability of A, and consumers will pay more activity A to get commodity B – a reinforcement effect. Decrease the demand for B, by increasing its availability more than A, and consumers will pay less A to get commodity B – a punishment effect. Of course, stronger punishing effects occur if the demand for B is zero or negative, and yet the consumer is forced to experience B whenever he engages in A.

### *1.4. Pavlovian-operant interactions*

Pavlovian conditioning, also known as classical conditioning, involves stimulus-stimulus pairings. Thus, no particular behavior is forced to occur in this process. However, Pavlov found that when an arbitrary stimulus (a conditioned stimulus, CS) was paired with a stimulus that elicited a consistent behavioral and motivational reactions (an unconditioned stimulus, UCS), aspects of the behavioral and motivational dispositions that occurred to the UCS soon began to occur after the CS. This reaction was called a conditioned response (CR). In a classic example of conditioning with a dog, Pavlov rang a bell and then, after a short delay, delivered meat powder. The meat powder elicited salivation and licking by the dog. In a short time the bell then began to elicit salivation in anticipation of the food powder. In effect, Pavlovian learning caused adaptive dispositions to be elicited by arbitrary cues.

In contrast to Pavlovian procedures, instrumental conditioning, called operant conditioning by Skinner, paired a specific action with a reward. Rats were commonly trained to press a bar to receive a food pellet. Pigeons were taught to peck a small key to receive grain delivery. Once trained the response began to occur much more often. However, operant studies required an initial bar- or key-press to trigger reinforcement. Given that these were considered arbitrary actions, the standard procedure for training them was to reinforce successive approximations to the desired action. For example, pigeons were given food for activities like approaching the location of the key, for looking at the key, for bobbing their head in front of it, and eventually for making beak contact with the key. This training procedure was called shaping. The thinking was that shaping was needed because the required actions were arbitrary and had to be built by rewarding simple approximations to the target response.

Skinner (1938) pioneered using pigeons in operant studies. For over thirty years, researchers began these studies by shaping the pigeons to peck a response key on the wall. However, Brown and Jenkins (1968) reported a study that changed that process. The authors got pigeons accustomed to eating grain from a short food-hopper delivery. Then, rather than shaping the pigeons to key-press, they set up a schedule in which lighting the response key for 8 s was followed by grain delivery. This procedure was then repeated on a variable 60-sec inter-trial interval. The authors found that simply pairing the lighting of a key with food delivery caused the pigeons to approach, look at, and eventually peck the key. All thirty-six subjects tested in the forward key-light-food pairing procedure pecked the key within 160 trials. Not surprisingly, Brown and Jenkins thus called this procedure *auto-shaping*. Subsequent studies showed that pairing a bar presentation with food delivery would cause rats to approach, contact, sometimes chew on, and eventually press a bar. If the bar-press was rewarded immediately, this process also resulted in automatic shaping.

The auto-shaping findings called into question the learning mechanisms by which responses were shaped. Pavlovian conditioning was thought to cause activities associated with a UCS to be directed at the CS. A common explanation was that the pigeons were redirecting their grain pecking to the response key. This was termed a Pavlovian stimulus-substitution explanation for auto-shaping. In the case of rats, contact with the bar seemed to be associated with food handling, not eating. Still, pairing presentation of the bar with food resulted in bar contact that also fit the stimulus-substitution model. However, Timberlake recognized that animals typically use a variety of search and investigatory activities when looking for food. Pigeons walk about and look for local areas to explore. In such areas they investigate the substrate with their beaks, and consume food when found. Investigation in rats involves moving around, digging, gnawing, handling, and in social situations may even involve following rats that predict food sources. Thus, a behavior systems explanation for auto-shaping predicted a greater variety of investigatory activities.

To show the relevance of the behavior systems model to auto-shaping findings, Timberlake used several variations of the auto-shaping paradigm. However, rather than using arbitrary cues as predictors of food, he used cues designed to elicit specific activities. For example, in one study Timberlake and Grant (1975) used the presentation of a rat to signal the delivery of food to another rat. A strict stimulus-substitution interpretation of this procedure predicted that rats should redirect pellet-feeding behavior toward the predictive rat, perhaps even gnawing and chewing on the rat. However, the behavior systems model suggested that the subjects would consider the predictive rat as a well-informed social partner. Thus, rats would be expected to approach and pay attention to the social partner.

Consistent with the behavior systems prediction, Timberlake and Grant found that rats oriented toward, approached, sniffed, and made social contacts such as touching, grooming, and even crawling over the predictive rat. They argued that this implied Pavlovian conditioning activated a whole system of species-typical behaviors related to a reward, and that what behavior was expressed depended on the nature of the stimulus and test situation. In line with this argument, they noted that Konrad Lorenz had reached a similar conclusion after hearing about an observation made in Pavlov's laboratory. It seems that after one Pavlovian conditioning study, Howard Liddell released a dog from the harness that normally held it in place for collecting salivation. The dog had been trained to salivate to a metronome CS. As Liddell reported, when free to move the dog ran directly to the metronome, began tail wagging, jumping up toward it, and barking at it. Lorenz noted that this behavior was characteristics of canid food begging, as if the whole system of food-related behaviors was activated by the conditioned stimulus, not just the salivary response that Pavlov chose to measure (Lorenz, 1969).

### *1.5. Conditioning and misbehavior*

In an extension of the auto-shaping paradigm in rats, a moving ball bearing was used to predict food delivery (Timberlake et al., 1982). The apparatus was designed so that when a ball bearing was released, it rolled down a track on the side of the chamber from the back to the front, where it exited through a small hole. When rats were exposed to this procedure, and food delivery was delayed until the time the ball bearing normally exited the chamber, the rats didn't just salivate. They chased the ball bearing, contacted it, often picked it up, chewed on it, and carried it around. In many cases they held the ball bearing in their paws while they ate the food pellet, and then continued to hold and chew on it. Timberlake delayed the next trial until after the ball bearing was released, but rats would often hold it for minutes. Eventually, he changed the rules so that food was not delivered until the ball bearing rolled out of the chamber. Even then, some rats continued to hold the ball bearing, thus delaying food delivery.

Timberlake recognized that chasing, capturing, and carry-chewing were aspects of foraging for moving prey. The ball bearing paradigm showed that these foraging activities were readily activated simply by pairing a moving ball bearing with food delivery. In a comparison across different species of mice, Timberlake and Washburne (1989) showed that the more a mouse species fed on moving prey, the more likely the mice of that species were to chase ball bearings that predicted food. In addition to linking foraging activities with the behavior systems model of Pavlovian conditioning, this paradigm also made contact with other common problems found in training some animals. Behaviors activated by behavior systems sometimes impose themselves into training paradigms even when they compete with the training goal. In a widely noted report on this problem, “The Misbehavior of Organisms”, animal trainers Keller and Marion Breland and Breland (1961) described this tendency for natural behaviors to “impose” themselves in conditioning procedures as *instinctive drift.*

In one example, the Brelands reported a case where they were training a raccoon to work to obtain coins and then to put the coins in a piggy bank. This behavior was planned to be part of a promotional display for a bank. Raccoons are smart and training their subject to obtain the coin was easy. The Brelands used standard operant shaping procedures. The next step was to get the raccoon to put the coin in the nearby bank to get food. All went well, except that the raccoon was reluctant to release the coin. He kept holding and rubbing it before letting it go. Eventually, they attempted to make the raccoon get two coins before putting them in the bank. Again, training the raccoon to get a second coin was easy, but when it came time to put them in the bank, two coins resulted in even more rubbing. Sometimes the raccoon would rub the coins for minutes at a time even though this delayed the reward. Occasionally, he would start to put a coin in the bank and then pull it back for more rubbing.

Constantly rubbing the tokens made the raccoon seem miserly and reluctant to trust the bank. And to the Brelands' dismay, the longer they trained him, the more time he spent holding the tokens. As a result, the plan to use the raccoon for a commercial promotion was abandoned. However, when we compare the raccoon's behavior, when coins were paired with food, and the rat's behavior, when ball bearings were paired with food, it is clear that it is not always natural for an animal to release physical objects that predict food, especially when food may be delayed. Cases of instinctive drift were not predicted by operant learning theories, but the appearance of extraneous foraging behaviors was completely compatible with a behavior systems account of foraging. The behavior systems model helped move instinctive drift from a curious artifact to a recognized part of modern learning theory. The message was clear. Conditioning doesn't just activate consummatory activities; it activates species-specific behavior systems for procuring and handling food, and they may not be adaptive in all contexts.

### *1.6. Superstition in pigeons*

In 1948, B. F. Skinner published an influential learning paper entitled “Superstition” in the Pigeon. In the study, pigeons were exposed to a periodic schedule of reinforcement every 15 s. Thus, there was no requirement for the pigeon to do any specific behavior to receive the reward. Nevertheless, Skinner reported that many pigeons developed idiosyncratic behaviors during the inter-food interval. Given his theory of reinforcement, Skinner proposed that these stereotyped interim behaviors were learned and maintained by accidental reinforcements. He likened this to superstitious behaviors that sometimes develop in humans, arguing that such superstitions illustrate the control that a few accidental reinforcements can produce.

While accidental rewards are clearly possible, Timberlake noted that the stereotyped behaviors of the pigeons did not appear completely arbitrary. In some cases they seemed like normal search activities. When the Brelands trained chickens to wait on a platform for 12–15 sec before they were fed, they noted that the majority of chickens developed a stereotyped pattern of scratching on the platform while waiting. The Brelands suggested this might be maintained by superstitious conditioning, but Timberlake noted that scratching the ground was a normal part of food search in chickens. It wasn't merely an arbitrary activity. Based on such insights, Timberlake and Lucas (1985) began a set of studies to explore the nature of superstitious behavior in pigeons. In these studies, we found that our pigeons developed a small number of stereotyped behaviors that were often similar to those Skinner reported. Thus, the behaviors were not as idiosyncratic as Skinner's accidental reinforcement interpretation suggested.

For example, in one study we specifically shaped some birds to peck on a 15-sec inter-reward schedule, while others were shaped to turn in a circle on that same inter-reward schedule. After those behaviors were well established, we removed the contingencies and simply delivered food on a 15-sec response independent schedule. However, rather than maintaining the initial behaviors that had been “accidentally” shaped by periodic rewards, the pigeons reverted to interim behavior patterns similar to those of pigeons who were never shaped. It seemed clear that something about the environmental situation influenced what behaviors were likely to appear. Many of the behaviors, like walking about the area during the inter-food interval, appeared to fit within the activities that pigeons engaged in during food search. However, we noted that one activity, the persistent bumping up against the feeder wall and head-waving there, didn't seem to fit within a foraging explanation.

To explore the wall bumping behavior, Timberlake and I engaged in two other kinds of studies. In one Timberlake decided we should examine the pigeon's foraging patterns in an open area. We cut the flight feathers on a few birds and let them search on the ground for food outside where we had placed a feeder in the ground. When food was delivered on a periodic 15-sec schedule, the pigeons tended to stay close to the feeder, but they walked around the area during the delay interval. This was typical of the pigeon's normal foraging activity. However, when we introduced a small wall-like barrier only 6 in. tall near the feeder, many of the birds began bumping against the wall. The wall did not prevent the pigeons from accessing food; it was just located near the feeder. However, it seemed obvious that bumping the wall was related to feeding. But exactly why pigeons bumped that wall was still not clear.

Taking another tack on the problem, I proposed that we raise pigeons in the lab so that we could observe their early feeding behavior. Timberlake agreed, and soon we had four breeding pairs of pigeons. Young pigeons are dependent on the parents for food, and the parents feed them by regurgitating partially processed food into the squab's mouth. However, as the squab get older, there is increasing competition among them for getting fed. When a parent arrives, the squab approach and bump up against the parent's breast while waving their heads for attention. Thus, we had our answer. The feeder wall delivered food. Bumping and head-waving against the wall were ways of begging for more feeding. Periodic reinforcers may sustain various activities in the superstition paradigm, but the activities most likely to emerge and be sustained were not completely arbitrary. In most cases, they were part of the pigeon's behavior systems for foraging and food-begging.

### 1.7. The anticipation of future food

A classic foraging problem is how long an animal should search in a patch before leaving for an alternative patch. In optimal foraging theory, this is called the *giving-up time* (Pyke et al., 1977). According to the marginal value theorem, foragers should leave a patch when the rate of finding prey there falls below the average rate of finding prey in alternative patches. But what if access to the alternative is delayed? From an optimal foraging model, a rational consumer should be willing to wait across a short delay, but less willing if the delay is longer. Indeed, it is commonly found that both animals and people tend to discount the value of access to easier reward schedules as an increasing function of their delay (Fantino and Abarca, 1985).

A common question in such studies is how long this discounting interval typically extends. In foraging studies, this period is commonly referred to as the *time horizon* of future food evaluation. Because Timberlake was concerned with how foraging systems interacted with standard learning paradigms, he was naturally interested in the time horizon over which schedule performance might be influenced by delayed access to food. This was important because in typical conditioning studies animals were food deprived. Thus, after a daily conditioning session they were routinely fed enough to maintain a standard deprivation level. However, it wasn't clear to what extent those later feedings could be influencing their performance during the conditioning schedule.

Timberlake addressed the time horizon issue using several strategies. The most direct procedure was to examine performance when access to food was delayed by an increasing response ratio. The schedule was arranged to mimic a decreasing patch, such that more work was required to access food over time. Following a delay, free food access was available in another patch. In the first of these studies, Timberlake (1984) did not find any evidence of reduced schedule intake when free-food was available after 1, 2, 4, 7, 10, 16, or 20 h, although he did find effects if the food was delayed 23 h. Given that a 23 -h delay resulted in feeding one hour before the subsequent session, this finding suggested that the rat's forward-looking time horizon was less than an hour under standard food deprivation, but that it was also influenced by a 1-hr pre-feeding, presumably because these meant the testing was done under reduced hunger levels.

In a subsequent study, Timberlake et al. (1987) focused on the effects of shorter delays. Again the initial patch provided food access using a progressive ratio schedule and the second patch involved nearly free access, in this case one food pellet for each bar-press. This second patch was available on the opposite side of the chamber after a delay. The delay to the start of the second patch was 4, 8, 16, 32, 64, or 120 min. The chamber was designed so that subjects could enter and test the second patch at any time. Under these conditions the rats occasionally tested the second patch, while continuing to respond in the first patch. However, time spent testing the second patch did not reduce overall intake in the first patch for delays longer than 16 min.

These results suggest that even when subjects may periodically leave the first patch, the added search competition is not significant enough to reduce food intake in the initial patch for delays longer than 16 min. In a second study Timberlake et al. (1988) specifically rewarded search of the second patch by providing access to the continuous reinforcement schedule if subjects avoided spending time in the initial patch for 2, 4, 8, 16, 32, or 64 min. No subject delayed responding in the initial path for 64 min. However, the contingency of rewarding time spent outside the initial patch allowed two subjects to extend their effective time horizon to 32 min. Taken together these studies suggested that the effective time horizon for food-deprived rats in a typical operant study is 16 min, but may extend to 32 min in some conditions.

Employing yet a different strategy, Lucas et al. (1988) used an anticipatory contrast paradigm to evaluate the rat's time horizon. In this procedure, hungry rats were given 5-min access to a 0.15% saccharin solution followed, after a delay of 4, 16, or 32 min, by access to a 32% sucrose solution. In their initial study, the authors found that saccharin intake in the first access period was suppressed before 4-min and 16-min delays to sucrose, but not for the 32-min delay. However, in subsequent studies, they found evidence of suppression at the 32-min delay: 1) if the testing environment was more stressful, conducted in bright light; or 2) if the sucrose feeding was soon followed by supplemental home-cage chow, effectively making the second feeding even larger. However, no suppression was found at the 32-min delay in the standard environment if the subsequent home-cage feeding was delayed 90 min after the session.

### 1.8. What behavior systems added

Adaptive and associative accounts of how behavior is organized differ markedly in their focus. The associative account emphasizes the role that stimulus and response pairings play in shaping what is learned. In many cases, this approach treats the behaviors involved as an index of conditioning strength and is less concerned with what response forms are learned. The strength of this account has been the discovery of a variety of conditioning strategies that facilitate training new activities. In contrast, the adaptive account, as incorporated in Timberlake's behavior systems model, emphasizes that animals bring pre-organized perceptual, motor, and motivational dispositions to conditioning studies. Thus, the behavior systems model is not a new account of learning per se, but rather a strategy for ensuring that adaptive predispositions are treated as organizational structures that influence and supplement the contingencies of the conditioning paradigm.

The strength of the behavior systems approach is in its ability to account for the appearance of biologically prepared stimulus biases and motivational properties. These biological dispositions include stimulus filtering, foraging sequences, specific motor programs, and motivational hierarchies that impose themselves on the conditioning paradigms. In fact, the nature of the reward, and thus the behavior system being activated, often determines what cues work best and what actions are most likely to be engaged. The behavior systems account also helps explain the sequential structure of foraging activities. It puts adjunctive activities, misbehaviors, and superstitious behaviors in an adaptive context. It even led Timberlake to search for an objective explanation of what makes an event a reinforcer. Timberlake was not the only theorist to adopt this approach to analyzing learning, but he was one of its strongest and most persistent proponents. For that, his work will long be remembered.

## 2. Attention systems and consciousness

It was some fifteen years after my work with Timberlake on behavior systems that I began looking into explanations of consciousness. When I began that work, it never occurred to me that my studies would bring me back to thinking about behavior systems. However, just as early explanations of learning and behavior were often divided into adaptive and associative accounts, I encountered a similar distinction between the two prominent neurological traditions for explaining consciousness. The *affect-based accounts of consciousness* focused on biologically adaptive dispositions and their role in conscious feelings. The *attention-based accounts of consciousness* focused on the associative processes of the thalamocortical architecture in bringing information to conscious attention. However, at the time I began this work, there was no obvious way to reconcile the different emphases of these two lines of reasoning. The biological dispositions underlying feelings didn't seem to be connected to the thalamocortical processes guiding attention.

Given that the *affect-based* and *attention-based* explanations of consciousness may not be familiar to some readers, I will start by highlighting the basic ideas from these approaches. I will then describe the finding of Murray Sherman and Ray Guillery (2006) that led me to recognize that the behavior systems strategy for reconciling the differences between adaptive and associative accounts of learning can be extended to reconciling the different emphases of the adaptive and associative accounts of consciousness. My intent is to show that just as pre-organized biological dispositions directed to motor programming regions (what we call *behavior systems*) have a major influence on the behavioral and motivational patterns acquired during learning, it is also the case that pre-organized biological dispositions directed to the attention architecture (what we might call *attention systems*) have a major influence on the topics and feelings of conscious attention.

### 2.1. Affect-based accounts of consciousness

Affect-based accounts for explaining consciousness are most closely associated with three long-time proponents, Antonio Damasio (1999, 2010), Bud Craig (2002, 2009, 2010), and Jaak Panksepp (1998, 2005). A common tenet of these approaches is that core feelings originate from biologically prepared adaptive dispositions for motivation, arousal, and motor actions. Thus, affect-based approaches often have an adaptive emphasis similar to that found in ethological models of behavioral expression. However, these approaches have little to say about the associative processes by which conscious features are bound together during attention.

Panksepp has noted that feelings not only originate in lower brain arousal and motivational systems, but that these networks are highly conserved across mammalian brains. Thus, he argues that the adaptive dispositions that lead to conscious feelings are likely to be shared broadly across mammalian species with similar affective systems. In particular, he emphasizes four broad categories of affect commonly found in vertebrates: 1) appetitive needs, food, water, sex, etc. and associated wanting, seeking, and rewarding dispositions, 2) aversive states, fear, and defensive activities, 3) anger, rage, protective states, and aggressive dispositions, and 4) social bonding, attachment, caring, separation distress, and panic (see Panksepp, 1998, chapter 3).

Craig notes that many affective dispositions originate as reflexive reactions in the spinal cord for senses like pain, itch, tissue temperature, and mechanical stress. These also project up the spinal cord to brainstem integration centers. Subsequent modules in the brainstem create a number of more complex sensing-reacting dispositions. These include networks for the many sympathetic *fight and flight* reactions in the body, and the parasympathetic *rest and digest* reactions. Yet more complex sensing-reacting combinations result in brainstem dispositions like anxiety, arousal, avoidance, stress, surprisingness, and vigilance. Many of the spinal and autonomic sensing-reacting modules are relayed on to the parabrachial nucleus (PBN) complex in the mid pons.

Some of these early dispositions are relayed on to emotional and homeostatic networks in the amygdala and hypothalamus and to thalamic nuclei that can send them on to the interoceptive cortices. Thus, there is a hierarchy of feeling-related sensing and reacting processes in the brain. Among humans, feelings of sadness, anxiety, risk, pain, disgust, craving, trust, rejection, and even the quality of music are associated with increased activity in this hierarchy and may reach the interoceptive cortices. As Craig (2009) notes, when subjects think about themselves or how they feel, these same networks are activated. And because there are downward projections from the interoceptive cortices and the basal forebrain back to the brainstem, these higher regions also participate in autonomic sensing and reacting. Thus, while many feeling-related networks are located in the lower brain, Craig makes it clear that both emotional and autonomic states are re-represented on multiple levels.

The theorist who most closely links feelings with conscious experience is Antonio Damasio. In fact, Damasio (1999) characterized consciousness as the *feeling of what happens* that occurs as an agent engages their world. This phrase is literally the title of his book and can be considered a general theme in affective explanations of consciousness. However, Damasio notes that not all potential sources of feelings reach consciousness. In particular, many of the autonomic sensing and reacting processes in the lower brainstem, like the constant adjustments for heart rate, blood pressure, and digestive activity, do not reach conscious awareness. It seems that only status and reactivity information integrated in the mid-pons and above become conscious.

To emphasize the importance of the sensing-reacting regions in the mid-pons and above, Damasio refers to them collectively as the *proto-self*. Proto-self regions include the upper pons, the midbrain, the hypothalamus, and the amygdala. The reason for calling these locations *proto-self* regions, rather than *self* regions, is that they do not appear to be the locus of conscious feelings, but rather the sources of feeling-related inputs which may reach consciousness. As Damasio (1999) notes, perceptual events and affective states begin as unconscious processes. Consciousness involves an *object-organism* integration in which an agent becomes aware of their own internal reactions as he or she engages the external world. In this process, the internal reactions come to be interpreted as a sense of self, while the external perceptions are interpreted as a sense of world. Obviously, much more is involved than simply detecting feeling-related modules. However, even in his more recent work (2010), Damasio remains uncertain as to exactly where and how this object-organism integration occurs.

### 2.2. Attention-based accounts of consciousness

A key point in these accounts is that conscious awareness emerges during states of attention. To be clear, *conscious attention* is a delayed outcome of the process. The focus of attention must be assembled and sustained for nearly a half second before it reaches consciousness. However, because the thalamocortical architecture is involved in managing attention, it follows that it must be essential for consciousness. Long-time proponents of the role of the thalamocortical architecture in consciousness include Gerald Edelman (1989, 1992, 2003; Edelman and Tononi, 2000), Francis Crick and Christof Koch (Crick, 1994; Crick and Koch, 2003), and Rodolfo Llinás (2001; Llinás et al., 1998). The emphasis of these theorists is on understanding how thalamocortical processes result in conscious awareness and not on the role of feelings. Edelman (2003), for example, argues that conscious attention results from re-entrant thalamocortical processing loops. He suggests that feelings are linked to this processing via “correlations” in the basal forebrain and cortex, but he doesn’t see feelings as playing a direct role in attention. Christof Koch seems even less concerned about feelings, suggesting that subjective feelings may not have a scientific solution (Koch et al., 1992).

The focus on this summary will therefore be on understanding the thalamocortical architecture of attention. Thirty years ago the thalamus was considered little more than a relay center that did some preprocessing as sensory and motor information was relayed on to the cortex. However, we now understand that the thalamus is much more complex. It not only contains nuclei that relay sensory and motor signals on to the cortex, but it also acts as a gatekeeper ensuring that only a small set of sensory and motor features reach the cortex at one time. When a sensory or motor signal in the thalamus passes the thalamic filter, it acts as a switch that activates the cortical column processing that feature. When the cortical column is activated, projections from that feature column to other parts of the cortex become active. The cortex also sends a return signal to the feature site in the thalamus. This signal results in an ongoing thalamocortical processing loop as long as the feature passes the filter. This loop appears to be essential for sustaining conscious attention. However, if a feature fails to pass the filter, as most usually do, then cortical activity for that feature remains inhibited.

Neurons from the thalamus to the cortex, and return paths from the cortex to the thalamus, send collateral signals to the thalamic filter. The filter, in turn, sends inhibitory signals back to feature sites in the thalamus. It appears the filter works by a reciprocal inhibition process, where stronger signals inhibit weaker signals, and as they are inhibited their ability to inhibit other signals is also inhibited. Thus, the strongest signals end up passing the filter, and the rest are inhibited. However, one way that a signal can be strengthened so that it is more likely to pass the filter is to bind it in activity with another signal. It turns out that there are *matrix* cross-connecting fibers in the thalamus that serve to bind coincident features together (Jones, 2001). Features bound together in this way can compete for passage through the filter as a group. As a result, connected feature sets, or *feature assemblies* as they are often called, compete with each other for attention.

Because feature sets are bound together in the thalamus, the features that pass the filter arrive in the cortex in synchrony with each other and they activate return loops from the cortex that are also in synchrony. These synchronous loops enhance thalamic and cortical processing for the feature sets bound together during attention, while features that lack synchrony fail to pass the filter and their cortical targets remain inactive. Synchronous activation is a novel method for managing feature processing. The associations formed during moments of attention are highly flexible and yet transient. As attention shifts, new features are bound in synchronous activity, while synchrony for unattended features is lost.

I describe this processing as being *associative* in character because features are bound together during attention. However, it is not the same kind of association that occurs in learning. Learned associations result from the strengthening of synaptic bonds and the associations persist. Synchronous associations result from the joint enhancement of thalamocortical processing. The enhancement is temporary, yet it has a profound effect on momentary awareness. Based on the prevalence of synchronous activity among features during attention, Llinás and colleagues (1998) proposed that synchrony was essential for conscious attention. This idea was soon widely accepted (see Crick and Koch, 2003; Edelman, 2003; Edelman and Tononi, 2000; Jones, 2001; Llinás, 2001).

All these theorists note that the synchronous binding of assemblies competing for attention typically takes some 300–500 ms to reach consciousness. Tononi (2008) argues that this delay occurs because the neural assembly must first reach a certain level of coherence before it can activate the extended synchronous links that result in consciousness. Extending this point, recent work suggests that this takes time because different brain processes operate at different base rates. As Gollo et al. (2015) have noted, there is a highly interconnected hub network in the cortex, the *rich club*, which monitors internal feelings of self. These networks tend to operate at *alpha* frequencies of 8–12 Hz. Some of the lower-level somatic mood networks that feed this hub operate at *theta* frequencies of 4–8 Hz or even lower. In contrast, sensory processing networks tend to operate at *gamma* frequencies of 30–60 Hz, and some local areas at *higher gamma* frequencies of up to 200 Hz. These higher frequencies appear to be needed to track rapidly changing events in the external world.

In between these perceptual and feeling frequencies are intermediate processing hubs that link perceptual activity with the feeling hub. These intermediate networks operate at what is often termed the *beta* frequency of attention, around 13–28 Hz. To be synchronously linked, rhythms for core features in each of these processes must be harmonically coupled with each other. Due to the complexity of coupling systems with varied gamma, beta, alpha, and theta frequencies together it is not surprising that it normally takes some 300–500 ms for such interconnected rhythms to stabilize (Tononi, 2008). Given the different time frames of these subsystems, it is also the case that they tend to unfold in a temporal hierarchy of cognitive changes, with perceptual processes often changing faster while moods and action plans change slower. Chaudhuri et al. (2015) note this local-to-larger scale time integration is exactly what is needed for cognition and action to be expanded into larger adaptive units.

### 2.3. A composite account of consciousness

The many associative processes discovered in conditioning studies led to those processes dominating thinking about how learning is organized. However, those learning mechanisms didn't explain all the behavioral characteristics that emerge during conditioning. Foraging patterns, adjunctive activities, and intrusive misbehaviors appear that are not explained by conditioning processes. It wasn't until the associative processes for binding features together in conditioning were supplemented with the adaptive dispositions of behavior systems that these emergent activities could be fit within a composite model of learning. In the same way, the associative processes discovered in thalamocortical studies of attention has led to those processes dominating explanations of how conscious attention is organized. However, those mechanisms don't explain all the features of consciousness. In particular, they don't explain the role of feelings and their prevalence in conscious experience. Something more was needed to connect the associative processes of attention with the adaptive dispositions of the affect-based accounts of consciousness.

I subsequently found evidence connecting the associative processes of attention with the affective dispositions of consciousness in work by neuroanatomists Murray Sherman and Ray Guillery (2006). These authors have done an extensive analysis of the structure of the thalamus. While the thalamus is known to relay incoming sensory and motor inputs on to the cortex, Sherman and Guillery found that less than ten percent of the synapses in each relay nucleus were from the sensory or motor sources to be relayed. For example, in the visual relay, the lateral geniculate nucleus, only about six to seven percent of the inputs come from the retina. Over ninety percent of the synapses are from processes that are thought to *modulate* the relay of information to the cortex.

One-third of these modulatory synapses are from sources within the thalamus itself. These connections are essential for the filtering and binding processes within the thalamus. Another third of the modulatory synapses are from the cortex. These are the top-down inputs involved in maintaining re-entrant thalamocortical processing loops during synchronous attention. Surprisingly, however, the remaining one-third of the modulatory synapses in the thalamic relays involve inputs from networks in the upper pons. This region is part of what Damasio (1999) called the proto-self, a source of pre-conscious sensing-reacting modules that I have characterized as life urges (Lucas, 2017). While there are only a few thalamic nuclei with life-urge drivers directly relaying interoceptive feeling inputs on to the cortex, life urges from the upper pons region project broadly to the thalamus as modulatory inputs. Thus, the scope of life-urge arousal to the thalamus has been largely underestimated.

Following Sherman and Guillery's findings, I assembled a composite model of how conscious attention emerges that includes brainstem life urges as major inputs to the thalamocortical architecture (Lucas, 2017). It is not my intention to provide a full description of that model here, or to explain the emergent nature of conscious feelings it addresses, but rather to illustrate how the addition of life-urge inputs to the thalamocortical architecture serves to reconcile the different emphases of the adaptive and associative accounts of consciousness. The key to this explanation is that while brainstem life urges are core components of the affect-based accounts of consciousness; they also play a critical role in the attention-based processes underlying consciousness.

Here is a brief overview of how the model in Fig. 2 is proposed to operate. Sensorimotor inputs project to various thalamic relays, but these driver inputs account for less than ten percent of the processing circuitry in each relay. The remaining inputs are all modulatory. About one third of the modulatory inputs come from within the thalamus. These inputs account for the filtering and binding circuits that manage the focus of attention. This focus ensures that only a small subset of features are passed on to the cortex for processing during each moment of attention. Cortical processing for the features that pass the thalamic filter results in the activation of return signals to the thalamus. These

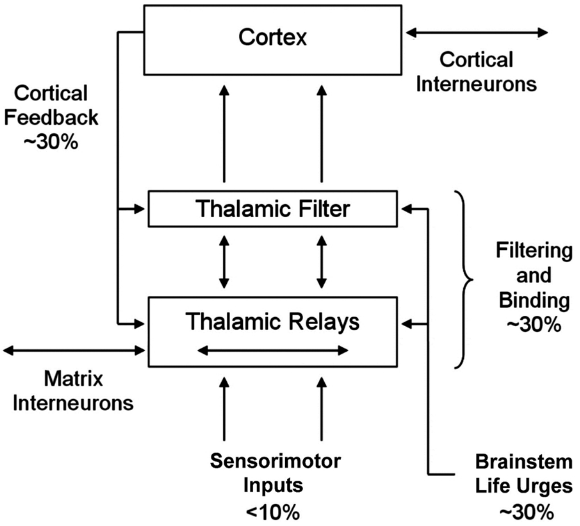

**Fig. 2.** A composite thalamocortical architecture for consciousness including brainstem life-urge inputs.

signals account for another third of the relay inputs and are proposed to hold the features at the focus of attention in synchronous loops that enhance their processing. The final third of inputs in each relay are from life-urge regions in the upper-pons. These signals provide modulatory arousal that helps to prioritize what features best compete for attention.

We have already noted that feature assemblies in the thalamus compete for passage through the filter as a group. Thus, when modulatory life urges are part of the assemblies that gain attention, they can be enhanced as background feelings. In addition, feeling-related inputs from the PBN project to the limbic thalamus. The nuclei in the limbic thalamus were generally thought to act as relays to and from the limbic cortex. However, there is growing evidence that such higher-order relays have a subset of relay cells that are driven by both cortical and peripheral inputs (Groh et al., 2014; Trageser and Keller, 2004). Thus, feeling-related life urges from the PBN also appear to engage activity in the limbic cortex along with cortical-cortical signals. As a result, return signals from the limbic cortex can engage synchronous activity with the limbic thalamus and with the inputs from the PBN that gain attention.

The limbic thalamus also has diverse outputs to other subcortical feeling areas including the nucleus accumbens, hypothalamus, and the amygdala. Thus, it can coordinate feeling-related activity broadly during attention. And because feeling-related life urges involve upward links to the interoceptive cortices and downward links to autonomic systems, all these regions will come to be activated in synchrony as attention stabilizes. In short, there are multiple paths by which the life urges that accompany attention may engage subjective feelings. Even something as simple as attending to music can result in changes in the interoceptive cortices, affective reactions in subcortical networks, autonomic adjustments in the body, and reports of feelings (Blood and Zatorre, 2001; Menon and Levitin, 2005).

The fact that feeling-related processing is enhanced during conscious attention is part of why consciousness is adaptive. However, conscious attention is selective and slow to take form, requiring some 300–500 ms to stabilize. All the features that compete for attention must first be processed unconsciously, and most of them never gain conscious awareness. So what makes this delayed outcome of attention so adaptive? Stanislas Dehaene (2014) argues that consciousness is like a self-amplifying avalanche of neural activity that results in the second-order integration of information. Conscious integration, he suggests, involves broad ascending and descending activations that highlight selected features and make it possible to become aware of their inter-relationships as they are activated together. It is this second-order awareness that enables agents to report on those inter-relationships.

Antonio Damasio (1999) makes a similar point about the second-order integration that occurs in consciousness. However, he emphasizes that consciousness involves an object-organism integration that enhances perceptual experiences in relation to the agent's own internal reactions to them. This makes conscious integration adaptive by prioritizing what gains attention based on the relationship between perceptions and biological life urges. This joint activation of perceptions and feelings accounts for what Damasio has called the *feeling of what happens.* As noted in the model above, this second-order integration is thought to result from the broad synchronous enhancement of perceptions and life urges during conscious attention, much as Dehaene suggests.

There is yet another aspect of neural synchrony that adds to the integrative effect of conscious awareness. Research has found that there are processing regions in the temporal-parietal junction of the cortex that detect synchrony among sensory, motor planning, proprioceptive feedback, and feeling changes. We now understand that agents treat synchrony among planning, proprioception, and feelings as evidence for self ownership of actions, while observed actions that lack this synchrony are attributed to a third-party agency (Decety and Lamm, 2007). In addition, agents treat synchrony among perceived body contacts and proprioceptions as evidence for their ownership of body parts (Blanke, 2012; Ionta et al., 2014). Further, they use synchrony among perceptions and actions for calculating self-location and engaging first-person perspectives (Blanke, 2012; Ionta et al., 2014). In effect, our brains have evolved to experience synchrony among perceptions and internal processes as dynamic features of self.

## 3. Discussion

The behavior systems approach for connecting adaptive dispositions with associative learning can serve as a model for thinking about how adaptive dispositions may influence other cognitive processes. Behavior systems argued that pre-organized adaptive dispositions don't simply motivate learning, they also bias what stimulus and response features are most likely to be engaged by particular motivational systems, and they promote temporal hierarchies of behavioral expression that are not required by associative contingencies. These sensorimotor biases and behavioral patterns presumably evolved to make associative learning more adaptive, although they sometimes appear as misbehaviors in conditioning paradigms.

In the second part of this paper, I have argued that there is a similar influence of pre-organized adaptive dispositions on attention. These attention systems don't simply motivate affective dispositions, as the affect-based models of consciousness propose, they also add modulatory biases that help prioritize what features are likely to win the competition for attention, and they introduce hierarchies of cognitive change that influence how attention may shift. These priorities and patterns of cognitive flow presumably evolved to make conscious attention more adaptive. Most importantly, they ensure that life urges are always part of the assemblies that gain conscious attention.

It also seems informative to consider how similar the adaptive components of the attention-system account of consciousness are to the adaptive components of the behavior-system account of learning. As I have characterized them, life urges are sensing-reacting dispositions. Behavior-system effects occur when life urges influence motor programming outcomes, whereas attention-system effects occur when life urges influence attention outcomes. However, other than their target effects, there appears to be no clear distinction between sources of these dispositions. Studies of the inputs that modulate visual attention indicate that many of them come from motor areas (Sherman and Guillery, 2006), presumably because it is important to attend to visual cues that support certain actions. Further, it is known that the dominant drive in a behavior system not only influences response dispositions, but also the sensory cues to which an agent is likely to attend. These findings suggests that there is an ongoing interaction between behavior and attention systems.

One feature of the behavior systems approach is its emphasis on the hierarchical nature of behavioral expression. It assumes that adaptive dispositions operate on multiple levels and that simpler modules are often nested within broader dispositions. For example, the dispositions for general search, focal search, handling, and consuming involve largely different lower-level behavioral modules. In a similar way, the local-to-larger scale time integration of conscious thought described by Chaudhuri et al. (2015) involves a sequential unfolding of dispositions guided by faster-changing cues and slower changing goals and feelings. This organization seems to map naturally to the observation that stimulus-guided behavior-system modules change faster than modes. Thus, the hierarchical structure of behavior systems may provide insight into the hierarchical structure of conscious processing.

Another difference between Timberlake's model of how behavior systems influence learning and my model of how life urges influence consciousness is that Timberlake focuses on the adaptive effects of life urges on learning and not on their connections in the brain. That was a topic that Timberlake never got around to exploring. However, Michael Fanselow's work on the behavior systems for fear-related behaviors in rodents describes not only their adaptive effects, but also grounds them in neural regions such as the amygdala and the periaqueductal gray (Fanselow, 1994). The neural grounding of behavior systems provides a mechanistic explanation of how fear-related behaviors are coordinated, while the adaptive dispositions that those behavior systems engage explain their functional nature. In a similar way, the neural grounding of attention biases via life urges provides a mechanistic explanation of how attention is prioritized. However, it is the adaptive dispositions that those life urges engage that explain the affective properties of conscious experience.

The parallels between Timberlake's behavior systems approach and my extension of that approach here as attention systems also suggests another likely similarity. The role that behavior systems played in guiding learning was slow to gain acceptance. Similarly, the role that life urges play in guiding conscious experience will also likely take time to gain broad acceptance. However, just as recognizing that life-urge dispositions were directed to motor programming networks gradually enhanced our understanding of learned performance in conditioning paradigms, recognizing that life-urge dispositions are directed to the attention networks should enhance our understanding of how attention is prioritized and why conscious feelings are adaptive.

## Declarations of interest

None

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