Habit and Nonhabit Systems for Unconscious and Conscious Behavior: Implications for Multitasking

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Abstract

The study of human consciousness has demonstrated that there are both conscious and unconscious systems. Other work, particularly in animals, has shown that there are habit and nonhabit systems and that these involve different brain regions and memory processes. Here we argue that habits can be equated with unconscious behavior and nonhabits with conscious behavior. This equation makes the extensive physiological literature on habit/nonhabit relevant to the less tractable issue of consciousness. On the basis of this line of reasoning, it appears that different parts of the BG and different memory structures mediate conscious and unconscious processes. It is further argued here that the unconscious system is highly capable; it can both process sensory information and produce behavior. The benefit of such a dual system is multitasking: The unconscious system can execute background tasks, leaving the conscious system to perform more difficult tasks.

INTRODUCTION

Two separate fields have studied the control of behavior and concluded that it is governed by dual systems. The field of consciousness studies (Dehaene & Changeux, 2011; Alkire, Hudetz, & Tononi, 2008; Berlin, 2008; Baars & Franklin, 2007; Crick & Koch, 2003; Frith, Perry, & Lumer, 1999) has demonstrated clear evidence for both conscious and unconscious processes. A different field of research has used physiological and behavioral methods to study animal behavior and also identified dual mechanisms, a habit system that controls automatic behavior and a nonhabit system that requires cognitive control (Ashby, Turner, & Horvitz, 2010; Graybiel, 2008; Yin & Knowlton, 2006). Here, we examine the question of whether these two fields can be unified. Such unification would make a substantial body of physiological work relevant to what differentiates conscious from unconscious behavior. In what follows, we will first review the evidence from both fields. We will then discuss the arguments for such unification, potential objections, and possible further tests. Our conclusion is that it is reasonable to equate the habit system with unconscious processing and the nonhabit system with conscious processing. We further argue that both systems are capable of sensory processing and action but utilize different brain regions, have access to different forms of memory, and excel at different computations. An important benefit of such a neural architecture is that it allows for efficient multitasking.

ELUCIDATION OF CONSCIOUS AND UNCONSCIOUS PROCESSES

The field of consciousness studies has made substantial progress in demonstrating that there is both conscious and unconscious vision. Participants are said to be consciously aware of a visual stimulus if they report that they see it (the “reportability” criterion). The sense that our consciousness has complete and continuous access to a visual scene is an illusion. Rather, experiments show that there is a configurable attentional window that allows only select information to pass into consciousness. Information not within this window cannot be reported, a phenomenon called “inattentional blindness” (Mack & Rock, 1998). Readers wanting to experience this blindness should view the demonstrations at www.simonslab.com/videos.html.

However, even if attention is focused on a stimulus, the stimulus can be prevented from reaching consciousness by at least 11 different experimental techniques (Lamme, 2006). One such technique is “backward masking” in which, for example, an image of a face is presented and then rapidly (within 50 msec) replaced by a second visual stimulus, the mask. Under these conditions, participants do not see the face.

Importantly, although a masked stimulus does not enter consciousness, it is nevertheless registered by unconscious processes (Higgins & Bargh, 1987; Kihlstrom, 1987). These unconscious processes can then influence even high-level behavior (Lau & Passingham, 2007). This phenomenon can be demonstrated by using a “priming” protocol. In one such study (Aarts & Dijksterhuis, 2002), participants were presented with images (primes) of either a fast or slow animal followed by a masking stimulus. The
participant was then shown pictures of persons and asked to judge their speed; persons preceded by a fast unseen animal were judged to be faster than those preceded by a slow unseen animal. Thus, although the primes did not reach consciousness, they affected judgments.

The ability to manipulate entry into visual consciousness has allowed experimental exploration of the mechanisms that underlie visual consciousness (Kouider & Dehaene, 2007; Dehaene et al., 2001; Pollen, 1999). The evidence indicates that presentation of a visual stimulus produces a rapid (within ~100 msec) bottom–up activation of neurons in primary visual cortex (VI) but that this activation is not sufficient for conscious vision. Achieving conscious vision requires an additional flow of information that is top–down, and it is this that is disrupted by the mask (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Fahrenfort, Scholte, & Lamme, 2008; Sergent & Dehaene, 2004; Pascual-Leone & Walsh, 2001). According to one theory, conscious awareness occurs when there is a match between bottom–up and top–down information (Pollen, 1999; see Graboi & Lisman, 2003, for how this match might be achieved). Once the match occurs, there is amplification of the local signal and the distribution of this signal to other brain areas (Dehaene & Changeux, 2011).

Some processes of unconscious vision have also been elucidated. In cases in which vision is made unconscious by a mask, the stimulus can still prime the detection of subsequent stimuli, a process that appears to depend on visual cortex (Koivisto, Henriksson, Revonsuo, & Raito, 2012). In contrast, the phenomenon of “blindsight,” which occurs after damage to VI (Goodale, Milner, Jakobson, & Carey, 1991; Sanders, Warrington, Marshall, & Wieskramt, 1974), appears to be mediated subcortically. Patients with this condition can make visual discriminations despite the fact that they claim to be blind, that is, they do not report the feeling of seeing (for an analysis of the controversies in this field, see Cowey, 2010). One possibility is that the unconscious processes that underlie blindsight are mediated by the superior colliculus, a subcortical midbrain region that receives direct retinal input and subserves primary visual function in lower vertebrates (Schneider, 1969). In support of this possibility, blindsight fails when color combinations are used that cannot be discriminated by the retinal pathway that innervates the colliculus (Tamietto et al., 2009). A recent review describes the role of the colliculus, pulvinar, and amygdala in these processes (Tamietto & de Gelder, 2010). Further evidence for subcortical vision comes from children born without a cortex who are nevertheless able to use visual information to guide behavior (Shewmon, Holmes, & Byrne, 1999).

The experiments described in preceding paragraphs show that there are conscious (reportable) and unconscious systems for the processing of visual stimuli and indicate that, as with other physiological systems, it is possible to investigate the neurobiological underpinnings. As discussed above, masked stimuli can produce fear, indicating that the unconscious system can influence behavior (for additional examples, see Prabhakaran & Gray, 2012; Galdi, Arcuri, & Gawronski, 2008). Indeed, even high-level behaviors can be influenced by unconscious processes (van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008). We will return later to a closer examination of possible actions mediated by the unconscious (see The Relationship of Habit/Nonhabit to Unconscious/Conscious: “Unconscious Driving” as a Case Study section and Other Behaviors Mediated by the Unconscious System section).

**HABIT VERSUS NONHABIT SYSTEMS FOR BEHAVIORAL CONTROL**

We now review work in human and animal behavior that similarly points to dual mechanisms, specifically to the distinction between habit and nonhabit behavior. Schneider and Schiffirin (Schneider & Shiffirin, 1977) showed that, when a task becomes highly practiced by human participants, it can be performed automatically and without attention. An important property of such automatic behavior is revealed when two tasks are performed simultaneously. If both tasks are novel, then performing them at the same time produces a degradation in performance compared with performing one task alone. In contrast, after one of the tasks becomes a habit, it can be performed together with the second task without interfering with the performance of the second task (Posner & Snyder, 1975). Thus, habit formation allows efficient multitasking.

Habits also develop in lower animals, and there are now specific tests that can be applied to identify behaviors that have become habit. For instance, when an action becomes a habit, an animal will continue to press a lever in response to a stimulus although the resulting food reward has been devalued by satiating the animal (Balleine & Dickinson, 1998). This property of habit has been most extensively studied in rats, but recent work shows that humans become similarly insensitive to outcome devaluation once a task becomes a habit (Tricomi, Balleine, & O’Doherty, 2009). Another approach for studying habits uses a plus maze (Figure 1) in which a rat starts in the south arm and gradually learns which arm of the maze (east or west) contains a reward at its end (Packard & McGaugh, 1996). Learning during the nonhabit phase is characterized by a particular behavior: The rat pauses at the choice point, often looking east and west, before making a choice. After many trials, the behavior enters the habit phase in which the rat turns toward the reward without a pause. Although habit behavior is thus faster, it has disadvantages. This becomes evident on “probe trials” in which the rat is started at the north arm of the maze rather than the south arm (Figure 1). If such a probe trial is made during the nonhabit phase, the rat utilizes spatial cues and correctly reaches the goal, although this now requires a right turn rather than a left turn (place strategy). If, however, the probe trial is given during the habit phase, the rat makes the habitual left turn, leading it east and away from the reward (response...
strategy). Thus, when acting through a habit, the rat does not utilize all of the available information to lead it to the goal. We will discuss later why such seemingly inefficient behavior may have evolved.

The ability to distinguish habit from nonhabit behavior in animals has made it possible to investigate the underlying brain processes. According to one major theory, nonhabit behavior involves the dorsomedial striatum, whereas the habit behavior involves the dorsolateral striatum (Yin & Knowlton, 2006). In support of this theory, task-dependent neural activity in the dorsolateral striatum builds up gradually over many trials. In contrast, dorsomedial striatum becomes less active once the habit phase is attained (reviewed in Yin & Knowlton, 2006). If a lesion is made in the dorsolateral habit system after habit formation, behavior on probe trials reverts from a response strategy to a place strategy (Yin, et al., 2004; but see Botreau & Gisquet-Verrier, 2010; Figure 1C). Similar conclusions have been reached about the role of subdivisions of the striatum in habit versus nonhabit behavior in monkeys and humans (Tricomi et al., 2009; Graybiel, 2008; Floyer-Lea & Matthews, 2004; Miyachi, Hikosaka, & Lu, 2002; Jueptner et al., 1997; Passingham, 1996). Exactly how the BG and cortex interact to produce habit behavior remains unclear (Pasupathy & Miller, 2005; Bottjer, Miesner, & Arnold, 1984). There is some evidence that, in the final stages of habit formation, behavior may be organized by the cortex without any further influence from the BG (Turner & Desmurget, 2010; Doupe, Perkel, Reiner, & Stern, 2005).

Another important set of advances provides a mechanistic understanding of why rats can find the goal on probe trials during the nonhabit phase but cannot find the goal once a habit is developed. Recall that, during a probe trial, the rat is started from the north arm rather than the south arm and must now make a right turn rather than a left turn to reach the goal. This behavior requires the sense of space provided by the hippocampus, a region where “place cells” (O’Keefe, 1979) represent positions in the environment. Indeed, if the hippocampus is inactivated during probe trials, the rat cannot find the goal even during the nonhabit phase (Figure 1B; Packard & McGaugh, 1996). The hippocampus, a key structure necessary for episodic memory (one-trial learning about specific events), is thus necessary for this form of nonhabit behavior.

Multielectrode recordings from the hippocampus have made it possible to observe the hippocampal recall...
processes that allow spatial information to be utilized to find a goal. The recall of a previous trip down an arm of the maze can be recognized by the sequential activation of place cells representing the sequence of positions down that arm (Figure 1A), a process organized by theta and gamma oscillations (Lisman & Redish, 2009; Johnson & Redish, 2007). During the nonhabit phase, rats pause at the choice point and serially recall prior trips down different arms of the maze (Figure 1A). Such serial recall appears to inform the decision in downstream targets (pFPC and striatum) about how to find the goal (van der Meer & Redish, 2011; Jones & Wilson, 2005). Once the behavior becomes a habit, there is no pause at the T-junction, and the hippocampal recall processes of the type shown in Figure 1A no longer occur. Taken together, these studies make the strong case that hippocampal information is used to guide behavior before a task becomes a habit but is no longer involved after the task becomes a habit.

The information summarized in this section has, we hope, convinced the reader that separate brain processes mediate habit and nonhabit behaviors and that substantial progress has been made in elucidating the mechanisms involved.

THE RELATIONSHIP OF HABIT/NONHABIT TO UNCONSCIOUS/CONSCIOUS: “UNCONSCIOUS DRIVING” AS A CASE STUDY

We now turn to the core question: Can conscious behavior be equated with nonhabit and unconscious behavior with habit? To examine this issue, it is useful to consider an experience that will be familiar to most readers: driving a car. An experienced driver on a well-known route may be deep in thought about matters not related to driving. A common occurrence is that the driver arrives at the destination with no recollection of events along the way. One colleague, who has two routes that he can take to work, often arrives at work and cannot recollect which route he took that day. It thus appears that, when consciousness is strongly turned to nondoning issues, such as an important meeting later that day, events related to driving are often not entered into long-term memory. Similarly, events stored in episodic memory, such as instructions to pick up a gallon of milk along the way, are often not accessed by the “unconscious driver.” Thus, like the habit behavior of the rat discussed previously, the behavior that occurs before habit formation may require the hippocampus, especially for complex tasks (Wise & Murray, 1999); however, once driving becomes a habit and the route is known, driving can be done without access to hippocampal episodic memory. Work on humans with hippocampal damage has led similarly to the conclusion that important aspects of human consciousness are dependent on the hippocampus (Clark & Squire, 1998; note that such contributions do not imply that consciousness would be absent without a hippocampus), whereas unconscious behavior is not (Smith, Hopkins, & Squire, 2006; but see Hannula & Ranganath, 2009).

It could be argued that, while driving, one is always fully conscious of the road and that memory is not always engaged. However, for some drivers, the experience of “tuning out” is more than just a memory problem; this becomes evident when attention returns to the road—there is the feeling of having been effectively blind during the previous inattentive state. Thus, even events that occurred seconds before cannot be reported. Given that reportability is the defining characteristic of conscious processing, it seems that driving can be done unconsciously. Experiments done using a driving simulator support this interpretation. It was shown that participants using cell phones often fail to report important targets, thus demonstrating inattentional blindness (Strayer, Drews, & Johnston, 2003). But if targets are not seen, why don’t accidents occur more frequently? Certainly, continuous visual processes are required to keep a safe distance from other cars. Experiments done with an eye tracker show that, when drivers become deeply involved in a cell phone conversation, there is no reduction in the shifts of gaze to targets, although there is a reduction in the number of targets reported (Strayer et al., 2003). It follows that there is an unconscious system with considerable ability to produce the eye movements necessary for driving. We argue that it is this unconscious system that is driving. It was described earlier that there is a form of vision (blindsight) that cannot reach consciousness. Blindsight patients move their eyes to targets that they do not report seeing (Poppel, Held, & Frost, 1973). Perhaps, the same mechanisms mediate “unconscious driving.” Later, we will propose a direct test of this possibility.

The advantage of having both unconscious and conscious capabilities is clear: The dual system allows efficient multitasking. When one is just learning to drive or when an experienced driver takes an unfamiliar route, the conscious system must be engaged. After the route becomes a habit, driving can be done unconsciously, allowing the nonhabit system to perform another task (e.g., preparing a lecture). An influential hypothesis (Daw, Niv, & Dayan, 2005) proposed that the habit and nonhabit systems provide different capabilities for optimally solving the same task. We argue that, to the contrary, the specific task being performed by habit is often performed suboptimally, especially if the task requires some degree of flexibility in the decision-making process (this is indeed the case during the probe trials on the plus maze when the animal systematically goes away from the goal). However, what makes suboptimal performance on the specific task acceptable is that an entire additional task can be performed simultaneously.

OBJECTIONS TO THE HYPOTHESIS

It might be argued that unconscious driving is not done by a system separate from the conscious system; rather, there may be a single system that simply directs a low amount of attention to a particular task. In this case,
“unconscious” driving would be better described as conscious driving with low attention devoted to driving. However, the memory processes that occur during unconscious driving are difficult to reconcile with this view. As noted earlier, unconscious driving does not have access to episodic memory. Furthermore, there are memory processes that can influence unconscious driving, and these have the slow learning properties characteristic of the procedural memory of the habit system. Witness what happens if a person’s route to work changes—it may take weeks before he or she stops taking the old route. These aspects of memory performance support a crisp distinction: Conscious driving utilizes episodic memory; unconscious driving uses procedural memory. Such a crisp distinction is difficult to explain in terms of a single system that simply gives low attention to driving. For related arguments, see Bargh and Morsella (2008); Reber and Squire (1994); Lewicki, Hill, and Czyzewska (1992); and Reber (1989).

A further argument against the single-system/low-attention model goes as follows: Although habits can be unconscious, it is certainly possible to focus attention on habit behavior. But, let us consider whether this helps or hinders performance. If there is a single system that devotes variable attention to a process, one would predict that increasing attention to that task should improve performance. However, contrary to this prediction, skilled athletes and musicians believe that it is detrimental to turn attention to their performance. Indeed, experiments on skilled golfers confirm this view; they perform better when their attention is pulled away from the process of stroke production (Beilock, Bertenthal, McCoy, & Carr, 2004).

A different objection to our argument is that equating the unconscious with habit violates people’s intuition that their unconscious can solve problems. Consistent with this intuition, experiments (Dijksterhuis, Bos, Nordgren, & van Baaren, 2006) indicate that the solution to complex problems (the authors asked participants to pick the best car based on comparisons of 12 qualities) can better be done without thought (but see Rey, Goldstein, & Perruchet, 2009). One explanation is that consciousness requires serial processing of memories, a process that may not be systematic. Indeed, as we have discussed, the downloading of different episodic memories from the hippocampus to the striatum and pFC is demonstrably serial. In contrast, the statistical learning that characterizes procedural/habit learning can be evaluated by parallel processes (Figure 2; Cisek, 2007). Thus, whereas episodic memory may focus on one or several events, statistical learning necessarily combines information from all relevant events and may thus, on average, have greater accuracy. Indeed, in the example given in Box 1, the statistically based parallel process arrives at a better solution than a serial process based on the best single trial recalled from episodic memory. These considerations suggest that the problem-solving capability that some people attribute to their unconscious could result from the unique capabilities of the unconscious system.

Figure 2. The unconscious can perform some mental operations better than the conscious. Here, we provide an example of how the unconscious system (using parallel access to procedural memory) could perform more optimally than a conscious system (using serial access to episodic memory). The example involves the problem of finding the optimal force for pulling a trigger on a gun. This decision is based on the memory of previous shots that used different forces (F) and that resulted in shots of different accuracy. We assume that accuracy is also dependent on a random process (e.g., wind). Using too little force lengthens the whole process and introduces error, whereas using too much force moves the gun and introduces error. What type of computation on past experience can lead the shooter to determine the optimal force? First, consider how this is solved consciously using episodic memory (which records the force and accuracy of each shot [F1 and A1, F2 and A2, etc.] as plotted above by black points). A conscious process could recall each shot serially and pick the force (F3 in the graph) that gave the single shot having the best accuracy (see arrow in top right). However, the accuracy of this shot was affected by the random wind, and the associated force on that shot may thus not be generally optimal. This is why the statistical learning (averaging over trials) that is characteristic of the unconscious can do better, as follows. Procedural memory stores the average accuracy for each force (red points in the graph); each average is represented in a neural network (shown at the bottom) by a synaptic weight (oval). Given the influence of these weights on the postsynaptic cells, a parallel winner-take-all process can find the most excited cell. This will be the cell representing force (F2), which is closer to the optimal force than the force chosen by episodic memory (F3).
would imply that unpracticed participants could change their response according to the feedback but would be unable to report that they had done so. We have not found any test of this prediction, but such behavior seems unlikely to us.

Another possible objection is that there may be nonhabits that are unconscious. For instance, participants on a treadmill were told to keep constant speed despite variable resistance on a treadmill; participants successfully compensated to maintain their speed yet were unaware of the changes in resistance for which they were compensating (Varraine, Bonnard, & Pailhous, 2002). This raises the possibility that nonhabit behavior can be unconscious. Alternatively, we suggest that the task of motor adjustment to resistance is one that over life may have developed into a habit. We suspect that, had the task involved something that never occurs in the environment (keeping constant speed despite changes in the direction of the treadmill), subjects would always be conscious of the direction change. For an interesting description of how habits can be directed by goals, see Dijksterhuis and Aarts (2010).

A final objection is that nonhabit behaviors such as shopping can be influenced by advertising without the person being conscious of it (Yoo, 2008) and might therefore be classified as an unconscious act. The problem with this critique is that it does not differentiate between the action itself and the processes that lead to that action. The fact that conscious decisions can be influenced by unconscious factors does not alter the fact that the decision itself is reportable and therefore conscious.

**PREDICTIONS OF THE HYPOTHESIS**

**The Role of an Unconscious System during Habit Driving**

We have argued that driving by habit is done by unconscious processes. How might this hypothesis be further tested? As mentioned, the subcortical mechanisms of the superior colliculus that have been implicated in blindsight have different color sensitivity than cortical vision. If unconscious driving (as during deep conversation on a cell phone) is done subcortically, target detection should come to have the color sensitivity of subcortical vision.

**Other Behaviors Mediated by the Unconscious System**

If dual systems govern behavior, one would expect some unusual conditions in which the conscious system is inactive, leaving only the unconscious system functional (i.e., with the capability of an unconscious driver). Such a person would be capable of sophisticated but limited interaction with the environment—sophisticated in the sense that tasks such as driving require vision and complex procedures, and limited in the sense that the behavior would be inflexible (based on procedural memory rather than episodic). Such a person would not use episodic memory. It seems possible that somnambulism is such a state (Koch & Crick, 2001). Sleepwalkers are capable of some sophisticated operations; they can speak, drive, and send e-mails (Siddiqui, Osuna, & Chokroverty, 2009; www.nytimes.com/2006/03/08/business/08ambien.html). However, as is characteristic of the unconscious system, sleepwalkers generally cannot use episodic memory and thus cannot have a two-way conversation during sleepwalking and report afterward what occurred (American Academy of Sleep Medicine, 2005).

If the unconscious system can speak during somnambulism, perhaps it also speaks during normal wakefulness. We urge readers to replicate an experiment that we have done, which suggests this to be the case. Passing a friend in the hall, the following type of interchange sometimes occurs: Your friend says, “How are you?” You say, “Fine.” Your friend then says, “Fine,” without being asked. After such exchanges, we have waited 10 sec and asked the friend to reconstruct the conversation. The initial part of the conversation is well remembered, but in no case (n = 8) did the friend recall saying “fine” or the odd fact that he or she replied without being asked. This is consistent with the hypothesis that “fine” was generated by the unconscious and not remembered because the unconscious does not store information in episodic memory.

**Multitasking in Rats during Habit Behavior**

We have argued that the function of the habit (unconscious) system is to allow a second task to be performed by the nonhabit system (multitasking). Because rats have both habit and nonhabit systems, rats should be able to multitask. We propose a test of this prediction that builds on the use of place cells in the rat hippocampus to monitor mental processes. These cells represent a given place by firing when the rat is at that place. However, there are periods when the cell fires elsewhere (Jackson & Redish, 2007; Olypher, Lansky, & Fenton, 2002), and this has been interpreted to mean that the rat is recollecting the distant place, a process that promotes memory consolidation (Girardeau, Benchenane, Wiener, Buzsáki, & Zugaro, 2009). In the proposed experiment, the rat goes through a novel premaze before entering the main maze. We predict that a rat can recollect a place in the premaze while moving through the main maze (thus demonstrating its ability to multitask) but that this will only occur after moving through the main maze has become a habit.

**COMMUNICATION BETWEEN THE CONSCIOUS AND UNCONSCIOUS**

A brain architecture in which there are conscious and unconscious systems implies that there must be mechanisms for communication between the two systems. In the section below, we review several lines of evidence.
that provide evidence for both normal and aberrant forms of such communication.

According to Antonio Damasio’s “somatic marker hypothesis,” our experiences leave unconscious physiological markers that affect future decisions. When we are in the midst of a decision, these markers may push certain alternatives to the forefront of our consideration before any conscious analysis has begun, creating a “gut feeling” that is accessible to consciousness (Damasio, 1996).

Another type of signal sent from the unconscious to consciousness is the feeling of familiarity. It is a common experience to meet someone and have no idea who he or she is yet be filled with a feeling of familiarity. Ways of measuring this feeling have been developed and are now a standard part of memory research in both humans and rats. Such experiments indicate that the feeling of familiarity results from regions in the temporal cortex that do not include the hippocampus (Sauvage, Fortin, Owens, Yonelinas, & Eichenbaum, 2008). Readers who experience déjà vu know what it is like to experience an aberrant familiarity signal. During déjà vu, one is filled with a feeling of familiarity, but logical analysis indicates that the feeling cannot be correct. Apparently, the pathway responsible for communicating familiarity from the unconscious to the conscious is generating a spontaneous signal. Experiments using direct brain stimulation have shown that déjà vu can be most easily evoked in the entorhinal cortex (Bartolomei et al., 2004).

The unconscious system can influence the emotions felt by the conscious system in surprisingly indirect ways. For instance, a complex pathway mediates the flow of information about fear from the unconscious to the conscious. As noted earlier, the unconscious system can detect a fearful stimulus, leading to activation of the amygdala. The amygdala then can lead to activation of the autonomic system, which results in increased sweating and heart rate (Flykt, Esteses, & Ohman, 2007; Esteses, Parra, Dimberg, & Ohman, 1994). Fear may then become conscious as a result of the perception of these peripheral autonomic changes. This example and another example involving the memory consolidation (McIntyre, McGaugh, & Williams, 2011) are remarkable in suggesting that, in some cases, there is no direct information flow between conscious and unconscious parts of the CNS; communication in these cases occurs only indirectly through peripheral changes.

A breakdown in communication between the unconscious and conscious systems may underlie schizophrenia. A common characteristic of this disease is the hallucination of voices. These are generated by subvocal articulation, which can be measured by transducers on the throat (Frith & Johnstone, 2003; McGuigan, 1966), but are unconsciously generated and not recognized as coming from the self. The reason, according to one class of models (Frith, 2012; Zhang, Yoshida, Katz, & Lisman, 2012; Stephan, Friston, & Frith, 2009; Mathalon & Ford, 2008; Feinberg, 1978), stems from the malfunction of a comparator that normally subtracts a corollary discharge (a signal sent from the motor system about the expected sensory consequences of speech) from the actual acoustic input. If there is cancellation, a “match” signal is sent to other parts of cortex, identifying the sensory signal as coming from self; if there is no cancellation, the output is “mismatch,” identifying the signal as coming from nonself. In schizophrenia, the corollary discharge or the comparator may malfunction, resulting in a mismatch signal. We argue that this is particularly problematic when speech is generated by the unconscious voice; a mismatch would lead conscious parts of the brain to conclude that the speech was generated by someone other than the self. Because no such individual could be identified, conscious processes would conclude that the speech must have been implanted in the brain by a technologically savvy organization (e.g., the FBI).

CONCLUDING REMARKS

Understanding how different brain regions function together to produce behavior is a major goal of modern neuroscience. We argue that a critical element of the solution will require delineation of conscious and unconscious processes and that the study of habit/nonhabit provides an experimental approach useful to achieving this goal. Figure 3 provides a tentative view of a brain architecture in which the conscious and unconscious systems are delineated. We emphasize that both systems can receive and process sensory information and that both can control behavior. However, the brain processes involved are different. Notably, only the conscious system can store information in the hippocampal episodic memory system, and only the conscious system can recall information from this store (using a serial recall process). The unconscious system, in contrast, uses parallel recall of the statistical properties of experience (Figure 2).

The effort to determine the brain regions and network processes that underlie the dual conscious/unconscious systems is just in its infancy, but there are promising approaches for making further progress. For instance, EEG recordings during somnambulism show that much of the brain remains in a sleep-like state, as judged by the slow waves that are characteristic of non-REM sleep. In contrast, the central cingulate cortex and motor cortex have an EEG characteristic of the awake state (Terzaghi et al., 2009), suggesting that these regions mediate the unconscious behavior seen during somnambulism. Another approach has found that direct electrical stimulation of some human brain regions cannot be detected consciously, whereas stimulation of other regions can be (Desmurget et al., 2009). The use of rats to study habit and nonhabit behavior will also be important. The role of the hippocampus in conscious recollection has been discussed; recent work in rats has delineated two regions, the pFC (Siapas, Lubenov, & Wilson, 2005) and the ventral striatum (Tort et al., 2008; Berke, Okatan, Skurski, & Eichenbaum, 2009).
that are recipients of the information recalled by the hippocampus and are thus likely to be part of the conscious system. Insight may also be gained from human behaviors that are not consciously willed. For example, smiles that occur spontaneously are triggered by the cingulate motor area, whereas willed (forced) smiles originate in the motor cortex (Purves et al., 2008, pp. 735–736).

If both the conscious and unconscious system can process sensory information and produce actions, there must be mechanisms that determine which system will control behavior. In some cases, the underlying logic is simple, as in multitasking; the unconscious controls the routine behavior. But, in other cases, the logic of control is less clear; you may decide to go on a diet yet suddenly find yourself removing ice cream from the freezer. The study of habit and nonhabit behavior in animals provides a path toward understanding how conscious and unconscious systems compete for control. Experiments in monkeys show that the presupplementary motor cortex is required for switching behavior from the habit to nonhabit mode (Hikosaka & Isoda, 2008). Experiments in humans implicate this same area in the control of willed actions (Haggard, 2008; Shibasaki & Hallett, 2006). The network mechanisms that determine whether an action is willed or performed automatically remain to be determined.

In summary, we have argued that there are separate systems for the conscious and unconscious control of behavior. These systems can be usefully mapped onto the nonhabit and habit systems that have been studied in animals by behavioral and physiological methods. We believe that this framework sets the stage for a strong experimental approach that will lead to the understanding of both conscious and unconscious systems.

Acknowledgments

We thank Dan Graboi, Gordon Fain, Paul Miller, Aline Newton, Dan Pollen, Chris Frith, and David Redish for comments on the manuscript. We thank Barbara Knowlton and Gerald Schneider for useful conversations. Supported by NIH/NIMH Conte Center grant P50 MH60450 and the European Commission Project 217148.

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