The Neuroscience of Goal-Directed Behavior

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If you ask average Americans to list their goals (as the website http://www.43things.com asks them to do) their answers run the gamut from “being happy” to “going on a road trip with no predetermined destination” (Table 2.1). Although people’s goals vary widely in what they aim to achieve and the obstacles that would be involved, they all have a few things in common. For one, they describe activities and outcomes with an abstractness and complexity far greater than what nonhuman animals probably would ever conceive. For another, it is clear that achieving any of their goals requires a system that can translate these abstract goals for a future state of the world into concrete actions in the present moment that are thought would get them there. This is no easy task. Not only must abstract goals (e.g., stop procrastinating) be translated into intermediate goals and actionable subgoals, but typically these (sub)goals require behaving in a way contrary to our ingrained habits and tendencies (e.g., turn off reality television until the book chapter is finished).

If we are interested in studying what brain mechanisms enable people to achieve their goals using these and other processes, then the types of goals we end up studying are necessarily a good bit simpler than “getting a tattoo” or “going to Europe.” A critical assumption behind this approach is that the neural systems studied in well-controlled laboratory settings are the same as those that are used to achieve more realistic and complicated goals in real life. For instance, one common goal is to quit smoking, in which individuals experience conflict between craving
cigarettes and their goal to curb their habit (Tiffany, 1990). In the laboratory, conflicts between goals and habitual tendencies are assessed by relatively simple tasks, such as the Stroop task, that are thought to depend on the ability to guide thought and behavior based on an internally maintained goal, which is known as cognitive control. In the Stroop task, as illustrated in Figure 2.1, individuals are asked to name the ink color that words are written in rather than saying the word. Our habitual tendency is to read words, and so conflict ensues as one is trying to override the habitual response with the instructed or goal-driven response to name the ink color. The assumption is that the kind of conflict that is experienced in this task is to some degree like the conflict experienced when trying to resist a cigarette, another piece of cake, or an angry impulse, and therefore engages the same neural systems involved in goal-directed behavior in the real world. In other words, the cognitive neuroscience approach involves breaking down goal-directed behavior into a set of constituent cognitive processes engaged in simple goal-directed laboratory tasks. It is these processes that laboratory tasks and everyday goals have in common.

This chapter provides a brief overview of the cognitive neuroscience of goal-directed behavior. We start by laying out some key functions that are required of

Table 2.1 Ten Popular Goals Listed on the Website http://www.43things.com

<table>
<thead>
<tr>
<th>1. Lose weight.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Stop procrastinating.</td>
</tr>
<tr>
<td>3. Write a book.</td>
</tr>
<tr>
<td>4. Fall in love.</td>
</tr>
<tr>
<td>5. Be happy.</td>
</tr>
<tr>
<td>6. Get a tattoo.</td>
</tr>
<tr>
<td>7. Drink more water.</td>
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<tr>
<td>8. Go on a road trip with no predetermined destination.</td>
</tr>
<tr>
<td>10. Travel the world.</td>
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</tbody>
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<table>
<thead>
<tr>
<th>Column 1</th>
<th>Column 2</th>
</tr>
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<tbody>
<tr>
<td>Red</td>
<td>Green</td>
</tr>
<tr>
<td>Purple</td>
<td>Red</td>
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<tr>
<td>Blue</td>
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<td>Blue</td>
<td>Purple</td>
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Figure 2.1 (See color insert following page xxx.) The Stroop effect. The Stroop effect illustrates the conflict that ensues when habits and task goals are at odds with each other. The task goal is to name the ink color of the words. For column 1, little conflict is produced because the responses produced by habitual tendencies to read the words are the same as those produced by the task goal of naming the ink colors. However, for column 2 habitual tendencies and task goals promote different responses, thereby eliciting greater conflict.
a system supporting cognitive control and the evidence from simple motor tasks for implementation of these functions in the brain. We then extend our discussion beyond the control of motor responses to consider the mechanisms that support cognitive control of memory and emotion. Finally, we highlight some of the open questions in this field.

CORE FUNCTIONS OF A CONTROL SYSTEM

Consider for a moment a system of neurons that fires in response to sensory changes in the environment, produces a cascade of firing patterns through the brain, and terminates with a behavioral response (Figure 2.2). The behavioral response then elicits a change in the environment that ultimately produces a positive or negative outcome, which in turn strengthens or weakens that particular cascade of connections from input to output. After multiple such events, the mapping between a sensory event and a behavior that produces a positive outcome would be strengthened. As a consequence of this process, the mappings from a particular sensory event to certain responses would be stronger than the mappings from that event to other responses.

An individual with this simple network can learn to engage in behaviors that usually help him or her, avoid behaviors that usually hurt, and ignore dimensions of the world that are usually irrelevant. For instance, over time the individual may learn to eat apples, avoid mosquitoes, and pay no mind to small bushes. At first, the association that maps seeing the apple to eating it may be weak. But through repeatedly receiving stronger positive outcomes for eating the apple relative to the other behaviors, this mapping becomes the strongest one. A simple network of this sort can also instruct that some events or behaviors lead to others that may help or hurt the individual. For instance, shaking a tree is associated with falling apples that can then be eaten.

Figure 2.2  Schematic of a simple stimulus-driven system. A simple stimulus-driven system, as represented by the simplified network above, may modify its connections over time to produce a more desirable stimulus response association. On trial 1, preexisting patterns produce a particular response (the shaded circle) to a given input. If over successive trials this pattern yields a maladaptive outcome, intermediary connections between this response given the input will be weakened and alternative responses may be strengthened to shift toward a more adaptive response.
For such a system, behavioral choice occurs strictly as a consequence of the stimuli that are encountered and their strongest associations. In this sense, the system is stimulus driven. Often, however, these strong associations are inappropriate, even damaging, given our goals and broader context. For instance, eating an apple may not always be the best idea if you have diabetes. In this case, how do we choose a weakly associated behavioral response when doing so is demanded by our broader context or goals?

An influential model of cognitive control that attempts to account for some aspects of controlled behavior is the biased-competition model (Desimone & Duncan, 1995; Miller & Cohen, 2001). This model begins by assuming that when presented with a stimulus, multiple response pathways are activated. For instance, seeing an apple may be associated with behaviors to eat it, as well as to juggle it, avoid it, or to give it to a friend. Left to its own devices, these pathways will compete for expression by mutually inhibiting one another until the strongest pathway succeeds in influencing behavior. In this case, the strongest pathway would be to eat the apple. To select an alternative pathway, a goal must be represented and internally maintained. This goal exerts its influence by biasing the goal-relevant pathway over any stronger ones (Figure 2.3). For example, someone with diabetes may represent and maintain the goal to avoid sugary foods, which biases against the dominant apple-eating pathway and in favor of another snack.

To achieve this basic ability, biased competition models share a set of core functions that we will consider here, along with their putative neural correlates:

1. Control systems have a “working memory” or the ability to internally maintain goals and contextual information important for engaging in goal-appropriate behavior.
2. Control systems require a means of “adaptive gating” in order to let only goal-relevant information into working memory and keep goal-irrelevant information out.

Figure 2.3  Schematic of a simple control system. A goal-driven system, as represented by the simplified network above, requires control nodes to maintain goal information (e.g., task instructions). According to the biased-competition model (Miller & Cohen, 2001), these nodes select for and strengthen the weaker pathway, which in turn gains enough strength to inhibit the stronger pathway such that the weaker pathway can be expressed.
3. Control systems require a mechanism to select goal-relevant and inhibit goal-irrelevant associations as a consequence of maintaining a goal.
4. Control systems require a means of determining when control needs to be deployed.

Although we recognize that these functions are likely to be just a subset of several central functions that go into a control system, we focus on them because they are among the most important functions highlighted in the literature to date.

**Working Memory: Keeping Goals in Mind**

One remarkable capacity we have is the ability to maintain goals internally and for extended periods of time. In other words, goals can be maintained without requiring an external stimulus to remind us to do so. A simple stimulus-driven system (as in Figure 2.2) is incapable of accomplishing this behavior. If such a system were given the instruction “don’t eat apples” but a few minutes later is shown one, it is likely to eat it simply because there is no inherent mechanism that can maintain this instruction over those minutes. It simply cannot maintain the goal. Hence, a system capable of following goals must require a means to maintain internally an online representation of information over time and in the absence of external reminders. Which neural regions could subserve this ability?

The ability to maintain internally information over a transient delay period has been studied in working memory tasks. In such tasks, a set of items (e.g., objects, words, locations) is presented that is relevant for a future response. These items then disappear, requiring individuals to maintain them internally over a delay (typically a few seconds), upon which a probe is presented in which individuals must use their memory for the maintained items to make the correct response.

In now classic studies involving single-cell recording in primates, cells in the lateral prefrontal cortex (PFC) have been shown to respond to holding information across a delay period in which the stimulus was no longer present in the environment (Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster, 1973; Goldman-Rakic, 1987). That is, they fired when the information was presented and continued to fire after the information disappeared until it was used to make a relevant response. Further, damage to the dorsolateral PFC causes delay-related impairments; if there is no delay, there is no impairment, but incorporating a brief delay of just a few seconds results in impairments (Buckley et al., 2009; Funahashi, Bruce, & Goldman-Rakic, 1993; Rushworth, Nixon, Eacott, & Passingham, 1997). This specifically implicates the dorsolateral PFC in the ability to maintain information over a delay period, rather than a more general deficit in representing the stimulus or required response since these remain intact without a delay. Human neuroimaging studies examining working memory activity have also shown activity in the lateral PFC (see Figure 2.4 for approximate locations of Brodmann’s areas and Figure 2.5 for locations of functional activations related to working memory; Curtis & D’Esposito, 2003; Wager & Smith, 2003).

Following from this, an important question is whether maintenance circuits in the lateral PFC are domain general, such that the same areas are capable of
Figure 2.4  (See color insert following page xxx.) Approximate outline of Brodmann’s areas in human prefrontal cortex.
maintaining various sorts of information, or whether they are domain specific, such that different areas of the lateral PFC maintain information for spatial, object, or verbal domains (Baddeley, 2003; Baddeley & Hitch, 1974; Goldman-Rakic, 1987, 1999). Cell-recording studies in primates have shown that individual neurons show selective maintenance of spatial and object information (Wilson, O'Scalaidhe, & Goldman-Rakic, 1993), but also that several neurons integrate across these two domains (Rainer, Asaad, & Miller, 1998a), and particularly so when the task goals require them to (Rainer, Asaad, & Miller, 1998b; Rao, Rainer, & Miller, 1997; Wallis, Anderson, & Miller, 2001).

Though working memory studies illustrate that information can be held internally over delay periods, information in these studies is typically arbitrary (e.g., a set of dots in particular locations). But how might this ability relate to goal-driven behavior? One possibility is that the lateral PFC is involved in maintaining the goals themselves in the form of an instructional set or stimulus-response mapping. To examine this, Macdonald et al. (2000) had participants complete a Stroop task in which instructions to either name the color of the word or to simply read the word were given prior to the presentation of each word. Results showed that activity in the lateral PFC was related to the instruction cue, prior to the presentation of a colored word. In another study, participants were presented with four different cues that signaled which set of stimulus-response rules were relevant (Bunge et al., 2003). For two rules, the match and nonmatch rules, the instruction cue indicated whether individuals should make a target response if the subsequently presented
stimulus and probe match or do not match. For the other two, they were instructed to make a left or right button press response regardless of the stimulus and probe. The first two rules had greater complexity of stimulus-response mappings relative to the simple response rules. Their results showed that the lateral PFC was sensitive to greater rule complexity as well as maintaining these rules over a delay. Working memory functions in the lateral PFC, then, could be useful for maintaining instructions and goals for implementing goal-directed behavior.

**Adaptive Gating: Updating Goals**

A system of neurons that actively maintains information online must have some mechanism to update its contents when that information is no longer required. Without such a mechanism, it would likely persevere on whatever goal it has in mind, even though it is no longer relevant, or conversely, it would be unable to keep salient but irrelevant information out of working memory. The basal ganglia has been hypothesized to play this role. Frontostrial loops, connections that loop through structures within the striatum and the prefrontal cortex (Alexander, Delong, & Strick, 1986), may serve a gating function that (a) prevents irrelevant information from interfering with the maintenance of relevant information, and (b) allows relevant information to update the contents of working memory (Braver & Cohen, 2000; Frank, Loughry, & O’Reilly, 2001; Miller & Cohen, 2001).

The general idea is as follows. Activation of thalamic connections to prefrontal cortex opens a gate for new information to enter active memory. However, thalamic input to the prefrontal cortex is generally inhibited by the globus pallidus. This allows the prefrontal cortex to maintain information robustly rather than being continuously updated. When an update is in order, the basal ganglia inhibits the globus pallidus, thereby disinhibiting the thalamic input to the prefrontal cortex and allowing the prefrontal cortex to update the contents of working memory. This model places the basal ganglia in the central role for controlling the updating of the lateral PFC (Hazy, Frank, & O’Reilly, 2006). Supporting this, McNab and Klingberg (2008) found that greater activity in the basal ganglia predicted whether lateral parietal regions involved in the maintenance of information additionally responded to irrelevant information.

The frontostriatal loops are dopaminergic, and central to this model is the multifaceted role of dopamine. In the lateral PFC, dopamine has more of a tonic influence on neural firing, whereas in the striatum, dopamine has a relatively more phasic influence on neural firing (Grace, 1991). This is due to several factors that differentiate the lateral PFC and the striatum, including the type and distribution of dopaminergic receptors, the presence of enzymes that break down dopamine, and reuptake mechanisms (Cools, 2006). It has been suggested that the tonic and phasic aspects of dopamine relate to the ability to maintain and update information, respectively (Braver & Cohen, 2000; Cohen, Braver, & Brown, 2002). Importantly, these two abilities are inherently competitive. That is, the ability to actively maintain information over delays and despite distractions is opposed by the ability to update what information is being maintained. The relative influence of tonic and phasic aspects of dopamine is believed to modulate the balance between...
the opposing alternatives. Indeed, modulation of the dopaminergic system has shown tradeoffs between maintenance and updating mechanisms (Bilder, Volavka, Lachman, & Grace, 2004; Cools, 2006; Mehta, Swainson, Ogilvie, Sahakian, & Robbins, 2001), supporting this idea.

Selection and Inhibition: Implementing Goals

The functions of internally maintaining goals and being able to update them aside, a goal-driven system must also have a way of using this information to influence behavior. Implementing control is thought to occur by selecting weaker pathways over stronger ones. This type of control is modulatory in that the control system guides connections within the stimulus-driven system. In other words, the system exerts influence over existing associative connections, but does not house or maintain the newly formed or reinforced associations in the long term.

A few key lines of evidence support the role of the lateral prefrontal cortex in the implementation of control (Miller & Cohen, 2001). First, the prefrontal cortex has reciprocal connections with much of the posterior cortex and subcortical regions (Pandya & Barnes, 1985; Petrides & Pandya, 1999; Petrides & Pandya, 2002). This indicates that the PFC is well positioned to exert a modulatory influence on the rest of the brain. Second, the PFC is commonly active under conditions in which a stimulus-driven response must be overridden by a goal-driven response, as in the Stroop task or a variety of other tasks requiring cognitive control (Wager, Jonides, & Reading, 2004). Third, damage to the PFC leads to deficits in the ability to exert control. This is evidenced by patients with frontal lobe damage who show reduced goal-driven behaviors (lethargy; Stuss & Benson, 1984), an inability to update to a new goal after having learned an earlier one (perseveration; Milner, 1963), and a tendency to be easily distracted and controlled by environmental stimuli (Chao & Knight, 1995), leading to stimulus-driven and stereotypic behaviors (a striking example of this is patients’ automatic tendency to grasp tools even though it’s not contextually appropriate; Lhermitte, 1983; Shallice et al., 1989). Importantly, damage to the lateral PFC does not generally influence the ability to perceive or produce well-learned behaviors (Milner, 1963; Stuss & Benson, 1984). This indicates that the PFC is necessary for modulating weaker connections between sensory representations and motor outputs, but is not required for the basic abilities to perceive stimuli, produce motor behaviors, or to store connections that produce well-learned or stereotypic behaviors.

Fourth, neural responses in the lateral PFC have several intriguing properties. Whereas neurons in the visual cortex respond to specific kinds of stimuli (e.g., line orientations in particular locations), neurons in the lateral PFC can acquire responses to stimuli, motor responses, or classes or categories of stimuli depending on the goals of the task (Bichot et al., 1996; Freedman et al., 2001; Watanabe, 1992). In addition, these neurons show response profiles to abstract relational rules, such as to select matching or nonmatching pairs of objects, which can be dissociated from specific stimuli or responses (Asaad et al., 2000; Wallis, Anderson, & Miller, 2001; White & Wise, 1999). Human neuroimaging studies have corroborated these results, illustrating greater activity in the lateral PFC to learning, maintaining, and
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representing stimulus-response mapping rules (Bunge, 2004). These findings suggest that lateral PFC neurons rapidly update their response profiles based on what is goal relevant. And fifth, elimination of PFC connections to posterior regions has been shown to eliminate modulatory influence in posterior cortical regions (Tomita et al., 1999). This result directly implicates the PFC in modulatory control.

An open question is what kinds of mechanisms guide this modulation? That is, exerting control may involve amplifying weaker pathways, inhibiting stronger pathways, or both. In the biased-competition model, prefrontal cortex is believed to amplify weaker associations with the consequence being that these weaker associations are then activated enough to locally inhibit the stronger associations (Desimone & Duncan, 1995; Miller & Cohen, 2001). Egner and Hirsch (2005) examined this hypothesis. They showed experimental participants faces of actors and politicians with names of other actors or politicians overlaid upon them. In different conditions, subjects were instructed to attend either to the names or the faces, and to indicate whether the target was a politician or an actor. In the congruent condition, the name and face were both of the same category (e.g., a picture of Bill Clinton with the name Fidel Castro overlaid upon it, both being politicians). In the incongruent condition, these were mismatched (e.g., a picture of Bill Clinton with the name Al Pacino overlaid upon it, one being a politician and the other an actor). They isolated activity in the fusiform face area, an area of the fusiform cortex that responds more specifically to faces (Kanwisher, McDermott, & Chun, 1997), and reasoned that if control occurred by amplification, then as control increases when instructed to pay attention to faces over names, increasing activity should be found in the fusiform face area. They found this to be the case. Activity in the fusiform face area increased when attending to faces with increasing control demands. They further examined whether control produced inhibition, too. For this, they reasoned that if control occurred by inhibition, then when names were attended to and faces were distractors there should be decreased activity in the fusiform with increasing control. However, the results did not support this hypothesis. Increasing control when attending to names had little effect on activity in the fusiform face area. Hence, their results suggest that control occurs through amplification of relevant information.

However, as noted by Aron (2007), functional neuroimaging results alone are insufficient for determining whether activation or inhibition is occurring in these regions since blood flow responses may relate to either process. Further, Aron remarks that inhibitory biological processes are commonly found throughout the body, suggesting that cognitive control through direct inhibitory mechanisms, while not hypothesized by current biased-competition models, is a reasonable means for exerting control. Much of the support for this notion comes from studies of response inhibition. Response inhibition has been examined by go-no-go and stop signal tasks (e.g., Rubia et al., 2001). In the go-no-go task, individuals are presented with a “go” stimulus roughly 80% of the time for which they simply press a button. This creates a tendency to push the button on the majority of trials. For the remaining 20% of trials, a nogo stimulus is shown for which they withhold or inhibit a response. Comparing the results of these trials with “go” trials shows which regions are involved in response inhibition. The stop signal task is similar
in that individuals are again presented with trials in which they make a simple
response to a presented stimulus. In some trials, however, a sound alerts them to
not press the button, thereby requiring them to withhold or inhibit their intended
response.

Neuroimaging studies using these tasks have shown a network of regions
including the lateral PFC, the dorsomedial PFC, and the anterior cingulate cor-
tex (ACC), which are associated with inhibition over noninhibition trials (Liddle,
Kiehl, & Smith, 2001; Rubia et al., 2001). However, a specific role has been
ascribed to the right ventrolateral PFC for its involvement in response inhibition
based on convergent findings from connectivity and neuropsychological studies
(Aron, Robbins, & Poldrack, 2004). Greater damage to the right ventrolateral PFC
produces greater deficits in stop signal task performance, and while damage to
other regions of the PFC were also correlated to performance, these correlations
did not hold up after controlling for the relationship in the right ventrolateral PFC
(Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003). These findings have been
corroborated in neuroimaging studies, which have shown that successful inhibition
was related to right ventrolateral PFC activity, whereas other commonly active
regions, including the dorsolateral PFC and the dorsomedial PFC/frontopolar cor-
tex, were more associated with failures to inhibit, which may reflect error detec-
tion (Menon, Adleman, White, Glover, & Reiss, 2001; Rubia, Smith, Brammer, &
Taylor, 2003). Following the neural circuitry involved in response inhibition, Aron
et al. (2004) suggested that connections between the right ventrolateral PFC to
the premotor cortex and the basal ganglia were responsible for successful response
inhibition. Such direct connections were not apparent in the dorsolateral PFC, fur-
ther supporting the specific role of the right ventrolateral PFC in response inhibi-
tion. In general, this set of findings provides good evidence for inhibitory processes
occurring in cortex. But the results of response inhibition studies notwithstanding,
alternative accounts have been offered (for a discussion see Aron, 2007), and
whether cognitive control is implemented by selection processes or both selection
and inhibition processes is currently being explored.

Another point to consider is that control can be implemented at different
moments in the information-processing stream. Early in the processing stream,
control may be used to attentionally select (or perhaps inhibit) what information
is more or less available to influence behavior. This is referred to as attentional
control, and it involves biasing how incoming information is processed. Neural
regions involved in attentional control have been studied by directed attention
paradigms, in which individuals are cued to attend to a particular stimulus dimen-
sions, such as a specific spatial location, feature (e.g., directions of motion, colors),
or kind of object (e.g., houses or faces). Neural regions involved in attentional
control should represent and internally maintain this cue over a delay period prior
to stimulus presentation and should modulate activity in subordinate areas that
respond to these stimulus dimensions. The superior frontal gyrus putatively in the
vicinity of the frontal eye field (FEF) and the intraparietal sulcus (IPS) both show
sustained response patterns for preparatory signals over delay periods, indicating
their involvement in attentional control (Corbetta & Shulman, 2002). And activity
in these regions precedes and modulates activity in the sensory cortex (Bressler,
Tang, Sylvester, Shulman, & Corbetta, 2008; Reynolds & Chelazzi, 2004). Late in the processing stream, control may help bias the selection (or inhibition) of a particular response over another. The response inhibition studies, as reviewed above, indicate that the right ventrolateral PFC is critically involved in this late stage of control.

Finally, in between early and late stages, control may involve reconsidering the information that is currently held in mind through selection or inhibitory processes. Across this spectrum, the dorsolateral PFC seems to be commonly engaged. In a meta-analysis of 47 imaging studies of control examining several different paradigms, ranging from paradigms involving greater attentional control to those involving greater response control, Nee, Wager, and Jonides (2007) found that the dorsolateral PFC was commonly activated across tasks, suggesting that this area may be central to all stages.

**Conflict Monitoring: Signaling the Need for Control**

The ability to maintain information and implement control does not necessarily imply the ability to know when control should and should not be implemented. How does the system know when to exert more or less control? One plausible mechanism to signal a greater need for control is to monitor for conflict between different candidate response pathways. Consider a case like the Stroop task wherein the correct pathway is color naming but where we have a habitual tendency to read words. As both the habitual and goal-relevant pathways are likely to be potentiated upon presentation of a colored word, there will be conflict between them. Thus, one way to signal control is to monitor for this conflict and up-regulate control once it is detected. If the selection mechanisms are successful and the goal-relevant pathway wins the competition, then there will no longer be conflict and thus no longer a need for control. Computational models of cognitive control that employ a simple conflict monitoring system have been designed that can regulate the need for control (Botvinick, Cohen, & Carter, 2004). Such models are useful because they show that control can be regulated without the need for a homunculus, or “little man,” inside the brain that simply “knows” when to engage in control.

Comparing neural activity for conditions that involve more conflict to those that involve less conflict may reveal regions that underlie such a mechanism. In the Stroop task, comparing conditions involving attending to the color of the word versus those involved in attending to the word itself reveals activity in the dorsal ACC (BA 24/32 at the rostral end; Pardo, Pardo, Janer, & Raichle, 1990; Nee, Wager, & Jonides, 2007). Given its association with conflict conditions, some have proposed that the dorsal ACC may support a conflict monitoring function (Botvinick et al., 2004; Carter & van Veen, 2007; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004).

Importantly, conflict monitoring refers to the change in how much control is needed, not simply whether a conflict is apparent. Thus, if the ACC is a conflict monitor, it should track the level of conflict rather than simply signaling the presence of conflict. Testing this idea, Botvinick et al. (2004) had participants complete sets of trials in a flanker task involving congruent trials, which require less control,
and incongruent trials, which require greater control. They reasoned that if the dorsal ACC is just sensitive to conflict across the board, then it should respond uniformly to incongruent trials. Alternatively, if the dorsal ACC is involved in conflict monitoring, then it should respond to the change in the need for control. This could be shown by comparing activity to incongruent trials that were preceded by congruent trials with activity to incongruent trials that were preceded by other incongruent trials. In the former case, the difference between the control required for the preceding congruent trial to the present incongruent one is large, whereas in the latter case, this difference is small. They found that dorsal ACC activity responded to the change in conflict, suggesting it plays a role in conflict monitoring.

This account of conflict monitoring involves reactive adjustments to control. That is, only when a change in conflict is detected is increased control subsequently implemented. However, increasing control in such a reactive manner may not suit every circumstance, particularly for situations in which making an error is costly or speed is at a premium. Alternatively, anticipating the upcoming need for control can be effortful and demanding. Ideally, appropriate levels of control would be engaged in the anticipation of circumstances that are more likely to result in errors. This idea was advanced by Brown and Braver (2005). They found that the dorsal ACC responded strongest to a context that was associated with a high likelihood of errors compared to contexts associated with a lower likelihood of errors. Moreover, over several trials dorsal ACC activity tracked with learning the likelihood of producing errors rather than detecting conflict. Their results suggest that the dorsal ACC is broadly involved in detecting the likelihood of errors and thereby uses this information to adjust proactively the amount of control required.

Further experiments have examined the link between the dorsal ACC and the lateral PFC in implementing control. If dorsal ACC activity modulates the need for greater control, then this should be shown to subsequently influence activity in the lateral PFC and enhance behavioral performance. Imaging results support these predictions (Carter & van Veen, 2007; Kerns et al., 2004). Additionally, damage to the ACC results in a poorer ability to adjust control based on the previous trial (di Pellegrino, Ciaramelli, & Ladavas, 2007). Overall, these results support the role of the dorsal ACC in detecting the likelihood of making errors and subsequently promoting the lateral PFC to exert greater control in such situations.

**Summary**

A control system requires several functions to modulate behavior successfully. Much of the work over the past few decades has examined their neural correlates. One key function is the internal maintenance of information over a delay and in a fashion that is resistant to distraction. This information can be used to implement control and guide behavior. Implementing control can occur at early stages, as in selective attention, or at late stages, as in response inhibition. The dorsolateral PFC is commonly engaged at both ends of the spectrum. Attentional control additionally engages the superior frontal gyrus (putatively in the frontal eye field) and the intraparietal sulcus, and response inhibition more specifically relies on the right ventrolateral PFC. Signaling the need for greater control may involve detecting...
conflict between response pathways. The dorsal ACC responds to this conflict and subsequently modulates the dorsolateral PFC to implement greater control. The contents of working memory must be updated when currently held information is no longer relevant or the presence of new goal-relevant information must be maintained. This updating is regulated by the basal ganglia through frontostriatal loops. The relative balance between maintaining and updating information is modulated by the tonic and phasic influences of dopamine in the lateral PFC and the striatum.

The purpose of this section was to provide an overview of some modal neural regions involved in cognitive control. In reference to everyday goals though, it is also worth pointing out that several of the tasks used to examine cognitive control fail to capture other aspects of goal-directed behavior, such as the self-initiation of goals, the motivation to do so, the social and emotional quality of many of our most important goals, and the abstract level at which self-initiated goals seem to be defined (Carver & Scheier, 1998; Higgins, 1997, 1998; Vallacher & Wegner, 1987). For instance, goals in the Stroop task are represented as specific, motivationally neutral, stimulus-response mappings (i.e., see a word, name the color), whereas common goals people have are represented with far greater emotional weight and abstractness (e.g., to be a good father). In these cases, it is difficult to specify precisely what the stimulus and response mappings are and to control the specific emotions and motivations that are key to its success. Importantly, this difference does not falsify the approach. Rather, it highlights several avenues for integrating aspects such as emotion and motivation into a more complete model of a control system. To further examine whether the systems described in this section generalize to other areas of research, we now turn to research on the neural bases of cognitive control in memory and emotion regulation.

**COGNITIVE CONTROL OF MEMORY**

We often try to remember things we have forgotten or forget things we have remembered. For instance, we may actively try to recall simply where the car was parked last, facts such as state capitals, or fond memories of friends or family. Or we may try to forget events that are no longer relevant, as in where the car was parked a week ago, facts that were remembered incorrectly, or the more embarrassing and negative moments in our lives. Stimulus-driven and goal-driven processes may also characterize these cases. For memory, stimulus-driven processes involve the automatic retrieval of associates based on the cues provided. Goal-driven processes then involve attenuating these stronger associative pathways and selecting for weaker but goal-relevant ones to be expressed.

**Implementation of Control in Memory**

Suppose one is trying to remember songs produced by a given pop star. The mere mention of her name may result in one or even several of her songs being effortlessly retrieved through stimulus-driven processes. But at other times, one may want to retrieve a less commonly known song. In this case, the weaker the association is, the more memory control would be required to allow alternative weaker paths to
be expressed and thereby retrieve the song. The ability to produce more associates beyond what is spontaneously provided is referred to as controlled retrieval.

In the lab, controlled retrieval can be assessed through manipulations of associative strength. Associative strength refers to how tightly interconnected two concepts may be to each other. For instance, perhaps in many people’s minds, pizza is strongly associated with soda, weakly associated with french fries, and not associated with airplanes. In one task paradigm that manipulates associative strength (Wagner et al., 2001), a cue word is presented with two probe words below. One of the probes is the target response and the other is a distractor. The participant is to choose the probe (ostensibly the target probe) that best matches the cue based on the overall relatedness of the cue to the probe. The key manipulation is to vary the associative strength between the cue and the target probe, and so the degree to which related information comes to mind, with minimal search. For instance, if “apple” was the cue, and “orange” and “wrench” were the targets, one would match “apple” with “orange” as these are more related semantically than “apple” and “wrench.” As the association becomes weaker, this places a greater demand on controlled retrieval to access information to assess the match. In this case, replacing “orange” with “tomato” may require greater controlled retrieval. That is, matching “apple” with “tomato” may require greater retrieval demand to obtain the relevant related information.

However, this particular paradigm may be limited in that it also involves additional processes or alternative strategies beyond controlled retrieval. For instance, a prime word is presented that can be semantically related to the target word or neutral (e.g., “map” for the prime related to “atlas,” or repeatedly presenting the word “blank” for all neutral primes). Primes that are semantically related to the target facilitate processing the target as shown by lower reaction times. By facilitating processing, they reduce demands on retrieval of semantic information when making the lexical decision judgment on the target word. Hence, activity that is greater for the neutral prime condition relative to the related prime condition should show areas that are related to retrieval demands.

An additional feature of this paradigm is that priming can occur automatically, such that a prime presented soon before the target (e.g., approximately 200 ms before) nonetheless facilitates processing the target, and through more controlled routes if the delay between the prime and the target is long enough to allow for them (e.g., approximately 1 s before; Neely, 1977, 1991). Hence, comparing priming
effects (effects of unrelated versus related primes on processing the target) for longer versus shorter delays reveals which neural regions are specifically associated with controlled retrieval. Relative to the task paradigm described earlier involving the probe and two targets, the priming paradigm is more streamlined in its engagement of controlled retrieval. That is, it does not engage additional comparison processes between items. Combined, both task paradigms show that increasing controlled retrieval demands produces greater activation in the left anterior ventrolateral PFC (approximately BA 47), implicating this region in controlled retrieval (Badre, Poldrack, Paré-Blagoev, & Insler, 2005; Badre & Wagner, 2007; Buckner, 2003; Gold et al., 2006; Wagner et al., 2001).

As more information becomes retrieved, one may begin selecting for information that is more pertinent to the goal. Using the example of remembering a specific song by a pop star, relevant information such as other song titles or albums or the year the forgotten song may have been associated with may be selected for, whereas irrelevant information such as the latest gossip or hairstyle about them which may not (or may, depending on your associates) help one remember may be selected against. This ability to choose specific goal-relevant information from that which has been provided by retrieval processes is referred to as selection (of memory).

Demands on selection can be increased when the judgment involves choosing along a specific feature or dimension. In a similar task paradigm as above for controlled retrieval, matching items on specific dimensions such as “size,” “texture,” or “color” instead of general relatedness would place greater demands on selection. This is because a relatedness judgment does not specify which dimension is relevant to making the decision. By contrast, a size judgment requires selecting information about size and against information that is irrelevant to size. Perhaps consistent with the greater selection demands required for the feature decision, comparison of a feature to a relatedness decision results in activation in the midventrolateral PFC (approximately BA 45).

Selection demands are even greater when the associative strength is contrary to the correct match based on the current retrieval rule. For instance, if the dimension were “texture,” then “apple” may be better matched with “table,” since both are similarly smooth. This choice would additionally involve having to select against the more general associative strength that “apple” has to “orange” and is associated with greater activation in the midventrolateral PFC.

Priming paradigms can also be used to examine selection processes. Here, selection demands are increased when the prime is unrelated to the target and hence activates additional irrelevant information that must be selected against, rather than selected for, when accessing information about the target for making a lexical decision. That is, when an unrelated prime is presented prior to the target (e.g., “lap” prior to “atlas”), it interferes with processing the target word relative to the neutral prime (again repeatedly presenting the prime “blank” for all neutral trials). Comparing interfering versus neutral primes in the longer versus shorter delay periods should activate neural regions that are related to selection processes. Selection demands manipulated in these ways result in increased neural activity in a more posterior region of the left ventrolateral PFC (approximately
Finally, in the event that one no longer wants the pop star’s song running through his or her mind, the person may try to actively suppress or inhibit it. Neural regions subserving the inhibition of memory have been explored using directed forgetting paradigms. Directed forgetting refers to intentionally putting something out of memory that has already been placed there, and these task paradigms simply involve instructing individuals to forget an association.

A study by Anderson et al. (2004) used a modified directed forgetting paradigm, the Think/No Think task, to investigate the neural regions involved in suppression of memory. Participants first learned word pairs (e.g., ordeal-roach). Then, while undergoing scanning, individuals were presented with one of the words (e.g., ordeal-_____), and simultaneously instructed based on the color of the word whether to retrieve (Think) or suppress (No Think) retrieval of the associate. Behavioral responses showed a suppression effect in an independent probe. In the probe, a cue and a word fragment were presented together (e.g., ordeal-r_ _c_), and participants were to complete the fragment with the first word that came to mind. Relative to control items, fragments were more frequently completed with the associated words in the Think trials. In the No Think trials, fewer associates were produced relative to the control items. This suggests that an active suppression is occurring, rather than just weaker memory strength.

Comparing the No Think versus the Think trials showed activity in several regions similar to those in response inhibition, including the dorsolateral PFC, the ventrolateral PFC, the ACC, and even motor areas including the pre-SMA, the dorsal premotor cortex, and the putamen (Anderson et al., 2004). Furthermore, they found that activity in the hippocampus, which is normally related to successful memory retrieval, was significantly reduced in the No Think condition. This further suggests that active suppression was occurring.

Of course, trying to forget simple word associates and trying to forget emotional events may be vastly different. Addressing this to some degree, another neuroimaging study extended these results to the pairings of faces with affectively negative images (Depue, Curran, & Banich, 2007). This study showed that memory suppression was related to greater activity in the right lateral PFC and decreased activity in the hippocampus, amygdala, and posterior sensory regions. The greater involvement of the right lateral PFC is further supported by an ERP study (Hanslmayr, Leipold, Pastotter, & Bauml, 2009). In brain-damaged patients, however, damage to the left or right lateral PFC resulted in an inability to show directed forgetting effects, though the right ventrolateral PFC ironically showed a pattern of better memory for the to-be-forgotten items than the to-be-remembered items (Conway & Fthenaki, 2003). In general, the evidence suggests that memory inhibition may also rely on the same right lateral PFC region as response inhibition.

**Mnemonic Conflict**

Just as with conflict detection in response control, memory control may also involve conflict from competing mnemonic associates. Is the ACC also involved in
detecting this conflict? Mnemonic conflict may be enhanced when retrieved mnemonic associates conflict with regard to the response or outcome they promote. An example of this involves proactive interference. In proactive interference, irrelevant prior information that was recently active interferes with mnemonic information that is relevant for the current trial.

Working memory tasks have been modified to examine the influence of proactive interference on neural activity (Badre & Wagner, 2005; Bunge et al., 2001; D’Esposito, Postle, Jonides, & Smith, 1999; Jonides, Smith, Marshuetz, Koepppe, & Reuter-Lorenz, 1998; Nee, Jonides, & Berman, 2007; Thompson-Schill, et al., 1997). Similar to standard working memory tasks, participants are shown a set of six letters to maintain over a brief delay of 3 s. Then, a probe consisting of a single letter is presented and participants had to indicate whether the probe was among those in the set. However, rather than presenting a fresh set of letters on the following trial, three of the letters in the prior set were included among the six letters in the subsequent set. Hence, whether the subsequent probe was in both sets, only in the current set, only in the prior set, or in neither set was manipulated. Behaviorally, reaction time is slower when the probe was only in the prior set relative to when the probe was in neither set, illustrating proactive mnemonic interference. Intriguingly, though imaging results consistently engage lateral PFC regions involved in the cognitive control of memory, increased activation in the dorsal ACC was not consistently found. These initial results suggest that dorsal ACC activity may specifically reflect response conflict rather than mnemonic conflict.

EMOTION REGULATION

Emotion regulation is our ability to control when, how, and to what extent we express our affective responses to a stimulus or event. For instance, we may try to reduce the fear and anxiety that is experienced when having to give a public speech, take an exam, or when jumping off the diving board for the first time. Alternatively, we may try to increase other emotions, as when having the explicit intention to savor and “get the most out of” a bite of chocolate cake or when trying to show more empathy for a friend’s misfortune than we may initially experience. Hence, emotion regulation can involve both up-regulating and down-regulating emotional responses depending on our goals, and can target emotional responses that range from mild to overwhelming, as when having to control anxiety or drug cravings in psychiatric or substance-using populations.

The initial thoughts and feelings one has toward an event are typically (though not always) stimulus-driven responses. For instance, upon seeing a spider, one might feel a rapid surge of arousal and fear and respond by jumping away, freezing, or screaming. This initial response to the spider results from an initial appraisal of it as potentially threatening within the context of any current or ongoing goals, wants, or chronic needs. Emotion regulation then involves attenuating or altering this appraisal to allow for alternative behavioral reactions (e.g., approaching the spider, capturing it, and setting it free outside).
Implementing Emotion Regulation

Multiple strategies may be used to attenuate this emotional reaction. As with cognitive control, these strategies can also be organized along a continuum where control processes may exert influence across early to late stages of the emotion generation process (Ochsner & Gross, 2005). At the early stage, selective attention can be used to influence how emotional or nonemotional aspects of a stimulus are brought into the appraisal process. For instance, while running a race, a competitor may selectively attend to the finish line and the anticipation of crossing it and away from the pain in his or her body. The context also shapes how we attend and respond to affective information in the environment. Whereas in most situations seeing someone in pain may draw attention toward that person, in the context of a race one might actively ignore the grimaces of others in the service of the goal to win. Other common examples include not looking down when walking across a narrow bridge or avoiding interactions with homeless individuals. Selective attention can be said to influence the impact of the initial appraisal by preventing it from taking full effect at the outset.

Experiments that examine selective attention typically involve attending to nonaffective information as the goal and then examining how task-irrelevant affective information interferes with this goal. For example, in the emotional Stroop task words with affective content (e.g., “death”) produce greater interference in color-naming than neutral words (e.g., “library”). Better performance on the task then involves selectively greater attention to the color of the words and lesser attention to the affective content of the words (Bishop, Duncan, Brett, & Lawrence, 2004; Bush, Lau, & Posner, 2000; Compton et al., 2003; Shin et al., 2001; Vuilleumier, Armony, Driver, & Dolan, 2001; Whalen et al., 1998). A few have further examined conflict within affective information, for instance, by showing a fearful facial expression with the word “happy” written across it, and having participants name the expression (Egner, Etkin, Gale, & Hirsch, 2008; Etkin, Egner, Peraza, Kandel, & Hirsch, 2006). Although differential activity to conflict has been found in several regions involved in emotional processing such as the amygdala and the ventral striatum, most consistent across studies and paradigms has been the ventromedial prefrontal cortex, suggesting that this area may play a special role in resolving affective conflict (Egner et al., 2008; Etkin et al., 2006). Ochsner, Hughes, Robertson, Cooper, and Gabrieli (2009) directly compared neural regions involved in both cognitive and affective conflict resolution and found that the ventromedial prefrontal cortex was specifically involved in resolving affective conflict, whereas the ventrolateral PFC was involved in resolving cognitive conflict. In common, both domains engaged the dorsal ACC and the dorsolateral PFC (Egner et al., 2008; Ochsner et al., 2009).

A second cognitive emotion regulation strategy targets the appraisal process itself and uses control processes to reappraise or reinterpret the meaning of a stimulus. Reappraisal takes advantage of the fact that situations can be construed in multiple different ways. Consider scoring poorly on an important exam, such as the LSAT. An initial appraisal may lead to feelings of dread. Reappraisal would involve rethinking the event so as to increase or diminish its emotional impact.
For example, to diminish its influence, one might subsequently consider that it can always be retaken, that law school was not the right match anyway, or that such exams do not really measure intelligence. Each of these thoughts involves reappraising the initial appraisal of the event so as to alter its emotional impact.

Correspondingly, experimental studies investigating reappraisal typically involve presenting individuals with affectively laden images or videos and instructing them to think of the stimulus in such a way as to enhance or reduce the initial emotional reaction to it. These studies have shown a common network of regions being involved in both increasing or decreasing emotional responses, including the lateral PFC and the dorsal ACC (Eippert et al., 2007; Goldin, McRae, Ramel, & Gross, 2008; Ochsner et al., 2004; Ochsner & Gross, 2005; Phan et al., 2005).

Given that these areas are involved in regulating emotions, then ostensibly a set of regions involved in triggering emotional responses should show corresponding changes, too. Two key areas involved in triggering emotion include the amygdala and the insular cortex (Kober et al., 2008). These areas show decreased activity when individuals are instructed to down-regulate feelings and increased activity when instructed to up-regulate feelings (Beauregard, Lévesque, & Bourgouin, 2001; Goldin et al., 2008; Ochsner et al., 2004). Moreover, increased activity in response to regulation in lateral prefrontal regions is associated with decreased activity in regions that are responsive to emotion, including the amygdala and the ventral striatum (Lieberman et al., 2007; Ochsner, Bunge, Gross, & Gabrieli, 2002).

A third cognitive regulation strategy targets the response phase of the emotional response by suppressing, amplifying, or otherwise altering the behavioral manifestation of emotional responses. The most commonly studied use of response control is the control of facial expression so as to not let anyone else know what emotions are being experienced. Expressive suppression, as it is called, is momentarily effective at reducing emotional expressivity but does so at the cost of increasing physiological arousal and impairing memory, presumably because one pays less attention to a stimulus and more to his or her own face (Gross, 1993; Richards & Gross, 2000). Via facial feedback, there is some evidence that expressive suppression can influence emotional experience as well, albeit not to the same extent as reappraisal (Davis, Senghas, & Ochsner, 2009, 2010; Goldin et al., 2008; Lévesque et al., 2003).

Imaging studies of expressive suppression show that when participants keep their face from exhibiting an emotional response while viewing affective stimuli, a familiar network of regions is activated, including the ventrolateral PFC, the dorsolateral PFC, and the dorsal ACC (Goldin et al., 2008; Lévesque et al., 2003). There are also likely to be important differences between expressive suppression and reappraisal. For instance, expressive suppression involves inhibition of motor responses such as facial expressions, whereas reappraisal may involve the retrieval of information that could be used to bias how an emotional event is perceived. In expressive suppression, the emphasis is on concealing the behavioral response to felt emotions, not on changing one’s appraisal of an event as arousing and affecting. Consistent with this, activity in the amygdala and insular cortex, though reduced by reappraisal, was not reduced by suppression (Goldin et al., 2008).
Against the backdrop of prior work, one expectation may be that the right ventrolateral PFC is involved in inhibitory control when one expressively suppresses, whereas the left ventrolateral PFC is involved in selection of new stimulus interpretations that help increase or decrease emotional responses when one reappraises. In one study that directly compared expressive suppression and reappraisal, Goldin et al. (2008) found that engagement of control regions differed based on the strategy, but this interacted with time. Early in presentation of the emotional stimulus, there was greater activity in control regions (the lateral PFC and the dorsal ACC) for the reappraisal condition, whereas late in the spectrum it was reversed. Moreover, greater early ventrolateral PFC activity in reappraisal was left-sided, and while greater late ventrolateral PFC activity in suppression also engaged left ventrolateral PFC, it also significantly activated the right ventrolateral PFC. These results suggest that the right ventrolateral PFC may be involved in inhibitory control of emotion, too, and matches the notion that behavioral suppression occurs at a late stage of the processing stream.

**Affective Conflict**

How does the system know when to exert greater regulatory control over feelings? In response control, the need for control is signaled by response conflict, which increases when the stimulus-driven response and the goal-driven response are at odds with each other. Similarly, affective conflict may occur when undesirable affective information or emotional feelings interfere with a desired goal-driven response. For instance, while trying to give a speech, the sight of yawning audience members or the feelings of choking up may signal affective conflict that must be overcome.

A handful of studies have examined the neural correlates of affective conflict. A central question of this research is whether regions that are involved in affective conflict overlap with those in cognitive conflict. In general, these studies have found activity in the dorsal ACC corresponding to affective conflict (Egner et al., 2008; Haas, Omura, Constable, & Canli, 2006; Ochsner et al., 2009). Two studies included cognitive and affective conflict conditions within the same experiment, allowing for more direct comparisons. In Egner et al. (2008), individuals were shown words superimposed over faces. The faces were either male or female with either fearful or happy facial expressions. Similarly, the overlaid words could be “male” or “female,” “happy,” or “fear.” In the gender task, the task was to indicate whether the face was male or female, and conflict was enhanced by superimposing the opposing word over the face (e.g., the word “female” over a male face) relative to a congruent word. In the expression task, it was the same except for facial expressions. Ochsner et al. (2009) used an affective variant of the flanker task, in which individuals were shown three words and categorized whether the central word (e.g., “triumph”) was positive or negative. Affective conflict was assessed by comparing when the flanker words were of the opposing valence as the central word (e.g., “triumph” surrounded above and below by “torture”), relative to the congruent condition (e.g., “triumph” surrounded by “ecstasy”). The cognitive version involved judging neutral words for whether they were fruits or metals. Both
tasks showed overlapping activity in the dorsal ACC for affective and cognitive conflict. This suggests a common role for the dorsal ACC in conflict detection across affective and cognitive domains.

**Summary**

While there is much less research examining the neural regions involved in emotion regulation, the available evidence suggests that there is considerable overlap between these regions as those involved in cognitive control. In both cases, the dorsal ACC is responsive to conflict, and the dorsolateral PFC is involved in implementing control. But there are differences in the control network, too. In particular, ventromedial prefrontal cortex may have a unique role in controlling emotional conflict, which makes sense given its strong connectivity to subcortical structures involved in emotion (Ongur & Price, 2000). Another difference is simply the posterior regions that are being regulated. In stimulus-response mapping tasks, this involves modulating activity in visual, parietal, and motor cortex. In emotion regulation, this involves the amygdala, insular cortex, and potentially several other regions involved in emotional experience.

**FUTURE DIRECTIONS**

In the introduction to this chapter, we raised the question of what kinds of behavior count as goal-directed behavior and what kinds do not. The point of raising the question was to introduce a prominent cognitive neuroscience perspective in approaching the question of goals. We contrasted goal-directed behavior with that which is stimulus driven and aligned the ability to override habits (e.g., quitting smoking) with overriding automatic responses in lab tasks (e.g., the Stroop task). We then outlined some key functions required of such a control system, specified the neural regions that may underlie this system, and asked whether they generalize across other domains of control.

Overall, neural regions involved in memory control and emotion regulation are generally shared with those involved in the control of simple stimulus-response mappings. Broadly speaking, lateral PFC and dorsal ACC regions responded to recruitment of control processes. This suggests that the network of regions involved in cognitive control is common across multiple sorts of domains, which in turn suggests it may be generalized to the everyday goals that people pursue.

However, there are also threads from each domain that suggest greater fractionation of the control network into regions that support more specific processes. For instance, in memory control the evidence suggests that the anterior ventrolateral PFC and the midventrolateral PFC may subserve distinct functions related to controlled retrieval and selection, respectively. And in emotion regulation, in addition to the dorsal ACC, the ventromedial prefrontal cortex also responds to affective conflict. Also, ambiguity remains in how to map some of the central functions involved in control onto each of these domains. In the case of emotion regulation, for example, it is unclear what information the control network is representing.
Future studies may attempt to distinguish various possibilities. For instance, we recently conducted a study that examined which neural regions were sensitive to heightened emotional arousal, awareness of emotion, and categorization of emotional states (Satpute, Shu, Weber, Roy, Ochsner, 2010). We found that increasing the emotional intensity of the stimulus led to greater activity in several regions, including the amygdala, the periaqueductal gray, and the insular cortex, all known to be involved in greater emotional arousal. However, we further found that the dorsomedial PFC and the ventromedial PFC, commonly activated across studies manipulating emotional intensity (Kober et al., 2008), were selectively activated to direct attention to emotion and categorize emotional states, respectively. Hence, these areas represent different aspects of experiencing an emotional event and therefore may play different roles when individuals regulate their emotional responses.

In general, few experiments have directly attempted to integrate the network of regions that underlie cognitive control across domains, and future experiments that do so would be helpful in determining whether the control network is domain general or domain specific to levels of control. On a broader level, however, it is important to note that goal-directed behavior involves a larger set of phenomena than can be captured by the functions we have highlighted and the tasks used to investigate them. That is, we have focused on the ability of a control system to override stimulus-driven behavior. Task paradigms used to study this aspect of goal-directed behavior typically involve giving participants a set of instructions they are to follow and a condition in which these instructions are at odds with their automatic tendencies. Hence, in a reductive sense, the experiments are studying the ability of individuals to merely follow instructions. Even in emotion regulation tasks, individuals are instructed to up- or down-regulate their emotions, regardless of what their own personal goals might be in reaction to the stimuli. But, considering all of what is involved when pursuing real-world goals as listed in Table 2.1, several other factors must also be critical. In the following sections, we review a few of these factors as future directions. Finally, much of what we have covered so far has been in the service of uncovering the neural mechanisms involved in goal-directed behavior. But, to point the finger the other way, how might knowledge of these neural systems subsequently inform our psychological understanding of goal-directed behavior? Has mapping out a neural system involved in goal-directed behavior helped us to understand the psychology and behavior of individuals?

Motivation in Goal-Directed Behavior

Beyond attempting to control stimulus-driven habits, goal-directed behavior can be thought of as behavior that is motivated by the personal wants, needs, or desires of an individual. This perspective has been the focus of research in social psychology and affective neuroscience. For instance, in experiments on stereotyping and prejudice, individuals are often presented with task conditions in which using stereotypes can help (or hurt) behavioral performance. It could be thought that individuals could simply follow task instructions, which essentially renders these experiments analogous to studies of semantic categorization more generally
GOAL-ORIENTED BEHAVIOR

(and makes them privy to the reductive criticism that the social cognition is merely categorization with social stimuli). However, individuals can also be aware that they are behaving stereotypically in these experiments. Indeed, individuals who are motivated to be egalitarian show distinct patterns of behavioral performance from those who are not (Moskowitz, Golwitzer, Wasel, & Schaal, 1999). This particular case highlights the distinction between the perspectives of goal-directed behavior as following task instructions from that of following one's personal wants, needs, or desires.

This aspect of goal-directed behavior has also been examined in reinforcement learning (Sutton & Barto, 1998). Here, goal-directed behavior has been defined as associations between a response and a desired outcome. This is held in contrast to associations between a stimulus and a response, which form the basis of habits. A paradigmatic example to distinguish these associations involves devaluation, in which behavioral responses are measured to an outcome that is no longer as desirable as it once was. Consider eating popcorn while watching a movie. Initially, one might be hungry, and so the response of reaching into the bag and eating some kernels produces the desired outcome. During the movie, one might keep snacking away at the popcorn, only to suddenly realize that at some point he or she was no longer hungry, and, moreover, that he or she was no longer hungry about 10 handfuls ago. Continuing this behavior even though the outcome is no longer desirable is attributed to the formation of a stimulus-response association, or habit. The bag of popcorn calls forth the behavior, even though the outcome is no longer desirable. In contrast, goal-directed behavior is defined as when the response–outcome association is driving behavior instead, assuming that the outcome is a desired target set defined by the goal. Using such devaluation paradigms, imaging and lesion studies have shown that response–outcome associations are associated with and rely on the orbitofrontal cortex (Balleine & O'Doherty, 2010; Gottfried, O'Doherty, & Dolan, 2003; Valentin, Dickinson, & O'Doherty, 2007). Hence, this area may be integral for assessing the motivational significance that a goal carries and potentially the extent to which it is ultimately pursued.

Goal Abstraction and Hierarchies

Goals can be considered as part of an action hierarchy (Vallacher & Wegner, 1987). These can be traversed by simply asking how and why an action occurs. Take “being a good father” as an example. Asking how takes us down a level to more concrete descriptions of behaviors, whereas asking why takes us up a level to more abstract descriptions of behaviors. Compare “by helping my child learn to read” versus “in order to help them be happy,” respectively. Most of the experiments reviewed above examining goal-directed behavior have operationalized rules as low-level and concrete stimulus-response mappings. The Stroop task, working memory tasks, and others are all examples of this. But clearly the system must be able to accommodate representations of actions at multiple different levels.

In a set of experiments designed to test the neural regions involved in goal abstractness, Badre and Wagner (2007) showed that increasingly anterior regions of the lateral PFC were engaged as action representations became more abstract.
Across all conditions, participants chose to press one of two buttons. In the low-level response control condition, individuals were presented with a colored frame that surrounded a fixation cross. They simply pressed one button for a set of colors and another button for a different set of colors. Hence, the colors directly controlled which response to make. This was taken up one level to have the colors represent feature control. Individuals were presented with different features, that is, shapes within the frames. How they responded to the shapes, however, depended on the color of the frame. Hence, the colors indicated which response to make when presented with the features. This study matches the notion of going up and down in an action hierarchy. In a sense, the colors controlled the meaning of the features, just as “being a good father” controls the meaning of “helping my child to read,” or “quitting smoking” controls the meaning of “avoiding bars.” And just as each level can increase or decrease in abstraction, Badre and Wagner (2007) implemented similar procedures to incorporate higher and lower levels in the hierarchy to encompass four distinct levels.

Neural activity tracked with the abstractness of the control that was implemented. The highest level of abstraction achieved in their study showed greater activity in the frontal pole. The lowest level of abstraction, response control, showed greater activity in the dorsal premotor area. Several prior experiments and theories have also postulated a caudal to rostral organization of lateral prefrontal cortex corresponding to increasing goal abstraction (reviewed in Badre, 2008). This notion provides a more unified view of lateral prefrontal organization by suggesting that regions that are caudal to the ventrolateral PFC are involved in lower-levels of control, whereas regions rostral to the ventrolateral PFC are involved in higher-levels of control.

Individual Difference Applications of the Model of Cognitive Control  A benefit of this model of cognitive control is that it raises several new possibilities to describe how individuals vary in their behavior. That is, how does variation in personality, age, or gender relate to components of the cognitive control system, such as activity in the lateral PFC or anterior cingulate? And how might this in turn relate to differences in behavior?

As we age, our ability to exert cognitive control gradually becomes worse. This is indexed by poorer performance on a host of tasks requiring executive control (Balota, Dolan, & Duchek, 2000; Moscovitch & Winocur, 1992; Salthouse, 1990). It could be the case that this simply reflects a general decline in all cognitive abilities across the board with aging. However, as noted below, neuroscience models of cognitive control suggest that different elements of the system tradeoff against one another, such that deficits in the operation of one element of the system may actually produce benefits in the operation of the other. This raises an intriguing question: Might there be cases in which older adults actually outperform younger adults?

This was shown in an experiment by Braver, Satpute, Rush, Racine, and Barch (2005). In their experiment, letters were shown on the screen one at a time. The instructions were to make a target response to the letter X if it was preceded by the letter A. Otherwise, a nontarget response was required. This produces four
trial types referred to as AX trials (the target trials), and BX, AY, and BY trials, all of which indicate nontarget responses. To engage maintenance demands, a delay of a few seconds was placed in between the letters, such that individuals had to maintain which letter they had just seen in order to respond correctly to the subsequent letter. Eighty percent of the trials were AX trials, promoting the expectation of target responses. The BY trials were relatively low conflict, since both the cue letter B and the subsequent letter Y promote nontarget responses.

The critical trials were the BX and AY trials. Relative to the BY trials, both produce a greater tendency to incorrectly make a target response since each has an element of the predominant AX stimulus. However, they do so for very different reasons. In the BX trials, the cue letter B basically indicates that no matter which letter is shown next, a nontarget response should be made. The better one is at maintaining the instruction that the cue letter B signifies, the less influenced they are even when an X appears. For these trials, younger adults outperform older adults, consistent with younger adults’ greater working memory maintenance abilities.

For the AY trials, stronger maintenance of the letter cue A coupled with the fact that 80% of the trials are AX trials produces a greater tendency to make a target response. Hence, when the subsequent letter ends up being a Y, conflict ensues and it becomes more difficult to subsequently make a nontarget response. For AY trials then, the model suggests that a poorer maintenance ability actually leads to better performance on these trials. Indeed, older adults outperformed younger adults on the AY trials. Hence, the same failure to maintain the letter cue impairs older adults’ ability on BX trials but aids their ability on AY trials. This finding illustrates a unique behavioral prediction made from a computational model that was inspired by neural mechanisms.

Apart from examining control processes during aging and development, a few studies have begun examining how to integrate neural models of cognitive control with basic personality theory. For instance, how might factors such as anxiety and neuroticism or extraversion and introversion relate to individual differences in the components of cognitive control, such as the ability to maintain or update information, or sensitivity to errors or conflict? Might variability in these processes relate to traditional self-report measures of personality?

In one study, Eisenberger, Lieberman, and Satpute (2005), addressed how neuroticism may relate to neural activity in the cognitive control network. To obtain neural measures, participants completed the odd-ball task. In this task, individuals are presented with letters one at a time. The majority of these letters, 80%, were Xs, for which the participant made no response. Any letter other than X was considered an odd-ball due to its infrequency, and participants were to make a target response to them. Comparing odd-balls to non-odd-balls in this task engages neural regions involved in cognitive control, including the dorsal ACC and lateral prefrontal cortex.

Neuroticism is intended to capture the tendency for some people to experience greater negative affect than others across situations. Negative affect can be thought of as indexing conflict and errors, as we tend to experience negative feelings when things go awry from what we intended or wished to happen. Given the
sensory dorsal ACC’s role in being sensitive to conflict and errors, it makes sense then that more neurotic individuals may have greater sensitivity in dorsal ACC. Indeed, this is what research has found.

The relationship between personality, neural activity, and cognitive control produces a number of intriguing questions. Eisenberger et al. (2005) further suggested that differences in neural reactivity may provide a better measure of individual differences than self-report measures. Indeed, self-report measures, though reliably related to actual behaviors, are only modestly so (Back, Schmukle, & Egloff, 2009). This may in part be due to several biases that can occur when people complete questionnaires about themselves. In contrast, neural measures may be less susceptible to these biases and more directly related to the underlying cognitive operations that distinguish individuals from one another (Eisenberger et al., 2005). In addition, this raises the possibility that standard descriptions of personality traits may be usefully reinterpreted in terms of neurocognitive processes, such as heightened sensitivity to errors or error likelihood in neuroticism.

Another study found that highly anxious individuals tended to show greater transient activity in the cognitive control network, whereas low anxiety individuals showed greater sustained activity (Fales et al., 2008). That is, whereas low anxiety individuals engaged control regions consistently during the course of a demanding working memory task, highly anxious individuals showed greater fluctuations to the onset of each individual trial. Fales et al. interpret sustained and transient activation as reflecting proactive and reactive control strategies, respectively. This suggests that highly anxious individuals may have difficulty maintaining attentional concentration on the task and hence resort to reaction to each stimulus as it arises rather than anticipating and maintaining a steady amount of control required more generally.

A limitation to these studies is the lack of a behavioral relationship that corroborates the interpretation of neural activity. Although personality has been related to differential activity in these neural regions, it has not been related to changes in behavioral performance on the cognitive control tasks. Without this link, it is unclear what the personality–behavior correlations reflect. For instance, an obvious expectation may be that individuals who show greater reactivity to errors in the dorsal ACC would subsequently adjust cognitive control resources more drastically and, therefore, influence behavioral performance on subsequent trials more readily. Without experiments to illustrate connections between personality, neural activity, and behavioral performance on measures of cognitive control, it is unclear how to interpret the relationships between personality and neural activity that have been found. Ultimately, the studies currently suggest the potential for describing personality in ways that are more reflective of the underlying cognitive processes.

Goal-Directed Behavior in the Absence of Awareness  A particularly fascinating behavioral finding that has received little attention in neuroscience is that goals can be activated without awareness (Bargh, Gollwitzer, Lee-Chai, Barndollar, & Troetschel, 2001; Custers & Aarts, 2010). That is, individuals can be primed to engage in goal-directed behavior without forming an explicit intention to do so. Chartrand and Bargh (1996) illustrated
this effect using an impression formation goal. They capitalized on a well-established finding that when people are shown a list of behaviors (e.g., “went skiing,” had a party,” etc.) and are instructed explicitly to form an impression of another individual rather than just memorize the list of behaviors, they show both better memory as well as a tendency to cluster concepts together into a trait-like representation (Hamilton et al., 1980). Chartrand and Bargh (1996) asked whether such effects were also observed if subjects were primed with the goal to form an impression rather than explicitly instructed to pursue it. In one experiment, they primed subjects subliminally with words that were related to the goal of forming an impression of another person (e.g., “opinion,” “personality,” “evaluate,” etc.) or just memorizing (e.g., “remember,” “retain,” “memory,” etc.). They asked subjects to then complete a second ostensibly unrelated task in which they were presented with the list of behaviors. Their results showed that priming subjects with words related to impression formation resulted in greater overall memory and tendencies to cluster the behaviors around traits. Hence, the results suggest that subliminal priming of goal-related words can produce the same effects as instructing subjects explicitly to pursue the goal.

It could be argued though that such effects are simply due to stimulus-driven processes. That is, priming these concepts may lead to automatic activations that ultimately lead to this sort of behavior without further requiring an impression-formation goal to be activated. However, experiments by Bargh et al. (2001) suggest otherwise. They reasoned that one central difference between the priming of goals versus nongoal concepts is that activation of nongoal concepts should naturally attenuate over time, whereas activation of goal-related concepts should increase over time so long as the goal is not being accomplished. That is, goals involve the pursuit and striving to acquire an outcome, and that over time this motivation maintains or even increases in strength until the goal is achieved or otherwise relinquished. They found that priming subjects with goal-related words resulted in greater motivation to accomplish the task after a longer delay rather than after a shorter delay. These studies and others have provided strong evidence that goals can be activated without awareness.

Although the behavioral findings are compelling, very little is known about whether neural pathways involved in goal-directed behavior can also be engaged without awareness (Custers & Aarts, 2010). Indeed, we know of only one study to date that has examined this question directly. Lau and Passingham (2007) investigated whether cues that resemble task instructions can influence the engagement of prefrontal cortical regions involved in cognitive control, particularly when processed without awareness. In their task, subjects performed a simple task in which they were shown a cue (the outline of a square or diamond) that indicated whether to process a subsequent word either for semantic or phonological content (i.e., abstractness, or number of syllables). They argued that the neural regions that subserve semantic and phonological processing engage different control regions in prefrontal cortex, including an anterior ventrolateral PFC region for semantic control and the ventral premotor cortex for phonological control. Prior to this instruction cue, a prime was presented subliminally that either matched the subsequent instruction cue or not (i.e., a filled-in square or
diamond). Their experiment tests whether the prime engages only perceptual encoding processes or extends its influence into regions involved in cognitive control. If this latter hypothesis were true, this would predict that subliminal cues that resemble instructions automatically engage neural regions involved in cognitive control pertaining to the relative tasks. And indeed, this is what they found. The prime when presented subliminally engaged prefrontal regions that were involved in phonological or semantic control, regardless of the actual instruction cue. Behavioral results mirrored this such that congruent primes facilitated performance and incongruent primes interfered with performance. Hence, Lau and Passingham’s study indicates that at least some neural regions underlying control processes can be engaged subliminally.

Overall though, more experiments in this area would be useful to examine the extent to which neural regions involved in cognitive control, including the lateral PFC and the dorsal ACC, can be engaged and implement control without awareness or intent. Along this line, Custers and Aarts (2010) have suggested that unconscious goals may be engaged through at least two distinct routes. In one, goal-related cues activate action representations that subsequently initiate pursuit of a goal as part of the neural code that represents an action. In another, these cues influence the reward value for various outcomes in the world and thereby influence the motivation to obtain these rewards. Intriguingly, prior studies have shown that neural regions involved in both action representation and reward value can be engaged subliminally, though it has yet to be shown that such activity promotes goal-directed behavior.

**CONCLUSIONS**

In the cognitive neuroscience approach to goal-directed behavior, the brain is considered to implement various processes that allow for the representation and maintenance of a goal and selection of goal-relevant information and behaviors. These processes have been studied by designing precise but low-level cognitive tasks that aim to manipulate their involvement, and thereby assess neural regions that may participate in these processes. Although the tasks themselves may seem far afield from the way we pursue our everyday goals, it is notable that more complex cases such as memory control and emotion regulation show overlapping neural circuitry. Current research continues to refine these models of cognitive control by examining how various regulatory regions interact and to extend this model to several other domains. For example, while not reviewed in this chapter, a great deal of this work has already been applied to clinical populations, many of which show differences in behavioral ability to perform specific processes as measured by these low level tasks (Braver, Barch, & Cohen, 1999; Ochsner, 2008). This approach has produced a wealth of knowledge as to how the brain accomplishes goal-directed behavior. Beyond attaining greater precision on how the control network interacts, future directions may also aim to explore the generality of this network, how it fractionates into additional subprocesses in various domains, and how it incorporates other aspects of goal-directed behavior such as reward learning, goal abstraction, and individual differences.
REFERENCES


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