Self Control in Society, Mind, and Brain
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Print publication date: 2010
Print ISBN-13: 9780195391381
Published to Oxford Scholarship Online: May-10
DOI: 10.1093/acprof:oso/9780195391381.001.0001

Damaged Self, Damaged Control: A Component Process Analysis of the Effects of Frontal Lobe Damage on Human Decision Making

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DOI: 10.1093/acprof:oso/9780195391381.003.0002

Abstract and Keywords

Frontal lobe damage can disrupt judgment, decision making, and self-control, often with devastating impact on the everyday life of the affected person. Studies of these phenomena can identify the specific brain regions important for self-control and can specify the component processes for which these regions are necessary. This chapter provides an overview of recent neuropsychological work on regional frontal lobe contributions to reinforcement learning and decision making in humans. These findings argue that self-control can be understood in terms of simpler component processes, including the ability to flexibly learn from reward and punishment, to track the value of potential choices, or to predict future events. Further, these processes have been shown to rely on particular brain regions, an important step in delineating the neural mechanisms underlying self-control.

Keywords: lesion, reversal learning, future thinking, prefrontal cortex, preference judgments, neuroeconomics

VARIETIES OF SELF-CONTROL

One of the central challenges in understanding a complex process like self-control is knowing how best to dissect this complexity. This becomes particularly important if the aim is to relate these aspects of behavior to their underlying brain substrates. Although at first glance self-control might seem like a tidy and easily operationalized construct, the existing cognitive neuroscience literature indicates the contrary. There are clearly multiple

levels and aspects of behavioral control (Stuss & Alexander, 2007; Yin & Knowlton, 2006), as well as multiple processes combining to generate the sense of a subjective "I" somehow in charge of that behavior (Gillihan & Farah, 2005). This complexity is not specific to self-control; similar challenges of definition and operationalization have been identified for other higher-order behaviors, such as impulsivity (Evenden, 1999). From this perspective, self-control might be optimistically considered an emergent property of the combined actions of these various component processes, or, more cynically, a *post hoc* gloss applied to give a sense of coherence to the mix of habit and stochastic choice tendencies that together constitute our everyday behaviors.

(p. 28) In part because of this complexity, cognitive neuroscience is not currently in a position to provide a "grand unifying theory" of self-control. However, it has the potential to guide our thinking about the nature of self-control, at the least providing insights into the potentially relevant component processes of this complex construct. This chapter describes potential component processes of self-control suggested by recent cognitive neuroscience studies of decision making. This vantage point means that self-control is here considered in relation to choice. I would argue that self-control is invoked only when there is more than one possible behavior, even if the choice in question is only the couch potato's dilemma of whether to act at all. It follows that adaptive, authentic *choices* are the expression of self-control. Within that framework, I will explore concepts that bear on self-control and on the relation of self-control to the brain.

Whereas I remain uncertain about the mappings between self-control and the brain, others have been less circumspect. Perhaps the dominant view of self-control and the brain is a hierarchical model of "top-down" (rational) control over "instinctive" or "impulsive" behaviors. I will begin by explaining why this model is unsatisfactory, and argue instead for a more integrative view of the neural substrates of decision making. I will then discuss recent findings from the cognitive neuroscience of decision making, primarily from studies of patients with frontal lobe damage, and suggest how these findings may be relevant to a brain-based understanding of self-control.

HIERARCHIES OF CONTROL

Human behavior is often framed as a struggle between "bottom-up" and "top-down" processes. When this terminology is applied in a neuroanatomical sense, the "bottom" refers to structures such as the brainstem, basal

ganglia, and limbic system, including the amygdala and hypothalamus. These areas are, in a literal sense, under the cortex, and are also phylogenetically older (and so more primitive) parts of the brain. The “top” refers to cerebral cortex in general, and often refers to the highest order association cortices—notably prefrontal cortex (PFC)—in particular (Mesulam, 2003). In such accounts, PFC grabs the top spot, lording it over not only subcortical structures but also over lower-order cortical regions. Even within PFC a hierarchy is often implied, with lateral PFC literally and figuratively above orbitofrontal cortex (OFC), the “seamy underside” of PFC that is most closely linked to the limbic system (Barbas, 2000), and hierarchies within lateral PFC have also been proposed (Badre, 2008).

The top-down/bottom-up dichotomy can also be expressed at the level of behavior. Here, these terms refer to a struggle between reflexive, environmentally triggered, or emotionally driven acts and abstract, rational, goal-directed pursuits that may require multiple steps, distant in both time and place, from the final intended outcome. The processes that support the latter are often subsumed under the umbrella term “executive functions,” a term that summons up reassuring images of business organograms and orderly chains of command.

Executive functions are, of course, linked to PFC, whereas reflexive, emotional, or habitual responses are related to subcortical and limbic systems. These relationships would seem to boil down nicely to a model of brain function in which simpler, more primitive circuits clamor to satisfy basic desires (or passing whims), with the prefrontal-executive system more-or-less successfully riding herd over this turmoil to allow the achievement of long-term, rational goals. Such a model would seem to provide a convenient framework in which to situate self-control. Indeed, the model appears to owe its very terms of reference to the concept of self-control. Sadly, this dichotomous representation of the brain basis of behavioral control is at best overly simplistic and arguably so misleading that it would be better to abandon it entirely.

On neural grounds, executive function is increasingly being viewed as a fractionated set of interacting processes, rather than a monolithic entity (Stuss & Alexander, 2007). Conceptually, the choices that reflect self-control need not involve top-down “struggles” over limbically mediated temptations. Limbic systems alone may have quite enough to struggle with, as **(p. 29)** potentially incommensurate homeostatic and environmental cues—never mind abstract goal states—prompt a variety of choice behaviors. Importantly,

such competing behavioral options can, in principle, be resolved without recourse to an “executive,” and nevertheless still be instantiations of self-control.

UNTANGLING MORE DISTRIBUTED MODELS OF SELF-CONTROL

If more nuanced models are needed, then cognitive neuroscience approaches are likely to be useful for generating them. Such work does double duty, providing new perspectives on self-control as a construct, and insights into the instantiation of these processes in the brain. A brain-based, component approach to self-control requires only that putative component processes be neurobiologically plausible; they need not fall within some pre-ordained and mutually exclusive “rational” or “emotional” category. The extent to which putative component processes are in fact distinct can then be tested with neuroscience methods. These methods can also specify the brain mechanisms that underlie these processes. For example, if injury to a particular region of PFC disrupts one component of executive function but leaves another intact, this at the least argues that two distinct processes are being measured and is a beginning to understanding the circuitry that underlies them (Bates et al., 2003; Chatterjee, 2005).

Among the several cognitive neuroscience methods that may be helpful in tackling the general question of the nature of (and neural substrates of) self-control, loss-of-function techniques can be particularly useful. These experimental approaches involve measuring the effects of a disruption of brain function on behavior. With sound design, these methods can support inferentially powerful “necessity” claims—that is, they can show that a particular brain region is necessary for producing a particular behavior (Fellows et al., 2005; Rorden & Karnath, 2004). Relatedly, as discussed above, they can speak to whether particular behavioral measures are capturing dissociable processes, and so provide strong tests of component process hypotheses. There are three such methods commonly used in humans: lesion studies, transcranial magnetic stimulation, and pharmacological manipulations. The latter help to specify the neurochemical, rather than the neuroanatomical systems supporting behavior, and are not the focus of this chapter. I have employed the lesion method to identify component processes of decision making and to determine the role of particular regions of human PFC in these processes. In the pages that follow, I will review this and related work, both to illustrate the general approach and to describe some specific, prefrontally mediated component

processes of decision making relevant to developing a neurobiologically based understanding of self-control.

FRONTAL LOBE DAMAGE AFFECTS ASPECTS OF SELF-CONTROL

Decision making is one lens through which to view self-control. Although decision making need not involve self-control, self-control—at least as I have defined it here—involves decision making. Non-arbitrary choices require generating or identifying options, evaluating one or more of these options, and deciding a course of action (Fellows, 2004). Of these stages, cognitive neuroscience work to date has focused primarily on "evaluation." Subjective value is not a fixed property of a stimulus. It depends on factors external to the organism (What else is available?), and internal information (Am I hungry?) (Izquierdo et al., 2004; O'Doherty et al., 2000; Padoa-Schioppa & Assad, 2006). It can change rapidly and may continue to change even after a decision is made. Value (or utility) is, of course, a central concept in economics. Economics and decision science have provided formal models of how value ought to be adjusted to take into account factors such as risk, ambiguity, and delay, and empirical work has described how these factors actually influence decision making (Baron, 1994).

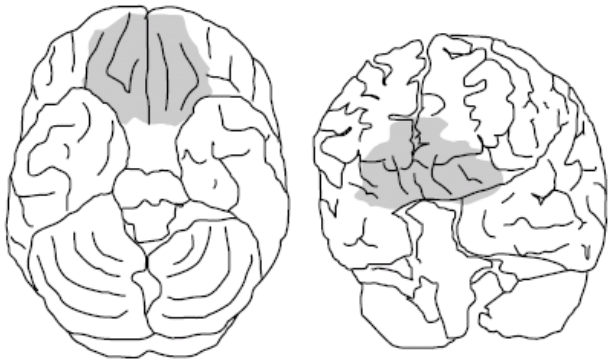

Figure 2–1. Schematic diagram of the brain, showing the region referred to in the text as the ventromedial frontal lobe (VM) in grey. The left panel shows a ventral view of the brain surface; VMF encompasses the medial aspect of orbitofrontal cortex. The right panel shows an oblique view, with the frontal poles cut away to show how VMF includes medial orbitofrontal cortex and the adjacent ventral aspect of the medial wall of prefrontal cortex.

These concepts and frameworks are being applied to inform neural models of decision making. This nascent field has been heavily influenced by clinical

reports of the effects of frontal lobe damage (Eslinger & Damasio, 1985; Loewenstein et al., 2001) and by experimental **(p. 30)** findings from human lesion studies (Bechara et al., 2000; Fellows, 2007), both of which have provided clues that the ventromedial region of PFC (VMF; *see* Fig. 2–1) may play a critical role in decision making. Efforts to understand the role VMF plays in decision making have provided interesting perspectives on the basic building blocks of self-control.

In the mid-1990s, Bechara and colleagues developed an experimental task in an effort to capture the clinically evident decision-making deficits of patients who had suffered damage to the ventral aspect of the frontal lobes (Bechara et al., 1997). Now known as the Iowa gambling task (IGT), the task succeeded in that patients with VMF damage had difficulty performing it, but the nature of that deficit has been much debated in the subsequent literature (Bechara et al., 2005; Dunn et al., 2006; Maia & McClelland, 2004). The task is a relatively complex card game, involving learning, ambiguity, risk, and integration of reward and punishment both within and across trials. This complexity has fuelled the debate about the interpretation of these findings. The task was initially framed as a test of the ability to anticipate future consequences, and the impairment of patients with VMF damage was taken as a reflection of "myopia for the future," a deficit in turn related to an impaired ability to "feel" risk—that is, to generate somatic signals in anticipation of potential losses (Bechara et al., 1997).

FLEXIBLE REINFORCEMENT LEARNING AS A MODEL OF ADAPTIVE SELF-CONTROL

Although "myopia for the future" has obvious resonance with ideas about self-control, the IGT is not a good test of such an ability. It is probably more straightforward to think of the task not in terms of anticipating the future, but rather of learning from past experience. The subject chooses from four decks of cards, learning by trial and error which decks are advantageous, which disadvantageous. Two decks are disadvantageous overall, in that choosing from those decks will lead to frequent wins but occasionally more substantial losses. The advantageous decks hold small wins, but even smaller losses, and so are the best bets over the long term. Importantly, card order in each deck is fixed, meaning the contingencies associated with each deck change partway through the task. The large losses associated with the disadvantageous decks are only experienced after several choices from those decks, and after both healthy and VMF-damaged subjects have established a preference for those decks. As these losses accrue, healthy

subjects tend to shift their preference to **(p. 31)** the lower win but overall advantageous decks, but VMF damage impedes this shift.

This pattern of performance is reminiscent of observations that had been made in non-human primates performing simple instrumental learning tasks (Butter, 1969; Jones & Mishkin, 1972). As far back as the 1960s a particular learning deficit had been observed after lesions to orbitofrontal cortex. Animals with such damage learn stimulus–reward associations as well as control animals but have difficulty adjusting their choices when the contingencies change. The paradigm that best illustrates this deficit is reversal learning. The usual design has two initially neutral stimuli, one paired with reward and the other with non-reward (or outright punishment). Once learning of these contingencies is demonstrated, the reinforcement contingencies are switched. Orbitofrontal cortex damage selectively impairs performance in this reversal phase of learning in rats, macaques, and humans (Murray et al., 2007). The process of learning new reinforcement contingencies associated with previously reinforced stimulus features is also termed “affective shifting,” in that it involves reassigning the motivational (or “emotional”) value of stimuli (Dias et al., 1996).

We asked whether this phenomenon explained the performance of patients with VMF damage on the IGT, and tested this possibility by administering a shuffled variant of the IGT to nine patients with VMF damage as well as a group with PFC damage-sparing VMF and a demographically matched healthy control group. The shuffled task was identical to the original with the exception that the card order did not lead to an initial tendency to favor the ultimately disadvantageous decks. Patients with VMF damage were impaired in the original task but performed as well as healthy subjects when the underlying requirement for reversal learning was eliminated from the task (Fellows & Farah, 2005a). This finding illustrates how components of a process as complex as the decision making required in the IGT can be identified and shows that such components can be relevant to understanding both the behavior and its relation to the brain. Reversal learning has been extensively studied in animal models, so connecting human decision making to this more basic construct allows this literature to be brought to bear.

A second important point arising from this and related work is that individuals may be impaired on the IGT because of fundamental deficits in various more basic processes. For example, patients with lateral PFC damage also have trouble with this task (Manes et al., 2002), but *not* because of its reversal learning requirement (Fellows & Farah, 2005a). It is likely that the

deficit in these patients is related, at least in part, to the working memory requirement of the task, although this remains to be definitively shown (Bechara et al., 1998). I emphasize this point because it highlights an inferential problem that dogs efforts to translate the lesion study results using this task to understand the neural substrates of "disordered self-control" in neuropsychiatric conditions such as addiction (Bechara, 2003; Bechara et al., 2002). Simply put, abnormal performance on the IGT does not necessarily mean that an individual has VMF dysfunction.

This work also serves as something of a cautionary tale, highlighting the potential pitfalls of moving from clinical observations to underlying mechanisms. Whereas some patients with VMF damage do have clinically evident difficulties in judgment and decision making that might be interpreted as a failure of self-control, and many with VMF damage show characteristic deficits on simple reversal learning tasks and, in turn, on the IGT, it remains unclear whether these clinical and experimental observations reflect a causal pathway or neuroanatomical coincidence (Fellows & Farah, 2003; Rolls et al., 1994).

Can these reversal learning findings inform thinking about self-control? These data highlight the existence of multiple neural systems for learning to make adaptive choices, acting over different timescales. When reinforcement contingencies change, well-learned rewarding "habits" can be quickly overridden, through a VMF-dependent mechanism. This flexibility to adjust to a rapidly changing reward and punishment "landscape" could be considered an aspect of self-control, and simple paradigms like reversal learning are a useful experimental tool for operationalizing self-control to understand the brain processes involved.

(p. 32) SURPRISE! BREACHES OF EXPECTATION AND DYNAMIC SELF-CONTROL

The ventromedial frontal lobe—particularly its OFC component—is heavily interconnected with two brain regions that play important roles in motivated behavior. One is the amygdala, a nucleus in the medial part of the temporal lobe that is involved in rapidly signaling the salience of emotionally laden stimuli. The other is the hypothalamus, a region important for signaling basic drives (e.g., hunger, thirst) and for coordinating basic behavioral and autonomic responses to stimuli relevant to satisfying those drives (Ghashghaei & Barbas, 2002). Although some work has been done to investigate how the amygdala and OFC might function together to support

learning and decision making in humans (Bechara et al., 1999; Hampton et al., 2007), this question has been addressed more extensively in studies in rats and non-human primates (Baxter et al., 2000; Murray et al., 2007). A recent, provocative finding in this regard comes from a dual lesion study in rats. Rats with lesions to OFC were impaired on a reversal learning task. Remarkably, when the basolateral amygdala was additionally lesioned, this reversal learning impairment was abolished (Stalnaker et al., 2007). The authors interpreted this finding as evidence that OFC serves a "gating" function, allowing rapid updating of amygdala-mediated stimulus–reinforcement associations. They propose that OFC, in this context, serves to detect breaches of stimulus–outcome expectation, in turn allowing other neural circuits to "learn something new."

Expectations of this kind might, in principle, be breached in one of two ways: either by delivery of an unexpected punishment (or omitted reward) or by the delivery of an unexpected reward (or omitted punishment). In practice, most of the work on this issue has examined responses to unexpected punishment (or omitted rewards), a type of feedback put in high relief in reversal learning tasks. A reversal trial provides a maximal "breach of expectation" signal, and it is the ability to rapidly respond to this signal that seems to be affected after OFC damage. This raises the possibility that OFC is critically involved primarily in learning from unexpected negative feedback.

We administered a reinforcement-learning task that allows separate measures of how much is learned from negative and positive feedback to patients with VMF damage to test this idea. The task requires learning to choose between pairs of arbitrary stimuli (Japanese Hiragana characters) through trial-and-error, with probabilistic feedback provided after each choice. Overall, one character in each pair was more often associated with positive feedback and the other with negative feedback. Once learning was demonstrated, subjects moved to the test phase of the task. This phase allowed the measurement of whether they had learned from positive feedback (i.e., to choose the most "correct" stimulus), from negative feedback (i.e., to avoid the most "incorrect" stimulus), or both (Frank et al., 2004). Healthy control subjects, and patients with frontal lobe damage outside VMF, learned almost equally from positive and negative feedback. Those with VMF damage learned normally from positive feedback but were very impaired in how much they learned from negative feedback (Wheeler & Fellows, 2008). This finding suggests that the contribution of VMF to reversal learning may rest on an even simpler component process: that of detecting

unexpected negative outcomes, in turn permitting rapid adjustments in behavior (i.e., learning) from these outcomes.

How can these results be related to ideas about self-control? At the least, they identify one potential mechanism underlying aberrant self-control in a particular clinical population: the ability to detect, and so rapidly adjust to, unexpected (negative) outcomes. This is a more nuanced perspective on the role of a particular region within PFC than the "top-down control over basic drives" caricature outlined earlier in this chapter. It is also interesting that the experimental paradigms that have been particularly useful in understanding VMF contributions to behavioral control have been reinforcement learning tasks. This provides a different perspective on self-control, underlining the importance of feedback (perhaps particularly negative feedback) and the fact that decisions take place **(p. 33)** in a dynamic context, with the results of past choices influencing the next.

FUTURE THINKING AND THE FRONTAL LOBES

Having argued that one major line of research on the role of the frontal lobes in human decision making concerns how past experience is applied to influence present choice, I now turn to the question of whether the frontal lobes play a critical role in future thinking. The proverbial "ant-and-grasshopper" choice between immediate gratification and delayed reward is a classic self-control dilemma. This type of problem is an attractive experimental target for a cognitive neuroscience understanding of decision making. It has a long history of study at the behavioral level, and lends itself to a component analysis. One likely component, the effect of delay on subjective value (so-called "temporal discounting") comes complete with defined experimental measures and well-specified theoretical models (Ainslie, 2001). Other components suggest themselves. For example, future rewards will carry less sway if they are more heavily discounted by delay. They will also carry less sway if the time at which they are to be delivered is outside the window of time considered as "the future." As an extreme example, a decision maker is likely to consider a reward delivered beyond his/her expected lifespan as worthless. Interestingly, the period of time spontaneously contemplated when individuals think about their own futures varies quite widely (Kastenbaum, 1961; Lessing, 1968).

We undertook an exploratory study of these two aspects of future thinking in patients with frontal lobe injury, as well as both healthy controls and a control group with nonfrontal focal brain injury. Temporal discounting

was measured with a widely used task that requires subjects to choose (hypothetically) from various sums of money delivered "now" or larger sums to be received after a delay of between 7 and 186 days. The task has previously been shown to detect tendencies to steeper discounting in drug addicts compared to non-addicted controls (Bickel & Marsch, 2001; Petry et al., 1998). Although we found large individual differences in our study population, focal brain injury, whether affecting VMF, dorsolateral frontal, or nonfrontal regions, had no systematic effect on temporal discounting rate (Fellows & Farah, 2005b). Thus, although fMRI data indicate that PFC is involved in intertemporal choice (Kable & Glimcher, 2007; McClure et al., 2004), no PFC region appears to be critical in setting temporal discounting rates.

In contrast, VMF damage affected the subjective window of time viewed as "the future." A task known as the "future time perspective" task was used to measure this construct. This task requires subjects to list a fixed number of events likely to occur in their own futures. Once listed, subjects are asked when these are likely to occur. The time to the most distant future event is the measure of interest. All subjects with brain injury had shorter future time windows than did healthy controls, presumably reflecting the effects of having experienced a serious illness. However, those with VMF damage (n = 12) had significantly shorter time windows compared to those with damage elsewhere (n = 26), suggesting a specific role for that part of the brain in the ability to envisage the more distant future (Fellows & Farah, 2005b).

This finding argues that when patients with VMF damage make choices that suboptimally emphasize present or near-term considerations, that may reflect a different view of time, rather than a steeper discounting of the value of future rewards. More generally, these findings make a case for the dissociability of these two aspects of future thinking, both of which are relevant to self-control as it is played out over time, but only one of which seems to rely critically on VMF.

SUBJECTIVE VALUE AS AN ANCHOR FOR SELF-CONTROL

An early view of the role of OFC was that it encoded the subjective (and relative) value of potential choices. For example, single-unit recordings from OFC in macaque monkeys indicated that a particular population of neurons might respond to the sight of a banana, with that activity suppressed and replaced by a **(p. 34)** different population encoding a second, more preferred option, if it was made available (Rolls, 2000). Subsequent work, using

different paradigms, have confirmed this basic idea. At least some neurons within OFC appear to be “tuned” to particular rewards, these rewards seem to be evaluated within the context of what else is available, and their value is modified by internal factors such as selective satiety (i.e., a banana’s value is reduced after the monkey has had the opportunity to eat several bananas) (Padoa-Schioppa & Assad, 2006; Roesch & Olson, 2004; Tremblay & Schultz, 1999). Functional MRI studies in humans have at least partially supported this view, although preference judgment has been related to activity within the ventral aspect of the medial wall of PFC, rather than OFC, in most such studies (Cunningham et al., 2003; Paulus & Frank, 2003).

Whereas these single unit and fMRI data indicate a correlation between VMF activity and value, they do not specify whether this activity is necessary for decision making, and if so, in what way. Given that relative evaluation would seem to be the very crux of most non-arbitrary choices, if VMF does play a crucial role in representing relative value, then damage affecting this region ought to affect even very simple forms of decision making. Perhaps the simplest form of decision making is preference judgment (e.g., chocolate or vanilla?), a choice that need not involve risk, ambiguity, or intertemporal considerations but that nevertheless can be difficult. There is some, albeit conflicting, evidence that OFC damage may affect the consistency of preference judgments in macaques (Baylis & Gaffan, 1991; Izquierdo et al., 2004). We tested this idea in humans with VMF damage using a simple preference task adapted from this animal work.

Subjects chose between all possible pairs within three categories of stimuli: foods, colors, famous people, answering the question “Which of these do you prefer?” There can be no objectively “wrong” answers to questions of subjective preference, but there can be inconsistencies. The overall rank order of preferences that emerged from these pair-wise choices was determined, and the number of individual choices that deviated from this order was taken as a measure of inconsistent choice. As predicted by the hypothesis that OFC represents relative value in the service of decision making, subjects with damage to VMF made more of these inconsistent choices than did either healthy controls, or those with damage to the frontal lobes that spared VMF (Fellows & Farah, 2007). These experimental findings of inconsistent preference after VMF damage have yet to be systematically linked to real-life behavior in these patients. However, independent clinical accounts of either a dramatic incapacity to choose at all (Eslinger & Damasio, 1985), or a tendency to whimsical or capricious choice after such damage, stretch back decades (Ackerly, 2000).

These results frame self-control in yet another way. If the ability to determine or compare value is disrupted, then resulting choices could be considered as somehow inauthentic. If you can't reliably represent value, is the resulting choice really "yours?" I suggest that one of the features that leads to the subjective sense of self is an at least broadly coherent set of preferences and choice tendencies—that is, "values," with value defined in the broad sense, rather than the narrower, moral sense. Inconsistent preferences after VMF damage can thus be conceived of as a form of aberrant self-control that is primarily an impairment of "self" rather than an impairment of "control."

SELF-CONTROL BEYOND DECISION MAKING

A complete understanding of self-control requires that these findings concerning basic elements of decision making be placed in a broader context. Although self-control involves choice, clearly it also involves other processes. Other component processes, also linked to PFC, including working memory, allocation of cognitive resources, maintenance and shifting of selective attention, and the inhibition of prepotent response tendencies are likely to be involved in at least some forms of self-control (*see* Chapters 1 and 6). Whereas it is beyond the scope of this chapter to review these in detail, there is now substantial evidence that these are dissociable and rely on distinct sectors within PFC (Miyake **(p. 35)** et al., 2000; Stuss & Alexander, 2007; Stuss et al., 2001; Tsuchida & Fellows, 2009).

That these processes can be dissociated should not be taken to mean that they normally occur in isolation. It is important to emphasize that the different sectors within PFC are directly interconnected, and interact as well through cortico-subcortical circuits (Barbas, 2000; Haber, 2003; Price et al., 1996). They are also extensively modulated by neurochemical inputs (notably dopamine, norepinephrine, and serotonin) that have their own influences on processes relevant to self-control (Chamberlain et al., 2006; Cools et al., 2006; Cools & Robbins, 2004; Frank et al., 2004; Schweighofer et al., 2008; Tanaka et al., 2007). The complex interactions within PFC, and between PFC and other cortical and subcortical regions that occur under normal circumstances put the lie to dichotomous "rational vs. emotional" or "cortical vs. limbic" accounts of self-control. Emotional and motivational processes are intrinsically linked to more conventionally "cognitive" processes and are in turn dynamically modulated by them.

The work reviewed here reflects an effort to reduce the complexity of self-control to tractable components. Relating these relatively new

neuroeconomic and decision-making findings to the better elaborated understanding of other aspects of frontal-executive function will be an important enterprise for research in this area in the medium term. This approach should lead to an integrated view of how humans more-or-less successfully navigate a real world offering a sometimes dizzying array of opportunities, temptations, and long-term prospects. Such a neurobiologically grounded understanding will put us in a position to analyze, and hopefully address, what goes wrong to produce self-defeating choices in illnesses like drug abuse or in more prosaic, but nonetheless important, contexts, such as overeating.

Martha Farah made substantial contributions to several of the studies reviewed here. I acknowledge support from the NIH (R21 NS045074, R21 DA22630) and CIHR (MOP 77583 and a Clinician Scientist award).

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