NEURAL SUBSTRATES OF INHIBITORY CONTROL: A REVIEW AND CRITIQUE

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Abstract

Inhibitory control is difficult to study in behavioral experiments because of its nature; a successful inhibition act does not manifest overtly, thus cannot be directly observed and measured (Kana, Keller, Minshew & Just, 2007). Some influential theorists have called the very existence of cognitive inhibition into question (MacLeod, 2007a). This is a case where brain-imaging research holds the promise to be able to shed light into the covert nature of inhibition, with potentially immeasurable impact on understanding and ameliorating conditions such as ADHD, addiction, and frontal lobe injuries.

A critical review of the literature shows that inhibitory control is subserved by a network of brain regions including as key components the inferior frontal cortex, the pre-supplementary motor area, and the sub-thalamic nucleus. It is argued that inhibitory control makes use of basic cognitive processes such as internalized speech. A common inhibitory mechanism for motor, speech and thought acts is proposed. Practical applications of research on inhibitory control are discussed such as brain plasticity exercises and electrical brain stimulation.

Cuvinte-cheie: control inhibitor, conectivitate, substrat neuronal.

Keywords: inhibitory control, connectivity, neural substrate.

1. INTRODUCTION AND BACKGROUND

We all know how itchy a mosquito bite can be. The urge to scratch it can be overwhelming. However, we know that scratching can make the itching worse, thus, we try hard (and sometimes succeed) to resist our strong tendency to scratch (Rougier, Noelle, Braver, Cohen & O'Reilly, 2005). Imagine you are about to press your car's accelerator but, as you begin, a bicycle appears in front of your car. Will you be able to countermand the motor command and avoid pressing the accelerator (Aron, 2008)? While taking the Stroop test, we cannot help but read the words that are presented on the screen and use these words to name the ink color in which they are written. When a word is incongruent with its color, we have to override the tendency to use the word and instead use the color name as a response (Stroop, 1935).

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The ability to inhibit inappropriate responses is one of the key functions of executive control (Friedman & Miyake, 2004; Miyake *et al*., 2000). Executive control is the ability to behave in accord with rules, goals, or intentions, even when this runs counter to reflexive or otherwise highly compelling competing responses (Rougier, Noelle, Braver, Cohen & O'Reilly, 2005). Inhibition is essential for development of executive functions. It provides the necessary delay for them to occur and develop. It sets the occasion for the engagement of executive functions, which then provides greater control of behavior by the internally represented information they generate (Barkley, 1997).

1.1. INHIBITION TASKS

Inhibition is measured by performance on tasks that require withholding of responding, delayed responding, cessation of ongoing responses, and resisting distraction or disruption by competing events (Barkley, 1997).

The Go-NoGo task requires inhibition of a motor response before the response has been started. Stimuli (usually letters) are rapidly and serially presented on the screen. Subjects respond as quickly as possible to every letter (Go trials), except for the letter "X". When the letter "X" appears on the screen, the subjects should restrain from responding (NoGo trials). The proportion of NoGo trials to Go trials is usually very low (e.g., 10/90). The lower this proportion is, the more difficult it is for subjects to withhold their Go response in NoGo trials. Of a particular importance are the errors of commission on NoGo trials, that is, responding as if they were Go trials. Since the reaction time (RT) for commissions is usually faster than RT for correct Go trials (Swick, Ashley & Turken, 2008), commissions are taken as an indication of impulsive behavior.

The Stop-signal task requires cancellation of a motor response during its execution. Participants always respond to Go signals unless they are followed by a stop signal. The stop signal occurs on 25% of the trials at various intervals after the go signal. These intervals are used to compute the "Stop signal reaction time" (SSRT) – a measure of the stopping speed (Logan, 1994). SSRT is used as a clinical index of inhibitory control, primarily in the study of attention deficit hyperactivity disorder (ADHD) (Schachar *et al*., 2007).

Other tasks that are thought to tap into inhibitory control are the Wisconsin Card Sorting Test (WCST), Random Number Generation, and Stroop. However, usually a cognitive task triggers multiple cognitive functions and sophisticated analyses are needed to isolate the inhibitory component (Aron, 2008; Bellgrove, Hester & Garavan, 2004; Juvina & Taatgen, 2009a).

1.2. IS INHIBITION A VALID PSYCHOLOGICAL CONCEPT?

There has been a growing interest in research on cognitive inhibition over the past decades. This growth is due to discovery of cognitive phenomena such as negative priming and inhibition of return and to advances in computational cognitive

modeling and cognitive neuroscience (MacLeod, 2007b). However, some authors have questioned the validity of the concept of cognitive inhibition (Egner & Hirsch, 2005a; MacLeod, 2007a; MacLeod, Dodd, Sheard, Wilson & Bibi, 2003). One of the arguments for opposing inhibition-related theories is that there are always alternative theoretical accounts that can explain the data without invoking an inhibitory process (MacLeod, Dodd, Sheard, Wilson & Bibi, 2003). A widely accepted theoretical account of how cognitive control operates (Miller & Cohen, 2001) postulates a top-down excitatory biasing mechanism that activates task relevant information, thus giving preferentiality to relevant over irrelevant information. There are elegant demonstrations of this account in both computational modeling (Herd, Banich & O'Reilly, 2006) and brain imaging (Egner & Hirsch, 2005a) literatures. These demonstrations suggest that there is no need for an inhibition concept to account for cognitive phenomena. According to Jonathan Cohen (personal communication) inhibiting irrelevant representations in order to select the relevant representation for the task at hand would be a very computationally expensive strategy, as there may be thousands of irrelevant representations for a given task. A more parsimonious strategy would be to over-activate the task relevant representation. Overriding a prepotent representation (e.g., the urge to scratch a mosquito bite) would be done by over-activating another arbitrary representation, and not by directly inhibiting the prepotent representation (Cohen, personal communication).

In contrast, there is empirical and computational evidence, showing that an inhibitory biasing mechanism is needed in addition to the excitatory biasing mechanism in order to account for performance in executive control tasks (Druey & Hubner, 2008; Grange & Houghton, in press; Juvina & Taatgen, 2009a). A more direct and compelling line of evidence comes from neuroscience. A study that measured the activity level of the cortical representation of muscles during a stop-signal task showed that both the agonist muscle and an irrelevant muscle representation in the cortex were suppressed by the requirement to inhibit the incipient response (Coxon, Stinear & Byblow, 2006). This suggests that stopping and presumably other inhibitory control processes are achieved via active inhibition of (potential) response tendencies rather than via over-activation of an arbitrary alternative representation.

1.3. ROLE OF NEUROSCIENCE AND NEUROIMAGING RESEARCH

Inhibitory control is difficult to study in behavioral experiments because of its nature; a successful inhibition act does not manifest overtly, thus cannot be directly observed and measured (Kana, Keller, Minshew & Just, 2007). As long as theorists have to infer either inhibition or alternative processes from behavioral data (MacLeod, Dodd, Sheard, Wilson & Bibi, 2003), the debate over the construct validity of cognitive inhibition will continue. Building computational models that attempt to account for behavioral data is a step in the right direction, in that it

favors only those theoretical accounts that are well specified and can be implemented at a computational level. However, the range of computational models that are able to account for the behavioral data can be very large and further constraints are needed in order to select those accounts that are biologically plausible.

Neuroscience and neuro-imaging research may be able to shed light into the covert nature of inhibition. The following section presents a review and a critique of the existing literature on the neural substrates of inhibitory control. The critique ends with the suggestion that inhibitory control can be seen as arising from internalized speech. Section 3 discusses the clinical and practical relevance of inhibitory control research.

2. INHIBITION NETWORK

The bulk of evidence regarding the neural substrates of inhibitory control comes from fMRI studies of tasks such as Go-NoGo (GNG), Stop-signal, and Stroop. However, fMRI is not the only source of evidence. Critical evidence comes also from lesion studies, connectivity analyses, single neuron analyses, and Trans-cranial magnetic stimulation (TMS).

2.1. ASYMMETRY AND HEMISPHERIC SPECIALIZATION

Brain activation found in inhibitory control tasks tends to be more pronounced toward the front of the brain. It is largely accepted that brain regions that are located toward the front of the brain exert control or bias over brain regions that are located toward the back of the brain (Egner & Hirsch, 2005b). In addition, numerous authors argue that inhibitory control functions are located in the right hemisphere; a meta-analysis of 39 studies confirms the right hemisphere dominance of inhibitory control (Swick, Ashley & Turken, 2008).

2.2. CONNECTIVITY

It is a commonly accepted view that performance on inhibitory control tasks is subserved by a network of interconnected brain regions. I will describe here the fronto-basal-ganglia network because it has received a considerable amount of attention in the literature on inhibitory control.

Multiple lines of evidence suggest that the right inferior frontal cortex (RIFC) (including the Operculum and Insula) is a critical region for response inhibition in the Stop-signal task (Aron *et al*., 2007; Aron & Poldrack, 2006; Chambers *et al*., 2006; Garavan, Hester, Murphy, Fassbender & Kelly, 2006; Kana, Keller, Minshew & Just, 2007). The RIFC sends a Stop command to intercept the Go process via the Basal ganglia. Let us first consider the Go process achieved through the *direct pathway* of the Basal ganglia. The motor plan in the frontal cortex activates the Putamen, which then projects to the Globus pallidus, then to the Thalamus, then to

primary motor cortex. Activations were found in regions consistent with this direct pathway when subjects responded to Go trials (Aron & Poldrack, 2006). The Stop process could be initiated in the RIFC and then activate the Globus pallidus via a projection from the subthalamic nucleus (STN). STN increases inhibition of the thalamus and thus blocks basal ganglia output to the primary motor cortex. This has been called the *hyperdirect pathway* (Aron *et al*., 2007). A third critical node for the stopping process is the dorsomedial frontal cortex including the presupplementary motor area (pre-SMA). It has been shown that pre-SMA damage affects stopping performance (Floden & Stuss, 2006; Nachev, Wydell, O'Neill, Husain & Kennard, 2007; Picton *et al*., 2007). On Stop trials, activations were found in STN, RIFC, and pre-SMA (Aron, Behrens, Smith, Frank & Poldrack, 2007). RIFC has anatomical connections with the motor system (Mostofsky & Simmonds, 2008) and the pre-SMA was found to be directly connected by white matter tracts with both the RIFC and STN (Aron, Behrens, Smith, Frank & Poldrack, 2007). The role of Pre-SMA could be monitoring and resolving response conflict (Aron, 2008; Nachev, Wydell, O'Neill, Husain & Kennard, 2007) or switching from automatic to volitionally controlled behavior (Isoda & Hikosaka, 2007).

2.3. COMMON MECHANISM FOR INHIBITORY CONTROL

Aron *et al*. (2007) presented irrelevant stop signals to subjects and found that their responses on Go trials were slowed, without complete cancellation. The degree of slowing corresponded to the degree of activation in the right pre-SMA, the IFC, and the STN region (Aron, Behrens, Smith, Frank & Poldrack, 2007). They concluded that slowing and stopping might occur via the same mechanism.

Is the inhibitory control mechanism described above (the fronto-basal-ganglia network) specific to tasks involving inhibition of manual responses? Evidence exists in support of the assertion that the same mechanism is involved in inhibition of saccadic movements (Isoda & Hikosaka, 2007) and speech acts (Xue, Aron & Poldrack, 2008). In addition, it has been shown that suppression of unwanted memories activates a network of regions that partially overlaps the network involved in motor and speech suppression (Ventro-lateral prefrontal cortex and pre-SMA) (Anderson *et al*., 2004; Levy & Anderson, 2008).

2.4. CRITIQUE OF THE LITERATURE ON THE NEURAL SUBSTRATES OF INHIBITORY CONTROL

The right hemisphere dominance of inhibitory control has become a commonly accepted view. What appears to be strong evidence in support of this view is that the degree of activation in the RIFC predicts the speed of stopping in the stop-signal task (Aron, 2008). However, evidence from brain lesion studies argues for the essential role of the left inferior frontal cortex (LIFC) in response inhibition (Swick, Ashley & Turken, 2008). Other authors report bilateral IFC activations in

inhibition tasks (Egner & Hirsch, 2005b). An interesting line of evidence comes from developmental psychology. Early in development, inhibitory control appears to be associated with LIFC regions, and the prominence of RIFC emerges only later in life (Bunge, Dudukovic, Thomason, Vaidya & Gabrieli, 2002). There is no evidence that the anatomical connections of the LIFC are different than the connections of RIFC (Swick, Ashley & Turken, 2008), thus there might not be any specific advantage of the RIFC for inhibitory control. These results suggest that the activation in the right hemisphere might be the result of a "spillover" from the left hemisphere homolog (Just & Varma, 2007).

The left hemisphere homolog of the RIFC includes Broca's area – the left inferior frontal gyrus (LIFG). This area has been shown to be involved in motor control by internalized speech (Morin & Michaud, 2007), resolution of proactive interference in working memory (Thompson-Schill *et al*., 2002), and resolution of Stroop interference (Novick, Trueswell & Thompson-Schill, 2005).

Given that the integrity of LIFG is critical for inhibitory control (Swick, Ashley & Turken, 2008), it can be argued that inhibitory control is achieved via internalized speech (Barkley, 1997). It has been suggested that vocal control for speech might share evolutionary origins with manual motor control for gesturing (Taglialatela, Russell, Schaeffer & Hopkins, 2008). Thus, in Go-NoGo and Stop-signal tasks, the internalized speech needed to control behavior on the NoGo or Stop trials is more complex. Perhaps the internalized speech would look like this: "Oops! I was just about to make a reaction as if it was a Go signal. But this is a NoGo signal, so I should not react. But I have all these motor preparations in place, what am I going to do with them?" It could also be a logically incoherent sentence, such as: "I am executing this motor movement and I see the Stop signal, thus I am not executing this movement". In both cases parsing and comprehending such internalized speech might be more demanding than in the case of a simple Go command, which explains why the right homolog of the LIFC have to be recruited. This case may by similar with the case of metaphor and irony comprehension (Eviatar & Just, 2006). For example, one can react to a rude comment by saying: "You are so polite… not!". There is obviously more complexity involved in parsing and comprehending such sentences. The last word "not" acts as a stop Signal – it reverses the meaning of the GO signal ("you are so polite").

Thus, inhibitory control might not be so different in nature than other cognitive processes and might be implemented by common mechanisms of executive control such as internalized speech.

3. CLINICAL AND PRACTICAL RELEVANCE

Another reason for the growing interest in inhibitory control, beside the reasons enumerated by MacLeod (2007b), is its clinical and practical relevance. Inhibitory control is essential for our daily functioning as social actors. Performance

on the Stroop test has been shown to correlate with our ability to resist expressing socially inappropriate opinions (Hippel & Gonsalkorale, 2005).

A deficit in inhibitory control seems to be the central impairment in attention deficit hyperactivity disorder (ADHD). ADHD appears to arise from abnormalities in the structure and function of the prefrontal cortex and its networks with other brain regions, especially the striatum (see Barkley, 1997, for a review). Children with ADHD are impaired in both Go-NoGo and Stop-signal tasks (Schachar *et al*., 2007) and they produce more errors of commission than other children on a large range of tasks (Barkley, 1997). Their brain size is altered in regions involved in inhibitory control such as the RIFC (Durston *et al*., 2004).

Another condition that is associated with impaired inhibitory control is traumatic brain injury (TBI) in the areas of the prefrontal lobes that are involved in inhibitory control. Patients with this condition show ADHD-like symptoms (Barkley, 1997). For example, patients with frontal lobe injuries are more likely than controls to manifest "utilization behavior" such as opening an umbrella found in an examination room (Barkley, 1997).

Thus, prefrontal lobe injuries can be seen as a form of acquired ADHD.

3.1. BRAIN PLASTICITY TRAINING AND MENTAL STIMULATION

Studying inhibitory control can suggest new ways of intervention in order to optimize behavior or ameliorate pathological conditions such as ADHD and TBI. Both ADHD and TBI produce relatively high rates of recovery (Barkley, 1997), and this can be attributed to brain plasticity (Doidge, 2007). By knowing what are the critical brain regions involved in inhibitory control and what are the mechanisms through which inhibitory control operates, one can design and experiment with brain plasticity exercises.

Males have a higher prevalence of impulse control disorders than females. In particular, the ratio of boys to girls in ADHD is 3 to 1 (Barkley, 1997). This fact is usually taken as evidence for a genetic component in the development of inhibitory control. However, fMRI findings suggest an alternative (or complementary) interpretation. Cortical activity in the inhibition network is greater in females and it increases with age (Garavan, Hester, Murphy, Fassbender & Kelly, 2006). If our "spillover hypothesis" is correct (i.e., inhibition is complex and requires recruitment of additional mental resources, see section 2.4.), females and older individuals may be better trained through their daily experience to handle inhibitory control tasks. Females and older individuals might have a higher level of exposure to social interactions that require modulations of speech acts. As a consequence, they might be better at recruiting the right resources for their inhibitory tasks at hand. This is potentially good news for patients with ADHD and TBI. They might be able to improve their inhibitory control skills if they practice enough. Children with ADHD and controls have comparable rates of improvement with age on executive tasks such as WCST (Barkley, 1997). It has been shown that the executive control

functions are trainable (Juvina & Taatgen, 2009b) and practice on executive control tasks produces lasting improvements on fluid intelligence (Jaeggi, Buschkuehl, Jonides & Perrig, 2008).

Other methods that might prove effective in improving inhibitory control include direct brain stimulation and use of psychoactive medications. Isoda and Hikosaka (2007) found that a group of pre-SMA neurons activated when subjects (Rhesus macaque monkeys) successfully switched to a controlled alternative action. Electrical stimulation in the pre-SMA replaced automatic responses with slower correct responses. A further test suggested that the pre-SMA enabled switching by first suppressing the automatic action and then boosting the controlled action (Isoda & Hikosaka, 2007). This result suggests a possible application of electrical brain stimulation in humans to improve their inhibitory control functions. Patients would be able to use a brain pacemaker when they recognize the need for self-control, for example, when their urge to take harming drugs is very strong and cannot be controlled by other means. Brain pacemakers are currently used in epilepsy, Parkinson's disease and severe depression.

4. CONCLUSION

Inhibitory control encompasses abilities that are considered to be inherently or predominantly human such as impulse control and deferred gratification. Deficits of inhibitory control are common in ADHD, drug abuse, TBI, and in everyday lapses in speech, action, thought and intention wherein behavior appears to be dictated by external cues or by habit (Garavan, Hester, Murphy, Fassbender & Kelly, 2006).

I have attempted to demonstrate that studying inhibitory control from the perspective and with the instruments of cognitive neuroscience is a profitable endeavor for both basic and applied science.

From a theoretical standpoint, I have provided a critical review of the existing literature on the neural substrates of inhibitory control. Although theorists are still debating on the validity of the cognitive inhibition construct, there is some evidence coming from the neurosciences to conclude that:

– The brain mechanism that implements inhibitory motor control is the fronto-basal-ganglia network with the direct and hyperdirect pathways.

– This mechanism acts directly by inhibiting the Go signal, and not indirectly by over-activating another representation.

– It appears to show right hemispheric dominance, although evidence for bilaterality exists.

– It shares resources with other cognitive processes and uses basic cognitive mechanisms such as internalized speech.

– It is likely that the same cognitive mechanism is involved in inhibition of motor, speech and thought acts.

From a clinical and practical perspective, I have discussed that conditions associated with poor inhibitory control such as ADHD and TBI can be ameliorated by brain plasticity exercises, psycho-active medications and electrical brain stimulations. I envisioned the possibility of using brain pacemakers to aid patients with impulse control disorders and other inhibitory control deficits.

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REZUMAT

Controlul inhibitor este dificil de studiat în experimente datorită naturii sale; un act de inhibiție care are succes nu se manifestă în comportament, deci nu poate fi observat şi măsurat în mod direct (Kana, Keller, Minshewy & Just, 2007). Unii teoreticieni de marcă au contestat însăşi existența inhibiției cognitive (MacLeod, 2007a). În acest caz, cercetarea prin scanarea creierului ar putea aduce lumină în ceea ce priveşte natura şi mecanismele inhibiției, cu posibilitatea de a avea un impact deosebit în înțelegerea şi ameliorarea unor condiții precum deficitul atențional cu hiperactivitate (ADHD), dependențele şi traumatismele lobilor frontali. O analiză critică a literaturii de specialitate arată că procesele de control inhibitor sunt implementate de o rețea de arii cerebrale incluzând ca şi componente cheie cortexul frontal inferior, aria motorie presuplimentară şi nuclei subtalamici. Se argumentează că procesele de control inhibitor se bazează pe procese cognitive de bază precum dialogul interior. Este propus un mecanism inhibitor comun pentru acte motorii, de limbaj şi gândire. Sunt sugerate câteva aplicații practice ale cercetării în domeniul controlului inhibitor precum exerciții de plasticitate mentală şi stimularea electrică a creierului.