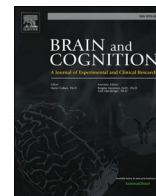




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A review on the electroencephalography markers of Stroop executive control processes

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ABSTRACT

The present article on executive control addresses the issue of the locus of the Stroop effect by examining neurophysiological components marking conflict monitoring, interference suppression, and conflict resolution. Our goal was to provide an overview of a series of determining neurophysiological findings including neural source reconstruction data on distinct executive control processes and sub-processes involved in the Stroop task. Consistently, a fronto-central N2 component is found to reflect *conflict monitoring* processes, with its main neural generator being the anterior cingulate cortex (ACC). Then, for cognitive control tasks that involve a linguistic component like the Stroop task, the N2 is followed by a centro-posterior N400 and subsequently a late sustained potential (LSP). The N400 is mainly generated by the ACC and the prefrontal cortex (PFC) and is thought to reflect *interference suppression*, whereas the LSP plausibly reflects *conflict resolution* processes. The present overview shows that ERP constitute a reliable methodological tool for tracing with precision the time course of different executive processes and sub-processes involved in experimental tasks involving a cognitive conflict. Future research should shed light on the fine-grained mechanisms of control respectively involved in linguistic and non-linguistic tasks.

1. Introduction

Executive control (EC), also called executive function or cognitive control, is constituted of a set of relatively heterogeneous cognitive processes that are involved in many high level functions of human cognition. EC is defined as the ability to flexibly adjust thoughts, actions and the processing of information to the challenges of a task at hand (Braver, 2012; Diamond, 2013; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). For example, this function allows human beings to flexibly adapt to task demands during goal-directed behavior. EC is thought to be a complex cognitive function composed of relatively separable processes, such as *inhibition*, *shifting* and *updating* (Miyake & Friedman, 2012) and their respective sub-processes, which are recruited to varying degrees in several tasks in order to provide the control required. EC is a core capacity of human cognition notably due to its domain-general nature, i.e. it is involved in numerous cognitive, affective/emotional and motoric processes. For instance, the relevance of executive control has been demonstrated for language processing (Fedorenko, 2014; Hagoort, 2016, 2017; Lambon Ralph, Jefferies, Paterson, & Rogers, 2016), and in particular, for bilingual language use

(Green & Abutalebi, 2013; see also the notion of *bilingualism advantage* in tasks involving executive functions), for motor and oculomotor coordination (Aron, 2007; Munoz & Everling, 2004), and for emotion processing and regulation (Ochsner & Gross, 2005), among others. Moreover, the executive control capacity and its neural bases are of considerable plasticity. On the one hand, over the lifespan, the frontal cortex – among other regions that are part of the neurocognitive executive control network – undergoes considerable developmental change from early childhood until young adulthood as well as with age-related alterations in neural processing. These neural changes are related to important functional variations not only in the capacity of executive control itself, but, due to the close interaction with various cognitive domains, such as language, motricity, or emotion, also in the capacity of domain-specific processing (Diamond, 2013; Liu, Yao, Wang, & Zhou, 2014; Zelazo, Craik, & Booth, 2004). On the other hand, it has been shown that not only developmental changes shape EC capacity, but also activities that engage EC can strengthen it in the long run. As an example, a rapidly growing body of research has provided evidence that challenging neurocognitive activities, such as bilingualism, musical practice or sportive activity that requires a high degree of coordination,

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can in the long run lead to an activity-dependent strengthening of EC (Aparicio, Heidlmayr, & Isel, 2017; Diamond, 2011; Dye, Green, & Bavelier, 2009; Green & Abutalebi, 2013; Heidlmayr, Hemforth, Moutier, & Isel, 2015). In contrast, individual differences in EC capacity cannot be fully explained by activity-dependent variation, but they are also largely determined by genetic factors (Anokhin, Heath, & Myers, 2004; Friedman et al., 2008).

Over the past decades, in cognitive neuroscience a rapidly growing literature has improved our understanding of the neurodynamics of executive control processes. The Stroop task (Stroop, 1935) is one of the paradigms that allowed gaining most valuable insight. However, a clear-cut picture of the neurophysiological signatures associated with the different sub-processes constituting the core of executive functioning has still not emerged in this field, certainly in part due to methodological issues, as it is sometime difficult to compare results of studies using different paradigms, tasks and populations, but also different typological distances between the first and second languages, in case bilingualism was under investigation. Given the importance of executive functions in various cognitive domains (e.g. language, emotion, motricity), the aim of the present review is to provide a state-of-the-art overview of the neurophysiological studies that have examined the electroencephalographical (EEG) signatures associated with the most discussed domain-general control processes – i.e., *conflict monitoring*, *interference suppression*, and *conflict resolution* – and their respective neural generators in the Stroop task. Here, we mainly concentrate on the Stroop effect, i.e., one of the most used tasks in cognitive sciences for approaching the issue of executive functioning in human beings. The question concerning the locus of the Stroop effect will be discussed by taking into consideration the neurodynamics as well as the neural bases of the different control processes thought to be involved for performing this experimental task. Our ultimate goal is to propose a precise description of the time course of these different executive processes. This description will be illustrated by a schematic presentation displaying for each process its electrophysiological signature and their possible neural generators.

In the Color Word Stroop task (Stroop, 1935), decision making is based on task-relevant information in the face of distracting information. Indeed, “two conflicting mental representations are active, each associated with a different response, and attention must be paid to only relevant cues” (Bialystok, 2006, p. 1342). Specifically, an ink color must be identified while ignoring the written word itself. Since word reading is more automatic than color naming, executive control is required to override the tendency to respond on the basis of the word rather than the ink color. The need of such control is reflected in slower responses when the word name is competing with the ink color (i.e. incongruent condition like the word green written in red ink) than when it is not (i.e. congruent condition like the word green written in green ink; see Heidlmayr et al., 2014).

EEG recordings of event-related brain potentials (ERPs) allow us to follow with a high temporal resolution, i.e. millisecond by millisecond, the electrical responses of the brain to time-locked events (Coles & Rugg, 1995). ERP data completed by a localization of their neural sources are particularly valuable for learning about the fine-grained spatio-temporal pattern of neural activity in different cortical areas sustaining the executive control network. Moreover, an improved neuro-functional understanding can be obtained when these findings are related to data on a spatially much more fine-grained scale obtained in the neuroimaging literature. For this reason, we refer to this literature in different parts of the current review. To the best of our knowledge, the present review is the first attempt to present a state-of-the-art overview of electroencephalographical studies examining a set of specific executive control processes including but extending beyond inhibition, their ERP markers and neural generators. In the first section, theoretical accounts and neurocognitive models of executive control are presented. Then, some of the most discussed executive control processes that play a role in managing conflict in linguistic (but also, marginally in non-linguistic) tasks in particular in the Stroop task, i.e. *conflict monitoring*, *interference*

suppression, and *conflict resolution* will be characterized.

2. Executive control: Theoretical accounts and neurocognitive models

The emergence and crystallization of research on cognitive control historically coincided with the development of connectionism, with both domains undergoing considerable progress since the 1980s (Botvinick & Cohen, 2014). However, the initial theoretical foundations of the two fields are substantially different, in that initial research on cognitive control was grounded in principles of symbolic representation, sequential hierarchical processing, and modularity, and strongly focused on the ‘top-down’ processes of control. Subsequently, computational modelling had a strong influence on theories of cognitive control. Modelling in this phase took into consideration the role of learning and environmental constraints, and consequently was interested in ‘bottom-up’ processes and in the way how adaptation takes place in the cognitive control system. Current research is, among others, interested in the reasons why the structure of cognitive control, involving its architecture, representations and operations, and its underlying neural substrate are shaped the way they are. An important yet unresolved question is how the structure of cognitive control reflects the structure of the task environment, which is of core interest given the role of cognitive control in the interaction with naturalistic environments (for a review, see Botvinick & Cohen, 2014). Currently, most psychological and neurobiological theories do not conceptualize cognitive control either as an unitary instance or as a system fractioned into different sub-processes, but mostly it is attempted to integrate elements of both approaches, unity as well as diversity of executive functions. In this vein, one of the most influential models has been put forward by Miyake et al. (2000). This model postulates a distinction of three main executive functions, namely inhibition of dominant responses (“inhibition”), shifting of mental sets (“shifting”) and monitoring and updating of information in working memory (“updating”; see also the “unity/diversity framework” by Miyake & Friedman, 2012). Miyake and Friedman (2012) claim that according to the level executive functions are looked at, one may find shared characteristics amongst the three of the main executive functions (i.e. *inhibition*, *shifting* and *updating*) or one may be able to subdivide each of the functions into more specific control processes. The different executive functions may be involved to varying degrees according to the experimental task at hand, in order to enable for optimal coordination of control (see also, Diamond, 2013; Miyake & Friedman, 2012). Experimentally, Stroop task is considered to tap *interference suppression* (Color words are presented in different ink colors; in case of incongruency between color word and ink color, the automatic reading of the color word produces interference on the controlled task of responding to the ink color; Stroop, 1935; see also, Fig. 1; other tasks like the Simon task, Simon & Ruddell, 1967) or the Eriksen Flanker task (Eriksen & Eriksen, 1974) also involve interference suppression). Here, we will particularly focus on the Stroop task. *Interference suppression* and *response inhibition* are generally considered to be reactive control processes, i.e. control processes that are active in reaction to an exogenous stimulus or signal.

3. Executive functions: Subprocesses

In the following, some of the most discussed subprocesses of domain-general executive control that play a role to manage conflict in linguistic or non-linguistic tasks will be discussed: *conflict monitoring*, *interference suppression*, and *conflict resolution*. Following the description of each of these control processes, a review for the ERP markers that are frequently associated with the respective process is given, i.e. the N2 component for *conflict monitoring* and *overcoming of inhibition*, the N400 component and the late sustained potential for *interference suppression* and *conflict resolution* respectively.

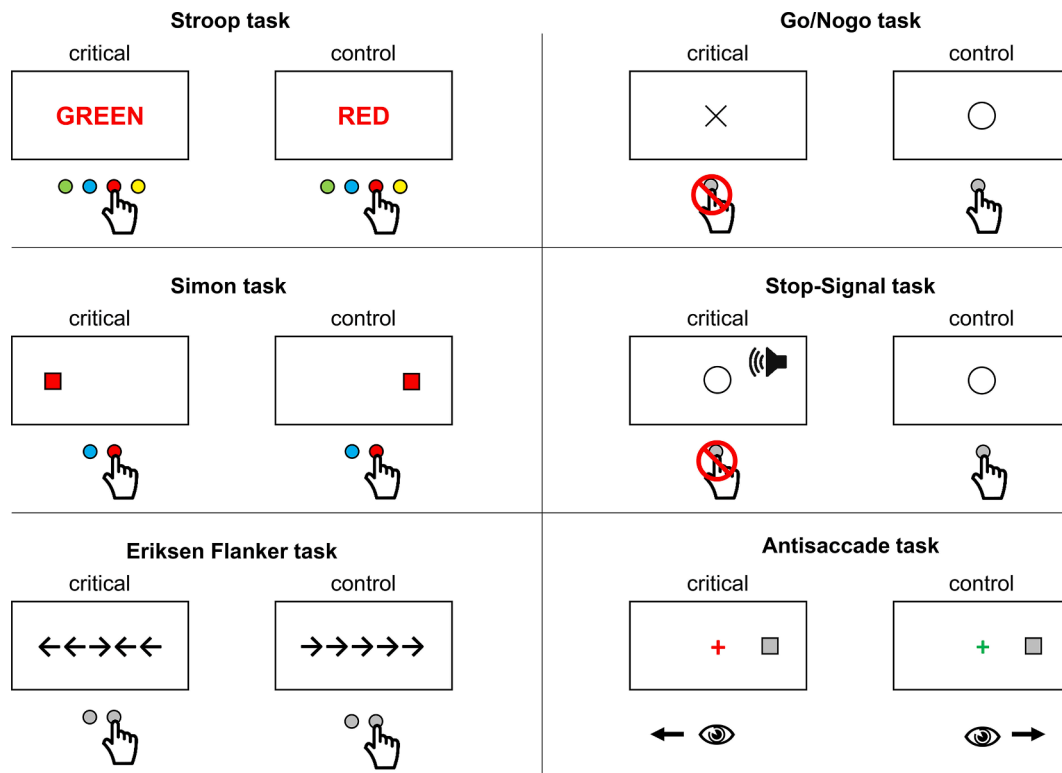


Fig. 1. The six most common tasks to study conflict monitoring, interference suppression and response inhibition. For each task, the most commonly used configuration and mechanistic interpretation of the underlying control processes is presented, but different variants of the tasks do exist in the literature. Stroop task (Stroop, 1935). The task is to respond to the ink color of the stimulus. In the critical, i.e. incongruent, condition the automatic process of reading the incongruent color word interferes with the more controlled process of responding to the ink color, which is not the case in the control, i.e. congruent, condition where the color word and ink color refer to the same color. Simon task (Simon & Ruddell, 1967). The task is to respond to the direction (left, right) coded by the color of the stimulus. In the critical, i.e. incongruent, condition the automatic process of responding to the physical position of the stimulus interferes with the more controlled process of responding to the direction as coded by the stimulus color, which is not the case in the control, i.e. congruent, condition where the physical position of the stimulus and the direction coded by the stimulus color are identical. Eriksen Flanker task (Eriksen & Eriksen, 1974). The task is to respond to the direction (left, right) indicated by the middle arrow that is positioned within a string of arrows. In the critical, i.e. incongruent, condition responding to the direction indicated by the middle arrow suffers from the inference from the incongruent direction indicated by the surrounding (flanking) arrows, which is not the case in the control, i.e. congruent, condition where the direction indicated by the flanking arrows is identical with the target arrow direction. Go/Nogo task. The task is to respond to a specific type of stimulus (e.g. circle) but to withhold the manual response when a different type of stimulus is presented (e.g. cross). In the critical, i.e. nogo, condition withholding the manual response requires the suppression of a prepotent response tendency, which is not the case in the usually much more frequent (e.g. 75% of trials) control, i.e. go, condition where the manual response can be executed. Stop-Signal task (Logan, 1994). The task is to respond to a specific type of stimulus (e.g. circle) but to stop the manual response when a specific signal is presented (e.g. beep). In the critical, i.e. stop, condition stopping the manual response requires the suppression of an already initiated response, which is not the case in the usually much more frequent (e.g. 75% of trials) control, i.e. go, condition where the manual response can be executed. Antisaccade task (Hallett, 1978). The task is to make an eye movement (saccade) towards or opposite the direction (left, right) of a target stimulus presented on the screen, depending on a preceding color cue. In the critical, i.e. antisaccade, condition the color cue (e.g. fixation cross in the middle of the screen) is red which indicates that a saccade in the direction opposite to the upcoming target needs to be executed, which requires the overcoming of a prepotent response tendency towards the target and a change of the motor program towards the opposite direction. This is not the case in the control, i.e. prosaccade, condition where the color cue is green, indicating that a saccade towards the target can be executed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. Conflict monitoring and overcoming of inhibition: The N2 component

In this section two control processes, i.e. *conflict monitoring* and in the N2 section also the switching-related *overcoming of inhibition* will be discussed. In electroencephalographical studies, the ERP marker that is most robustly associated with these control processes is the N2 component and a review over these studies will be presented subsequently.

3.1.1. Conflict monitoring

Conflict monitoring has been defined as the process of monitoring for the occurrence of conflict in information processing and is on the evaluative side of cognitive control. Conflict monitoring serves to translate the occurrence of conflict into compensatory adjustments in control, i.e. the conflict monitoring system evaluates the levels of conflict and communicates this information to systems responsible for control

implementation (Botvinick, Braver, Barch, Carter, & Cohen, 2001). However, conflict monitoring is in most cases one of several control processes involved for realizing a task. Most theoretical frameworks of cognitive control distinguish conflict monitoring from inhibitory control and their respective underlying sources and electroencephalographical markers. However, a strong relation between the two control processes as well as their neural underpinnings is usually assumed. The conflict monitoring theory of cognitive control proposed by Botvinick (2007) as well as by Carter and van Veen (2007) postulates a primordial role of the ACC in detecting conflicts while the dorsolateral prefrontal cortex is thought to modulate cognitive control over the suppression of task-irrelevant information. In the same vein, MacDonald, Cohen, Stenger, and Carter (2000; see also, Green & Abutalebi, 2013) suggest that a widely distributed neural network may be activated in cognitive control processes but that specific subprocesses of control are reflected by spatially and temporally distinguishable activations, i.e. the anterior

cingulate cortex (ACC) shows activation in conflict monitoring while the dorsolateral prefrontal cortex (DLPFC) is active in control implementation. Several fMRI studies lend support to the hypothesis that ACC plays a crucial role in (1) detecting conflict (i.e. conflict monitoring) and processing cognitive conflict as well as in monitoring action outcomes (Botvinick, 2007; Botvinick et al., 2001; Carter et al., 2000; Chen, Lei, Ding, Li, & Chen, 2013; Gruber, Rogowska, Holcomb, Soraci, & Yurgelun-Todd, 2002; Kerns et al., 2004; Leung, Skudlarski, Gatenby, Peterson, & Gore, 2000; Pardo, Pardo, Janer, & Raichle, 1990; Peterson et al., 2002; van Veen and Carter, 2005, 2002a; Yeung, 2013; for a review on the controversial findings in neuropsychological studies, see Yeung, 2013) and (2) attentional control in cognitive and emotional processes (Bush, Luu, & Posner, 2000; Ochsner, Hughes, Robertson, Cooper, & Gabrieli, 2009).

3.1.2. N2a

The N2 (or N200) component is a negative-going component peaking at around 200 ms after stimulus onset. According to task-specificity and topographical distribution at the surface of the scalp, a distinction of three different subcomponents of the N2 has been suggested (Folstein & Van Petten, 2008). These subcomponents vary in scalp distribution and are thought to reflect different cognitive processes: (1) a fronto-central component reflecting novelty or mismatch (i.e. mismatch negativity (MMN); tasks: e.g. oddball task), (2) another fronto-central component reflecting cognitive control (e.g. conflict monitoring, response inhibition, response conflict and error monitoring; tasks: Eriksen Flanker task, Stop-Signal task, Go/Nogo task), and (3) a posterior component reflecting some processes of visual attention (for a review, see Folstein & Van Petten, 2008).

In the present review, we will only focus on the control-related N2 component, and more specifically on the N2 to reflect *conflict monitoring*. The control-related N2 effect thought to reflect specifically *conflict monitoring* has previously been found in studies using a Stroop task (Boenke, Ohl, Nikolaev, Lachmann, & van Leeuwen, 2009), Simon task (Chen & Melara, 2009), Eriksen Flanker task (van Veen & Carter, 2002a), and the Go/Nogo task (Donkers & van Boxtel, 2004; Jonkman, 2006), with a large consensus of the ACC, as well as IFC and PFC, as the main neural generators of the N2; for a review, see Table 1. However, even within the control-related N2 effects functional distinctions can be found, e.g. despite a large similarity between the control-related N2 reflecting *conflict monitoring* and an error-related fronto-central negativity (ERN) - which is elicited by participants' errors and by negative feedback about task performance - the two components show a clearly distinct functional sensitivity and are distinguishable by principal component analyses (Nguyen, Moyle, & Fox, 2016) and can thus be considered as two distinct subcomponents (Nguyen et al., 2016). The main neural generator of the control-related fronto-central N2 is the medial frontal cortex, more specifically the anterior cingulate cortex (ACC; Folstein & Van Petten, 2008; van Veen & Carter, 2002a). Importantly, the ACC is the main neural generator in both, the N2 reflecting *conflict monitoring* as well as the ERN, though future research may possibly identify specific subregions of the ACC to be involved in each of these processes (Folstein & Van Petten, 2008). In contrast, the main neural generators of the auditory MMN include fronto-temporal regions, i.e. among others superior temporal regions including the primary auditory cortex; interestingly, in MMN paradigms involving a linguistic component, left hemispheric regions are more strongly involved (for reviews, see Garrido, Kilner, Stephan, & Friston, 2009; Pazo-Alvarez, Cadaveira, & Amenedo, 2003).

To sum up, in electroencephalographical studies, the N2 component is the main ERP marker associated with *conflict monitoring* and with some complex processes involving inhibition, such as the switching-related *overcoming of previously applied inhibition*, which is required in tasks such as negative priming or in tasks that involve language switching or non-linguistic switching of tasks or task rules. In Table 1, an overview of studies documenting an N2 effect in cognitive control tasks

is proposed.

3.2. Interference suppression: The N400 component and the late sustained potential (LSP)

In this section, we will focus on the control process called *interference suppression*. The ERP marker usually associated with this process is the N400 component, and in the Stroop literature sometimes also the late sustained potential (LSP). Now, a review of the literature on the functional role of these components will be presented.

3.2.1. Interference suppression

The resistance to distractor interference is the ability to prevent interferences from information in the external environment that is irrelevant to the task at hand and which could disrupt ongoing processes (Friedman & Miyake, 2004). The capacity to suppress distractor interference is usually assessed using tasks such as the Stroop task (Stroop, 1935; see also, Fig. 1), the Simon task (Simon & Ruddell, 1967) or the Eriksen Flanker task (Eriksen & Eriksen, 1974). For example, in a Stroop task, color words printed in an incongruent ink colors are presented to the participant (e.g. GREEN), who usually has to manually or verbally indicate the ink color of the stimulus. In this condition, a conflict arises between the automatic language process of word reading, which disturbs another process, of a more controlled nature, i.e. ink color naming. Hence, the interfering automatic process needs to be inhibited for correct performance in the task. Alternative accounts claim that Stroop is not necessarily to be considered as a task on interference suppression, but that it is rather a task involving prepotent response inhibition, i.e. the capacity to deliberately inhibit dominant, automatic, or prepotent responses when necessary (Miyake et al., 2000; for a review, see Friedman & Miyake, 2004). Concerning neuroanatomical localization of executive processes, some fMRI studies have also demonstrated the involvement of dorsolateral prefrontal cortex (DLPFC) activation in tasks evoking cognitive conflict, such as the Stroop task (Chen et al., 2013; MacDonald et al., 2000; Milham, Banich, Claus, & Cohen, 2003; Peterson et al., 2002; van Veen & Carter, 2005). Moreover, ERP source localization analyses have identified the ACC (Liotti, Woldorff, Perez, & Mayberg, 2000; Markela-Lerenc et al., 2004) and/or the PFC (Bruchmann, Herper, Konrad, Pantev, & Huster, 2010; Qiu, Luo, Wang, Zhang, & Zhang, 2006) as potential neural generators involved in interference suppression. In ERP studies, interference suppression is frequently associated with an effect on the N400 component (cf. Section 3.2.2) and a late sustained potential (cf. Section 3.2.3).

3.2.2. N400a

The N400 (or N4, N450 or N_{inc}) component is a negative-going component at posterior sites peaking at around 400 ms after stimulus onset. In psycholinguistics, this ERP component has first been shown by Kutas and Hillyard (1980; see also Federmeier & Laszlo, 2009; Kutas and Federmeier, 2011, 2000) as reflecting difficulties of lexical semantic integration (e.g., *He spread the warm bread with *socks.*) during the visual integration of words in English sentences. (for reviews, see Kutas & Federmeier, 2011; Lau, Phillips, & Poeppel, 2008).

However, beyond the sensitivity of the N400 to semantic anomalies, an N400 effect has also been observed in cognitive control tasks involving a linguistic (semantic) component, and it has been interpreted to reflect of inhibitory processes and interference suppression. For example, in language switching tasks, an N400 effect has been suggested to reflect inhibitory processes. More precisely, in semantic comprehension tasks, e.g. a bilingual semantic categorization task (Alvarez, Holcomb, & Grainger, 2003; Chauncey, Grainger, & Holcomb, 2008) or a task involving the evaluation of the semantic expectedness of sentence-final words (Proverbio, Leoni, & Zani, 2004), a larger N400 was found for language switching compared to repetition conditions, either in one switching direction (L1 to L2; Alvarez et al., 2003) or in both directions (L1 to L2 and L2 to L1; Chauncey et al., 2008; Proverbio et al., 2004).

Table 1

The functional significance attributed to the N2 effect in tasks involving cognitive control. Time window indicates the time window in which an N2 effect was observed. Included were ERP studies that found a conflict-monitoring related N2 for which source localization analyses were conducted and/or which made use of a paradigm that allows to functionally specify the function of the N2. Studies are presented in alphabetical order of author names. ACC, anterior cingulate cortex; IFC, Inferior-frontal cortex; ITC, Inferior-temporal cortex; MCC, midcingulate cortex.

N2 effect in tasks involving cognitive control					
Reference	Paradigm	Time window	Surface topography	Functional attribution	Neural generator
Boenke et al. (2009)	Stroop	268–360	Fronto-central	Cognitive control processes involved in conflict detection and monitoring	Medial frontal cortex, including ACC
Chen et al. (2008)	Partially incongruent categorization task	240–300	Fronto-central	Conflict detection	ACC
Chen and Melara (2009)	Simon	360–400	Central	Working memory; disruption in working memory due to Stimulus-Response (S-R) conflict; conflict in information held in working memory	–
Donkers and van Boxtel (2004)	Go/Nogo	200–350	Fronto-central	Conflict monitoring	–
Enriquez-Geppert, Konrad, Pantev, and Huster (2010)	Combined Go/Nogo - Stop-Signal task	20 ms around peak in window 200–350;	Fronto-central	Conflict monitoring	IFC, MCC
Frings and Groh-Bordin (2007)	Negative priming	170–270 (P2/N2 complex)	Frontal, fronto-polar	Selection of previously inhibited stimulus against incompatible distractors	–
Gajewski, Stoerig, and Falkenstein (2008)	Response-cueing task	200–320	Fronto-central	Response selection	–
Groom and Cragg (2015)	Flanker	250–350	Fronto-central	Response conflict processing	–
Heidlmayr et al. (2016)	Antisaccade task	160–200	Frontal	Conflict monitoring	ACC, PFC
Heidlmayr et al. (2015)	Negative priming	200–300	Fronto-central	Overcoming of inhibition	ACC, IFG
Huster et al. (2011)	Stop-Signal	150–250	Fronto-central	Conflict monitoring	MCC
Iannaccone et al. (2015)	Flanker	223–323	Fronto-central	Conflict monitoring	Pre-SMA, bilateral IFC, right ITC
Jackson, Jackson, and Roberts (1999)	Go/Nogo	~150–200	Frontal	Associated with the withholding of a manual response	IFC
Jackson, Swainson, Cunningham, and Jackson (2001)	Language switching	Peak at 320 ms after stimulus onset	Fronto-central	Inhibitory processes (response suppression similar to inhibition in a Go/Nogo task) during language switching	–
Jonkman (2006)	Go/Nogo	240–260	Fronto-central	Conflict monitoring/detection	–
Kopp, Rist, and Mattler (1996)	Flanker	250–350	Fronto-central	Avoidance of inappropriate action and selection of appropriate action	–
Koussaie and Phillips (2012)	Stroop	220–360	Fronto-central	Conflict monitoring	–
Koussaie and Phillips (2012)	Flanker	260–420	Central	Conflict monitoring	–
Krämer, Knight, and Münte (2011)	Flanker – Stop/Change-Signal	220–280	Frontal	Inhibition (N2 effect absent in change trials)	–
Lavric, Pizzagalli, and Forstmeier (2004)	Go/Nogo	235–256	Fronto-central	Inhibition	vPFC, dlPFC; vPFC-dlPFC connectivity, ACC-PFC connectivity
Maguire et al. (2009)	Go/Nogo involving conceptual-semantic component	150–300	Frontal	Inhibitory processing	–
Melara, Wang, Vu, and Proctor (2008)	Simon	175–325	Fronto-central	Attentional disruption caused by S-R conflict in working memory	–
Moreno, Wodniecka, Tays, Alain, and Bialystok (2014)	Go/Nogo	270–320	Fronto-central	Conflict detection or inhibition	–
Mueller, Swainson, and Jackson (2009)	Antisaccade task	180–244	Parietal	Current inhibition	–
Naylor et al. (2012)	Between-within language Stroop	200–350	Fronto-central	A stage in conflict processing/inhibitory control parallel to N400 that facilitate the resolution of conflict at the LSP (late sustained potential, cf. Section 3.2.3)	–
Nguyen et al. (2016)	Go/Nogo	200–350	Fronto-central	Error monitoring	–
Nieuwenhuis, Yeung, Van Den Wildenberg, and Ridderinkhof (2003)	Go/Nogo	250–350	Fronto-central	(Response) conflict monitoring	ACC
Siemann, Herrmann, and Galashan (2016)	Flanker	240–260, 280–300 (relative positivity)	Central	(Response) conflict monitoring	ACC
van Veen and Carter (2002b)	Flanker	340–380	Fronto-central	Conflict detection	ACC
Yeung and Nieuwenhuis (2009)	Flanker	Negative peak ~ 300 ms after stimulus onset	Fronto-central	Conflict monitoring	Medial frontal cortex, including ACC

Furthermore, an N400 effect was also observed in several EEG studies examining temporal dynamics underlying the interference arising in the Stroop task (Stroop, 1935) and has been argued to reflect inhibitory processes or interference suppression. This effect reflects a larger negativity in the incongruent condition in comparison to the congruent condition or a neutral condition (a non-color word or a string of characters written in one of the ink colors; Appelbaum, Meyerhoff, & Woldorff, 2009; Badzakova-Trajkov, Barnett, Waldie, & Kirk, 2009; Bruchmann et al., 2010; Coderre, Conklin, & van Heuven, 2011; Hanslmayr et al., 2008; Liotti et al., 2000; Naylor, Stanley, & Wicha, 2012; Qiu et al., 2006; West, 2003; for a review, see Table 2). However, it remains unclear whether this component does reflect partially shared cognitive processes with the classic N400 first identified by Kutas and Hillyard (1980; Siltan et al., 2010). The so-called N400 Stroop effect usually mirrors the behavioral Stroop effect, i.e. longer response times in the incongruent compared to the congruent condition, response times to neutral stimuli lying in between. A larger negative deflection in the incongruent compared to the congruent and neutral conditions in the time window 400–500 ms post stimulus onset (N400 effect) is interpreted to sign the higher cognitive cost in responding to stimuli in the incongruent condition – usually causing a conflict between the two sources of information, the color word and the ink color. Some studies investigating the localization of the main neural generators of the N400 Stroop interference effect have shown that the difference of N400 amplitude between the incongruent and congruent conditions mainly originates in the ACC (Badzakova-Trajkov et al., 2009; Bruchmann et al.,

2010; Hanslmayr et al., 2008; Liotti et al., 2000; Markela-Lerenc et al., 2004) and the prefrontal cortex (PFC; Badzakova-Trajkov et al., 2009; Bruchmann et al., 2010; Hanslmayr et al., 2008; Liotti et al., 2000; Markela-Lerenc et al., 2004; Qiu et al., 2006). In contrast, the typical semantic N400 is mainly generated by superior and middle temporal, anterior temporal, medial temporal and dorsolateral frontal regions (for a review, see Kutas & Federmeier, 2011). Table 2 displays a review of the functional interpretation of the N400 effect in the Stroop task and related tasks requiring cognitive control. The largely differing but partially shared (e.g. frontal) localization of the neural generators of the semantic and executive N400s suggests that the underlying processes of these ERP components may be considerably different but also share some aspects of control.

3.2.3. Late sustained potential (LSP)

In several electroencephalographical studies using a Stroop task – i.e. a cognitive control task considered as involving a linguistic (semantic) component –, a further ERP component was found in the time window of about 550–800 ms, that is a sustained fronto-central negative-going potential, i.e. a late sustained potential (LSP; Hanslmayr et al., 2008; Heidlmayr et al., 2015; Naylor et al., 2012; West, 2003; note that this component has varying names with the different authors, e.g. late negativity (LN; Hanslmayr et al., 2008), sustained negativity (SN; Naylor et al., 2012), conflict sustained potential (SP; West, 2003), or late positive complex (LPC; Donohue, Appelbaum, McKay, & Woldorff, 2016)). It is to be noted that some studies also found an additional

Table 2

The functional significance attributed to the N400 effect in tasks involving cognitive control. Time window indicates the time window in which an N400 effect was observed. Included were ERP studies that found a control-related N400 for which source localization analyses were conducted and/or which made use of a paradigm that allows to functionally specify the function of the N400. Studies are presented in alphabetical order of author names. ACC, anterior cingulate cortex; IFC, inferior frontal cortex; IPS, intraparietal sulcus; PFC, prefrontal cortex.

N400 effect in tasks involving cognitive control					
Reference	Paradigm	Time window	Surface topography	Functional attribution	Neural generator
Appelbaum et al. (2009)	Stroop	450–500	Centro-parietal	Central executive control processes (detection and/or resolution of response conflict); semantic incongruency	ACC (posterior part), left parietal regions
Badzakova-Trajkov et al. (2009)	Stroop	370–480	Centro-parietal	Attentional allocation/conflict identification and resolution	ACC
Brass, Ullsperger, Knoesche, Von Cramon, and Phillips (2005)	Task-switching	440–520	Central	Task-set updating, incongruency between task meanings conveyed by current vs preceding cue	IFC, IPS
Bruchmann et al. (2010)	Stroop	396–576	Centro-parietal	Conflict monitoring and processing	ACC, right PFC
Coderre et al. (2011)	Stroop	400–500	Centro-parietal	Conflict detection	ACC
Donohue et al. (2016)	Stroop, Flanker	323–621 (Stroop) 303–479 (Flanker)	Fronto-central	Response conflict processing	–
Feroz, Leicht, Steinmann, Andreou, and Mulert (2017)	Emotional Stroop	326–426	Fronto-central	Task/stimulus (task-irrelevant emotional meaning) conflict processing	Dorsal and rostro-ventral ACC
Frings and Groh-Bordin (2007)	Negative priming	330–420	Left-lateralized	Enhanced semantic processing	–
Hanslmayr et al. (2008)	Stroop	400–500	Fronto-central	Interference detection and elicitation of central executive processes (rather than semantic incongruency)	ACC
Heidlmayr et al. (2015)	Stroop	400–500	Centro-parietal	Interference suppression	ACC, PFC
Larson, Kaufman, and Perlstein (2009)	Stroop	Voltage at the most negative peak between 350 and 500 ms (420–440)	Fronto-medial	Conflict monitoring processes	–
Liotti et al. (2000)	Stroop	350–500	Medial-dorsal	Suppression or overriding the processing of the incongruent word meaning	Dorsal ACC
Markela-Lerenc et al. (2004)	Stroop	350–450	Left fronto-central	Conflict monitoring, control implementation	Left inferior PFC, ACC
Naylor et al. (2012)	Between-within language Stroop	350–550	Medial-central	A stage in conflict processing/inhibitory control parallel to N2	–
Qiu et al. (2006)	Stroop	350–550	Fronto-central	Conflict processing, response selection	PFC
West (2003)	Stroop	450–500	Parietal	Conflict detection	ACC, left frontal cortex
West, Jakubek, Wymbs, Perry, and Moore (2005)	Stroop, counting, digit-location tasks	400–450	Negative deflection: central	Conflict processing	–

centro-parietal positive deflection in the incongruent compared in the congruent condition (Appelbaum et al., 2009; Coderre et al., 2011; Hanslmayr et al., 2008; Liotti et al., 2000; West, 2003). The sustained centro-parietal positivity and/or frontal negativity was discussed to reflect either engagement of executive processes (Hanslmayr et al., 2008), conflict resolution processes (Coderre et al., 2011; Heidlmayr et al., 2015; Naylor et al., 2012; West, 2004), semantic reactivation of the meaning of words following conflict resolution (Appelbaum et al., 2009; Liotti et al., 2000) or response selection (West, 2003, 2004). Source localization has rarely been done for the late sustained negative-going potential but there is some evidence of its main neural generators in the middle or inferior frontal gyrus and the extrastriate cortex (West, 2003). West (2003) suggests that the left middle frontal gyrus and extrastriate cortices are responsive to the presence of conflict, while the right middle frontal gyrus may be sensitive to conflict arising from the less dominant dimension (i.e. color) and may support some aspect of conflict resolution. In Table 3, a brief overview of studies documenting a late sustained potential in tasks involving cognitive control is given.

4. A unified neurocognitive model of the executive control time course

The aim of the present article is to provide an overview of the

electroencephalographical studies that targeted the examination of ERP signatures associated with the most discussed domain-general control processes (i.e., *conflict monitoring*, *interference suppression*, and the switching-related *overcoming of inhibition*) and their respective neural generators. Fig. 2 displays a description of the time course of these different executive processes and their ERP signatures and neural generators. The selection of these specific control processes is justified by the fact that these processes were considered most relevant in the literature, and therefore the most discussed. We agree that further control processes beyond those reported presumably also play an important role and should obtain more focus in future research.

Moreover, it is important to note that there is no single explanation of the control mechanisms in cognition, in particular in bilingual mind, which is characterized by joint activation of the two languages. In a recent review on bilingual adaptation, Bialystok (2017) claimed that attention system should also be considered to better understand the underlying mechanisms enabling bilingual mind to select the appropriate language and avoid interference from an unwanted language. Interestingly, Sholes et al. by investigating neurochemical basis of attentional control showed that acute serotonin and dopamine depletion are able to improve attentional control in healthy individuals as behaviorally attested by a significant Stroop interference decrease. Beyond the neurochemical issue, this study clearly showed that

Table 3

The functional interpretation of the LSP (late sustained potential) effect in tasks involving cognitive control. In the column presenting surface topography, it is indicated at which sites the incongruent condition shows a positive or a negative deflection relative to the congruent condition. Time window indicates the time window in which an LSP effect was observed. Included were ERP studies that found a control-related LSP for which source localization analyses were conducted and/or which made use of a paradigm that allows to functionally specify the function of the LSP. Studies are presented in alphabetical order of author names. ACC, anterior cingulate cortex; PFC, prefrontal cortex.

LSP effect in tasks involving cognitive control					
Reference	Paradigm	Time window	Surface topography	Functional attribution	Neural generator
Appelbaum et al. (2009)	Stroop	850–900	Positive deflection: parieto-occipital	Processing of semantic meaning of words	–
Brass et al. (2005)	Task-switching	600–800	Positive deflection: Centro-parietal (after 680 also frontal)	Integrating the new contextual information to activate the relevant task set in case of incongruency between task meanings conveyed by current vs preceding cue	–
Chen and Melara (2009)	Simon	480–520	Positive deflection: parietal	Maintenance of current stimulus–response relations in working memory rather than conflict resolution	–
Coderre et al. (2011)	Stroop	600–900	Positive deflection: Centro-parietal	Conflict resolution or post-resolution processes	–
Donohue et al. (2016)	Stroop, Flanker	630–1000 (Stroop) 566–1000 (Flanker)	Positive deflection: Centro-parietal	Allocation of attention, conflict resolution	–
Feroz et al. (2017)	Emotional Stroop	626–726	Negative deflection: fronto-central	Response conflict processing; also: emotional arousal involved in late attentional processes that engage higher-order cognitive control to overcome interference	Dorsal and rostro-ventral ACC
Hanslmayr et al. (2008)	Stroop, Negative priming	600–800	Negative deflection: fronto-central; Positive deflection: parieto-occipital	Engagement of central executive processes	ACC
Heidlmayr et al. (2015)	Stroop	540–700	Negative deflection: fronto-central	Conflict resolution	PFC
Larson et al. (2009)	Stroop	650–850	Positive deflection: parietal	Conflict processing (conflict resolution processes)	–
Liotti et al. (2000)	Stroop	500–800	Negative deflection: anterior frontal; Positive deflection: Left superior temporo-parietal scalp	Reactivation of the meaning/Retrieval of semantic meaning of the incongruent word	Left posterior generator (s) (left temporo-parietal cortex)
Markela-Lerenc et al. (2004)	Stroop	600–1000	Positive deflection: parietal	–	–
Naylor et al. (2012)	Between-within language Stroop	550–700	Negative deflection: fronto-central	Conflict resolution (possibly facilitated by efficient N2 inhibitory control processes)	–
West (2003)	Stroop	750–850	Negative deflection: lateral-frontal; Positive deflection: centro-parietal	Conflict processing	Middle or inferior frontal gyrus, left extrastriate region
West et al. (2005)	Stroop, counting, digit-location tasks	600–700	Negative deflection: lateral-frontal; Positive deflection: parietal	Response selection rather than conflict resolution	–

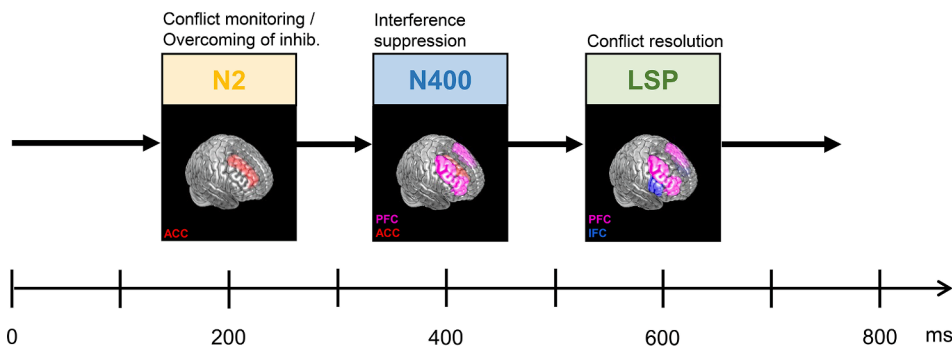


Fig. 2. A unified neurocognitive model of the executive control time course in the Stroop task. A fronto-central N2 component is consistently found to reflect conflict monitoring processes or overcoming of inhibition, with its main neural generator being the anterior cingulate cortex (ACC). For cognitive control tasks that involve a linguistic component, such as the Stroop task, the N2 is followed by a centro-posterior N400 and subsequently a late sustained potential (LSP). The N400 is mainly generated by the ACC and the prefrontal cortex (PFC) and is thought to reflect interference suppression, whereas the LSP plausibly reflects conflict resolution.

variations of attentional control influence the performance of a cognitive test involving interference control. More recently, Laeng, Ørbo, Holmlund, and Miozzo (2011), using pupillometry (i.e., the measurement of changes in pupillary diameter) also demonstrated a link between visual attention and control of interferences in a Stroop task. Laeng et al. reported that pupil diameters increased for color distractors that differed from color responses, while they reduced for color distractors that were identical to color responses. The replication of the Stroop effect with recording of pupillary diameter, i.e. a marker of attention-grabbing stimuli (for a review, see Loewenfeld, 1993) reinforces the idea that attentional resources (here, visual attention) may play a role in interferences control.

To sum up, the fronto-central N2 component is robustly found in tasks requiring conflict control, e.g. the Stroop, Simon or the Eriksen Flanker task, and is interpreted to reflect conflict monitoring processes as well as switching-related overcoming of previously applied inhibition, as in negative priming or in tasks that involve language switching. The neural generator of the N2 is thought to be the anterior cingulate cortex (ACC), the inferior frontal cortex (IFC) and the prefrontal cortex (PFC). Next, the posterior N400 has also been found in tasks requiring conflict control and has been suggested to reflect different processes, involving conflict monitoring and control implementation, i.e. interference suppression. However, intriguingly, the N400 effect has mainly been found in cognitive control tasks involving a linguistic (lexical) component, e.g. the Stroop task (see detailed discussion below), whereas for non-linguistic interference control tasks, e.g. the Simon or Eriksen Flanker task, mostly P3 effects have been reported. As the main neural generators of the N400 have been identified the ACC and the prefrontal cortex (PFC). Moreover, in several electroencephalographical studies using a Stroop task – i.e. a cognitive control task involving a linguistic (lexical) component –, a further ERP component was found in the time window of about 550 – 800 ms, that is a sustained fronto-central negative-going potential, i.e. a late sustained potential (LSP). However, the functional attribution of this component is less univocal and it has been thought to reflect the engagement of conflict resolution processes, semantic reactivation of the meaning of words following conflict resolution, or response selection. As neural generators for this component have been identified the middle or inferior frontal gyrus and the extrastriate cortex, which have been argued to respond to the presence of conflict and to underlie some aspect of conflict resolution.

From the present review we can draw inference about the following neurocognitive time courses of cognitive control as reflected in ERP patterns (see Fig. 2). Based on the present review, a fronto-central N2 component is consistently found to reflect *conflict monitoring* processes or *overcoming of inhibition*, with its main neural generator being the anterior cingulate cortex (ACC). Interestingly, three distinct neurocognitive patterns emerge for the subsequent ERP components. On the one hand, for cognitive control tasks that involve a lexical component, the N2 is followed by a centro-posterior N400 and subsequently a late sustained potential (LSP). The N400 is mainly generated by the ACC and the prefrontal cortex (PFC) and is thought to reflect *interference*

suppression, whereas the LSP is probably generated by the middle or inferior frontal gyrus and the extrastriate cortex and plausibly reflects *conflict resolution*. Moreover, in some studies and paradigms specific ERP components and their functional attribution cannot be unambiguously disentangled (e.g., Donohue et al., 2016). This is partially due to a certain heterogeneity in the literature concerning the identification of ERP components and the role that is attributed to them. With the present review article, we hope to have provided a contribution to a clearer characterization of ERP components and the cognitive functions that they have been suggested to reflect.

To conclude, the present review on electroencephalographical markers of executive control processes is intended to provide a comprehensive overview of our current knowledge on ERP markers of control and their neural generators in Stroop task (i.e. *conflict monitoring*, *interference suppression*, *conflict resolution*). Future research should shed light on the fine-grained mechanisms of control respectively involved in linguistic and non-linguistic tasks. But they should also look in to oscillatory activity and their functional significance with respect to cognitive control processes. Recently there has been much progress in our understanding of the functional significance of specific frequency bands with respect to cognitive and motor control, with theta (4–7 Hz) emerging as a marker of cognitive control (e.g., Cavanagh & Frank, 2014; Hanslmayr et al., 2008; Mückschel, Stock, Dippel, Chmielewski, & Beste, 2016), alpha (8–12 Hz) as a marker of inhibition (e.g., Jensen & Mazaheri, 2010; Klimesch, 2012; Waldhauser, Johansson, & Hanslmayr, 2012), or beta (13–30 Hz) as a marker of the maintenance of the current sensorimotor or cognitive state (e.g., Engel & Fries, 2010; Heidlmayr, Doré-Mazars, Aparicio, & Isel, 2016).

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