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Simulating Event Related Potentials in Tasks Involving Conflict Resolution: A Neural Network.

Tesi in Sistemi Neurali

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Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Table of Contents

Abstract	
Introduction	7
Executive Control	
The Role of Prefrontal Cortex	
Executive Control Theories	
Behavioural Tasks	
The Stroop Task	
The Eriksen Flanker Task	
The Error Related Negativity	
The Conflict Monitornig Account	
The Reinforcement Learning Accont	
Expectancy, Significance and Detectability	
Adjustment of selective attention following errors	
A neural network for a Flanker Task	
First implementation	
Simulations and Results	54
Introducing Conflict	
Parameters	
Simulations and Results	
The effect of Flanker Size	
Sensitivity Analysis of Parameters	75
Attentional Layer Parameters	75
S Layer Parameters and Intralayer Competition	
Noise Parameters	
Attentional Enhancement Parameters	
Threshold	
General Discussion	
Conclusions	
Appendix A	
Appendix B	
Appendix C	
References	

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Abstract

In this thesis, the main Executive Control theories are exposed. Methods typical of Cognitive and Computational Neuroscience are introduced and the role of behavioural tasks involving conflict resolution in the response elaboration, after the presentation of a stimulus to the subject, are highlighted. In particular, the Eriksen Flanker Task and its variants are discussed. Behavioural data, from scientific literature, are illustrated in terms of response times and error rates. During experimental behavioural tasks, EEG is registered simultaneously. Thanks to this, event related potential, related with the current task, can be studied. Different theories regarding relevant event related potential in this field - such as N2, fERN (feedback Error Related Negativity) and ERN (Error Related Negativity) – are introduced. The aim of this thesis is to understand and simulate processes regarding Executive Control, including performance improvement, error detection mechanisms, post error adjustments and the role of selective attention, with the help of an original neural network model. The network described here has been built with the purpose to simulate behavioural results of a four choice Eriksen Flanker Task. Model results show that the neural network can simulate response times, error rates and event related potentials quite well. Finally, results are compared with behavioural data and discussed in light of the mentioned Executive Control theories. Future perspective for this new model are outlined.

Nel presente elaborato si discutono le principali teorie riguardanti il Controllo Esecutivo. Vengono presentati i metodi delle Neuroscienze Cognitive e Computazionali con particolare attenzione ai task che implicano la risoluzione del conflitto nell'elaborazione di una risposta successiva alla presentazione di uno stimolo, in particolare l'Eriksen Flanker Task e le sue varianti. Vengono illustrati i dati comportamentali di letteratura dai quali si ricavano tempi di reazione medi e percentuali d'errore. Durante gli esperimenti si ha la registrazione congiunta dell'EEG grazie alla quale è possibile valutare i potenziali evento - correlati relativi al task stesso. Vengono presentate le teorie riguardanti i potenziali evento correlati N2, fERN (feedback Error Related Negativity) e ERN (Error Related Negativity). Per far luce sui meccanismi riguardanti il controllo esecutivo, che includono il miglioramento della performance, i meccanismi di individuazione dell'errore, gli aggiustamenti che seguono l'errore e il ruolo dell'attenzione selettiva, è stata sviluppata una rete neurale originale atta alla simulazione dei processi oggetto di studio. Viene quindi illustrata l'implementazione di tale rete neurale per la simulazione di un Eriksen Flanker Task a quattro risposte. I risultati mostrano che la rete permette di simulare tempi di risposta, percentuali d'errore e potenziali evento - correlati. In fine, vengono discussi i risultati ottenuti dalle simulazioni alla luce delle attuali teorie e dei risultati degli studi comportamentali. Vengono delineate successive prospettive di sviluppo in tale ambito.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Introduction

Cognitive Neuroscience and Computational Neuroscience are two thriving research fields of our times. The former regards the study of the neural mechanisms of mental processes. It includes experimental and theoretical works stretching from perception, attention, memory and language to action, decision-making, emotions, and social cognition. The latter concerns theoretical neural modelling of brain function, including neural networks model, which span from biophysically realistic simulations of neurons and synapses to high-level abstract models and from the simulation of the activity of a single neural cell to neural masses models which take neural populations into account. Thanks to Cognitive Neuroscience a growing body of experimental works, behavioural tasks and relative collected data is now available. This led to the formulation of several cognitive theories regarding themes such as learning, executive control, performance monitoring and so on, that are continuously updated and tested. Computational neuroscience has a complementary role in this scenario: simulating a neural model and replicating behavioural results is needful if one wants to understand the underlying mechanisms that make a given behaviour or capability arise. Modelling a cognitive process means having a direct insight on all the involved parts, on how they are interconnected and on what is the exact role carried out by each. Results may confirm current available theories. Alternatively, unexpected results or new rising hypotheses may lead to new behavioural studies, defining an interacting relationship between those two sides of Neuroscience.

The study here presented regards Executive Control. This term enclose different high level human behaviours, such as motor control, motor planning, performance monitoring, performance improvement, selection of appropriate behaviours, environmental variables control, attentional enhancement, etc. Cognitive Neuroscience elaborated through the years different theories regarding how this Executive Control is implemented. Those theories are illustrated in this paper along with behavioural tasks used and relevant event related potentials description. Behavioural tasks are a useful instrument in the understanding of the main features of mind processes.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

In this field two tasks are mainly used: the Stroop Task, which is a colour naming task with interfering stimulus meaning, and the Eriksen Flanker Task, which is a non search task where the subject has to identify the central target excluding interfering flanking elements. Attention was focussed on this latter task and experimental results and variants from literature are presented. As regards relevant event related potentials, evaluated from EEG signal, theories regarding N2, fERN (*feedback Error Related Negativity*) and ERN (*feedback Error Related Negativity*) are introduced.

The study undertaken in this final thesis had the purpose to understand and clarify some aspects of Executive Control. This aim was pursued building a new neural network. In its first implementation, the network was composed by three layers encoding respectively attention, stimuli mapping and response mapping; no controlling variables were defined and the network had a feedforeward structure from the attentional layer to the response layer, with intra – layer competition. In its second implementation, response conflict was chosen as a performance monitoring variable. The need for a new network with this cognitive feedback was motivated by the inability of the previous network to explain results regarding attentional errors properly. Conflict is defined as the extent of the overlap of the activation of two (or more) responses due to the simultaneous activation of incompatible representations in the stimulus processing. That is why the Eriksen Flanker Task is best suited for this study: activation of the target letter and of left and right flanker letters in the response elaboration represents the basis of this conflict signal. The network implemented a four choice Flanker Task, so that other aspects relative to attentional errors and noise errors could be distinguished and analysed.

Network simulated results proved a good fitting of several behavioural results, such as response times and error rates. Furthermore, conflict time – patterns were compared to mentioned event related potentials. Overlapping features was found between this simulated signal and ERN, in particular variations in amplitude in different condition and timing features. In the General Discussion some of the main questions in this research field are discussed in light of the theoretical accounts reported and of the simulated results obtained by this new model simulations.

> Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Executive Control

Cognitive Neuroscience aim at the knowledge of mental and behavioural processes in terms of structure and function of the Central Nervous System. A branch of this discipline particularly concerns the ensemble of cognitive processes which we refer as Executive Control.

Executive control is responsible for flexible behaviours pursued by the subject in respect of afferent stimuli, environment and current goals, Figure 1 shows a schematic of the involved processes. This system allows humans to interact with the external environment in an appropriate way, by changing their behaviour whenever there is a change in external conditions. In the absence of a system like this, all actions would be carried out in an automatic way and will be stereotyped. In fact, there are connections between sensorial stimuli and the corresponding responses aimed at creating precise and habitual behaviours that do not require special attention. The automatic mode predominates in animals, because of their limited prefrontal cortex, and in humans that have a prefrontal damage. This implies impairment in adaptation, learning, performance improvement and task switching.



Figure 1. Processes involved in goal-directed behavior and cognitive control. Flexible adaptations can be viewed as a feedback loop in which weighted differences between expected and real action outcomes are used to trigger appropriate adjustments and to improve outcome prediction. During an action, events indicating unexpected difficulties or decreased likelihood to succeed can also trigger adaptation. (Ullsperger et al., 2014)

> Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The Role of Prefrontal Cortex

The prefrontal cortex (PFC) is the cerebral cortex which covers the front part of the frontal lobe. It contains Brodmann areas 9, 10, 11, 12, 46, and 47. PFC is a richly interconnected system with extensive projections to and from many other parts of the brain and is involved in the executive control. Its position appears to be ideal for the control of many aspects of behaviour. In particular, the PFC has a leading role when the required behaviour consists in achieving a defined goal or when the external environment is rapidly changing and the subject is asked to react properly (Ridderinkhof et al., 2004). The PFC is also involved in following appropriate behaviour, particularly as regards interacting appropriately with others and/or with objects in the environment.

The medial part of PFC (mPFC) is critically involved in both higher cognitive function and psychopathology, yet the nature of its function remains in dispute. A univocal theory able to account for the variety of effects observed with a broad range of methods does still not exist. The most relevant of those theories will be discussed further and includes conflict based theories, reinforcement learning theories, error signalling theories, etc. Thus a central open question is whether all of these varied findings can be accounted for by a single theoretical framework. First of all, medial PFC may be central to forming expectation about actions and detecting surprising outcomes. A growing body of literature casts mPFC as learning to anticipate the value of actions. This requires both a representation of possible outcomes and a training signal to drive learning as contingencies change. A mechanism is needed to detect discrepancies between actual and predicted outcomes and update the outcome predictions appropriately. A number of studies suggest that mPFC, and anterior cingulate cortex (ACC) in particular, signal such discrepancies.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna

Gabriella Cefalù



trends in Cognitive Sciences

Figure 2. Anterior cingulate cortex (ACC) anatomy. The upper right part of the figure contains a reconstructed MRI of the medial surface of the right hemisphere of a single human brain (anterior towards the left, posterior towards the right). A schematic representation of cytoarchitectural areas (numbered) of ACC is shown on the enlarged section (left). Cognitive approximated division areas are outlined in red and affective division areas are outlined in blue. A schematized flat map of actual anterior cingulate cortical areas is shown in the bottom right panel. The borders of each sulcus appear as thin unbroken black lines, whereas a combination of broken and dotted lines outline cingulate areas. (Bush et al., 2000).

The anterior cingulate cortex is the frontal part of the cingulate cortex that surrounds the frontal part of the corpus callosum (see Figure 2). It consists of Brodmann areas 24, 32, and 33. ACC is a part of a circuit involved in a form of attention that serves to regulate both cognitive and emotional processing. Several neuroimaging studies showed that separate areas of ACC are involved in cognition and emotion (Bush et al., 2000). Cognitive and emotional information are processed separately. It is possible to distinguish the dorsal cognitive division (ACcd, areas 24 b9-c9 and 32) from the rostral - ventral affective division (ACad, rostral areas 24 a-c and 32, and ventral areas 25 and 33). The distinction is based on convergent data from cytoarchitectural, lesion and electrophysiology studies, combined with a knowledge of differential connectivity patterns and imaging studies. The cognitive subdivision is part of a distributed attentional network which includes strong reciprocal interconnections with lateral

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

prefrontal cortex (BA 46/9), parietal cortex (BA 7), and premotor and supplementary motor areas. Various functions have been ascribed to the ACcd, including modulation of attention or executive functions by influencing sensory or response selection (or both); monitoring competition, complex motor control, motivation, novelty, error detection and working memory. The affective subdivision, by contrast, is connected to amygdala, periaqueductal gray, nucleus accumbens, hypothalamus, anterior insula, hippocampus and orbitofrontal cortex, and has outflow to autonomic, visceromotor and endocrine systems. Thanks to this pattern of connection ACcd is involved in assessing the salience of emotional and motivational information and the regulation of emotional responses.

Also, ACC is responsible for detecting and identifying events that require more resources to be processed. How this process occurs is still under investigation. Flexible adjustments of behaviour and learning based on reward associations require a continuous assessment of the current actions and the related outcome. This is critical in order to optimize the decision - making processes. In particular, the area of the rostral cingulate cortex (RCZ) is involved in the monitoring of adverse consequences related to the action: wrong answers, response conflict and uncertainty in decision making. The objects of this monitoring all share a common thing: they point out that the goal in a task and the eventual related reward may not be achieved unless the level of cognitive control is increased. These aspects are discussed in different cognitive theories which build their assumption through specific behavioural task. These will be presented further. If the reward that was expected is not actually obtained, the prediction error is encoded by the midbrain dopamine system (MDS). Failure in reward is encoded as follows: if the events are better than expected phasic activity of MDS increases; in the opposite case it decreases. These signals are sent to RCZ where mechanisms for the improvement of the performance are implemented. RCZ is also involved in the monitoring of the conflict related to the response. The response conflict occurs when a cognitive task activate two or more competitive answers.

> Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Executive Control Theories

Several theories have been developed through the years regarding how executive control is implemented, which structures are involved and how they work together dynamically. A comprehensive theory of executive control should account for the entire body of evidence accumulated by a variety of scientific methods. As regards ACC function, it should be considered that cingulate cortex includes specific processing modules for sensory, motor, cognitive and emotional information. As a whole, cingulate cortex integrates input from various sources (including motivation, evaluation of error, and representations from cognitive and emotional networks) and through its connection with other brain regions modulates cognitive, motor, endocrine and visceral responses.

Currently two main types of theories explain the function of dorsal ACC: *evaluative theories* and *response selection theories*. Evaluative theories hold that dorsal ACC monitors ongoing behaviour to detect error conflict. Those theories are largely motivated by event-related brain potential (ERP) and hemodynamic neuroimaging data. They holds that dACC monitors ongoing performance to detect errors or conflict. Such evaluative theories propose that dACC is not directly involved in response selection but rather evaluates the success of ongoing behaviour during the task. On the other hand, response selection theories hold that dACC is directly involved in decision making process, particularly those theories suggests that dACC uses reward prediction error signals carried by the midbrain dopamine system to decide which of several competing motor control systems should be given control over the motor system itself. These two types of theories are antithetical to each other: whereas evaluative theories hold that this function must occur elsewhere in the brain, such as in the basal ganglia.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Representative of the evaluative account is the *Conflict Monitoring Account*; representative of the response selection theories is the *Reinforcement Learning Account*. Before going into the assumptions and the claims of these two account, it is fundamental understand the investigation methods used in this field, which include the building up of proper behavioural tasks to collect behavioural and EEG data from human subjects and modelling proper neural networks to simulate the underlying processes of interest.

Behavioural Tasks

Behavioural tasks are built specifically to study certain aspects of cognition. Generally, the subject is instructed to respond to a target stimulus and response times and/or error rates are detected. The type of stimulus can vary: it could be a letter, a light, a sound and so on. The stimulus – response mapping could be known or unknown a priori and during the task the mapping itself can be steady or dynamical (random or described by a function or a criterion). Accordingly to the purpose of the study, a feedback or a reward can be released to subjects. In this case, as well as for stimuli – responses mapping, responses – reward mapping can be fixed or variable. The Stroop task and the Eriksen Flanker Task are two relevant tasks in the executive control research area.

The Stroop Task

The Stroop task (Stroop, 1981; Stroop, 1938; MacLeod, 1991) is a colour naming task, that consist in saying what colour is the given stimulus. The stimulus is a word with its meaning inconsistent with respect to the colour with which it is written, for example: RED. Other examples are shown in Table 1. The subject is asked to tell what colour the word is written with (in the example the correct answer is 'green'). The interference arises from the parallel processing of the two components of the stimulus: the reading component, which is more immediate, and the colour component, which suffers from the interference of the spoken word that leads the subject to respond incorrectly (in the example, the interference can cause the wrong answer 'red').

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Stroop Task Stimuli	Control Card Stimuli
RED	RED
YELLOW	YELLOW
GREEN	GREEN
BLUE	BLUE

Table 1. Examples of Stroop stimuli and of control stimuli

Usually the results of the tasks show slower answers in incongruent (meaning and colour inconsistent) stimuli and higher error rates, with respect to congruent (meaning and colour consistent) stimuli as shown in Table 2. Typically, subjects are tested only on naming colours of incompatible words and of control patches. Interference is expressed as the difference between the times on these two types of cards.

		Experimental: words in color		Cont words i	rol: n black	<u>r</u>	
Experiment	Sample size	Μ	SD	Μ	SD		
Stroop (1935)	70	43.30	6.15	41.00	4.84		
MacLeod (1986)	50	41.58	6.98	41.16	7.12		

Table 2. Mean times M in seconds with standard deviation SD for reading color words in the experimental condition (incompatible colored inks) and in the control condition (black ink only). (MacLeod, 1991)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The Eriksen Flanker Task

The basic idea of the Eriksen Flanker Task is to 'flank' the target stimulus with an interfering stimulus, expecting that the accuracy and speed in identifying the target will vary according to the relationship existing between the target and noise stimuli called *flanker* (Eriksen & Eriksen, 1974). Usually, subjects are required to recognize or detect a target embedded in a display of noise consisting of other flanker letters or forms. Speed and accuracy in those type of task have been found to depend upon the number of noise elements present in the display, the similarity of these noise elements to the target, the dimension of target and of flanking elements, the delay between target and flanker presentation (Eriksen & Shultz, 1979). Flanker stimuli weaken and sometimes compromise the processing of the target. Selective attention is, in fact, unable to eliminate completely the effect of extraneous stimuli.

The first types of stimuli used were letters and they are still used even though there are versions of the task with symbols. The stimulus is composed of a central letter, the target, and a number of identical letters in the right and left side of the stimulus (see Table 3). Each target letter is mapped in a different button. The complete stimulus is located immediately above the fixation point, that is why we refer to this type of task as a non – search task. In this sense, evaluated response time reflect only the elaboration of the stimulus in all its parts. The flanker letter can be congruent with the target (target letter flanked by the same letter) or incongruent (target letter flanked by different letters). Flanking elements could also be neutral, which means letters or symbol that are not mapped with a responding button.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Condition		Example					
Congruent	Н	Η	H	H	H	H	Η
Noise same as the target.							
Incongruent	K	K	K	H	K	K	K
Noise different from the target.							
Neutral	%	%	%	H	%	%	%
Noise same as the target.							
T= target letter; f= flanker letter.	F	F	F	Т	F	F	F

Table 3. Examples of flanker stimuli. Each letter is mapped in a response button or key. Neutral symbols are not mapped in any possible response. Flanker/Target size may vary such as letter spacing or disposition on screen.

The results of the test show primarily an effect called *congruency effect* (see Figure 3): when the target letter is flanked by another letter mapped in a different response, reaction time to the target letter is markedly increased relative to when the noise letters are the same as the target. The neutral noise letters produce an intermediate effect upon reaction time, with the magnitude of their effect depending upon the number of features they shared with the target letter. They also show that the parallel processing of the flanker letter leads the subject to commit more errors. In conclusion, the result of a flanker task show that subjects cannot restrict their attention to process only a single letter, even when the location of the letter itself is clearly designated. Also, the task shows that the noise letter is processed along with the target. That is why incongruent stimuli produce greater impairment in reaction time and in error rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 3. Mean latency for the target conditions as a function of noise compatibility in three conditions: Condition 1, the target and flanker share the same size. In condition 2 flanker has a larger size; in condition 3 flanker has a smaller size. (Eriksen & Shultz, 1979).

Using this two tasks and their variation, it is possible to show a lot of effects that can help us understanding the executive control mechanisms.

> Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The Error Related Negativity

An important aid understanding the executive control and the performance monitoring mechanisms comes from the analysis of EEG data. Usually, in fact, a behavioural experiment involves the simultaneous recording of the EEG. Furthermore, EEG is usually registered simultaneously with Electromyogram (EMG) and Electrooculogram (EOG). The first is used to detect the start of the response using the muscular activating signal of the limbs involved in the response. The EOG is used in signal conditioning to remove artefacts due to eye movements. The analysis of EEG data involves tracking interesting epochs (e.g. 100 ms before the response onset and 500 ms after the response) and averaging those data by condition (e.g. congruent/ incongruent stimulus or correct/error response) according to the task : thanks to data conditioning it is possible to study three main event related potential (ERP): the Error Related Negativity, the Feedback Error Related Negativity and the N2. Those ERPs are shown in Figure 4 and will be widely discussed in the following.

Humans (and other animals) use feedback to learn how to behave. Such learning depends crucially on the ability of the organism to discriminate between positive feedback, indicating that the behaviour was appropriate, and negative feedback, indicating that the behaviour was in some way inappropriate. A variety of sources indicates that the brain responds differentially to positive and negative feedback. This differential neural response is evident in measures of the event-related brain potential called *Feedback Error Related Negativity* (fERN). Following negative feedback, the analysis of the ERPs in a given task shows a more negative potential with respect to trials that lead to positive feedback delivery. This negativity was isolated by subtracting the response to positive feedback from the response to negative feedback. The resulting waveform had an average amplitude of between 5 and 10 μ V and a peak latency of between 230 and 270 ms.

The *Error Related Negativity* (ERN) is a negative deflection that appears only when the subject commit an error during a trial and error reaction time tasks, with or

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

without the explicit delivery of a feedback signal (Falkenstein et al., 1990; Gehring et al., 1993). It is a negative deflection of approximately $10\mu V$ of amplitude that starts parallel to the subject's response and peaks 100 ms after the start of the response itself. Using a Flanker Task, it was firstly identified as a manifestation of a system associated with the accuracy monitoring of the response and for error compensation. ERN is visible, related to incorrect answers, in the RCZ channel and is not visible in correct trials.



Figure 4. Event-related potentials associated with performance monitoring. A: prototypical ERPs in response to errors (ERN, response-locked), negative feedback (FRN, feedback-locked), or preresponse conflict (N2, stimulus-locked) at midline electrodes FCz and Cz. B: corresponding topographies of difference waves from A. C: source localizations ERN, FRN, and N2. (Ullsperger et al., 2014)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Tasks in which is emphasized accuracy elicit larger ERN; this phenomenon is limited if speed is emphasized with respect to a neutral condition. These results support the hypothesis that the ERN is associated not only with the error detection, but also with the importance in accuracy given by the subject during the task. Using techniques of sources identification, different studies have shown that ERN is generated in the rostral part of the ACC. On the significance and on the role of this particular ERP several theories have been developed. Some accounts regard the ERN as correlated with the evaluation of the error or with the behavioural adjustments following error detection. Other theories regard ERN as the actual manifestation of the error detection itself. According to the timing and the location of fERN and ERN, it was proposed that the negativities following response errors and negative feedback were associated with the same neural and cognitive error detection process.



Figure 5. Electrical studies of error-related negativity (ERN). (a) Scalp distribution of the error related negativity (the purple area shows the centre of scalp negativity following an error). (b) Electrical tracing showing that errors produce the largest ERN, but later responses, owing to strong conflict, produce some ERN. (Bush et al., 2000)

In the following sections, two different account explaining ERN are introduced. Both accounts assert that an evaluation component, that monitors information processing in a given task, is needed. While *Conflict Monitoring Theories* holds that this monitoring role is carried out by ACC and that ERN is the EEG correlate of response conflict, *Reinforcement Learning Theories* holds that basal ganglia monitor for performance/reward, sending to ACC a dopaminergic signal, which is responsible for ERN. ACC, according to this account, select directly the appropriate motor controller.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The Conflict Monitornig Account

The Conflict Monitoring Account (CM; Botvinick et al., 2001; Botvinick, 2007; Yeung et al., 2004) asserts that, there must be a system monitoring for the amount of conflict generated in the elaboration of the given stimulus. The core of the conflict concept is the crosstalk interference. If two non-overlapping stimuli are processed, those two processes can run in parallel and without interference; instead, if both stimuli have some overlapping elements, the separate processing of the two of them will interfere one another involving the activation of two or more responses. The result of a crosstalk usually imply a slowing in the development of the response and in an increased frequency of error in a given task. The CM system is used to translate the occurrence of a conflict in a series of cognitive adjustments in order to minimize and prevent conflict itself. This conflict detection is up to the ACC. Conflict quantifies the extent of the overlap of the two (or more) processed stimuli and is due to the simultaneous activation of incompatible representations. The cognitive control intervenes to prevent conflicts and the conflict itself is considered, according to this account, as the trigger that activates a specific area of the brain, the ACC. The most likely neural generator of ERN ,then, is ACC itself.

Experimental data show that participants are faster in expressing the correct response after an error than in signalling that an error has occurred (Rabbit 2002). The error - correcting response is often very fast (20 ms after the original incorrect response). According to this account error correction is given by the accumulation of information over time even after the initial error: that is why the mechanism is fast and automatic. There is a correction tendency even when the subject is not instructed in correcting an erroneous response. Actually the rate of error correction increases with the duration of the stimulus confirming this account.

Main aspects in the study of ERN are its amplitude, the type of stimulus, the stress on accuracy, the frequency of the correct/error response in the task, the emotional component or the significance of the error itself. In general, ERN features vary according to the experimental conditions. It follows error regardless of the stimulus and of the

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

response modality and its amplitude is related with subjective judgement of response accuracy: according to experimental findings ERN is larger in the accuracy condition, in fact more strict response criterion and more attentional focussing produce lower error rate and longer response time. It is smaller in the speed condition, which causes shorter response times but higher error rates. Furthermore ACC result activated in its caudal part even in correct trial where multiple responses compete for the control of action. So the role of the ACC would be related with conflict detection and signalling the need of attentional enhancement.

In their work, the authors used a connectionist model to explain how executive control is implemented in a flanker task (see a schematic of the model in Figure 6).



Figure 6. Illustration of a model for a flanker task. The conflict monitoring feedback loop was added to simulate the role of ACC in performance monitoring and adjustment of attentional control. (Botvinick, 2001)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Simulated ERN is taken as the difference between conflict in correct and error trials following the response. In the simulated model, activation of the correct response continues following the error response and there is also a brief period following incorrect response in which both response units are activated and this leads to a large conflict signal. In correct response, conflict was found to be restricted to the period prior to the response, before inhibition from the correct unit response totally suppressed incorrect responses activity. According to those results, ERN could be a consequence of continued processing of the stimulus that leads to post-error activation and which is eventually involved in error-correcting activity. The difference between congruent/incongruent correct trials is largest in the period before the response. On correct trials any negativity associated with conflict should be observed before the response reflecting the conflict related to stimulus processing. A good candidate for this conflict related ERP is the N2. It emerges 250 ms after the presentation of the stimulus, it has a frontocentral scalp topography and is larger on incongruent trials, as shown in Figure 7. The localization of this ERP is in ACC.



Figure 7. The N2. Top: Stimulus-locked waveforms for correct trials, separately for congruent and incongruent stimuli. Data are shown for electrode FCz, in an epoch running from 200 ms before until 600 ms after the stimulus. Bottom: Scalp topography for congruent and incongruent trials, and the difference between these conditions observed 344 ms after stimulus presentation. (Yeung et al. 2004)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Using the neural model two prediction were tested: N2 should be similar to the ERN in terms of scalp topography and neural source and N2 and ERN should differ in latency (N2 preceding and ERN following the response).

The model also explains the empirically shown larger ERN related to congruent error trials. A greater ERN results from a more activated correct response unit. The activity of the incorrect response falls more quickly following the response on congruent rather than on incongruent trials (see Figure 8).



Figure 8. Activity in the network on correct and error trials. Response conflict (simulated anterior cingulate cortex activity), upper graphs, is the scaled product of the activity in the correct response unit (middle graphs) and the incorrect response unit (lower graphs), bounded at zero. Left panels show the activity in the model averaged across trials aligned to stimulus onset. Right panels show corresponding response synchronized averages, where trials are aligned with the response. (Yeung et al. 2004)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

In Figure 9 the relative timing and features of both N2 and ERN are shown in congruent or incongruent correct trials and in error trials as well.



Figure 9. The relative timing of the N2 and ERN. The upper panel shows response synchronized waveforms at FCz for correct congruent, correct incongruent, and error trials. The ordinate indicates the time of the response. The other panels show scalp voltage maps for error trials, correct congruent trials, and correct incongruent trials at 88 ms before the response (middle panel) and 56 ms after it (lower panel). (Yeung et al. 2004)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As mentioned above, another parameter influencing ERN is frequency: in experimental data participants were sensitive to frequency manipulation responding more quickly and accurately to frequent stimuli. ERN was larger on frequent incongruent trials, intermediate on infrequent congruent trials and smallest on infrequent incongruent trials: behavioural and simulated results are shown in Figure 10. In frequent incongruent condition participants expected to perform a correct response, if it wasn't so a large ERN was observed. Difference in simulated ERN across condition fitted experimental data as a direct consequence of changes in the dynamics of task processing according to task demand.



Figure 10. Error-related negativity amplitude as a function of response accuracy across stimulus conditions. The results are shown alongside the empirical data from Holroyd and Coles (2002). IFI = frequent incongruent trials; III = infrequent congruent trials; FIF = infrequent incongruent trials; 'data' = empirical results; 'sim' = simulation results. (Yeung et al., 2004)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Finally, the response conflict model predicts a very close relationship between ERN and error correction. Error correction is defined as the threshold crossing in the correct response unit that follows the threshold crossing in the incorrect response unit. It was found that error correction rates vary as a function of at least two factors: the degree to which attention is effectively allocated to target information; the degree to which participants commit to their first response. The simulated results showed that high error activity was found on those trials on which error is not subsequently corrected. The greater the activity of the incorrect response, the less likely is that the correct response will overcome it and correct error. In this sense, ERN should be not intended such as an explicit signal that an error has occurred, but it is rather a signal that there is response conflict. The monitoring for response conflict might represent a simple method for detecting errors: this system should signal that an error has occurred whenever the amount of conflict in the post- response period exceeds a threshold.

According with the results, explicit error detection involves the computation of conflict after an error is committed. This process is found to be slower than the automatic error correction. Experimental data shows that participants responds more quickly and efficiently with a correcting response than when making a common detection response to all errors (error correction is visible within 10-20 ms of the error) confirming the previous assumption. CM model is consistent with two intuition:

- Error correction may occur automatically in a system in which the information flow is continuous and increasingly accurate over time
- Error correction may precede error detection.

The proposed mechanism for detecting errors makes use of a simple and quite general property of human information processing: that is the fact that the representation tend to become increasingly accurate over time.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The Reinforcement Learning Account

A possible alternative to the CM account is the theory of Reinforcement Learning (Barto & Sutton, 1997). This theory is based on the role of the Mesencephalic Dopamine System (MDS). The MDS is composed by a small collection of nuclei (SNc and VTA, among the others) that project diffusely, acting as reinforcement, to the basal ganglia and to the prefrontal cortex, where the processes necessary to facilitate ('reinforce') the development of adaptive motor programs take place. This system can facilitate long - term potentiation and long - term depression. It also encodes the hedonic aspect of reward with a phasic response that acts like an error signal which, according to the RL, is used to indicate the need for increased ACC control. However, the engagement of the ACC is limited to the first part of the performance in a task, when it is new or particularly difficult. As soon as the subject begins to learn how to behave, its contribution decreases and other areas of the prefrontal cortex become more activated.

According to the RL (Holroyd et al. 2002) then, the human nervous system is provided with various motor controllers that act independently and in parallel. A schematic of this model is reported in Figure 11. All these structures have projections to the ACC and each one deal with the problem – solving task in a different way. The cingulate motor controller decides which is best suited to the task on the strength of the dopaminergic reinforcement signals. The main hypothesis assumes that when human participants commit errors in reaction - time tasks, the mesencephalic dopamine system, including basal ganglia, conveys a negative reinforcement learning signal to the frontal cortex, where it generates the ERN by disinhibiting the apical dendrites of motor neurons in the ACC. Furthermore, error signals are used to train ACC, ensuring that control over the motor system will be released to a motor controller that is best suited for the task at hand.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna

Gabriella Cefalù



Figure 11. A schematic of the RL model. The corresponding neural substrate is given in parentheses below each component label. (Holroyd et al., 2002)

Fundamental for the RL account is the fact that ERN is generated by a high - level generic error processing system. Its amplitude is sensitive to the importance of error commission to the participant. In task in which an explicit feedback was given to participants, the onset of the feedback stimulus indicating that a wrong response has occurred elicited an ERN (Miltner et al., 1997). Because in those experimental set up the feedback was delivered some time after the response occurred, the ERN elicited by the feedback was dissociated from the response generation process. This result demonstrates

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

that the ERN is not elicited by the process that causes the error in the first place, nor by the execution of a remedial action made in conjunction with the error (e.g. error signalling or error correcting response). It is concerned with an aspect of error processing that is not directly tied to error commission. This function might include detection of the error itself or the use of the error information to prevent future error repetition. The system is equally sensitive to different output modalities of error commission and it is indifferent to the input modality of the error information. When speed is emphasized ERNs are also elicited by late responses. ERN was found to be abnormal both in individuals with obsessive– compulsive disorder and in individuals with dorsolateral prefrontal damage, conditions that are associated with executive dysfunction.

Several groups of investigators have noted similarities between the phasic activity of the MDS and a particular error signal, called temporal difference error (TD error), associated with a reinforcement learning algorithm called the *Method of Temporal Differences*. This algorithm is the generalization of the Rescorla – Wagner rule to continuous time domain. In neural network models, TD errors are computed by an adaptive critic, which associates a value with the ongoing events and outputs a TD error when it changes its own prediction:

- Positive TD errors indicate that ongoing events are better than expected;
- Negative TD errors indicate that ongoing events are worse than expected.

Typically, a response selection module called actor or motor controller uses the error signal to reinforce behaviours that elicit reward. TD errors propagate back in time from the reward to the conditioned stimulus with learning. Also, like the phasic dopaminergic activity, a negative TD error is elicited by the absence of an expected reward. These observations led naturally to the hypothesis that the mesencephalic dopamine system carries a TD error.

On the whole, RL assumes that the nervous system is composed by multiple motor controllers acting in parallel with each one of these corresponding to neural structures that project to ACC, and each one approaching the solving of an high level motor control

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

problem in its own way. ACC at the confluence of all this information decides which motor commands are best suited learning to recognize the appropriate controller with reinforcement signals conveyed via MDS. Basal Ganglia implements the role of adaptive critic, which computes the value and the change in value of ongoing events and, finally, ERN is generated only on error trials and reflects the transmission of a reinforcing signal carried by MDS used to train the ACC to optimize performance on the task at hand.

The fundamental behavioural difference between those two accounts, the CM and the RL, is the role given to the ACC: according to the CM, the ACC has the role of monitoring the conflict and answers in order to decrease the extent of conflict in future presentations of the same stimulus that had caused it previously; according to the RL, the ACC is responsible for choosing the best executive path in a given task, the choice is made considering the dopaminergic signal that acts as reinforcement, based on the outcome of the actions carried out before.

To understand the relationship between error ERN and feedback ERN, Holroyd and Coles (2002) used a probabilistic learning task. On each trial in this task, an imperative stimulus appeared in front of the participant on a computer screen. The participant was then required to make a two-choice decision by pressing one of two buttons. At the end of the trial, a feedback stimulus indicated to the participant the correct or erroneous outcome. The participants were not informed of the appropriate stimulus–response mappings and had to infer the optimal response strategy by trial and error.

The task had three possible condition:

- 100% mapping, in which the association rule was fixed;
- 50% mapping, in which the subject has the fifty percent of probability to receive a negative feedback, irrespective of the stimulus;
- Always correct/always incorrect mapping, which means that an always positive/always negative feedback signal was delivered independently from the given response.
Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

In the model, the adaptive critic computes the value of ongoing events and give as output a TD error when it detects a change in this value. The simulated ERN was defined proportionally to the amplitude of the TD error. For comparison with the empirical results the effective simulated ERN was determined by subtracting the simulated ERN on trials with positive feedback from the simulated ERN on trials with negative feedback.



Figure 12. Simulated and empirical ERN amplitudes in the probabilistic learning task. A: 50% mapping condition; B: 100% mapping condition; C: always correct/always incorrect (AC/AI) mapping conditions. (Holroyd et al., 2002)

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

According to the results (see Figure 12) in the 100% mapping condition, as the system learned the associations between response and feedback, the ERN associated with the response increased, whereas the ERN associated with the feedback decreased: the subjects learns to rely on its own prediction of the outcome of the current trial. In the 50% mapping condition the system needs to wait for the feedback to determine the outcome of the trial itself: that is why negative feedback stimuli in this condition continue to elicit the ERN throughout the course of each block. Finally, in the last condition, as the system learns the associations between the imperative and the feedback stimuli, neither the response nor the feedback should elicit the ERN: whatever is the behaviour pursued by the subject, this will not affect the performance in any case. The fact that neither the response nor feedback ERNs decreased by much in the empirical data suggests that an additional cognitive process must have been at work in the human system, continuing the search for an appropriate response strategy even after the simpler system had given up.

In the same study, the authors used a modified Flanker Task to test the effect of frequency on ERN amplitude. The possible stimuli are shown in Table 4.

Condition		Example						
Compatible	Н	Η	Η	H	Η	Η	Η	
	S	S	S	S	S	S	S	
Incompatible	Н	Η	Η	S	Η	Η	Η	
	S	S	S	H	S	S	S	

 Table 4. Example of stimuli in the experimental task. (Holroyd et al., 2005)

Half the participants saw each of the stimuli with a central H on 10% of the trials and each of the stimuli with a central S on 40% of the trials; the remaining half of the participants saw the same stimuli with the converse set of probabilities. Stimuli in which the central and flanker letters are the same are referred to as *compatible*, and stimuli in which the central letter is different from the flankers are called *incompatible*. Likewise, the highly probable stimuli are called *frequent* and the less probable stimuli *infrequent*. There are four possible conditions: *infrequent compatible* (III), *infrequent incompatible* (FIF), *frequent incompatible* (IFI), *frequent compatible* (FFF).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The RL account predicted that the amplitude of the ERN would be smaller on error trials in the incompatible conditions than in the compatible conditions, because the error detection process should be compromised when the flanking letters differs from the central target letter. This was not confirmed by results. For both the model and the experimental data, ERN amplitude is larger on incompatible trials, frequent incompatible (IFI) error ranking 1st, infrequent compatible (III) ranking 2nd and infrequent incompatible error trials (FIF) ranking 3rd (see Figure 13).



Figure 13. Average error-related negativity (ERN) amplitudes as a function of accuracy (percentage correct) for the empirical (ERN, in μV) and simulated (temporal difference; TD) data. The solid line represents empirical data; the dashed line represents simulated data. IFI, frequent incompatible condition; III, infrequent compatible condition; FIF, infrequent incompatible condition. (Holroyd et al., 2005)

The understanding of those results was the basis of further investigation that took in account new relevant elements such as *error expectancy*, *error significance and error detectability*. Those aspect could explain the variability of ERN amplitude.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Expectancy, Significance and Detectability

The modulations of dopaminergic activity and subsequent behavioural changes, according to several studies on animal, are stronger for less expected outcomes. RL theory predicts that the ERN should be larger for less expected errors. However, larger ERNs for less expected outcomes have not been consistently reported. Maier et al. (2012) showed that this could be due to the confusion between the expectancy of an outcome and the significance for the current task goal. For example, if accuracy is emphasized over speed, than error are not only less frequent but also more significant because they violate the goal to respond accurately! In another study, participants were informed before each trial whether a correct response would entail a small or a large monetary reward, making errors more significant in the latter case (Hajcak et al., 2005). The two case shared the same frequency. Errors on high-value trials elicited larger ERNs than errors on low-value trials. Error expectancy and error significance in this task where well distinguished and it was found that the ERN was determined by error significance, suggesting an important role of motivational factors in performance monitoring. For further investigation, the authors defined a new modified flanker task, with four possible choice.

Stimuli were strings of seven letters in Arial font. The central letter in each string was designated as the target, and the remaining letters were designated as the flankers. Target letters were B, K, P, R, M, V, W, and X. Couples of letters (B and K, P and R, M and V, W and X) where mapped in 4 possible response keys. Responses had to be given by pressing the "W," "S," "L," and "P" keys of a standard computer keyboard. For each target, flankers were six identical letters associated with a different response than the target were associate (e.g., the targets B and K could be combined with one of the letters P, R, M, V, W, or X). This resulted in 48 possible target - flanker combinations (e.g., PPPBPPP, RRRBRRR, etc.). An example is given in Figure 14. Participants were instructed to respond to the identity of the target and to ignore the flankers. Each trial started with the presentation of a fixation cross for 250 ms. The stimulus array was then presented and remained on the screen until a response was given. A black screen for 1,200 ms followed the response before the start of the next trial. This interval was restarted if further responses (e.g., spontaneous error corrections) occurred during this time.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna

Gabriella Cefalù



Figure 14. Stimulus response mappings and classification of responses in the four-choice flanker task. Each of the four response fingers (fourth line) was associated with two target letters (third line). Given a specific stimulus, each response was classified as either a correct response, a flanker error, or a nonflanker error (second line). In the present example, the stimulus consists of the target letter 'M' and the flanker letters 'R' (first line). Given this stimulus, a response with the right index finger would be classified as a correct response, a response with the left index finger would be classified as a flanker error, and a response with the remaining fingers would be classified as a non flanker error. (Maier et al., 2011)

Thanks to this new version of the task it was possible to distinguish *flanker errors* from *non flanker errors*:

Incongruent stimulus P P P B P P P	Target: B Flanker: P
Flanker error	Response letter P/R
Non flanker error	Response letter M/V or W/X

Tab 5. Flanker and Non Flanker error example.

- Flanker errors are predominantly attention errors, they occur because selective attention is mistakenly allocated to the flankers. This kind of error violates both the goal to respond accurately and to ignore the flanker;
- Non flanker errors occur due to other reasons, such as response confusion induced by time pressure. This kind of error violates only the goal to respond accurately.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Flanker errors might have a greater significance for ongoing behaviour than non flanker errors. Indeed, in accordance with the error significance account, previous studies have shown that the ERN is larger for flanker errors than for non flanker errors (Maier et al., 2008, 2011) but they also were less frequent and therefore less expected than non flanker errors(43% in Maier et al.,2008, and 46% in Maier et al.,2011). So this result were also consistent with the error expectancy account. Manipulating the size of the flankers relative to that of the target it was possible to dissociate the effects of error expectancy and error significance. In particular increasing flanker size increases interference, this leads to increased frequency of flanker errors: flanker errors become now 'expected'.

Two possible account are outlined: the *expectancy account* and the *significance account*. The former holds that ERNs should be smaller for flanker errors with large flankers (error is more expected in this case) than for flanker errors with small flankers (error is less expected); the latter holds that larger ERNs should be elicited for flanker errors with large flankers (error assume great significance since the subject is instructed in ignoring the flanking stimuli) than for flanker errors with small flankers. Furthermore, an increased flanker size implies that the proportion of attention errors among flanker errors is increased: as asserted before flanker errors are *predominantly*, and not only, attentional errors. Because flanker interference should not affect the frequency with which responses are confused due to time pressure, the proportion of non flanker errors should be unaffected by flanker size according to both accounts. Results have shown that ERN was larger for flanker errors with large flankers than for all other conditions (see Figure 15). These results support the idea that performance – monitoring processes as measured by the ERN evaluate errors with respect to their significance for the current task goal.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 15. Response-locked grand-averaged waveforms at electrode FCz for correct and nonflanker error trials with small and large flankers (A), and for correct and flanker error trials with small and large flankers (B), as well as scalp topographies of the peak-to-peak Ne/ERN amplitude quantified as the difference between the most positive peak in an interval of -100 ms and 0 ms relative to the button press and the most negative peak in an interval of 0 ms and 120 ms relative to the button press (C). ms = milliseconds; $\mu V = microvolt; R = button press.$ (Maier et al., 2011)

The stimulus – locked N2 component was evaluated too and was found to be smaller for non flanker errors with small flankers than for non flanker errors with large flankers, whereas no effect of flanker size was obtained for flanker errors. This result provides support for the assumption that there are qualitative differences between flanker errors and non flanker errors.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 16. Stimulus-locked grand-averaged waveforms at electrode FCz for correct and nonflanker error trials with small and large flankers (A), and for correct and flanker error trials with small and large flankers (B), as well as scalp topographies of the N2 amplitude quantified as the most negative peak in an interval of 250 ms to 350 ms following stimulus onset (C). ms = milliseconds; μV = microvolt; S = stimulus onset. (Maier et al., 2011)

If more than two responses are possible, conflict depends on the number of competing responses that became active during response selection:

- for non flanker errors 2 responses are active if the error is due to response confusion, but 3 responses are active if the error is due to confusion and attention error (the actual response, the correct response and the flanker response are simultaneously active). So, non flanker errors with large flankers are associated with larger N2 amplitude;
- for flanker errors, the number of competing responses is always two, so N2 amplitude is independent on flanker size.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As regards ERN and the error detection, which mean the ability to recognize when an error has occurred in a given task, there are different theories. In the RL account, as previously reported, ERN is the correlate of error evaluation or of the behavioural adjustment that succeeds the detection of an error; in the CM account ERN is the correlate of error detection in terms of post - error conflict, which arises when the intended correct response becomes activated during continued stimulus processing after an error; other theories hold that ERN is the correlate of error detection itself, in this sense ERN represents the mismatch between the actual response and the intended correct response. As regards the last two theories, which we refer as error detection theories, they assert that the greater the amount of mismatch or conflict the greater the probability that the error is detected. So ERN amplitude should reflect the *detectability of errors*. ERN amplitudes of detected errors should be larger than those of undetected errors.

To investigate this relationship ERN amplitude was compared across error types differing in detectability. Errors that are detected more efficiently should show larger ERN amplitudes than errors that are less detectable. According to Yeung et al. (2004) computational model, an error is detected whenever the cumulated conflict exceeds a criterion. Because both the ERN and error detection are assumed to depend on the amount of post - error conflict in the CM account, ERN amplitudes and error detection rates should be correlated across errors differing in post - error conflict. By comparing ERN amplitudes and error detection rates across these errors, one can examine whether increased detectability is accompanied by increased ERN amplitudes. Maier et al. (2008) used the same four choice flanker task, with flanker/non flanker errors as defined above. Detectability of both the error types was measured by signalling responses. The authors argued that detectability of flanker errors is reduced because these errors occur particularly on trials on which too much attention is allocated to the flankers, which, in turn, impairs error detection. In fact, a negative component in the pre-response phase that was larger for flanker errors than for non flanker errors was found and it is consistent with frontal N2. This means that an increased pre - response conflict on flanker errors is consistent with the idea that flanker errors are due to an increased allocation of attention to the flankers.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Other results showed that error detectability was higher on non flanker errors but ERN amplitudes were larger for flanker errors. ERN amplitudes were generally smaller for non signalled errors than for the signalled ones. Moreover, non signalled errors showed no significant difference between flanker errors and non flanker errors. In conclusion, it seems that ERN amplitude is not related with error detectability.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Adjustment of selective attention following errors

The mechanisms of error detection change how the subject reacts on ensuing trials. At least three types of behavioural post-error adjustments have been observed: *post* - *error slowing* (PES), *post - error reduction of interference* (PERI) and *post - error improvement in accuracy* (PIA). Apart from these behavioural changes, post - error adaptations have also been observed on a neuronal level with functional magnetic resonance imaging and electroencephalography (Aron et al., 2007).

For what concerns PERI and PIA, the former was described for the first time as the reduction of difference in RTs between compatible and incompatible trials in an Eriksen Flanker task (Ridderinkhof et al. 2002) and it is thought to reflect cognitive control processes leading to improvements in interference resolution; the latter was described in interference tasks where there are short - term or trial - to - trial adjustments that lead to decreasing error rates directly after error commission (Laming, 1968; Danielmeier et al., 2011; Maier et al., 2011).

PES describes the prolonged reaction time in trials subsequent to an error compared to RTs in trials following correct response (Rabbitt, 1966; Laming, 1968). This has been observed in a variety of different tasks (Flanker and Stroop task, among the others). However, some studies reported conditions under which no PES effects were observed or they are observed only in conditions where error trials are infrequent, while observing post - correct slowing when correct trials are infrequent. Thus, it is yet unclear under which conditions PES can be observed, and what the underlying mechanisms are. There are three main theories on this phenomenon: according to CM, PES is related to cognitive control mechanisms which are implemented after the commission of errors (Botvinick et al., 2001); according to the orienting account PES reflects an orienting response following infrequent events like errors (Notebaert et al., 2009). Additionally, an inhibition account is supported by functional and structural anatomical studies and EEG experiments showing that motor inhibition is related to PES (Ridderinkhof, 2002). Again, using a flanker task in which we can separate flanker error from non flanker error can be useful to explain how post error adjustment are engaged (Maier et al., 2011).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Accordingly, errors due to insufficient attentional selectivity should be more frequent among flanker errors than among non flanker errors. A relative frequency of flanker errors exceeding 33% (in a four choice flanker task) would provide evidence that a portion of flanker errors is due to insufficient selective attention. Analyses demonstrate that without distinguishing flanker errors and non flanker errors, no substantial adjustments of selective attention following errors were obtained. Investigating whether adjustments of selective attention were different for trials following flanker errors and non flanker errors showed that attentional selectivity was stronger on trials following flanker errors than on trials following non flanker errors or trials following correct responses. The congruency effect, that can be considered an index of attentional selectivity, was reduced on trials following flanker errors as compared to trials following non flanker errors.

Adjustments of selective attention were closely related to the ERN amplitude: ERN amplitude was increased for flanker errors, that is, for errors that led to stronger adjustments of selective attention. Also, those finding give evidence to the truly adaptive mechanism underlying those behavioural adjustments, in contrast with the orienting account. Given that adjustments of selective attention are initiated only following errors due to insufficient attention, it is plausible to assume that performance monitoring not only implies that errors are detected, but also that the source of these errors is evaluated.

Although those results clearly revealed a relationship between the ERN and adjustments of selective attention, the exact data pattern suggests that this relationship is rather complex. In particular it was found that after non flanker error the attentional selectivity increase when associated with large ERN while after flanker error the attentional selectivity increase regardless of ERN amplitude. The adjustments of selective attention could be triggered either by the identification of a flanker error or by a large ERN amplitude.

It was then proposed a two stage account, according to which error evaluation occurs on an early stage preceding the ERN but it also takes place on a late stage succeeding ERN. During task processing, the early stage system continuously estimates the risk of specific error types by monitoring the current state of system parameters. In

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

particular, this system monitors for attentional selectivity inferring that poor attention allocation produces a higher risk of error. If the error detection system then signals that an error has occurred, the early evaluation process indicates that this error is due to insufficient attentional selectivity, and initiates adjustments of selective attention reflected by an increased ERN amplitude.



Stimulus

Response

Figure 17. Two-stage account of error evaluation. During task processing, an early evaluation stage continuously estimates the risk for specific errors (e.g., errors due to insufficient selective attention) by monitoring the current state of system parameters. Upon detection of an error by the error detection system, this process initiates appropriate adjustments which is reflected by the Ne/ERN. After execution of a response, a late evaluation stage evaluates the error source by matching memory representations of executed responses and stimuli. By initiating further adjustments according to the estimated error source, this stage can compensate for misses by the early evaluation process. (Maier et al. 2011)

This kind of system often produces false alarms, for example adjustments for non flanker errors. After a response has been executed and the ERN has been generated, the late stage system can evaluate errors more reliably. If an error is due to insufficient selective attention, adjustment is initiated and it is possible to recognize error missed in the early stage (flanker error with small ERN amplitude). This new interesting theory summarized in Figure 17, should be further investigated by means of collecting more behavioural data and simulating the dynamics of both the error evaluation systems through a new model.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

A neural network for a Flanker Task

Until now, executive control theories were explained considering behavioural tasks used in this area regarding fundamental concepts such as error detection, conflict, attentional adjustments and so on. The concept of ERN was then introduced and the importance of EEG data analysis was shown through the mentioned experimental works. A prominent role in the investigation of neural mechanism is carried out by neural network models. Modelling a neural network for a designed purpose complete the methods typical of Cognitive Neuroscience giving a direct insight through the processes of interest. The neural network implemented in this paper, simulates the four – choice flanker task described above. It was built using Matlab 2012b.

First implementation

In its first implementation, the model, shown in Figure 18, was made up of three layers. The *Attentional Layer* represents the effect of selective attention. It is composed by three neurons that encode the allocated attention on the central letter and on the two lateral parts of the stimulus.

The *Stimuli Layer* is composed by three groups of neurons, each one for the possible location of the letters and so a first group for the central target, a second group for the left flanker and another group for the right flanker. Each group in made by 14 neurons which represents the 8 possible letter plus the 6 neutral symbols. Even in the central block the neutral symbols were included but not used: the central position in the task can be occupied only by one of the 8 possible letters.

The *Response Layer* consist of four neurons, which represents the 4 possible response in which the 8 letters are mapped.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 18. The first implementation of the neural network for a 4 choice flanker task. The explanation of the mode of operation of the model is referred to text.

As the network receives an input stimulus, such as the incongruent example in the black box in Figure 18, the neurons associated with target letter and flanker letter grow in excitement. Moreover, the central block of stimuli receives the attentive input from the attentional layer, this acts such as an attentional enhancement focussing attention itself on the target letter, while the lateral blocks receive a small but non zero attentional input. Thanks to attentional input, the competition in the stimuli layer frequently ends with the target letter as the winner, overcoming the strong flanker input. This means that the neuron in the R layer which encodes the right response beats the flanker activated response and reaches a defined threshold (see parameter list, Table 6) faster. Otherwise, thanks to noise added in both S and R layers, the flanker or one of the possible non flanker responses can win over the correct one. Sometimes, strong attentional enhancement can lead to error correcting response. Other example of how the network works in the possible different conditions will be further discussed along with the results.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Each neuron is described by a first order differential equation and with an activation function (Equation 1 - 4).

$$\tau \frac{d}{dt} v_i^S = -v_i^S + I_{Si} + \sum_{a=1}^3 A_{ia} y_a^A + \sum_{s=1}^{42} L_{is} y_s^S + N_i^S$$
(1)

$$y_{i}^{S} = \frac{1}{1 + e^{-k(v_{i}^{S} - \theta)}}$$
(2)

$$\tau \frac{d}{dt} v_i^R = -v_i^R + \sum_{s=1}^{42} W_{is} y_s^S + \sum_{r=1}^{4} H_{ir} y_r^R + N_i^R$$
(3)

$$y_i^R = \frac{1}{1 + e^{-k(v_i^R - \theta)}}$$
(4)

Equations (1) and (2) regard the stimuli layer (i=1,...42); equations (3) and (4) describe the response layer. State variable used are V_i^S for the stimuli layer and V_i^R for the response layer. The exit variable are evaluated through a sigmoidal activation function (equation (2) and (4)). They are Y_s^S (s = 1,2,..., 42) and Y_r^R (r =1,2,..., 4) respectively for the stimuli layer and for the response layer. Y_a^A (a=1,2,3), the attentional layer variable, is fixed.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

A represents the matrix of sinaptic weights between the attentional layer and the stimuli layer, with the generic element A_{ij} (conventionally assuming that i indicates the postsynaptic neuron, while j indicates the presynaptic neuron from now on). A dimensions are 42 rows for 3 columns. It has the first and the third columns set to a low value (see parameter A_{low} , Table 6), while the central column is set to a high value (see parameter A_{hight} , Table 6). In this way, attentional input y^A (which is a column vector made up of three elements) is appropriately weighted and this gives a higher input to central S layers neurons and a lower input to lateral S layer neurons.

W represents the matrix of sinaptic weights between the stimuli layer and the response layer, with the generic element W_{ij} . W dimensions are 4 rows and 42 columns. Columns encode stimuli and rows encode responses. Each row has the three elements associated with the correspondent response letter (e.g. B right, B central and B left correspond to columns number 1, 15 and 29 respectively and are mapped in response 1, 'BK') set to a high value (see parameter W_{hight} , Table 6), the other elements are set to a low value (see parameter W_{low} , Table 6). This structure is repeated for all the four columns.

In this model, stimuli layer and response layer are competitive layer. Consequently two other matrices were defined: L and H. Those matrices contains the coefficients of self-excitation and inhibition between the neurons of the stimuli layer and of the response layer respectively. Both matrices share a common structure: the principal diagonal elements are set to a common value (see parameter L_{ex} and H_{ex} , Table 6) which encodes the self excitation value for each neuron; the other elements are set to a different common value (see parameter L_{in} and H_{in} , Table 6), that encodes the strength with which each neuron inhibits all other neurons of its belonging layer.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

 I_i^s (i = 1,...,42) is the binary value given as input to the i – th letter of the stimuli layer, accordingly to the current simulated stimulus, varying during the task. N^s and N^R represents added noise in stimuli and response layer. k and θ are respectively slope and threshold of the activation function. τ is the time constant of both layers.

Critical to this type of models, is the setting of the synaptic weights, time constants, thresholds and all other parameters in general. The model was simulated using Euler method.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Simulations and Results

The following exemplary simulation of the network shows the activation of the neurons layer by layer. In Figure 19 an example relative to a single incongruent trial is shown.





A



Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 19. Example of the mode of operation of the network with input stimulus "MMMBMMM". A. Early stage. Three neurons are activated, corresponding to the two flanker letter (M) and the central one to target (B) in the S layer. B. Middle stage. Target in the S layer becomes more active. Flanker are still stronger so, in the R layer, error response (MV) seems to win over the correct response (BK). C. Late stage. Target now overcomes the lateral noise stimuli that are consequently suppressed. In the response layer the correct response emerges and inhibits the erroneous one. D. Time-pattern of the outputs in the R Layer. Note that y axis is not the same for the four possible responses. BK, the correct response, rises till full activation. MV, the flanker error response, rises early and is then inhibited by the correct response. PR and WX, the non flanker error response, do not reach relevant activation.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The example in Figure 19 shows a correct trial, in which the correct response overcomes the flanker response. Adding noise, sometimes the network produces error responses that can be flanker errors or non flanker errors. Running a simulation over 1440 trials, including ten tasks for ten participants of 144 each, one can compare behavioural data to simulated results by means of mean response times and error rates. We refer to 144 stimuli considering 48 congruent, 48 incongruent, 48 neutral.

As regards the congruent and the incongruent condition, simulated data were fitted with behavioural data from Yeung et al. (2004, second simulation). The comparison is reported in Figure 20 in terms of error rates and response times on correct trials.



Figure 20. Congruency Effect: a comparison between behavioural data (Yeung et al. 2004) and simulated data both showing lower error rates on congruent trials than on incongruent trials, and faster responses in the congruent condition with respect to incongruent condition on correct trials. Response time was calculated adding 400 ms to simulation results.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Neutral condition in literature is compared with the incongruent one. Simulated data show the same trend as regards error rates and response times (see Figure 21). Simulated results do not prove satisfactory in the comparison of flanker and non flanker error rates during incongruent trials, as well as response times in this two types of error with behavioural data. For completeness, those results are reported in Figure 22.



Figure 21. Congruency Effect: a comparison between behavioural data (Maier et al. 2008) and simulated data both showing lower error rates on neutral trials than on incongruent trials, and slightly faster response in the neutral condition with respect to incongruent condition on correct trials. Response time was calculated adding 400 ms to simulation result.

Looking at the result it is immediate to notice that neutral condition is an intermediate condition between the congruent and the incongruent case. That is due to the presence of the neutral flanker, which in mapped in none of the response, impairing partially the performance. The simulated results show a global tendency towards higher error rates: this could mean that more central attention should be recruited.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 22. Flanker and Non Flanker Errors: in the left panel, simulated error rates show the opposite trend compared with behavioural data. In the right panel, simulated response times of non flanker error results faster than the behavioural, vice versa as concerns flanker errors.

Flanker error in those simulation double the respective behavioural results. This also accounts for the hypothesis that a greater amount of central attentional enhancement is needed so that the major suppressing of flanker interference will result in a lower proportion of flanker error and, accordingly, a higher proportion of non flanker error. Global error rate on incongruent trials should decrease as well.

See table 6 in the following for an explanation of all parameter used. See also *Appendix* A for the complete table of simulated results and for assigned parameters values.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Introducing Conflict

The aim of the present work was to build a new neural network with the purpose of investigating the ERN source and to understand what feature is monitored by executive control. It was assumed that a good candidate to this latter purpose can be conflict. A feedback from the response layer to the attentional one was then added in the network. The signal brought to the attentional layer is what we have defined *response conflict*, evaluated as the Hopfield energy function in the response layer:

$$Conflict = \sum_{\substack{i, j=1 \ i \neq j}}^{4} y_i^{R} y_j^{R}.$$



Figure 23. Introducing conflict in the neural network. Inputs are not showed in figure. Different line width show qualitative different degrees of activation (from the thinner to the bolder activation increases).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The new implementation of the network is shown in Figure 23. The attentional layer has now its own activation function, taking conflict as input. As a consequence, the selective attention on the central target enhances accordingly to the amount of conflict itself (Equation 6,7). The dynamic of this process is assumed instantaneous: since it acts within the trial, the relative time constant should be much more lower then τ (time constant of the network, see Equation 1 and 3).

$$v_{i}^{A} = C_{i} \sum_{\substack{i, j=1 \ i \neq j}}^{4} y_{i}^{R} y_{j}^{R}$$
(6)

$$y_i^{A} = A_{max} (1 - e^{-k v_i^{A}/\tau_A}) + A_{min}$$
 (7)

C represents the matrix of synaptic weights between the response layer and the attentional layer, with the generic element Ci (i = 1,2,3).

When two or more responses are activated, response conflict becomes significantly greater than zero. This signals that more control is needed and the subsequent attentional enhancement through the activation function helps the target to overcome noise. This leads to an increased activation of the correct response that inhibits the error response, reducing the amount of conflict. Coefficients C_1 and C_3 are set to zero, which means that there is no enhancement nor suppression for the flanking elements. Coefficient C_2 is set to one, accordingly central attention on target will increase whit A_{max} as weighting parameters. A_{min} is defined as the attentional input, the same for lateral and central letter, when conflict is zero.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Parametres

Table 6 shows all the parameters of the network. The values used will be reported along with the discussion of the results, when necessary, or in *Appendix* A and B.

Attentional Laver	AHIGH	Coefficients of matrix A. Ahigh encodes high attentional enhancement flow encodes low					
j •-	ALOW	attentional enhancement.					
Stimuli Layer	WHIGH	Coefficients of matrix W.					
	WLOW						
Stimuli Layer- Competition	LEX	Coefficients of matrix L Lex is the auto- excitement coefficient. Lin is the inhibition coefficient. Each					
	LIN	neuron excites itself and inhibits all the other neuron within the layer.					
Response Layer- Competition	HEX	Coefficients of matrix H. Hex is the auto- excitement coefficient. Hin is the inhibition coefficient. Each					
	HIN	neuron excites itself and inhibits all the other neuron within the layer.					
Sigmoid Parameters	S	S is the slope parameter while teta is the threshold					
	ТЕТА	s is the stope parameter, while teld is the intestion.					
Noise	STS	Standard deviation of noise input in the stimuli layer, sts, and in the response layer, str.					
	STR						
Time Constant	TAU	Tau is the same for all neurons of all layers.					
Attentional Parameters with Conflict	AMAX	Amax is the weighing coefficient of Conflict. Amin is the basal attentional level when conflict is					
	AMIN	introduced: it is the minimum attentional input received by the S layer when conflict is zero					
Threshold	ТН	Threshold value is the same for all neurons. If neura activation of one of the possible response crosses th then a response has been given. If in the same task another possible response crosses th, then a correction is been made.					

Table 6. Model Parameters.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Simulations and Results

Introducing conflict in our network, as defined in Equation 6 -7, permit the study of how conflict itself can vary in the response period across different conditions. Thanks to this it is possible to compare this conflict signal with relevant ERPs in this field, such as ERN and N2. Since experimental work regards only neutral and incongruent trials (Maier et al. 2008, 2011, 2012), from now on only this two conditions will be considered.

An example of simulation is presented in Figure 24. It shows activation layer by layer in a single incongruent trial and conflict shape. In an early stage of simulation (panel A, Figure 24), the target letter and the two flanker are activated. Other letters due to noise result slightly activated too in the S layer. In the R layer, the correct response is rising up, together with the flanker error response (which has higher activation value due to the contributes of both flanking letters) and one of the two possible non flanker response. In the final simulation stage (panel B, Figure 24), flanker letters and noise – activated letters are suppressed by target, and so the correct response wins in the R layer over flanker and non flanker error responses. The activation of the response neurons has the time trend reported in panel C.



A

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 24. Example of the mode of operation of the network with input stimulus "VVVBVVV". A. Early stage. Three neurons are activated, corresponding to the two flanker letter (V) and the central one to target (B). In the response layer the correct response is slightly activated, the flanker error response leads the competition. A non flanker error response (MW) is also activated thanks to noise. B. Late stage. Target overcomes the lateral noise stimuli that are suppressed. In the response layer the correct response emerges and inhibits both the erroneous ones. C. Time – pattern of the outputs in the R Layer. Note that y axis is not the same in the four possible response. BK, the correct response, rises till full activation. MV, the flanker error response, rise early and is then inhibited by the correct response. The same thing happens to the non flanker error response WX. PR, activated by noise, is immediately suppressed.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The evolution of response conflict is depicted in Figure 25. It is easily explainable considering its definition and the activation of the R layer neurons. 200 - 300 ms before the response onset, response are slightly activated. The concomitant rising up of three responses, 150 ms before the response onset, makes conflict grow. Peak value is reached when the three neurons reach their reciprocal maximum activation value, 70 - 100 ms before the response onset. This peak could be representative of the N2 event related potential. According to CM account, this potential could be the correlate of response elaboration: this hypothesis is supported by the current simulation.



Figure 25. Response Conflict Wave: Correct response. Time is referred to response onset.

As regard erroneous trials, an example of flanker error is shown in Figure 26, where the R layer activation waveforms are illustrated. The correct response does not reach threshold and is slowly suppressed by flanker error response. This results in the conflict shape depicted in Figure 27. Pre response conflict is not high because of the prominent and fast activation of the flanker response. Typically error responses result faster than the correct ones (Eriksen & Eriksen, 1974). After the response onset, conflict peaks 50 - 70 ms after to error commission. This could be a good candidate to simulate ERN. As the correcting response slowly decreases, the conflict consequently remains different from zero and decreases slowly as well.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 26. Time – pattern of the outputs in the R Layer with "VVVBVVV" as input stimulus. Note that y axis is not the same in the four possible responses. BK, the correct response, is slightly activated but then suppressed by the emerging flanker response, MV. This results in a flanker error. The correct response slowly decreases, so no correcting response is given. PR and WX, activated by noise, are immediately suppressed.



Figure 27. Response Conflict Wave: Error response. Time is referred to response onset.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Simulations were repeated with the new model over 960 trials: 48 neutral stimuli and 48 incongruent stimuli per 10 simulated participants. Results consist of response times and error rates, sorted by condition, neutral or incongruent (see Figure 28). As regards erroneous incongruent trials, errors are divided in flanker type and non flanker type (see Figure 29). It should be noted that flanker error rates is now lower than non flanker error rates (see Figure 22).



Figure 28. Behavioural data (Maier et al. 2008) and simulated data both show lower error rates on neutral trials than on incongruent trials, and slightly faster response in the neutral condition with respect to incongruent condition on correct trials. Response time was calculated adding to simulation result 400 ms.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 29. Flanker and Non Flanker Errors. The network simulates appropriately both error rates and response times. Response time was calculated adding 400 ms to simulation result.

Finally ERN amplitude was compared with response conflict amplitude in the mentioned condition. Results are reported in the following figures. For a complete discussion see the *General Discussion* section.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 30. ERN amplitude (Behavioural) compared with response conflict (Simulated) in the neutral/incongruent condition. Simulated conflict values were multiplied for a scalar coefficient in order to compare the results.



Figure 31. ERN amplitude (Behavioural) compared with response conflict (Simulated) in the flanker/non flanker conditions. Simulated conflict values were multiplied for a scalar coefficient in order to compare the results.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The effect of Flanker Size

As mentioned in the *Expectancy*, *Significant and Detectability* paragraph, varying flanker size can be helpful in the understanding of important features of the ERN, such as its amplitude. For example, in a single trial simulation, varying flanker size from the smaller to the larger, one can notice that response times became slower on correct trials. The effect of different sizes was modelled varying the *attentional parameters ratio*, which means A max /A min . If flanker becomes too large, then, using the same parameters and the same noise, a correct response turns into a flanker error as shown in Figure 32.



Figure 32. Activation of R Layer in 5 different simulations with different flanker size (increasing size from simulation 1 to simulation 5). Input Stimulus = 'BBBPBBB'. Correct response =PR. Flanker Response =BK. Note that y axis have a different scaling and that a logarithmic scale was used to allow a better visualization. From 1 to 4 the response is correct. Case 5 show a flanker error response. All simulation shared the same parameters, except the attentional parameters ratio (see Appendix C for a detailed description).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As regard conflict shape, increasing the flanker size a higher peak is visible preceding response onset in the correct response condition. Figure 33 shows an example.



Figure 33. Response conflict in 4 condition with increasing flanker size from 1 to 4. Response onset (R.O.), in dotted lines, is shown for each case.

From those considerations, simulations of the network were performed with different flanker size. For more information about the parameter used see complete data in *Appedix* C. Results include, as well, response times, error rates and conflict amplitude. Only the incongruent condition was investigated.
Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As the size of the flanking letter increases, behavioural data show slower responses, higher error rates and greater ERNs amplitude. Furthermore, increasing flanker size, the number of flanker error increases. Experimental results are summarized in Table 7 (from Maier et al. 2011).

	Smal	l Flanker	Larg	ge Flanker
	correct	error	correct	error
Error Rates (%)	80,76	19,24	79,67	20,33
Response Times (ms)	577	535	602	557
Error Type	Flanker	Non Flanker	Flanker	Non Flanker
Error Rates (%)	6,81	12,43	8,18	12,15
ERN Amplitude (µV)	6,31	6,84	8,23	6,51

Table 7. Behavioural results from Maier et al. (2011). Error rates and response times are reported in both small and large flanker conditions. Error trials are sorted in flanker error and non flanker error: relative error rates and ERN amplitudes were evaluated.

Simulations were repeated 480 times (48 incongruent stimuli for 10 simulated subjects) and response times, error rates and conflict amplitudes were evaluated. The effect of different flanker sizes was obtained changing one parameter only: central attentional weight A_{hight} . A similar result would have been obtained if it was kept high and fixed A_{hight} and A_{min} was slowly increased (see *Appendix* C).



Figure 34. Error rates and response times simulated compared with behavioural data (Maier et al. 2011) considering two possible flanker size, which we refer as 'small flanker' and 'large flanker'.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

The model fits error rates and response times quite well. In Figure 35, error rates in the flanker error condition are compared with the simulated results: the network overestimate flanker error in the small flanker condition; by the way, the global trend asserts that increasing flanker size increases the number of simulated flanker errors. For what concerns conflict peak amplitude, it was compared with ERN amplitude in the general small and large flanker conditions. Large flanker stimuli are associated with higher response conflict with respect to small flanker stimuli in the behavioural data as well as in the simulated ones.



Figure 35. Error rates in the flanker error condition.

Finally, within those two condition, flanker errors and non flanker errors conflict amplitude were compared separately with the respective behavioural data (see Figure 36 and 37). Simulated results follow behavioural trends. Differences in ERN amplitudes was more pronounced with large flanker, this result was partially confirmed by simulations.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 36. ERN amplitude (Behavioural) compared with response conflict (Simulated) in the small/large flanker condition, incongruent error trials. Simulated conflict values were multiplied for a scalar coefficient in order to compare the results.



Figure 37. ERN amplitude (Behavioural) compared with response conflict (Simulated) in the flanker/non flanker condition in the two cases of study: small flanker (left panel) and large flanker (right panel). Simulated conflict values were multiplied for a scalar coefficient in order to compare the results.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Sensitivity Analysis of Parameters

Sensitivity analysis is fundamental for understanding the behaviour of a non - linear model and to assess how the obtained results depend on individual factors. For each parameter sensitivity analysis was preformed, varying one parameter at a time in a defined range, with fixed step. For each parameter value, a whole simulation of 960 trials was performed. Response times and error rates are calculated at each step and plotted along with parameter range values. Referential parameters values are those used in the first simulation with conflict added, for more details see Appendix B. Relevant results are here reported and discussed. Note that reported times refer to simulation time.

The effect of Flanker Size

Attentional parameters are A high and A low. Those parameters encode the amount of attention given to the central letter and the lateral letters respectively. S-Figure 1 shows error rates and responses times in the neutral and in the incongruent condition along with increasing A hight values. Figure S-Figure 2 shows error rates relatives to flanker and non flanker errors. Varying A hight from a lower value to a higher value, means increasing the attentional weight on central target. Consequently performance improves in terms of faster response times and lower error rates. The attentional enhancement effect is confirmed by flanker error rates, which gets lower as the value of the parameter increases.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



S-Figure 1. Sensitivity analysis on parameter A hight. Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates, neutral condition.



S-Figure 2. Sensitivity analysis on parameter A hight . Flanker and Non Flanker error rates.

Varying A_{low} , one could expect symmetrical results. Actually, increasing A_{low} value worsen only the performance on incongruent trials, leaving unchanged neutral error rates. This because in the incongruent condition more attentional error are committed.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Accordingly the number of flanker error increases along with increasing parameter values. Results are shown in S-Figure 3 and 4.



S-Figure 3. Sensitivity analysis on parameter A_{low} . Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates, neutral condition.



S-Figure 4. Sensitivity analysis on parameter A_{low}. Flanker and Non Flanker error rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

S Layer Parameters and Intralayer Competition

S layer parameters are W_{hight} and W_{low} . As concerns W_{hight} increasing the weight between a stimulus input and its response results in improved performance as regards response times and error rates, for both neutral and incongruent stimuli. Since flanker response receives a strong flanker stimuli input during the trial, the proportional number of flanker error increases (see S-Figure 5 and 6).



S-Figure 5. Sensitivity analysis on parameter Whight. Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel =error rates, incongruent condition. Right lower panel = error rates, neutral condition.



S-Figure 6. Sensitivity analysis on parameter Whight. Flanker and Non Flanker error rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As regards W_{low} , increasing values of the parameter result in higher error rates for both conditions. Not significant variation affected flanker and non flanker error rates in this range.



S-Figure 7. Sensitivity analysis on parameter Wlow. Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates, neutral condition.

Intralayer competition parameters do not affect performance significantly. The only reported effect is the shortening of response time along with greater excitation parameters values (L_{ex} and H_{ex}). The opposite result is found assigning a less negative value to inhibition parameters (L_{in} and H_{in}).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Noise Parameters

Noise parameters are st_s and st_r, standard deviation of noise in the stimuli layer and in the response layer respectively. Mean values of added noise is always set to zero in both layers in all the reported simulations of this paper. Varying st_s in a close range (0 - 1), no relevant effects was found. Increasing the range amplitude, it was found that high st_s value result in dramatic performance impairment (see S-Figure 8).



S-Figure 8. Sensitivity analysis on parameter sts. Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel =error rates, incongruent condition. Right lower panel = error rates, neutral condition.

Variations of str have significant effect on performance. The absence of noise in the response layer lead to all correct responses. Rising noise results in increased error rates as expected. This parameter does not affect significantly response times. As regards flanker error and non flanker error, increasing noise result in a higher error rate in the non flanker error type. See S-Figure 9 and 10.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



S-Figure 9. Sensitivity analysis on parameter str. Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates, neutral condition.



S-Figure 10. Sensitivity analysis on parameter str. Flanker and Non Flanker error rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Attentional Enhancement Parameters

Two parameters are used in the definition of the mechanism of attentional enhancement by means of response conflict: A $_{max}$ and A $_{min}$. As it could be predictable, increasing the weight of conflict by A $_{max}$ rapidly improves the performance in terms of response times and error rates. For higher values of A $_{max}$ error rates seems to grow. This could be due to noise in the central part of the stimuli layer: that is also confirmed by the higher non flanker error rates. Flanker error rates decreases as attention overcomes flanking letters interference. Results are reported in S-Figure 11 and 12.



S-Figure 11. Sensitivity analysis on parameter A_{max} . Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates, neutral condition.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



S-Figure 12. Sensitivity analysis on parameter Amax. Flanker and Non Flanker error rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As concerns A_{min} , setting this parameter to zero means that in the early stage of each trial no attentional enhancement is given to central letter since A_{max} and A_{min} lose their role multiplied by zero. As shown in S-Figure 13, performance improves from this situation to parameter value 2, whereas a high attentional input results in an increased number of error responses due to noise.



S-Figure 13. Sensitivity analysis on parameter A_{min} . Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates neutral condition.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



S-Figure 14. Sensitivity analysis on parameter Amin. Flanker and Non Flanker error rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Threshold

Threshold is a fundamental parameter if one wants to compare results of trials in which accuracy is emphasized over speed or vice versa. In fact, giving a lower value to this parameter resembles the condition in which the subject is required to produce faster responses. This results in reduced response times on correct responses but in a higher error rate. Higher value of th resemble the condition in which accuracy is emphasized. So response times become slower and error rates decrease. The network reproduce both behavioural findings (see S-Figure 15). Threshold parameter does not affect flanker and non flanker error rates.



S-Figure 15. Sensitivity analysis on parameter th. Left upper panel = response times on correct trials, incongruent condition. Left lower panel = response times on correct trials, neutral condition. Right upper panel = error rates, incongruent condition. Right lower panel = error rates. neutral condition.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

General Discussion

In this section simulated results using the described new neural network are discussed in light of the exposed Executive Control theories.

In its first implementation, the network, as depicted in Figure 18, can explain some behavioural effects. The most relevant is congruency effect, defined as the impairment in performance on incongruent trials with respect to congruent trials. During a congruent trial, three neurons of the S Layer encoding the same response result activated. This makes the activation of the correct response stronger and faster, consequently it is less likely that noise wins the competition, producing an error response. In the incongruent condition, if not enough attentional control is engaged, flanker can compromise stimulus processing leading to slower correct response or to erroneous response. The same thing can happen if noise strongly activates an erroneous response, in both congruent or incongruent condition. It is possible, then, to say that the difference in error rates of incongruent trials is due to attentional errors, since noise contributes to error responses number in the same measure in both conditions.

The four choice flanker task allowed the distinction between flanker and non flanker error. Attentional errors make, in normal condition, raise flanker errors rate above the 33%. In fact, if all errors were due to noise action, then each response should share with the other 1/3 of the error trials. Consequently it would be found that flanker errors (one response in the four possible) cover the 33% of all errors and that non flanker errors (two responses in the four possible) cover the residual 66%. This simple feedforeward model based on intra – layer competition, does not account for the attentional enhancement required on incongruent trials. While the network simulate quite well error rates and response times (see Figure 21), flanker errors result overestimated. This can be explained considering that not enough attention is allocated on target and flanker suppression is consequently inefficient increasing the amount of attentional errors (see Figure 22 or comparison in Figure 38).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

From this point, it was possible to assert that a controlling variable is needed to recruit attentional enhancement when necessary: this is the same fundamental statement of the exposed Executive Control theories. The chosen variable was conflict, as suggested by the Conflict Monitoring account. Response conflict was evaluated from the value of activation of neurons in the R layer (a similar signal was used in Yeung et al., 2004). The general idea is that conflict monitoring during the trial is the best and easier way for online evaluation of good or bad outcome. For example, one could consider a trial in which the correct response is activated as well as noise responses (indifferently flanker or non flanker). In the initial part of the trial conflict would be high, because two or more response are activated. Proportionally, attentional input would grow exciting central target and so the correct response. As a consequence of competition within the layers, noise responses would be inhibited. Conflict during the trial would, then, turn lower in amplitude and its peak value should lay before the response onset: from that point on, the winning neuron could finally overcome other neurons in the R layer and conflict would tend to zero. If flanker letters activation results too strong (this could be due to insufficient attentional input or to noise), then the error response would compete with the correct one which is raised by attention as well. The production of an erroneous response should be then accompanied by a greater amount of conflict peaking after the response onset, since two or more responses will result still activated even after error commission, due to attentional enhancement.

In conclusion, monitoring for conflict should improve performance in the sense that those trials in which conflict is high should see the enrolment of a greater amount of attention that should result in a better performance and in a lower conflict during the trial itself. Our results confirm this assumption, in fact the number of flanker error decreases accordingly introducing the feedback. In Figure 38, Figure 22 is compared with Figure 29 showing flanker and non flanker error rates estimated with and without conflict. Hypothesis on conflict shape in correct and error trials was confirmed (see Figure 39).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 38. Flanker and Non Flanker. Comparison between simulated results from the first implementation of the network (left panel), without conflict, and the second implementation of the network, with conflict added (right panel). Behavioural data are the same in both figures.

The recent neuroscientific literature debates whether ERN is the correlate of a conflict signal or of a reinforcing signal, as underlined explaining the major claims of conflict monitoring and reinforcement learning respectively. The main features of the response conflict time pattern simulated by this network were then compared with relevant ERPs: N2 and the ERN in particular. What seems sure is the relationship between conflict on correct trials and N2 event related potential. N2 is believed to be related to stimulus processing and so it could also represent the early activation of competing responses before an open response is given. As regards ERN, it should peak soon after the response onset of incorrect trials. Conflict - time pattern simulated by this network, are depicted in Figure 39. Conflict on correct trials could be a good candidate to simulate N2: it peaks before the response onset and its amplitude is smaller than ERN (for the relative timing and shape of N2 and ERN together see Figure 9). Conflict peak amplitude on error trials is higher than on correct trial and this maximum value is reached after the response onset. Those conflict features resemble ERN.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*



Figure 39. Time – pattern of response conflict in the correct and in the error case, average values in neutral and incongruent condition per correct and error responses type. Trials with error correction or late response (simulation time > 400 ms) were excluded.

Simulated results showed that conflict amplitude results lower in the neutral condition with respect to the incongruent condition, in agreement with behavioural data (see Figure 30). Time – pattern of conflict in the neutral and in the incongruent condition are reported in Figure 40. This results support the hypothesis that conflict is directly correlated with the error related negativity.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna

Gabriella Cefalù



Figure 40. Time – pattern of response conflict for correct responses (top panel) separately for neutral and incongruent condition. Time – pattern of response conflict error trials (bottom panel) separately for neutral and incongruent condition. Trials with error correction or late response (simulation time > 400 ms) were excluded.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Looking at the flanker and non flanker condition, simulated data shows the same pattern of behavioural results in this two types of error (see Figure 31 and Figure 41 for simulated conflict shapes). This result is in contrast with what Conflict Monitoring theories holds. Some authors suggest that non flanker error should be associated with a higher conflict peak value because the commission of a non flanker error implies that three responses are activated: the correct one, the flanker one and the non flanker one (Steinhauser et al., 2008; Maier et al., 2012). On flanker error case, only the correct response and the flanker error response are simultaneously activated and this results in a lower conflict on those trials.



Figure 41. Time – pattern of response conflict for flanker and non flanker errors. Trials with error correction or late response (simulation time > 400 ms) were excluded.

According to the structure of this network, it is possible to explain the results considering that in the non flanker error case, it is true that three responses are activated, but the neurons in the R layer inhibit one another: this would eventually results in a global lower activation of all response in the game! In the flanker error condition strong flanker activation in the S layer and a great attentional input can lead to high activation of both responses, the correct one and the flanker one, leading to a resultant conflict signal a bit higher. Moreover, the difference in ERN amplitude reported in literature is of course significant but not huge, proving that the dynamics of competition in this two type of errors could not be so different in terms of activation amplitude, as simulated results confirm.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

As regards the features that can affect ERN amplitude, flanker size was investigated. The results are in accordance with behavioural data (Maier et al. 2011), fitting experimental results quite well. Increasing flanker size induced a greater amount of conflict, either in correct trials and in error trials, as shown in a single simulation in Figure 33 and for a whole block of trials in Figure 42. This is another point for the hypothesis that conflict is a well suited candidate to explain ERN features.



Figure 42. Time – pattern of response conflict for correct responses (top panel). Small flanker compared to large flanker. Time – pattern of response conflict error trials (bottom panel). Small flanker compared to large flanker. Trials with error correction or late response (simulation time > 400 ms) were excluded.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Behavioural data regarding ERN amplitude in flanker and non flanker conditions show an inversion in the conflict simulated amplitude of this two types of errors. In particular, in the small flanker condition both simulated and behavioural data show a higher amplitude of conflict and of ERN respectively in the non flanker case. Actually this result could be explained by considering the greater excursion of flanker error amplitudes from the small flanker condition to the large flanker condition. In other words, non flanker amplitudes do not change much along with flanker size. The opposite thing happens to flanker error, to such an extent that amplitudes of flanker errors in both behavioural and simulated data result lower than non flanker errors values with small flankers.

If the hypothesis reported above is correct, this result could be justified considering that a smaller flanker means a less activated flanker response. In the large flanker condition, flanker error response is strongly activated and the same happens to the correct response since high response conflict means greater attentional enhancement. This translate in a lower worsening in performance along with greater ERN amplitude enlargement (or conflict amplitude, if one considers simulated data), explaining both simulated and behavioural data. See activation pattern in the large flanker and in the small flanker conditions in Figure 43.

Beyond those considerations the simulated results support the error significance account. ERN, then, represents the correlate of an error detecting system which evaluates the type of error, its value in the current task and in this sense error significance. Conflict, as defined in this paper, seem to have all the right properties to explain ERN features over a wide range of behavioural findings.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna Gabriella Cefalù



Figure 43. Time – pattern of response conflict for flanker and non flanker errors in the small flanker condition (top panel) and in the large flanker condition (bottom panel). Trials with error correction or late response (simulation time > 400 ms) were excluded.

100

ms

50

0

-150

-100

-50

response onset

150

200

250

300

350

> Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Conclusions

The new neural network described in this thesis was used to fit several empirical results. It proved to be suitable for the explaining of different Eriksen Flanker Task variants and their relative behavioural results. Moreover, the introduction of conflict as performance monitoring signal allowed the simulation of relevant event related potentials. In particular, analogies between ERN and conflict time – pattern were found. Just like ERN, conflict signal shows a higher peak value on incorrect trials soon after the response onset. Conflict amplitude varies according to the type of stimulus resembling ERN amplitude variations in tasks involving neutral and incongruent stimuli or in tasks with different flanker size. In conclusion, conflict signal explain quite well some ERN features and this model provides a new framework in which Executive Control processes can be investigated and understood.

A new hypothesis that could be taken into account is that conflict is a *partial* ERN correlate. It should be noticed that ERN, such as other event related potential registered on the scalp, is fundamentally the sum of the neural activity of neural populations. In this sense, it may be the sum of different signals, including in this list response conflict. Future development of the model could consider, for example, the sum of activation of S layer and R layer, or a weighted sum of the two conflict signals of both layers, evaluated for each one separately as Hopfield energies. This new signal could provide a better correlate for ERN, helping in the explaining of its features in different types of task.

In the future development of this neural network, it could be possible build an *inter* – *trial* attentional enhancement system using conflict signals in order to explain performance improvement trial by trial. With 'inter – trial' is intended a mechanisms that enhances attention trial by trial if an error is committed. The mechanism implemented so far with conflict feedback was an *intra* – *trial* attentional enhancement, which means that more attention was recruited if needed within the trial, and no improvement in performance could be evaluated in a block of trials. An inter – trial attentional enhancement can be considered a sort of reinforcing signal and, through this, mechanisms related to reward and punishment could be included and investigated with this network.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Finally, it would be interesting the inclusion of an hebbian learning rule in the synapses between R layer and S layer. In this sense, once a correct response is given, the relative synapse would be straightened whether when an error is committed the relative synapse would be weakened. This new mechanism should allow the simulation of post error adjustments, such as post error slowing, helping elucidating the nature of those processes.

Introducing those modification could, through simulated results, support the conception of a new cognitive theory that reconciles conflict monitoring accounts and reinforcement learning accounts aiming at the explaining of as much behavioural results as possible. With a simple model based on lateral *intra* – *layer* inhibition, on *intra* – *trial* conflict monitoring and on *inter* – *trial* reinforcing signals, it would be hopefully possible to explain a wide range of Executive Control mechanisms.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Appendix A

In this appendix parameters and complete results obtained from simulations of the neural network depicted in Figure 18 are illustrated. Reported data in A – Table 2 are shown in Figure 20. A – Table 1 shows value assigned to parameters.

Ahight	Alow	Whight	Wlow	Lex	Lin	Hex	Hin	Amax	Amin	th
4.5	3	6	0.1	3	-9	3	-5	4	1	0.6

S	Teta	Sts	Str	Tau
1.6	2.5	0.5	1.6	100

A - Table 1. Parameters Values.

	Cong	ruent	Incon	gruent
	Correct	Error	Correct	Error
RT (ms)	106.4723	100.0345	118.9945	100.5214
STD	29.1870	29.1870	36.5217	65.4684
%	93.9583	6.0417	75.6250	24.3750
Correction %	100	100 0		0
N° of not given resp	onses = 0			

A - Table 2. RT= Response Times. STD = Standard Deviation. %= Error Rates. Correction % = correction rates: correct correction means that the right response is been given, error correction means that the response was followed by an erroneous response, whether the first response was correct or not. A not given response is a response that does not reach threshold (parameter th).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Reported data in A – Table 4 are shown in Figure 21. Reported data in A – Table 5 are shown in Figure 22. A – Table 3 shows values assigned to parameters.

Ahight	Alow	Whight	Wlow	Lex	Lin	Hex	Hin	Amax	Amin	th
4	2	6	0.1	3	-9	3	-5	4	1	0.6
		S	Teta	ı	Sts	Str	Ті	<i>u</i>		
		1.5	2.5		0.5	1.9	1	00		

A - Table 3. Parameters Values.

	Neuti	al	Incongruent			
	Correct	Error	Correct	Error		
RT (ms)	121.4653	112	118.108	136.5963		
STD	44.6323	38.4208	86.8968	97.4973		
%	77.6151	22.3849	76.8085	23.1915		
Correction %	23.3813	0	29.3578	0		
N° of not given resp	onses = 10					

A - Table 4. RT = Response Times. STD= Standard Deviation. % = Error Rates. Correction % = correction rates: correct correction means that the right response is been given, error correction means that the response was followed by an erroneous response, whether the first response was correct or not. A not given response is a response that does not reach threshold (parameter th).

	Flanker	Non Flanker
RT (ms)	113.9914	101.9565
STD	40.1934	25.8860
0⁄0	83.4532	16.5468

A - Table 5. RT = Response Times. STD = Standard Deviation. % = Error Rates.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Appendix B

In this appendix parameters and complete results obtained from simulations of the neural network depicted in Figure 23 are illustrated. Reported data in B – Table 2 are shown in Figure 28 and 30. Reported data in B – Table 3 are shown in Figure 29 and 30. Reported data in B – Table 4 are shown in Figure 39. B – Table 1 shows parameters values used.

Ahight	Alow	Whight	Wlow	Lex	Lin	Hex	Hin	Amax	Amin	th
10	3	6	0.1	3	-6	3	-5	4	1	0.6
		S	Teta	l	Sts	Str	Та	<i>u</i>		
		15	2.5		0.5	19	1	00		

B - Table 1. Parameters Values.

	Incong	gruent	Neutr	al
	Correct Error		Correct	Error
RT (ms)	132.5457	113.2069	131.3680	124.0095
STD	51.5344	60.3976	62.9250	65.0452
%	75.6813	24.3187	78.1250	21.8750
Conflict Amplitude	0.0646	0.0767	0.0573	0.0718
Conflict Peak Time (ms)	101	168	100	162
Correction %	31.0345	0	27.6190	0

N° of not given responses = 10

B - Table 2. Table 6. RT = Response Times. STD = Standard Deviation. % = Error Rates. Conflict Amplitude = max value reached by conflict time – pattern (average value). Adimensional. Conflict Peak Time = the time value corresponding to Conflict Amplitude. Correction % = correction rates: correct correction means that the right response is been given, error correction means that the response was followed by an erroneous response, whether the first response was correct or not. A not given response is a response that does not reach threshold (parameter th).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

	Flanker	Non Flanker
RT (ms)	101.6000	122.0000
STD	37.7235	72.1042
%	43.1034	56.8966
Conflict Amplitude	0.0861	0.0737
Conflict Peak Time (ms)	248	181

B - Table 3. RT = Response Times. STD = Standard Deviation. % = Error Rates. Conflict Amplitude = max value reached by conflict time – pattern (average value). Adimensional. Conflict Peak Time = the time value corresponding to Conflict Amplitude.

	Correct Trials	Error Trials	
Conflict Amplitude	0.0609	0.0742	
Conflict Peak	101	164	

B - Table 4. Conflict Amplitude = max value reached by conflict time – pattern (average value). Dimensionless. Conflict Peak Time = the time value corresponding to Conflict Amplitude. Correct Trials = all correct responses irrespective of stimulus type. Error Trials = all erroneous responses, irrespective of stimulus type.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Appendix C

In this appendix parameters and complete results obtained from simulations of the neural network depicted in Figure 23 are illustrated. Reported data in C – Table 2 are shown in Figure 34 and 36. Reported data in C – Table 3 are shown in Figure 35 and 37. C – Table 1 shows parameters values used in the *Small Flanker* condition.

Ahight	Alow	Whight	Wlow	Lex	Lin	Hex	Hin	Amax	Amin	th
25	0.1	6	0.1	3	-6	3	-5	4	1	0.6
		S	Teta	ı	Sts	Str	Та	<i>nu</i>		
		1.2	2.5		0.5	1.7	1	00		

C - Table 1. Parameters Values.

	Incongruent	
	Correct	Error
RT (ms)	126.0517	124.3370
STD	58.5625	51.4648
%	80. 7933	19.2067
Conflict Amplitude	0.1077	0.2121
Conflict Peak	106	168
Correction %	42.3913	6.5217
N° of not given respon	ses = 1	

C - Table 2. RT = Response Times. STD = Standard Deviation. % = Error Rates. Conflict pattern Amplitude = value reached by conflict time _ (average value). max Adimensional. Conflict Peak Time = the time value corresponding to Conflict Amplitude. Correction % = correction rates: correct correction means that the right response is been given, error correction means that the response was followed by an erroneous response, whether the first response was correct or not. A not given response is a response that does not reach threshold (parameter th).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Flanker	Non Flanker
119.1143	127.5439
64.4204	41.9149
38.0435	61.9565
0.1559	0.1931
160	206
	Flanker 119.1143 64.4204 38.0435 0.1559 160

C - Table 3. RT = Response Times. STD = Standard Deviation. % = Error Rates. Conflict Amplitude = max value reached by conflict time – pattern (average value). Adimensional. Conflict Peak Time = the time value corresponding to Conflict Amplitude.
Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

Reported data in C – Table 5 are shown in Figure 34 and 36. Reported data in C – Table 6 are shown in Figure 35 and 37. C – Table 4 shows parameters values used in the Large Flanker condition.

Ahight	Alow	Whight	Wlow	Lex	Lin	Hex	Hin	Amax	Amin	th
15	0.1	6	0.1	3	-6	3	-4	4	1	0.6
		S	Teta	St	'S	Str	Таи			
		1.2	2.5	0.	.5	1.8	100			

Incongruent		
Correct	Error	
48.0550 1	31.3854	
55.4775	75.0348	
79. 7933	20.2067	
0.1181	0.2662	
109	245	
59.3750	0	
	Incongrue Correct 48.0550 55.4775 79.7933 0.1181 109 59.3750	

C - Table 4 Parameters Values.

 N° of not given responses = 0

C - Table 5. RT = Response Times. STD = Standard Deviation. % = Error Rates. Conflict Amplitude = max value reached by conflict time – pattern (average value). Adimensional. Conflict Peak Time = the time value corresponding to Conflict Amplitude. Correction % = correction rates: correct correction means that the right response is been given, error correction means that the response was followed by an erroneous response, whether the first response was correct or not. A not given response is a response that does not reach threshold (parameter th).

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

	Flanker	Non Flanker
RT (ms)	113.3243	142.7119
STD	34.7443	90.1889
%	39.5417	60.4583
Conflict Amplitude	0.1911	0.1733
Conflict Peak	199	185

C - Table 6. RT = Response Times. STD = Standard Deviation. % = Error Rates. Conflict Amplitude = max value reached by conflict time – pattern (average value). Adimensional. Conflict Peak Time = the time value corresponding to Conflict Amplitude.

Tesi di Laurea Magistrale - Alma Mater Studiorum di Bologna *Gabriella Cefalù*

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