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Authors
Kallioinen, Petter
Sikstrom, Sverker

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Negative Subsequent Memory Effect in ERP: Modeling and Data

Sverker Sikström (sverker.sikstrom@lucs.lu.se)
Petter Kallioinen (petter.kallioinen@lucs.lu.se)
Lund University Cognitive Science (LUCS), Kungshuset, Lundagård
Lund, 222 22, Sweden

Abstract

The subsequent memory effect (SME) is the ubiquitous phenomena that stimulus that are later retrieved show a more negative going ERP wave than stimulus that are not retrieved. Two basic findings in neurophysiology are that cells respond weaker to repeated stimulation (e.g. synaptic depression) and that the response differentiates during familiarization. This paper presents a computational theory of SME based on synaptic depression and cell differentiation. SME occurs because synaptic depression is stronger for stimuli with larger cell differentiation and these stimuli are also easier to retrieve. The model also predicts a negative subsequent memory effect (NSME) so that a stimulus that are not preceded with other stimuli are recovered from synaptic depression, better recalled, and have a more positive ERP. The model is tested on ERP data collected during study of short lists followed by free recall.

Keywords: ERP, model, cell, depression, differentiation, LTP/LTD, negative subsequent memory.

Introduction

Subsequently remembered stimuli evoke more positive going ERPs during study than stimuli that are not remembered (Sanquist, Rohrbaugh, Syndulko and Lindley, 1980; Johnson, 1995; Rugg, 1995). This effect is called the difference due to memory (DM) effect or the subsequent memory effect (SME, Paller, Kutas and Mayes, 1987). SME has been found with different stimulus material and with different test procedures (e.g., Sanquist et al., 1980; Besson and Kutas, 1993; Fabiani and Donchin, 1995). Topographically, two classes of SME have been found, one with centroparietal and one with frontal maxima. Frontal subsequent memory effect are associated with elaborative encoding strategies, particular right frontal effects may be related to associative processes (Karis, Fabiani and Donchin, 1984; Fabiani, Karis and Donchin, 1990), whereas centroparietal subsequent memory effects are associated with rote encoding (Fabiani et al., 1995).

This paper proposes a neurophysiologically based model to account for the subsequent memory effect. This model is based on the empirical finding of synaptic depression and cell differentiation and it is therefore called the differential depression (DD) model. It also predicts that for certain experimental conditions a more negative ERP may also be associated with successful subsequent memory.

First, a brief review of synaptic depression and cell differentiation is provided. Then the DD model is presented along with the predictions. Finally, the model is tested in a list learning experiment with of high and low frequency words where ERPs are measured during study.

Synaptic Depression and Cell Differentiation

Synaptic depression is the strongest form of short-term plasticity (Nelson, Varela, Sen and Abbott, 1997). The underlying mechanism of synaptic depression is not fully understood. However, one mechanism is believed to be presynaptic depletion of transmitter substances, which is stored in the release-ready pool of vesicles. With this depletion, pre-synaptic action potentials have reduced efficiency on the post-synaptic activity. Synaptic depression depends on activity so that higher levels of recent pre-synaptic activity tend to the decrease the efficiency of transmission.

Synaptic depression can be simulated by a simple depletion model. This model assumes that a portion of the available resources needed for transmitting a signal are consumed with each neural spike (Tsodyks and Markram, 1997).

Cell differentiation is the empirical phenomena that the neural representation becomes increasingly distinct, and that the overall activity decreases, as a stimulus material is familiarized (Miller and Desimone, 1994; Desimone, 1996). This phenomenon has been studied using single cells recordings in the temporal and frontal lobes of monkeys performing the delayed match to sample task. In this paradigm the monkey is first presented to a matching stimulus, followed by a sequence of sample stimuli. The monkey is rewarded for pressing a lever when the sample stimulus matches the matched stimulus. For example, Rainer and Miller (2000) used either novel or familiarized pictures and found that approximately 56% of the cells showed increased activity compared to baseline for novel stimulus whereas the corresponding percentage for familiarized stimulus were 24%. Cells with decreased activity following familiarization are here called suppressed cells; whereas cells with maintained or increased activity are called static cells.

The primacy effect

The primacy effect is the empirical phenomena that the first few items in a list are better recalled than items in the middle of the list (Murdock, 1960). The primacy effect is often accounted for by rehearsal in short-term

memory, where full attention can be maintained to the first presented item, whereas items later in the list compete for attention with earlier presented items present in the short-term buffer. A problem with the rehearsal account is that a primacy effect typically is obtained when rehearsal is eliminated (see for example, Wixted and McDowell, 1989). The primacy effect typically lasts for fewer serial positions when rehearsal is eliminated, however, the magnitude measured as the relative decrease from the first position typically is as large as under conditions when rehearsal is allowed. Here it is argued that synaptic depression may play a role in the primacy effect.

The Differential-Depression Model

The Differential-Depression (DD) model is based on synaptic depression and cell differentiation. The aim of the model is to account for the stimuli evoked change in neural activity depending on various psychological variables and at the same time account for the memory performance at the behavioral level. The model represents neural activity using rate coding in single neural cells.

The postsynaptic activity of a cell is simply the presynaptic activity, times the conductance between the pre and postsynaptic cells, times the amount of resources available for transmitting the presynaptic signal to the postsynaptic cell. The presynaptic activity is assumed to rise slowly at an exponential rate following stimulus onset.

The available resources are assumed to be consumed proportionally to the post-synaptic activity, and to recover spontaneously at an exponential rate in absence of post-synaptic activity. Resources are assumed to be fully available prior to the onset of the first stimulus, and reaches to an asymptotic value over the first few items in a list of stimuli.

The conductance between the pre and post-synaptic cells is assumed to be undifferentiated for novel stimulus, so that suppressed and static cells have the same conductance. Following familiarization static cells increases their conductance, whereas suppressed cells decrease their conductance. The change in conductance is assumed to be modulated by long-term potentiation (LTP) and long-term depression (LTD) of synaptic efficiency (for reviews see, Lynch, 2003)

Because the synaptic depression depends on the post-synaptic activity, the DD model assumes a pre-synaptic expression of LTP and LTD. Evidence for presynaptic involvement of synaptic depression includes, LTP activates PKA presynaptically (Tong, Malenka and Nicoll, 1996), Genistein inhibits LTP by acting presynaptically (Casey, Maguire, Kelly, Gooney and Lynch, 2002), LTP enhances Externally Regulated Kinases (ERK) activation presynaptically (Casey et al., 2002), LTP activates cAMP response element binding protein (CREB) presynaptically (Gooney and Lynch, 2001). Although, evidence for post-synaptic expression of LTD / LTP is also available (for a review see Lynch, 2003).

Basic mechanisms in the DD-model

The increase in synaptic plasticity for static cells following familiarization is assumed to be balanced by the decrease in conductance for suppressed cells, so that the expected sum of the conductance for all cells is constant over time. However, familiarization decreases the post-synaptic activity for suppressed cells more than it increases the post-synaptic activity for static cells, so that the summed activity for suppressed and static cells decreases with familiarization (see Figure 1). This occurs because static cells are more influenced by synaptic depression (because they are more active) than suppressed cells (that are less active). This phenomenon is henceforth coined *differential depression*, because the
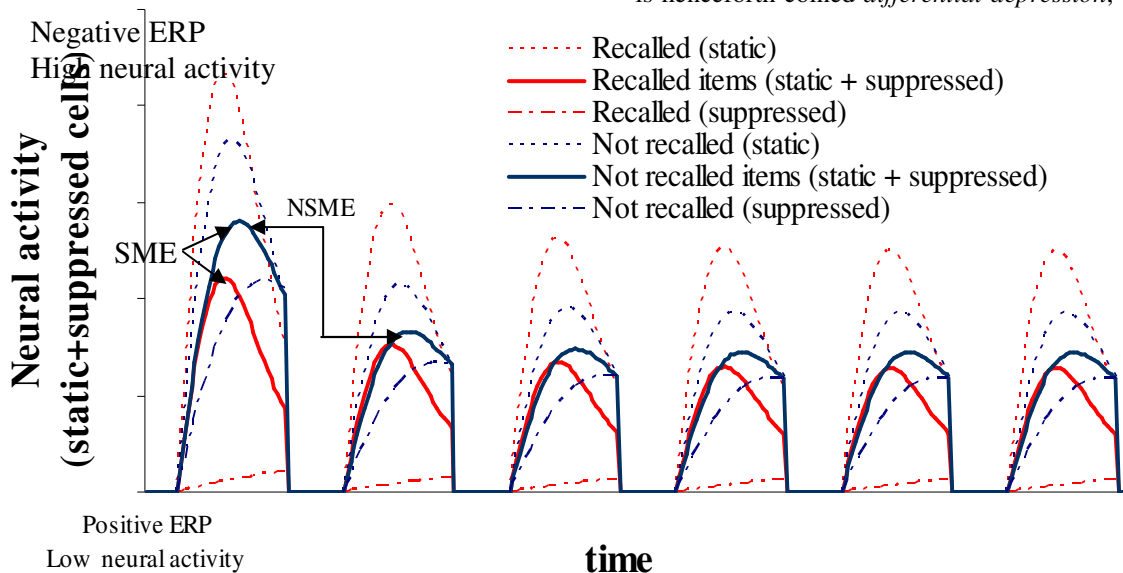

Figure 1. Neural activity in the DD-model during the presentation of six subsequently recalled (red) and not recalled (black) stimuli. The upper dotted lines represent static cells, the lower dotted lines suppressed cells, and the solid lines represent static and suppressed cells. .

static and suppressed cells are differently influenced by synaptic depression.

Mapping neural activity and cell differentiation to ERP and performance

We limit the DD-model to account for the N400 component of the ERP-wave. Earlier components (i.e., N100, P200) are largely influenced by characteristic of the stimulus, and is therefore of minor importance because the goal here to capture more cognitive processes. Furthermore, we are not interested in discrimination studies where a P300 component typically is evoked.

The mapping between ERP waves and the underlying neural activities are complicated by a number of factors such as the alignment of neural cells, and that different components may map differently to activity. However, in the DD-model it assumed that the amplitude, or the degree of negative potential in the N400 component, is proportional to neural activity. Evidence for this assumption comes from simultaneous single cells recording and scalp ERPs, for example during seizure activity in cats (Caspers and Speckmann, 1969; Caspers and Speckmann, 1972; Caspers, Speckmann and Lehmenkuhler, 1980) and response to visual flashes in recording in cortex and thalamus of rats (Coenen and Eijkman, 1972).

The DD-model assumes that free recall performance is directly proportional to cell differentiation, i.e., the difference in neural activity between static and suppressed cells.

Predictions

The DD-model makes the following predictions of the ERP wave and free recall performance. It is assumed that there is a stimuli dependent variability in cell differentiation. Stimuli with a high cell differentiation have a lower neural activity, a more positive N400

potential, and are more likely to be recalled than stimuli with low cell differentiation. That is a subsequent memory effect (SME) is predicted.

Furthermore, synaptic depression is assumed to be low in empirical conditions where stimuli are not preceded with other stimuli. That is the first stimuli in a list will have a lower synaptic depression, a higher neural activity, a more negative N400 potential, and a better free recall performance compared to stimulus in the middle of the list. This prediction is called a *negative subsequent memory effect* (NSME) because good performance is associated to conditions with negative, rather than positive ERPs.

Notice that the SME effect occurs when the ERPs are divided into stimulus that will, or will not, be subsequently recalled. It is stimulus specific and the effect is predicted because particular stimulus utilizes a unique subset of the synaptic connections. In contrast, the NSME effect is found when the ERPs are divided into conditions that are, and conditions that are not, preceded with other stimuli. It is less, or not, stimulus specific because it depends on the synaptic depression accumulated over previously presented stimuli. A SME effect is predicted at all serial positions, including the first serial position, whereas the NSME effect mainly occurs as the difference between the first and the following serial positions.

Finally, the DD-model assumes that high frequency stimuli have a higher cell differentiation compared to low frequency stimuli. That is high frequency stimuli is predicted to have a lower neural activity, a more positive ERP, and a better recall performance compared to low frequency stimulus.

An experiment was setup to test the predictions, where participants studied a short list of low and high frequency words followed by a free recall test. ERPs and free recall performance data were collected.
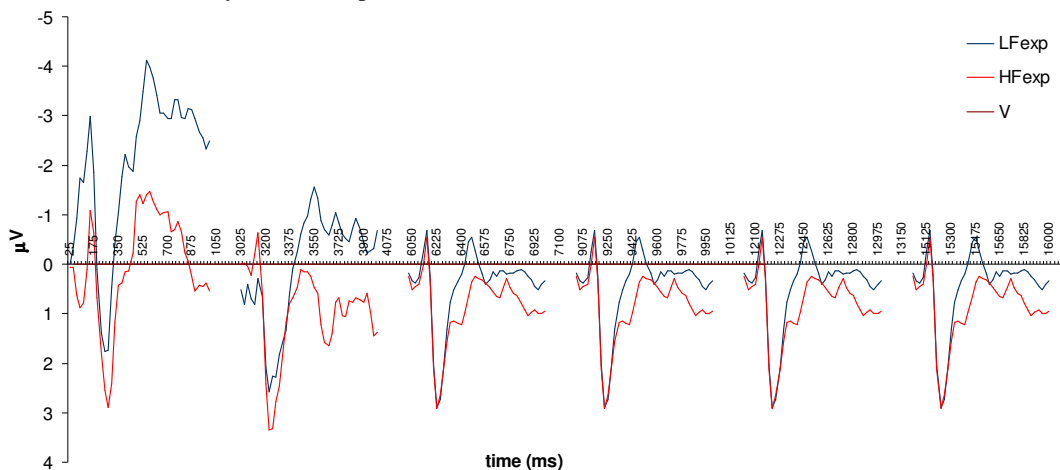

Figure 2. Experimental ERPs potentials for the Fz electrode as a function of serial position divided into high (red) and low frequency (black) words.

Method

Participants. Ten participants with a mean age of 26 (sd 7) were recruited. Five were woman and ten were right handed.

Material. Four-hundred and eighty words were collected from the Stockholm-Umeå-Corpus (SUC) (Ejerhed and Källgren, 1997). Half of the words were low frequency (i.e., 3 occurrences per million) and half high frequency words (100 times or more per million). The words were divided into 80 lists, each consisting of 6 words. One fourth of the lists were pure high frequency words, one fourth pure low frequency words, and the remaining half were mixed with intervening high and low frequency words.

Procedure. Subjects were instructed to focus their attention to the currently presented word and to avoid rehearsal of previously presented words. This was done to minimize rehearsal as an alternative account for the primacy effect. Each word was presented for 1250 ms in white on a black background. A "+" sign served as a fixation point and was presented in a random interval from 1500 to 2000 ms prior to stimulus onset. Following the presentation of the six words a random number signaled the start of a ten second distractor task consisted of counting backwards in steps of three starting with the presented number. This was followed by a 30 second oral free recall test of the previously presented list. The same procedure was repeated with the eighty lists and each list was randomized for each subject.

ERP-data collection. ERP data was collected using a 129 electrode channel Geodesic Sensor Net (EGI. Inc Eugene, OR Tucker, 1993) sampled every 4 ms and filtered from 0.5 to 80 Hz. Epochs were extracted from 200 ms prior and 1000 ms following stimuli onset. Channels in an epoch with ERPs exceeding an absolute value of 50μV were automatically excluded and epochs with more than 10 excluded channels were removed. Furthermore, artefacts were removed using the ICA algorithm as implemented in the EEGLAB software (Delorme and Makeig, 2004). Average references were used and baselines were removed.

Results

Free recall. A primacy effect was found so that the first serial position had a higher percentage correct recall compared to the third serial position (one tailed paired t-test, $t_{(9)} = 3.9$, $p = .001 < .05$, MSE = .03). Furthermore, the last serial position had a higher percentage correct recall compared to the third serial position (two tailed paired t-test, $t_{(9)} = 2.95$, $p = .011 < 0.05$, MSE = .04). Finally, low frequency words were better recalled than high frequency words (two tailed paired t-test, $t_{(9)} = 3.5$, $p = .004 < 0.05$, MSE = .019).

Discussion of the free recall data. As predicted, a primacy effect was obtained despite the fact that subjects were instructed not to rehearse previously presented words, indicating a support for the DD-theory that other mechanisms than rehearsal may play a role in the primacy effect. A recency effect was found so that the last serial position had a higher performance than items in the middle of the list. This indicates that the distractor task was not sufficiently long or strong to totally eliminate the recency effect. Low frequency items were better recalled than high frequency items. This effect can largely be attributed to the mixed lists where earlier studies have either found a low frequency advantage or no frequency effect (Gregg, 1976).

ERP data. Electrodes along the midline of the brain were chosen to study and grouped into four sets along the posterior - anterior dimension. Each set consists of the following six to eight electrodes, labeled according to the EGI sensor net system, starting from the most posterior to the most anterior set (occipital O = [68 67 73 78 72 77 76], parietal P = [32 81 54 55 80 61 62 79], central C = [13 6 113 31 7 107 106], and frontal F = [19 16 10 20 11 4 12 5]).

A 2 X 3 X 2 X 4 X 4 ANOVA was conducted with the following factors; frequency (high, low), serial position (position 1, position 2-5, position 6), subsequent recall performance (correct, incorrect), time windows (100-150 ms, 150-375 ms, 375-600 ms, and 600-825 ms), and electrode sets (O, C, P, and F). All comparisons were made with Greenhouse-Geisser corrections. The following significant effects were obtained. A main effect was obtained for time periods ($F_{(2.34, 29.3)} = 11.7$, $p = 0.00$, MSE = 28.5). A main effect was found for frequency ($F_{(1, 9)} = 4.8$, $p = 0.050$, MSE = 31) where high frequency obtained a more positive going ERP than low frequency words from 200 ms poststimulus. There was no main effect for subsequently recalled words (see Figure 2).

An interaction effect was found for time periods and serial position ($F_{(2.8, 21.9)} = 7.1$, $p = 0.001$, MSE = 14.3). A planned t-test revealed a significantly more negative potential (over the four sets of electrodes) for serial position 1 compared to serial position 2-5 in the 375-600 (one-tailed, $t_{(9)} = 2.25$, $p = 0.022$, MSE = 0.33) and the 600-825 time periods (one-tailed, $t_{(9)} = 2.71$, $p = 0.008$, MSE = 0.50); however, there were no significant difference for the 100-150 and 150-375 time periods.

Discussion of the ERP data. Consistent with the DD-model a negative subsequent memory effect was found for the first serial position compared to the following positions. That is the first serial position had a more negative going ERP in combination with a better performance compared to the following serial positions. The DD-model interprets this as that the first serial position has a larger neural activity (more negative N400 potential) and a stronger cell differentiation leading to better recall performance.

Furthermore, consistent with the DD model the ERPs for the high frequency words were more positive going compared to the low frequency words. This finding is

consistent with earlier studies (Smith and Halgren, 1987; Rugg, 1990). This is interpreted as high frequency words evoke less neural activity than low frequency words. This occurs because high frequency words have a greater cell differentiation leading to more synaptic depression in high than low frequency static cells.

However no subsequent memory effect was obtained. This finding was unexpected because earlier studies typically obtained this effect (Sanquist et al., 1980; Johnson, 1995; Rugg, 1995).. The reason for why no subsequent memory effect was found is unclear.

Discussion

This paper has suggested a neurophysiologic based model of ERPs and behavioral data. The model is based on the empirical finding of cell differentiation and synaptic plasticity. The neural activity is predicted to decrease with cell differentiation because static cells show a smaller increase in neural activity than the decease in activity of suppressed cells as consequence of synaptic depression. Items that are subsequently recalled will have a larger cell differentiation and lower neural activity than items that are not subsequently recalled yielding a subsequent memory effect. Furthermore, the cell differentiation is larger at the first serial position leading to better performance, and more negative N400 potentials for the first serial position compared to the following serial positions. This so called negative subsequent memory effect was also obtained in the experiment. However, no subsequent memory effect was found.

The DD-model yields a different account of why the neural activity diminishes during familiarization compared to current theories. According to Desimone (1996) familiarization of a stimulus causes a sharpening of the neural representation of the static cells and at the same reduces the pool of cells that respond to the stimulus by diminishing the number of stimuli specific cells. Both accounts share the idea of cell differentiation; however, Desimone 's account does not include synaptic depression and furthermore it is a verbally stated theory whereas the DD-model is a computationally implemented model.

We hope that further empirical ERP and single cell recording data in combination with computational modeling will shed light in this complex and interesting field.

Acknowledgments

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