

The neural correlates of evidence accumulation and summed similarity in EEG oscillations

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Abstract

Several studies have indicated a link between scalp EEG oscillations of 4 to 9 Hertz and decision making. An unequivocal connection has been lacking, however, as this theta activity has shown a strong correlation with evidence accumulation irrespective of stimulus similarity in a perceptual decision making task, but also increased with the summed similarity of a probe item to studied items in a recognition decision making task. This current study was to deconfound these two variables by recording scalp EEG activity in participants executing two tasks of roughly equal difficulty, but with different similarity computations. The results should provide grounds for establishing a clearer link between either theta oscillations and evidence accumulation independent of stimulus structure, or between theta oscillations and the summing of similarities. In this present study, we showed left parietal theta activity was linked to direct similarity in a perceptual task, and central alpha activity was correlated to response time in a memory task.

Introduction

Countless evidence-based decisions are made by us on a daily basis. A deeper understanding of how the decision making process works would provide useful information that could have broad implications for many aspects of our lives. It could affect the way we look at accumulating and assessing evidence for decisions with multiple options, such as governance and business policy decisions. It could even have influence on more mundane tasks that involve evidence-based decision making, such as driving or flying.

Multiple models have been proposed to explain the decision making process. The drift diffusion model (DDM; Ratcliff (1978)) is a stochastic differential equation that assumes decisions are made by slowly accumulating evidence over time until one of multiple thresholds is reached. Each threshold corresponds to a response alternative, and the time at which it is reached determines the response time. A graph representation of this process can be seen in figure 1.

Summed similarity models (SSM) state that each

memory is a trace. A memory or stimulus can be represented by a vector of the features that make up that memory:

$$\mathbf{p} = \begin{bmatrix} p(1) \\ p(2) \\ \vdots \\ p(L) \end{bmatrix}$$

Each vector element, $p(1), p(2) \dots p(L)$, represents a single feature that can be individually compared to the corresponding feature of another stimulus. More similar items have a shorter vector distance between them, and thus higher similarity. To decide whether a stimulus is part of a memorized collection, the similarities of each of the stimulus' features to the corresponding features of each element in that collection are assessed. All similarities are summed and the resulting summed similarity is compared to a threshold. Only if the summed similarity value is above the threshold, the stimulus is assumed to be in the collection. This summed similarity model has been successful in accounting for experimental data concerning recognition memory and categorization (Hintzman, 1988). Recognition

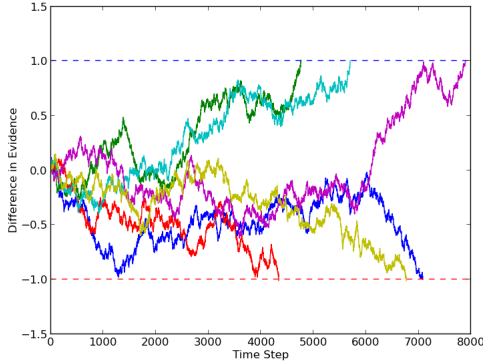


Figure 1: A graphical representation of the Drift Diffusion Model. *Each colored line represents a decision making process. The dashed lines at 1.0 and -1.0 represent decision thresholds. When one of these thresholds is reached, enough evidence has been accumulated to make a decision, and the decision making process stops. The stochastic nature of the DDM can be seen in the form of the swaying of the lines.*

accuracy of test subjects appears to change along with the mean similarity among study items, with higher summed similarity increasing the probability of endorsing an item as a target (Kahana and Sekuler, 2002), and a probe’s similarity to studied items correlates to subjects’ false alarm rates (Kahana et al., 2007; Nosofsky and Kantner, 2006). This is explained by the fact that, even though a probe may not have been one of the studied items (a lure), if it has enough features similar to studied items, its summed similarity will be close to the threshold, causing subjects to often falsely report it was one of the studied items.

Previous studies indicate a connection between decision making and brain activity measured by EEG. Since EEG measures cranial electromagnetic potential, the oscillations measured can be divided in frequency ranges, such as alpha (9-14 Hz), beta (14-31 Hz), gamma (>32 Hz), delta (<4 Hz), and theta (4-9 Hz). Research by Guderian and Düzel (2005) found that post-stimulus theta oscillations (4-9 Hz) increase during recollection of personal events, and concluded theta oscillations are related to the binding of distributed cortical representations. This means theta oscillations seem to play a role in exchanging information between different brain regions, and in integrating infor-

mation from different sources into a whole. Jacobs et al. (2006) have shown, among other things, that theta oscillatory power correlates with decision making confidence at central electrodes in a memory retrieval task, with memory recognition at left-parietal electrodes, and with memory load at widespread electrodes. Intracranial theta activity in the medial temporal lobe has been shown to increase with summed similarity, demonstrating direct neural correlates of similarity computations (van Vugt et al., 2012a). Theta oscillations also strongly correlate with evidence accumulation in a perceptual decision making task, and the rate of power decrease in the theta band covaries with individual differences in drift rates obtained from behavioral data (van Vugt et al., 2012b).

In these previous studies, evidence accumulation for decision making was confounded with similarity-based information: higher summed similarity correlated with an increase in deciding a probe matched studied items. This current study is to deconfound these variables by using two tasks of roughly equal difficulty, but with different similarity computations. In the perceptual task, participants had to directly decide whether or not two presented stimuli were the same. In the memory task, participants first were presented with two different stimuli to memorize. After a short interval, they were shown a probe, and had to decide whether it was one of both memorized stimuli. This means that, in the perceptual task, decision information consists of direct similarity, whereas in the memory task, decision information consists of summed similarity. Thus, the results of this study should provide grounds for establishing a link between either theta oscillations and evidence accumulation independent of stimulus structure, or between theta oscillations and summed similarity. This is possible because, if theta oscillations reflect decision evidence accumulation in general, their power should increase equally in both tasks. However, if theta oscillations reflect summing similarities, they should increase with decision evidence in the memory task, but decrease with decision evidence in the perceptual task.

Methods

Participants

Twenty-three healthy right-handed participants between ages 17 and 28 had volunteered for paid participation in this study. Each participant spent about an hour on the experiment itself, requiring up to an hour of EEG preparation beforehand.

Procedure

Each participant did one session, in which he or she had to perform two different decision making tasks: a perceptual task and a memory task. Participants did twelve four-minute blocks, with two blocks of the memory task followed by one block of the perceptual task, again followed by two memory blocks and one perceptual block, etc.

Participation was rewarded with €12 per hour. As the time taken per participant was around two hours, (approximately one hour of subject preparation and one hour for the actual experiment) this made for a total base reward of €24. Additionally, participants received a small amount per correct decision, on average totalling €10, with a range of €8–12.

Stimuli

Both tasks had artificial faces as stimuli, created using the Basel Face Model (Paysan et al., 2009). This model creates faces from a long vector of shape values. To do so, it uses a vector that represents an “average” face, and a set of 199 principal components of this vector, each of which can be varied by an amount of standard deviations. This makes it possible to create systematic variations in the generated faces.

For the perceptual task, faces were created with the first three principal components each varied by -2 , 0 and $+2$ standard deviations from the mean, generating a set of 27 different faces. The faces for the memory task were generated in the same fashion, but with -4 , 0 and $+4$ standard deviations. This was done to make the faces more easily distinguishable, so the difficulty of the memory task more closely matched that of the perceptual task. Examples can be seen in figure 2.

Established knowledge about similarity judgements indicates that more similar stimuli are more difficult to distinguish. This means more similar faces in our task (i.e., faces that only differ on 1 principal component, instead of 2 or 3, or faces that differ by only 2 standard deviations instead of 4) would also be harder to distinguish. The fact that faces were randomly combined, meant our experiment had trials with varying difficulty. Lower similarities of presented faces made for easier trials, and higher similarities for more difficult ones. This provided the possibility to investigate the effects of similarity on response times and accuracy.

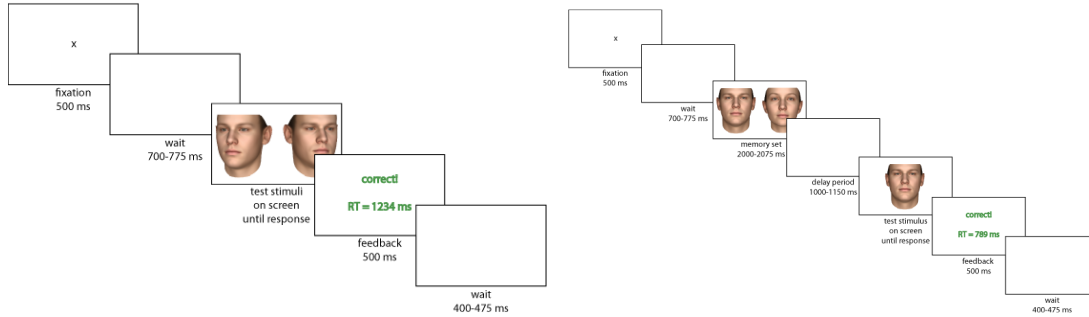
Experiment setup

Perceptual task

The perceptual task consisted of viewing two faces simultaneously, to decide whether they are the same or different. To make this task slightly more difficult, both faces were rotated facing slightly outwards, facing away from one another. Each trial started with the well known fixation cross at the center of a blank screen, presented for 500 ms, followed by a delay of 700 to 775 milliseconds, randomly chosen. Then, the two faces were shown, which stayed on screen until the participant pressed one of two keys on a keyboard. With their right hand, the participant was to press the M-key if he or she decided both faces were the same. If both faces were thought to be different, the Z-key was to be pressed. The decision was followed by a 500 ms feedback presentation, and then a randomly chosen 400–475 ms wait before the start of the next trial.

Memory task

The memory task used the Sternberg recognition memory paradigm (Sternberg, 1966), in which participants were presented with a memory set of two faces, to be remembered for a delay period, followed by a test stimulus (the probe), a single face. The participants’ task was to decide whether the test stimulus was part of the memory set or not. Each trial began just as in the perceptual task, with a 500 ms fixation period, followed by a wait of 700–775 ms. Thereafter, the memory set was presented for 2000 to 2075 ms. This was followed by a delay of 1000–1150 ms, after which the probe was shown



(a) Example stimuli in the perceptual task.

(b) Example stimuli in the memory task.

Figure 2: Example stimuli. *In the perceptual task, participants were shown two faces slightly rotated away from one another, and had to decide whether these were equal or not. In the memory task, participants were presented two different faces, and after a brief interval, were shown another face. For this last face, participants had to decide if it was one of the two faces shown first.*

until a recognition decision was made clear, again by pressing the M- or Z-key. Each trial ended with feedback, shown for 500 ms, followed by a 400–475 ms wait until the next trial. In both tasks, times were jittered to prevent accidental temporal correlations between EEG measurements and task events that might occur when rhythms are fixed.

Stimulus presentation

The presentation order of faces was determined semi-randomly, with a few restrictions. Quite obviously, sets to be memorized in the memory task should not contain two identical faces. Also, in both tasks half of the trials were randomly assigned to be target trials. This meant that, in the perceptual task, both faces shown were the same, and in the memory task, the probe face was part of the memory set. Consequently, the other half of the trials were non-target (lure) trials in which the two faces were different, or in which the probe was not identical to any face in the memory set. Furthermore, in half of the cases in the memory task, again picked randomly, target trials had the target be the face presented on the left, and on the right in the other half. Finally, the same face couldn't reappear with any less than 2 trials in between each appearance. These restrictions were implemented for each four-minute block separately, so each block itself was balanced, with an equal amount of target and non-target trials, and equally many memory trials with the target face on the left as trials with

the target face on the right.

Each participant was shown the same 12 blocks as the others, but in random order, and always as two memory blocks followed by one perceptual block. This makes for a total of four perceptual and eight memory blocks per participant.

EEG recording

Data was recorded in 34 EEG channels, of which thirty were from electrodes in an EEG cap, placed according to the 10/20 system, providing the actual scalp EEG activity. The other four channels originated from six separate electrodes, four of which facial electrodes that recorded horizontal and vertical eye movements in two channels, and two electrodes located on the mastoid process, to record both channels used for re-referencing all data. One more electrode, located on the left clavicle, provided a ground source. All electrode channels were adjusted to have impedances lower than 50 k Ω .

The sampling rate for recording was 500 Hz, with AC line noise removed off-line using a 48–52 Hz filter. To be able to link behavioral events to EEG recordings, the task generating computer sent trial-encoding pulses that were recorded along with the EEG activity.

After recording, artifact removal was done upon manual inspection of the data. Bad channels were also detected manually, and events that were unusable because of high noise, eye blinks or participant movement were rejected (only a few percent).

Data processing

For all further processing, only events with correct responses and reasonable response times (no more than 2500 ms) were used, which on average was 76% of all events, and target trials and lure trials were processed separately. To aid in processing, FieldTrip* and EEGLAB† were used.

Theta activity was extracted from the EEG data by a wavelet-transformation for frequencies of 4 to 9 Hz, using Morlet wavelets. Each trial was baseline-corrected by using the average activity of the 500 ms before the start of the trial. Then, for each trial, the similarity of the presented faces was calculated. This was based on the method described in Kahana and Sekuler (2002), and defined as:

$$\eta(\mathbf{s}_1, \mathbf{s}_2) = e^{-\|\mathbf{s}_1 - \mathbf{s}_2\|}$$

with \mathbf{s}_1 and \mathbf{s}_2 being the coordinate vectors of each image, and each element $\mathbf{s}_i(k)$ the amount of standard deviations by which the corresponding principal component of the average face was changed to generate the relevant face.

To evaluate the relation between theta activity and similarity, for each subject a regression model was established, fitting theta activity to similarity values calculated using above formula. Each model's regression coefficients were then used for an across-subject t -test, with the Multiple Comparison Problem overcome by using a cluster-based permutation method on the t -statistics (Maris and Oostenveld, 2007). Clusters were used because the probability a found result is real is higher if adjacent EEG channels show similar results. The cluster-based t -statistic was calculated by comparing the significance of each channel's regression coefficients t -test to a threshold of 0.025. For each cluster, the t -values of its channels are summed, and compared to a permutation distribution. This distribution is generated by assigning trials from both experimental conditions (perceptual and memory trials) to a single set and repeatedly randomly drawing as many trials from it as

originally in the trial set. For each of these random partitions, the t -statistic is re-calculated. The proportion of random partitions with a higher t -value than the observed one is the cluster significance value. If this p -value is below the critical alpha-level, set to 0.05, the difference between both experimental conditions is concluded to be significant.

Results

Behavioral results

The behavioral data show a fairly linear connection between the probability a participant responded 'yes' (i.e., presented faces are identical) and the (summed) similarity value of presented faces, independent of the experimental condition, as can be seen in figure 3.

Electrophysiological results

EEG data was analysed for correct lure trials only, using the cluster-based t -statistics. Only these trials were analyzed because similarity values close to the threshold increase the likelihood the participant incorrectly responds the probes are equal. This higher difficulty is expected to increase any observed effects on the theta oscillations.

Average response time for correct lure trials was 1.11 s for the perception condition, and 0.86 s for the memory condition. For the perceptual task, a significant positive relation between theta activity and similarity values was found from 1.6 to 1.65 seconds ($p = 0.04$), as can be seen in 4a. This suggests a link between evidence accumulation in the perceptual task and observed theta activity in the left parietal cortex. Also, a significant relation between theta activity and response time was found at 1.2 seconds ($p = 0.0368$) for the perceptual task. This result can be seen in 4b.

As an extra check, alpha (9-14 Hz) and delta (2-4 Hz) activity was analyzed, to see if they showed any relation to either of the experimental tasks. No link was found for delta activity, but a positive link ($p < 0.05$) was found between alpha activity and response time in the memory task (4c, 4d).

*A MATLAB software toolbox for MEG and EEG analysis, developed at the Donders Institute for Brain, Cognition and Behaviour at the Radboud University Nijmegen. It can be found at: <http://fieldtrip.fcdonders.nl/>.

†An interactive Matlab toolbox for processing continuous and event-related EEG, MEG and other electrophysiological data, found at: <http://sccn.ucsd.edu/eeglab/>.

Discussion

This study was to establish a link between either theta oscillations and evidence accumulation independent of stimulus structure, or between theta oscillations and summed similarity. We observed increased left parietal post-stimulus theta activity when subjects were able to correctly identify lures in a task that required direct evidence accumulation. This corresponds with earlier studies linking theta activity to decision making processes (van Vugt et al. (2012b), Jacobs et al. (2006)). Similar to the findings of Jacobs et al. (2006), it involves left parietal post-stimulus theta activity in a decision making process, but where they relate this to memory recognition, this present study finds it in relation to a perceptual decision making task. This is broadly in line with Nosofsky et al. (2012), who posit that categorization and recognition are mediated by largely overlapping neural memory systems.

Central post-stimulus alpha activity was correlated to response time in a memory task, where subjects had to rely on summing similarities. Decision making has already been linked to central theta activity (Jacobs et al., 2006), and now alpha also seems connected.

In this current study, all relations found were a substantial amount of time after the response. Future studies might clarify this, and establish a clearer link between theta oscillations and evidence accumulation independent of stimulus structure, theta oscillations and the summing of similarities, or both.

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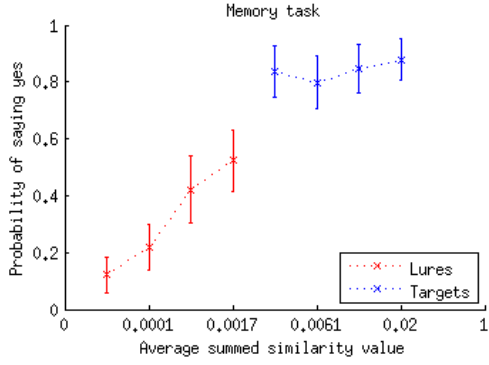
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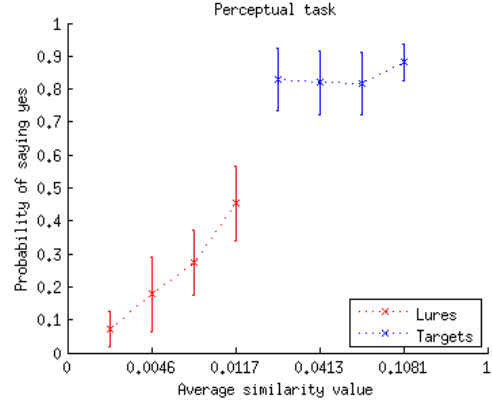
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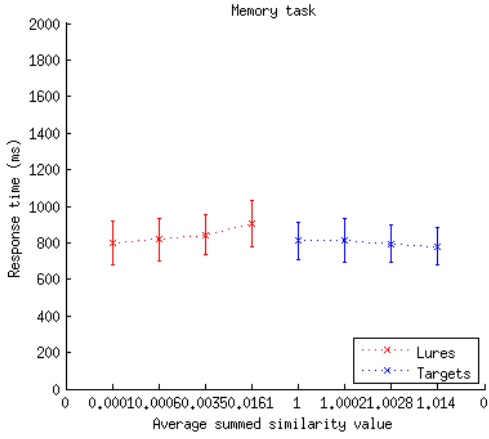
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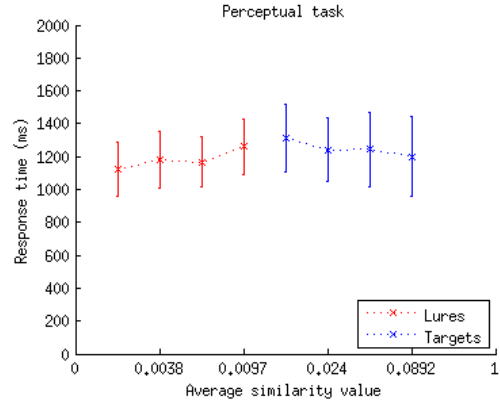
(a) Average accuracy in the memory task.



(b) Average accuracy in the perceptual task.

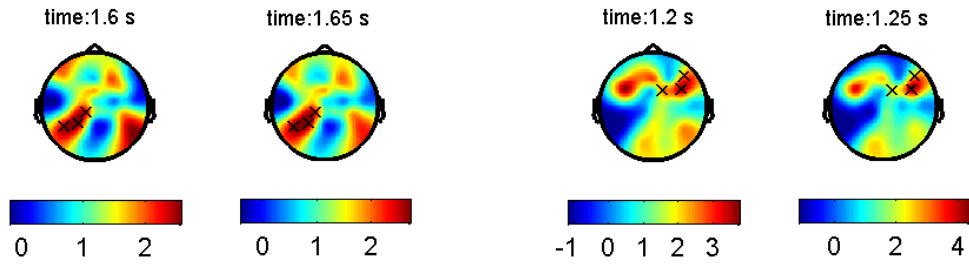


(c) Average response time in the memory task.

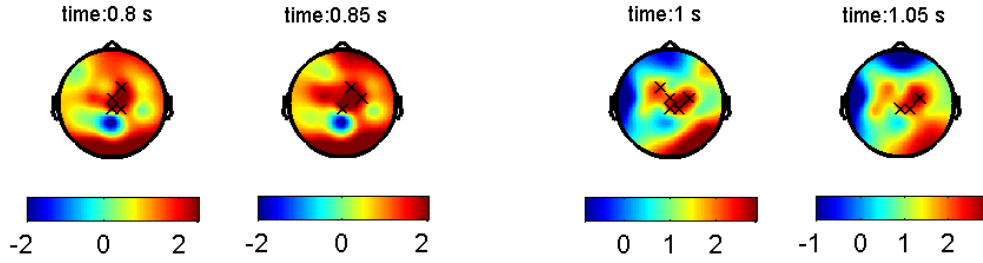


(d) Average response time in the perceptual task.

Figure 3: Average accuracies (3a, 3b) and response times (3c, 3d) for (summed) similarity values at each task. The plots are generated with a histogram-like method. Data is averaged over all participants. For each trial, its (summed) similarity value is calculated and added to an ordered vector. This similarity vector is then split into eight equal parts, each treated as a single data point. For each of these parts, the average (summed) similarity value is shown on the x-axis, and its average value and standard deviation on the y-axis.



(a) Significant ($p = 0.04$) post-stimulus theta activity in the perception task, using similarities as regressor. (b) Significant ($p = 0.0368$) post-stimulus theta activity in the perception task, using response time as regressor.



(c) Significant ($p = 0.0436$) post-stimulus alpha activity in the memory task, using response time as regressor. (d) Significant ($p = 0.0332$) post-stimulus alpha activity in the memory task, using response time as regressor.

Figure 4: Significant post-stimulus theta (4a, 4b) and alpha (4c, 4d) activity, found by the across-subject cluster-based t -test. The colors denote the values of the t -statistics. 'X' denotes $p < 0.05$.