

Event-related potentials in humans during spatial navigation

Matthew V. Mollison

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Department of Psychology
Brandeis University

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Abstract

Computer-generated, three-dimensional environments were used to study implicit landmark recognition by having participants take on the role of a taxi driver. During the task, electrical activity on the scalp was measured at 128 locations, and behavioral data on actions within the environment was recorded. Event-related potentials (ERPs) were calculated for a time period surrounding the appearance of target and non-target locations on the computer screen, showing the cortical activation during the implicit recognition of these landmarks. Statistical tests reveal that scalp-recorded stimulus-locked voltage fluctuations are significantly greater during the viewing of target as opposed to non-target locations, with a positive-going deflection in the ERP waveform at approximately 300 ms showing strongly on the right parieto-occipital area of the scalp. This effect, called the P300, is seen throughout the related literature, and is associated with stimulus processing. These findings provide evidence for significant differences in neural activity between two related, but functionally different, conditions in a complex spatial navigation task.

Background

Spatial navigation is a complex process that all people must integrate into their daily lives. With it, we are able to construct what might be considered a “cognitive map” that allows us to accurately direct ourselves within our environment, be it throughout a city or within a building, in an automobile or on foot (Tolman, 1948; Newman et al., in press). We observed and recorded how people react within a realistic virtual environment while performing a task that tests their navigational abilities. This paper will demonstrate that it is possible to record reliable data during a visually and conceptually complex navigation task and that statistical differences exist between the data for the occurrence of specific events. Furthermore, our research supports other findings common among visual recognition tasks.

Event-related potential literature review

An integral aspect of many studies in cognitive neuroscience is that electrical fluctuations measured on the scalp, the recording of which is known as electroencephalography (EEG), are induced by neural activity in the brain that can be associated with specific cognitive processes (Rugg & Coles, 1995; Friedman & Johnson, 2000). One way to analyze this electrical activity is to calculate event-related potentials (ERPs) for the occurrence of specific events. An ERP is calculated by averaging many epochs of EEG signal that are time-locked to the occurrence of an event in the experiment, usually the appearance of a stimulus (Rugg & Allan, 2000; Handy, 2005). The visualization of the resulting averaged values is known as an ERP waveform and is plotted as voltage¹, in microvolts (μV), over time, in milliseconds (ms). The waveform gives a detailed temporal account of neural activity induced by the presentation of a particular stimulus. ERPs are calculated by averaging over many events so that the random noise of the background EEG, being uncorrelated with

¹Voltage is unit of electrical potential equal to the difference between two points. Here, the difference is measured between a location on the scalp and a “reference,” resulting in an event-related potential.

the event of interest, will be averaged out, while the inherent aspects of ERP waveforms (called components or peaks) that are common among the individual epochs of EEG signal will become more profound (Handy, 2005). This approach also helps to eliminate any effects created by muscle or eye artifacts – fluctuations in electrical activity resulting from sources other than the brain (Coles & Rugg, 1995). In principle, ERPs are effective, multi-faceted tools that are useful in memory research. Among the advantages offered by ERPs are the following (Rugg, 1995): (1) their high temporal resolution allows the observer to view them at the ms level. (2) Their ability to record voltage fluctuations that correlate behavioral conditions with underlying brain activity without the need for an overt reaction from an experimental participant is a convenience not provided by behavioral testing. (3) They permit the comparison of patterns of neural activity at different locations on the scalp, giving insight into the possibility of functionally distinct processes at different locations.

Because the EEG is measured at the scalp, spatial aspects of this data are sometimes difficult to interpret with respect to underlying neural activity. The electrical signal from the brain must travel through the three layers of tissue surrounding the brain (the meninges), as well as the skull in order to be detected on the surface of the scalp. Since, like any tissue, these layers can absorb, deflect, and distort electrical activity, a scalp EEG recording is made up of voltage fluctuations from approximately the first two or three centimeters of brain tissue (the cortex) (Mangun & Hillyard, 1995). Even so, the underlying populations of neurons, in which synchronous activity is required to produce perceptible electrical fluctuations, may not necessarily be oriented toward the surface of the skull, and consequently may not be recorded on the surface of the scalp (Otten & Rugg, 2005). However, electrophysiological and cognitive analyses and comparisons of people in normal and brain-injury populations have allowed researchers to recognize specific scalp locations as regions in which neural activity for certain cognitive processes should occur. For example,

visual tasks are associated with activity in the posterior scalp areas; this observation makes sense because the visual cortex is located in the occipital lobe (Slotnick, 2005).

With prior knowledge about ERPs and their components, comparison of the waveforms for two or more conditions can lead to an informed differentiation of stimulus processing for different events. Two aspects of waveforms are commonly compared in ERP analyses: amplitude and latency. Peak latency in an ERP, which is the amount of time from stimulus onset to the maximum amplitude of a peak, informs us about when and under what conditions specific neural activation occurs (Handy, 2005). Comparison between two experimental conditions of when a peak begins, known as the peak onset latency, is also common. With respect to this value, the location on the scalp at which two ERPs differ might reveal that different conditions or stimuli within the experiment elicit different processes at different cortical locations (Rugg & Coles, 1995). The amplitude of specific components is examined two ways. First, a “peak amplitude measure” is the measure of the voltage at the peak latency. In a “mean amplitude measure” the voltage values across a restricted period of time centered around the peak latency of a specific component are averaged to compute one value. Mean amplitude measures, being less sensitive to noise, can be compared between conditions or stimuli without well-defined components (Picton et al., 2000; Handy, 2005). Rugg and Coles (1995) have hypothesized that peak amplitude reflects the amount of processing occurring at that location, which may possibly indicate how relevant the observed stimulus is to the task.

Specific cognitive processes are caused by specific neural activity. If two conditions have different effects on their respective ERP waveforms, and if it is assumed that ERPs are a visualization of underlying cortical activity, then it is inferred that differing evoked potentials signify differences in the cognitive processes involved (Rugg & Coles, 1995). Moreover, two different cognitive processes – and, consequently, cortical sources – may

produce scalp topographies of electrical changes that look the same, or an infinite number of other topographies, but a single cognitive process cannot produce two different scalp topographies (Slotnick, 2005). Therefore, it should be noted that ERPs calculated from simple experimental conditions do not necessarily represent the neural processes that occur in a real-world situation. The reason is that, as humans, we observe the world at an extremely dynamic level; the constantly changing interpretations of our surroundings alter our complex behavior within these environments. ERP studies can and will be applied to more real-world situations if we make progress in the study of this dynamic process – for example, by developing controlled experiments that have more ecological validity (that is, to more closely emulate the conditions under which the task is normally performed) or by creating tools to better analyze EEG data under these conditions.

Most ERP studies in the history of human electrophysiology have employed straightforward laboratory models, and have looked at the cortical activity elicited by memory tasks or by certain types of stimuli. The behavioral aspects have almost always been previously analyzed so that certain neural activity can be correlated with certain behavior. Previous ERP experiments have laid the groundwork for the next generation of electrophysiological experiments, analyses, and interpretations. They have been key steps in bringing us to our present level of understanding of electrophysiological research, and in showing the importance of this useful analysis. For example, a study done by Neville, Kutas, Chesney, and Schmidt (1986) showed that accurate predictions can be made about subsequent word recall in a free recall experiment. These authors determined that the more positive the P300 component is in the centro-parietal and centro-frontal areas of the scalp at the time of encoding of a particular word, the more likely it is that word will be subsequently recalled. A P300 is a positive-going deflection denoting increased voltage that occurs around 300 ms after stimulus onset. Sutton, Braren, Zubin, and John (1965) found differences in ERP

waveforms for various types of stimuli and noted certain waveform characteristics during the viewing of an unexpected stimulus. However, though these kinds of experiments may allow psychologists to use ERPs to look at neural activity during memory encoding and recall or at physiological reactions to different types of stimuli, they cannot necessarily elicit the same type of behavior in humans that would be experienced in a real-world situation. Two realizations underlie the present study. First, the more we study brain activity during realistic situations, the more we can learn about how to approach such theories. Second, it is important to not lose sight of previous, seemingly elementary findings that analyses of more complex data will take into account.

Spatial navigation literature review

Though spatial navigation and spatial memory in rodents have been studied for decades (Tolman, 1948; O'Keefe & Dostrovsky, 1971; O'Keefe & Conway, 1978), only recently has there been a strong interest in studying behavioral and electrophysiological aspects of navigation and spatial memory in humans (Newman et al., in press; Caplan et al., 2003; Ekstrom et al., 2003). Behavioral research in the field has determined that people orient themselves in an environment by using landmarks (salient objects) and the spatial relationships between landmarks (geometrical properties), which are designated egocentric and allocentric associations, respectively. An egocentric association is the contextual relationship formed upon viewing specific salient objects from a particular location, thereby creating a "perceptual snapshot" (Shelton & McNamara, 2001). An allocentric association is the spatial relationship between one salient object and other objects in that environment (Hartley, Trinkler, & Burgess, 2004; Burgess, Spiers, & Paleologou, 2004), a concept related to the "cognitive map" theory mentioned earlier. Research by Shelton and McNamara (2001) supports the idea that allocentric associations are updated during egocentric

experience as a person moves within his or her environment. Newman et al. (in press) provide evidence for spatial learning by showing that the path length to specific locations within a virtual environment varies inversely with the amount of exposure; that is, a person can navigate more adeptly to a desired landmark once he or she has learned the spatial layout of the environment, by forming allocentric and egocentric associations. Salient locations, with which the participants interact, are particularly important in building one's "cognitive map." This study by Newman et al. (in press) prompted the examination of correlations between landmark recognition and neural activity.

Electrophysiological research on spatial navigation can provide insight into the neural basis of way-finding within an environment. Because an experiment looking at ERPs for implicit landmark recognition during spatial navigation has never been published, we turn to relevant portions of the literature on oscillatory analyses of virtual navigation tasks. Oscillations are created in the brain when the synchronous activity of populations of neurons causes large positive and negative voltage fluctuations. Specific oscillatory rates, such as the theta (θ) band (defined in humans as activity in the 4 - 8 Hz range) (Caplan et al., 2003), are elicited during certain cognitive functions. θ is usually associated with successful memory encoding, but it is also involved in navigation. A spatial navigation study by de Araujo, Baffa, and Wakai (2002) used magnetoencephalography (MEG) to look at θ oscillations. These investigators found an increase in θ during periods of movement within a virtual environment, compared to control conditions. Though they did not find θ to be associated with any particular event, Bischof and Boulanger (2003), using scalp EEG, found θ to increase when new spatial information is acquired. Caplan et al. (2003) also looked at θ rhythms during spatial navigation, and used the same virtual taxi paradigm employed by Newman et al. (in press), on which the current experiment is based. These researchers made intracranial recordings in epileptic patients, and found a particularly strong increase

in θ specifically during periods of integration between sensory information (such as optic flow during movement) and motor planning (such as finding a target location). It should be noted that passive viewing of movement within a virtual environment elicited only a very small increase in θ (de Araùjo et al., 2002).

Research by Klimesch et al. (2004) reveals that oscillations are capable of “phase locking,” or resetting, and therefore building a larger wave, to create the positive and negative components in an ERP waveform. A significant increase in phase locking in the alpha (α , 8 - 12 Hz) and θ bands occurs during the same epoch as the P1 and N1 waves, which are positive and negative waves at approximately 100 ms after stimulus onset, respectively, and therefore these oscillations have a large affect on P1 and N1 amplitude. The P1 and N1 components have been associated with early visual recognition, and are evoked by stimuli presented in different parts of the visual field (Townsend, Harris, & Courchesne, 1996). A prominent late positive component (LPC) is normally seen after the appearance of the early visual response peaks (Makeig et al., 1999). The P300 is considered a LPC in the ERP waveform. α is associated with a resting state (periods of lowered cognitive activity) and is negatively correlated with latency onset of the P1-N1 complex. Klimesch, Doppelmayr, Schwaiger, Winkler, and Gruber (2000) hypothesized that a relation between an increase in oscillations and a P300 ERP component would be seen in an old/new recognition memory task involving words. They found an increase in θ and delta (δ , 1 - 3 Hz) for words correctly identified as “old” (targets) – that is, for remembered words – during the same time interval and at the same locations on the scalp as the P300.

Literature concerning ERP analyses during a visual oddball-stimulus task is also relevant to the analyses in this paper. In this paradigm, infrequent target stimuli are interspersed throughout the presentation of a series of standard stimuli (Squires, Squires, & Hillyard, 1975). These unexpected stimuli elicit a P300 with a larger amplitude than

do the standard (frequent or expected) stimuli (Swick, 2005). Katajama and Polich (1999) found that a P300 occurs in the centro-parietal area of the scalp for both auditory and visual oddball-stimulus tasks. These and many other studies with similar findings have led researchers to believe that the P300 wave denotes attentional activity (Sutton et al., 1965; Donchin & Coles, 1988; Duncan-Johnson & Donchin, 1977).

Donchin and Coles (1988) have proposed a context-updating model in which stimuli that are more rare and task-relevant than other stimuli will produce a larger P300 component in the ERP waveform at electrode locations on the right parieto-occipital portion of the scalp. The same posterior parietal effect has been observed by Alexander et al. (1995) during viewing of infrequently presented target stimuli (as opposed to infrequently presented novel stimuli or frequently presented standard stimuli). Their research also suggests that the activation they observe at the right frontal portion of the scalp is related to initial stimulus processing.

These findings from previous studies form the foundation for this thesis. We examine how electrical activity in the brain correlates with the occurrence of salient behavioral events in a spatial navigation paradigm – that is, how and at which scalp locations ERPs differ during viewing of a target store versus a non-target store. We show that we can measure evoked potentials during a realistic, dynamic, and conceptually complex task and that the difference in the ERP waveforms for the two proposed conditions is significant in regions associated with processing of visual stimuli.

Methods

Participants

Fourteen young adults (ages 19 to 27, mean = 22.9; seven male, seven female) participated for monetary compensation. All were right-handed native-English speakers and had

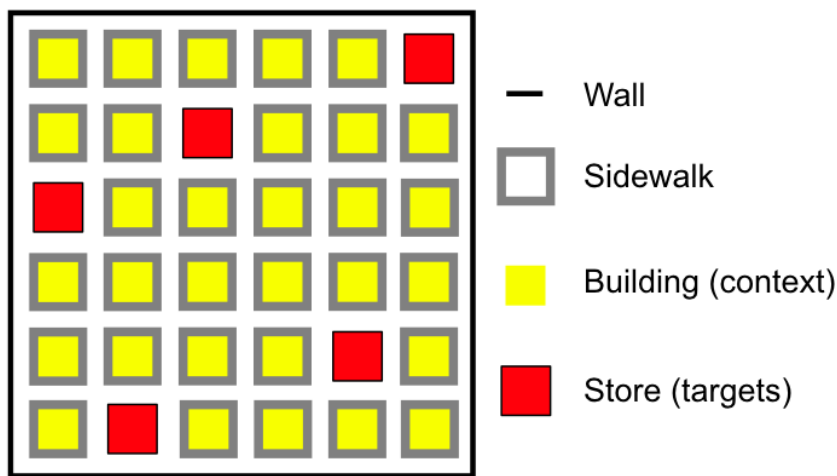


Figure 1. Top-down view of a possible town layout

normal or corrected-to-normal vision. Each experimental session, including application of the electrode net and running in the task, lasted approximately ninety minutes. To provide motivation for doing well in the task a monetary bonus was given to the participant based on how quickly and accurately the passengers were delivered. The research protocol used was approved by the institutional review board at the University of Pennsylvania, and informed consent was obtained from the participants.

Construction of virtual towns

Together with Josh Jacobs and Igor Korolev, I designed a task, “YellowCab II,” in which a participant plays the role of a taxi driver within a virtual, three-dimensional town². The driver maneuvers within a virtual town while looking for passengers. Once a passenger is picked up the participant must take the passenger to the requested destination, which is always a store within the town.

²We wrote the entire experiment in Python using OpenGL as the graphics rendering library. Our software may be downloaded from <http://memory.psych.upenn.edu>.

Each of three virtual towns is laid out on a 6×6 grid of blocks, with a single store or building on each block. There are five stores and thirty-one buildings in a town, for a total of thirty-six landmarks. An example of a sample town layout is shown in Figure 1. Each building is surrounded by a sidewalk and is centered within the block. Buildings may vary slightly in width and height, and a unique façade is mapped onto all four walls of each building. These structures provide a rich visual context for the virtual towns. The stores also have a single storefront image mapped onto all four sides. Each store is uniform in size and is centered within a block. Unlike buildings, stores are not surrounded by a sidewalk but rather by paved roads on which participants can drive up to complete a delivery. An image of a blue sky is used as the ceiling of the environment. The outer boundary of the town, beyond which no other visual information can be seen, has the image of a brick wall mapped along its length.

All three towns are randomly generated during the task, taking into account constraints on how close one store could be to another. The constraints are as follows: (1) there must be at least two buildings between each store in the same row or column. (2) There must be at least one building between each store in each diagonal direction. (3) There cannot be a store in all four corners of the town at the same time. The first two constraints prevent stores from being located within close proximity to each other, which would allow the participant to see multiple stores at one time. We want to avoid this situation for the sake of subsequent analyses, so that there would not be many stores on the screen at the same time. The third constraint prevents the town from becoming symmetrical, or very near symmetrical, thereby causing confusion to the driver. The second test-town is completely different than the first except for grid size, with no repeated stores, buildings, or topographical layouts. Not repeating the stimuli or layout keeps each town as unique as possible. The third test-town has the same layout, buildings, and stores as the first test-

town. This approach allows the assessment of the transfer of learning from the first town to the third town when a distraction town exists between them. This choice was also made for the sake of subsequent analyses (not presented in this paper).

The behavioral aspects of this experiment are designed as an extension of the second experiment in Newman et al. (in press), and are similar to the tasks in that experiment involving navigation to specific locations within a virtual town. In the current experiment, participants take on the role of a virtual taxi driver; they search for randomly placed passengers (“foraging” phase) and deliver them to a specific location within the town (“goal-seeking” phase), and in doing so they earn “points.” The monetary bonus given to each participant is based on the number of points earned throughout the experiment. Though this task may sound simple, participants are given a considerable degree of freedom within the environment to move about and make choices. Participants are urged to find the goal locations as quickly and accurately as possible by learning the individual layout of each town and its landmarks. Many realistic stimuli are also involved, including cab-hailing passengers, interactive stores, and static buildings – all within a rich visual context simulating a small city. To make the towns appear as realistic as possible, a digital photograph was taken of each stimulus, and then edited with a graphics editor to account for distortions. What most distinguishes this experiment from the previously mentioned experiment is that we measured voltage fluctuations across the scalp during the task, thereby adding another dimension to our analyses. We then used this scalp EEG data to calculate ERPs, and by doing so delineated the underlying neural activity.

Navigation

Participants navigate from a first-person perspective using a computer-game controller. The field of view is $60^\circ \times 60^\circ$, with a screen resolution of 800×600 pixels. With



Figure 2. A passenger within the virtual town. It is possible to see a store, the Butcher Shop, on the right side of the figure, and buildings in the middle and left portions.

the width of the road defined as one *unit*, the size of the town is 19×19 units. Each building, including the sidewalk by which it is surrounded, measures 2×2 units, and each store measures $1 \text{ unit} \times 1 \text{ unit}$. The turning rate of the virtual taxi is $51.6^\circ/\text{s}$, and a full rotation takes approximately 7 s. The taxi moves forward at $0.9 \text{ units}/\text{s}$, while the reverse speed is $0.25 \text{ units}/\text{s}$. It is possible to turn the taxi while moving forward or backward, thereby making an arcing turn. The controller can be held comfortably with both hands resting in the lap, therefore eliminating most or all arm movements that could cause muscle artifacts in the electrophysiological recordings. The controller was modified to be as simple as possible by removal of any extra buttons. No participant had any problems using the controller, and all participants became adequately skillful in using it in the practice environment. The practice environment was implemented to minimize any learning-to-learn effects associated with the controller or the task (Keppel, Postman, & Zavortnik, 1968).

For the first delivery of every town, a passenger is placed directly in front of the virtual taxi, so as to prevent the large amount of initial exposure experienced in Newman et al.

(in press). During the remaining foraging phases, six potential passengers wait in randomly chosen locations on sidewalks surrounding the buildings. Passengers are placed so that their location is not within the line of sight of either the previous or the upcoming target store; thus, upon passenger pickup the participant cannot see the current destination or use the previous target store as a cue for orientation. Each passenger is randomly assigned a specific destination; each store must have a passenger delivered to it before it is visited again. When the passenger is picked up, a text screen instructs the participant to take the passenger to a specific target store and notes that upon doing so, the participants will receive 50 points. The participant then pushes a button on the controller to return to the virtual town.

Participants are asked to earn as many points as possible by moving quickly and efficiently within the town. As soon as the passenger is delivered, a text screen informs the participants that they were successful and instructs them to look for another passenger. Participants begin the task with 300 points and are awarded 50 points for each delivery. They are docked one point for every three seconds spent moving, turning, or standing still. This provision motivates them to continue toward their current goal. Their earnings are continuously displayed in the upper right corner of the screen. In the upper left, a short description of their current goal is shown (e.g., “Find a passenger” or “Find The Coffee Store”).

To complete the first test-town participants are required to pick up and deliver 15 passengers – three passengers to each of the five stores. Between each of the three test-towns participants do the second practice task (viewing and reading names of the store fronts) again. The second and third test-towns likewise require delivery of 15 passengers.

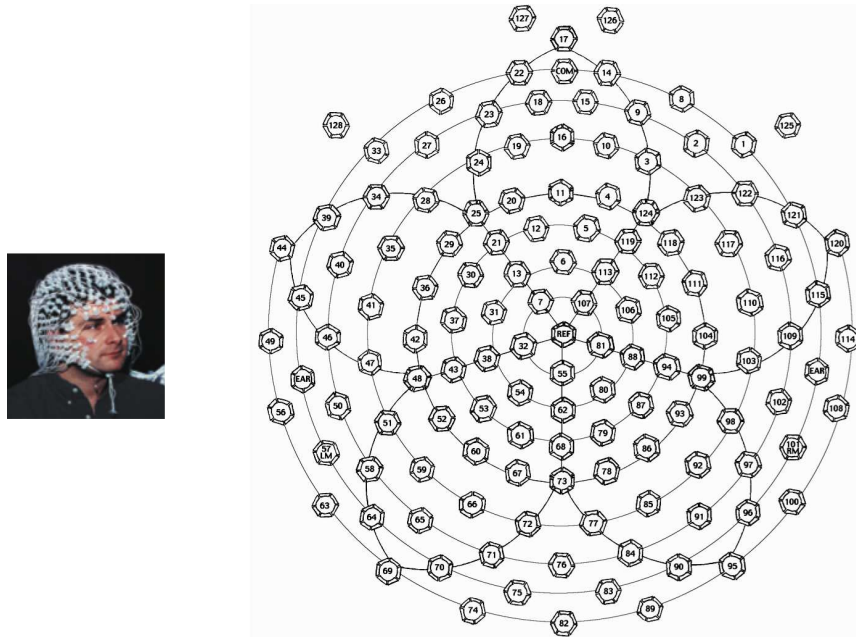


Figure 3. The Geodesic Sensor NetTM used to measure electrical potentials

Electrophysiological recordings

A 128-channel Geodesic Sensor NetTM (Tucker, 1993) was used to measure the EEG at the scalp at 500 Hz, or 500 *times/s* and was connected to an AC-coupled, 128-channel, high-input impedance amplifier (200 M Ω , Net AmpsTM, Electrical Geodesics, Inc., Eugene, OR). Before being placed on the participant's head, the net was soaked in an electrolyte solution made up of distilled water, potassium chloride, and shampoo to promote the conductance of the signal to the electrodes. The net uses silver-silver chloride (Ag/AgCl) electrodes, and each surrounded by a small sponge to hold electrolyte solution. The 128 electrodes were adjusted until impedances were less than 50 k Ω . NetStationTM, the data acquisition and analysis application made by Electrical Geodesics, Inc., was used to save the EEG data to our recording computer.

Procedure

Before encountering the test-towns, participants completed two different practice tasks. In the first task, participants delivered four passengers, one to each of four stores, in a practice town. The practice town was a 3×3 grid, with one store in each corner. These stores were not used in the test-towns. The four stores were surrounded by open road, allowing movement in these areas without obstructing the view of the stores. Navigating this small practice environment familiarized participants with the controls of the task and with the method for picking-up and delivering passengers.

In the second practice task, participants viewed two-dimensional, static images of all ten storefronts that would be encountered in the three subsequent test-towns. Below each image, the name of the store was displayed; passengers later used these names to communicate where they wanted to go. Participants looked at each picture and read its name silently. The list was presented five times, each time in a new random order. This practice task was designed to familiarize participants with the appearance of the stores before entering the towns.

The experimenter remained in the testing room during the entire session, and answered questions (unrelated to strategy) immediately following the first practice task. Once both practice tasks were completed the participants were asked to not talk unless necessary, as any unnecessary movements could create muscle artifacts in the EEG data.

ERPs: computation and statistical tests

This experiment is considered to have a *repeated-measures*, or *within-subject*, design because it compares two related conditions from a single population. The average ERPs for each participant were calculated by averaging over the voltage values for a 1000 ms window surrounding the occurrence of each event. Because we hypothesized that more activation

would occur during the viewing of target stores, one-tailed paired-sample t tests were used to calculate the statistical difference between the grand average ERPs for target and non-target store views, producing p values for each time point. A grand average ERP is the mean of each participant's average ERP. An artificial baseline was calculated by averaging over the EEG for 200 ms prior to stimulus onset to eliminate any direct current (DC) shifts, which would result in an overall positive or negative shift of the wave. When comparing across averages of specific epochs of EEG for multiple participants, one-tailed paired-sample t tests were used. When comparing epochs of EEG for events within an single participant independent-sample t tests were used because the number of events being compared varied for each of the two conditions. The resulting p values for each were then used to create topographical plots of the difference in electrical activity on the scalp for the specified epoch. Matlab (The MathWorks, Natick, MA) versions 7.0.1 and 7.0.4 were used to perform all calculations.

Selecting events

Our current behavioral analyses can calculate the percentage of the screen occupied by a particular object at any given time point, but not the percentage of a particular object on the screen. We tested the different percentages of the screen occupied by an object identified three percent as an ideal threshold for denoting the time point at which seeing an object is marked as an event; this threshold gave us an acceptable number of events for our purposes. Thus, an event for viewing a target store starts at the time when three percent of the screen is occupied by the store. An example of a store occupying three percent of the screen is shown in Figure 4. Because we do not know exactly where a participant is looking, some latency variability may exist in the appearance of a store on the screen and the participant's recognition of the store. For example, a participant might be looking at a

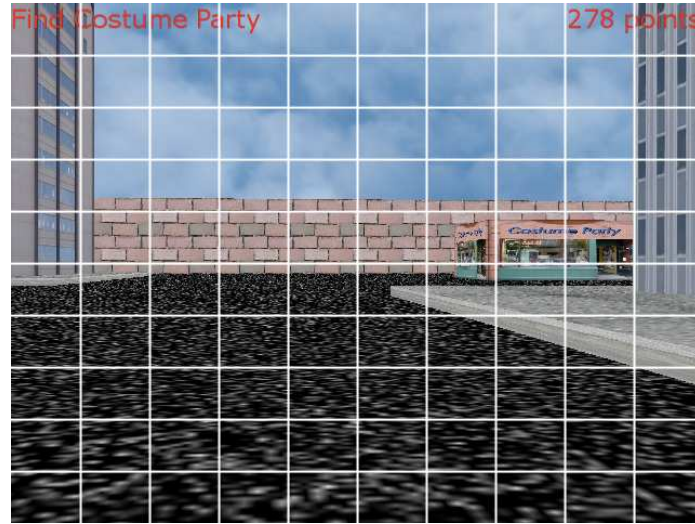


Figure 4. The store in this figure occupies approximately three percent of the screen. Each rectangle covers one percent of the screen.

building on the right side of the screen when a target store shows up on the left side. Even though his or her attention will not be directed to the target store for a certain period of time, this appearance of the target store is still considered an event and is included in the average ERP. This approach has led to some complications that are discussed later. All epochs surrounding events for the viewing of a target store or a non-target store with a duration of less than 1000 ms were excluded from the analysis.

Post-processing of EEG data, including electro-oculogram (EOG) detection, bad-channel detection, and average rereference, was performed offline and after the experiment was complete. Those event epochs containing eye-movement or eye-blink artifacts (EOG over $100 \mu\text{V}$) were excluded from the analysis. The EOG was assessed with one channel above and one channel below each eye, for a total of four electrodes detecting eye artifacts. In bad-channel detection the EEG data was first split into 1000 ms segments. A channel was then marked bad if voltage was greater than $100 \mu\text{V}$ for more than 20% of the segments – a standard procedure for finding bad channels. Two participants contributed

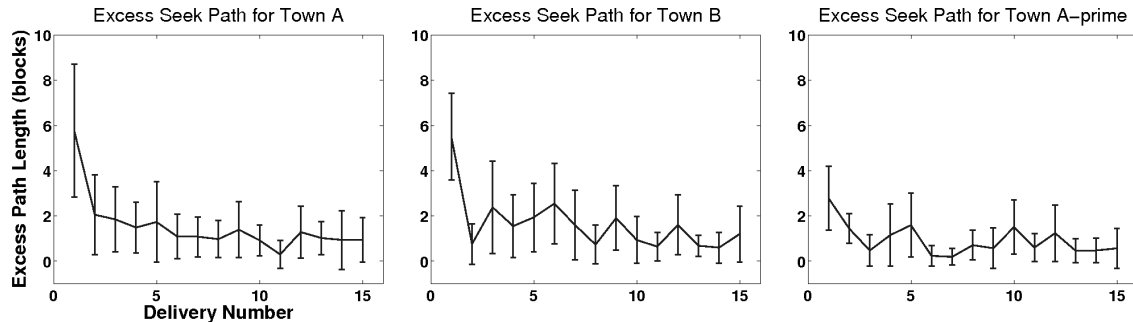


Figure 5. Average excess path length during the seeking phase across all participants

a majority of the bad channels, but their EEG data was not excluded from the analyses, because during the task most of their electrode impedances were less than $100\text{ k}\Omega$. Averaged over all 14 participants, approximately 20% of the channels were marked bad in post-processing ($M = 25.0$, $SD = 32.0$); without data for the two previously mentioned participants, approximately 12% were found to be bad ($M = 14.67$, $SD = 5.88$). Though a vertex reference (Cz) was used during recording, an average rereference was performed to account for distortions in electrical activity at Cz. Segments of EEG data that were marked “bad” in post-processing were not included in the analyses.

Results

Behavioral measures

The task was designed such that all participants were able to finish without difficulty. Using behavioral analyses it is possible to look at specific aspects of the data, such as the amount of learning done within a town. To estimate the amount of learning done during the task in a particular town we can look at the excess path length for each delivery (the same method of estimating learning as used in Newman et al. (in press)). Excess path length for the seeking phase is calculated by subtracting the distance to the target store

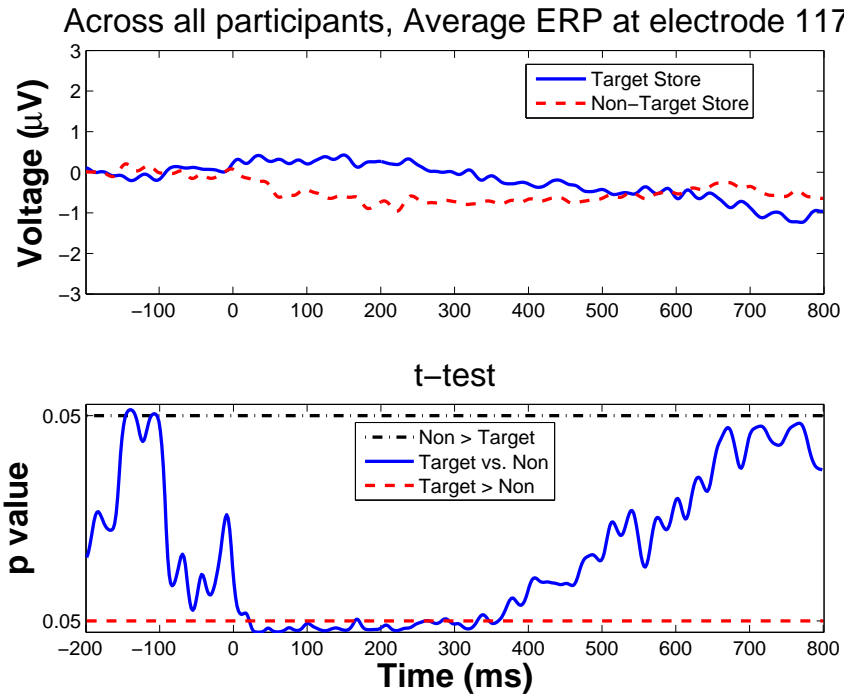


Figure 6. Average ERP and corresponding p values for an electrode in the right frontal area with early activation

at the passenger pickup location from the actual distance driven by the participant to the target store. The graphs in Figure 5 show that almost all learning of the town's spatial layout is done during the first three deliveries. Error bars are 95% confidence intervals.

Electroencephalographic measures

The grand average ERPs of the two events of interest reveal a discrepancy between the typical shape of an ERP waveform and the ones presented here (see discussion below and Figures 6, 7, and 8). However, the effect seen in the waveform is a positive-going deflection exhibiting a maximum amplitude at around 300 ms ($M = 328$, $SD = 49.78$) for channels in the right posterior area of the scalp and continuing on for several hundred milliseconds. Even though my analyses do not cover oscillatory phase locking, it is possible that this is

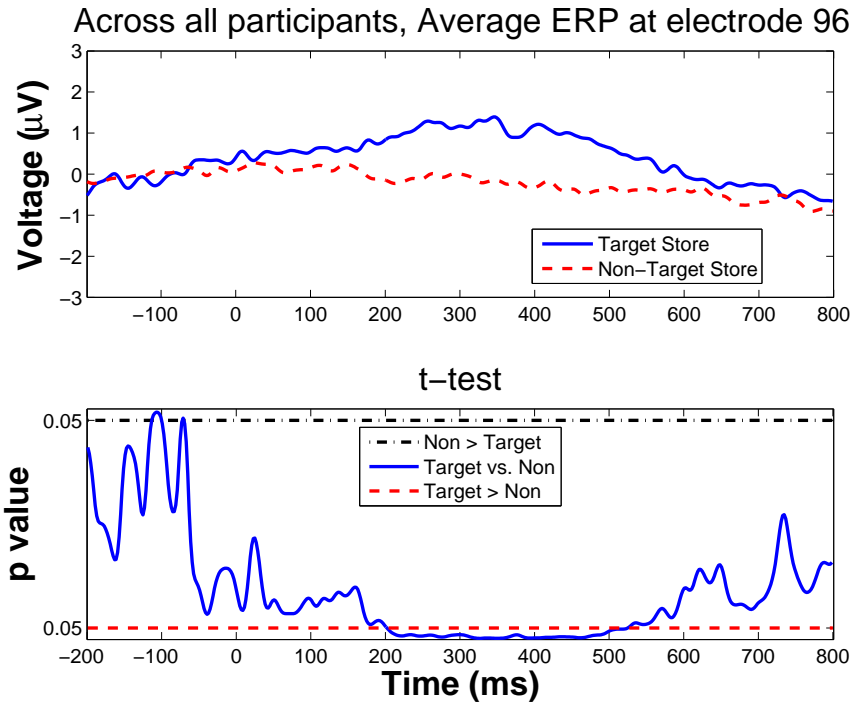


Figure 7. Average ERP and corresponding p values for an electrode in the right parieto-occipital area with mid-to-late activation

occurring and contributing to the P300 effect seen in the ERP waveforms. Analysis of t tests on the ERP amplitudes at the three electrode locations reveals that the two conditions are most different at the following times: right frontal (Figure 6), 124 ms, $t(13) = +2.88$, $p < 0.01$, one-tailed; right parieto-occipital (Figure 7), 328 ms, $t(13) = +2.81$, $p < 0.001$, one-tailed; centro-parietal (Figure 8), 622 ms, $t(13) = +5.32$, $p < 0.0001$, one-tailed.

It is difficult to see any real components produced in the grand average ERPs, and because of this the data should be looked at in other ways. Recording from a dense electrode-array like the one used in this experiment allows the spatial distribution of activity across the scalp to easily be analyzed. This gives a better idea as to what kind of neural activity is happening at different locations on the scalp for a single point in time. Figure 9 shows a topographic plot of p values at three specific time points averaged across all participants.

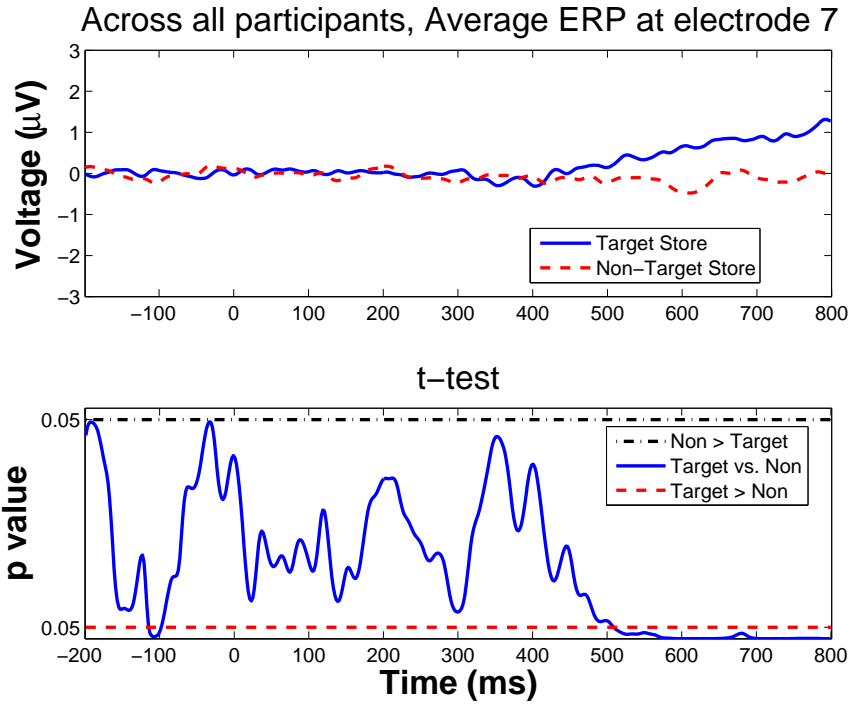


Figure 8. Average ERP and corresponding p values for an electrode in the centro-parietal area with late activation

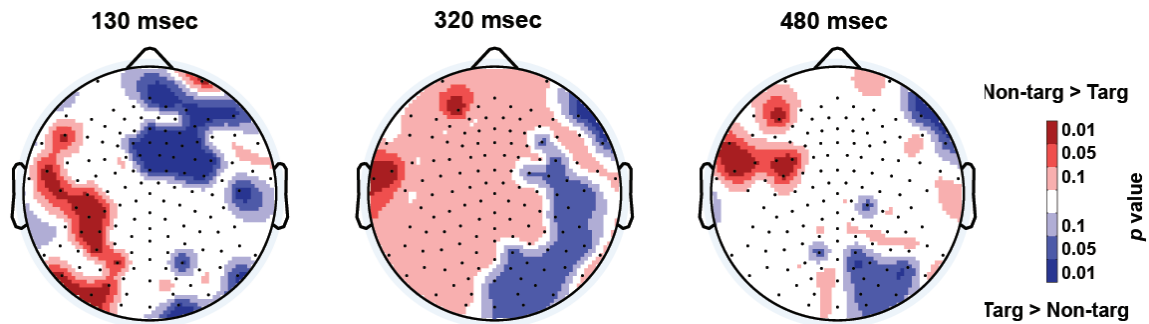


Figure 9. Topographical plots of significance values at 130 ms, 320 ms, and 480 ms after the event occurred, averaged across all participants

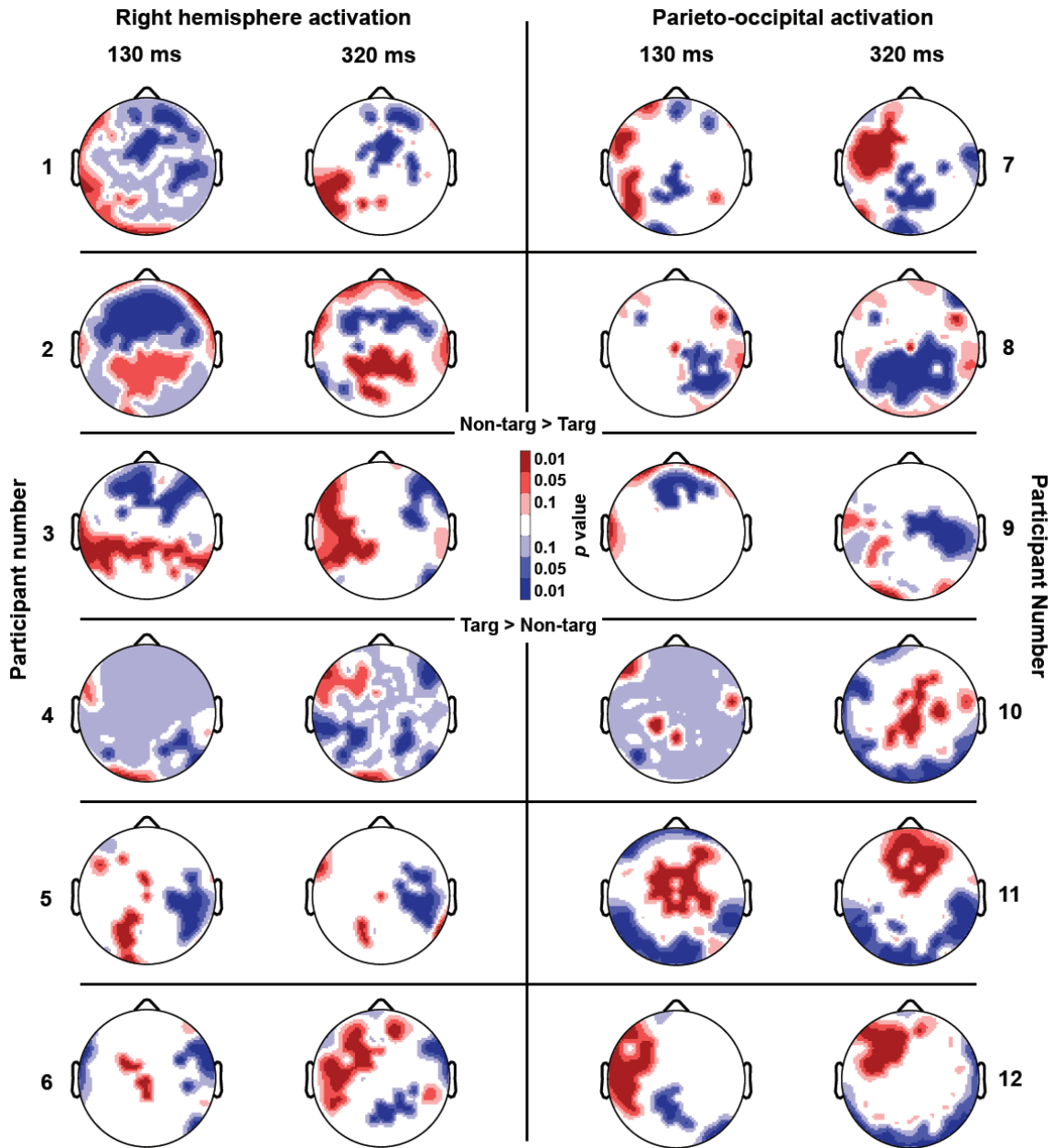


Figure 10. Topographical plots of significance values for each participant

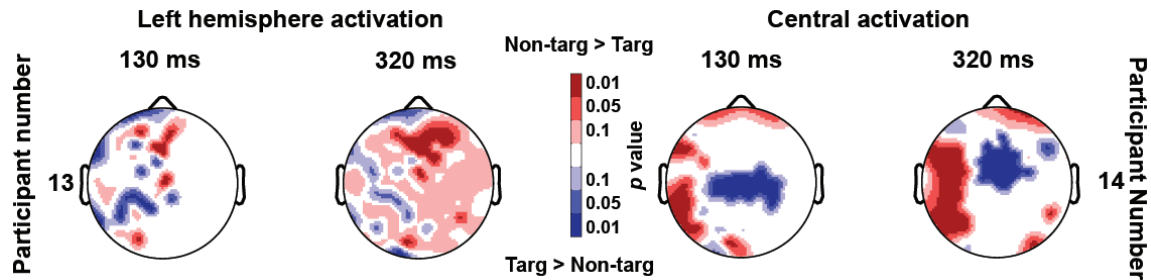


Figure 11. Topographical plots of significance values for the two participants not included in the activation-area groups

There is a significant ($p < 0.01$) amount of activation at 130 ms in the right frontal and temporal areas, and at 320 ms and 480 ms ($p < 0.05$) in the right parieto-occipital area during viewing of a target store versus a non-target store. These effects, that is, the early positive component in the frontal area flowing into late positive components in the posterior area, are consistent with the oddball task literature discussed earlier. However, considering the fact that not all human brains have exactly the same structure, these topographic plots are also looked at on a per-participant basis to see if individual differences exist.

Figure 10 shows topographic plots of each individual participant at two specific time points; the plots have been grouped by the area in which the most activation is seen. Two distinct topographies are found, with six of the 14 participants showing activation in mostly the right hemisphere, and another six showing activation in either only the right parieto-occipital area or moving from the right frontal lobe to the right parieto-occipital area. The activation-area groups were created by hand according to where on the scalp the most significant activation was seen, and the subsequent analyses are based on these two groups. The two remaining participants were inconsistent in their activation-areas with the previously mentioned participants and were excluded from the group-averaging; their topographical plots can be seen in Figure 11.

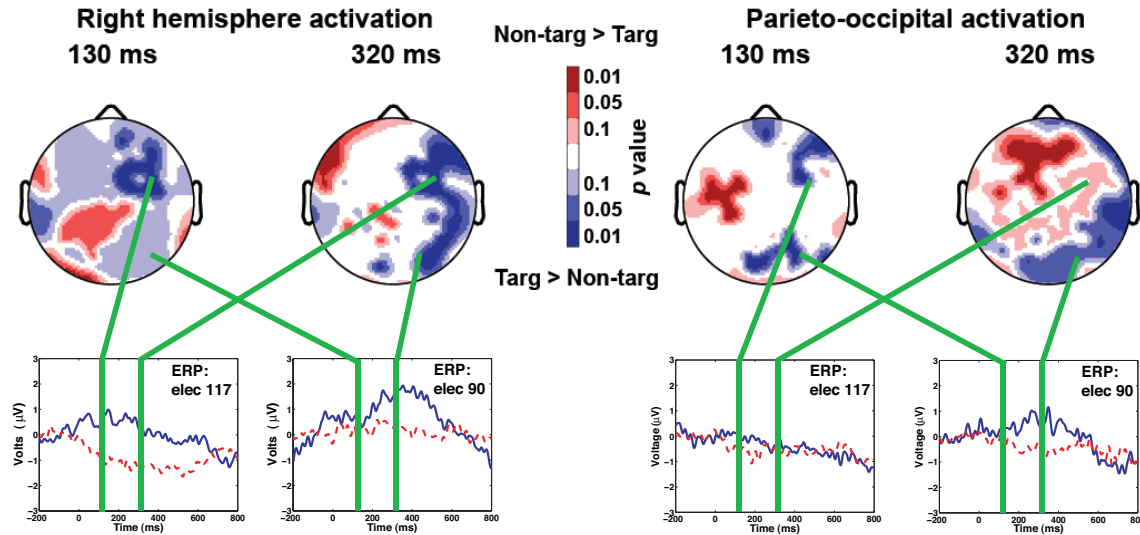


Figure 12. Topographical plots averaged across the two activation-area groups with ERPs for frontal and posterior electrodes

Figure 12 is shown as a comparison to the earlier grand average topographic plots presented in Figure 9. It shows topographical plots averaged across the two activation-area groups at two specific time points. ERPs are provided for two specific electrodes, one frontal and one posterior, and are marked at the times for which the topographic plots correspond. The topographies of activity in this figure are very similar to the grand averages.

Though the averaged topographic plots presented above have shown effects consistent with related literature, these plots may have over-simplified the analysis. To present this data in more detail, Figure 13 consists of three topographic plots for a particular participant, number nine in Figure 10, with six ERPs marked at the times for which the plots correspond. This participant had exemplary neural activity, clearly showing the flow of activation from the right frontal scalp area to the right parieto-occipital area, again, consistent with the visual oddball paradigm literature. It must be kept in mind that the ERPs for this individual are much more subject to noise because they are averaged over a smaller number of events.

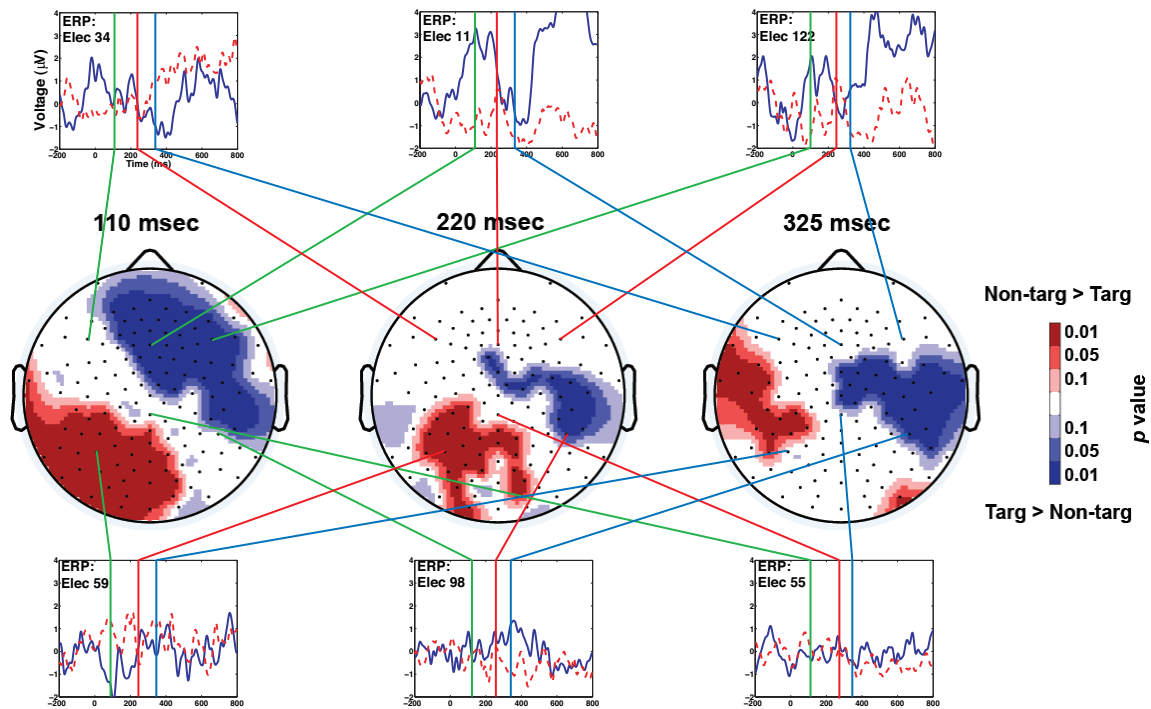


Figure 13. Topographical plots and corresponding ERPs for a single participant

Also, it should be noted that the frequency of the waves in the ERPs presented in Figure 13 appears to be in the θ band (4 - 8 Hz), arguing for the θ oscillation phase locking presented by Klimesch et al. (2004), though this is only a conjecture and more research would need to be done to provide any actual evidence.

Discussion

Epochs of EEG corresponding to the occurrence of behavioral events for the two conditions of interest were lined up (stimulus-locked) to allow for proper averaging over many events; however, because some time variability (latency jitter) occurs between the time that a target or non-target store appears on the screen and the time that the participant

directs his or her attention to this store, these events are not synchronized³ as events traditionally are in ERP experiments. As stated previously, when averaged, inconsistent components, such as positive or negative peaks that are not synchronized, will decrease and the similarities between the waveforms will become more profound. We believe this is the reason for the relatively flat grand average ERPs.

However, as shown above, statistical tests reveal that the latency variability between event onset and actual store viewing is not significant. Seeing a target store evokes an ERP component that is significantly greater in amplitude than when a non-target store is seen. This component appears at around 300 ms and seems to represent the formation of a P300 complex. According to Katajama and Polich (1999), visual target stimuli elicit a larger P300 component than non-target stimuli. The ERP waveforms that we have calculated display a significant voltage increase in the parietal area when a target store is seen, confirming these observations. Donchin and Coles (1988) have proposed a context-updating model, in which a set of environmental relationships, or allocentric associations, is restructured when “strategic” information is received. This strategic information (as opposed to “tactical” information which applies to immediate reactions) allows the individual to subconsciously modify behavioral aspects such as attentional levels, biases, and the setting of priorities (Donchin, Ritter, & McCallum, 1978). When this more task-relevant information is received, a larger P300 is seen, especially upon viewing a relatively rare target stimulus. It follows, then, that the P300 has an attentional basis – a statement which can be applied to our task, in that, as the participant drives around the town, the target store is attended to and the non-target store is ignored.

Furthermore, it has been found in other experiments that the latency of a participant’s explicit response does not affect the appearance or latency of the P300 (McCarthy

³To produce latency-corrected ERP averages we would need to use a filtering algorithm to synchronize the components of the waveforms; this is discussed later.

& Donchin, 1981). This observation reinforces the idea that the P300 is associated with information processing. Research by Alexander et al. (1995) also suggests that the P300 is involved during stimulus processing and that this activation occurs in the right-frontal hemisphere. The infrequent target stimuli, infrequent novel stimuli, and frequent standard stimuli used by these investigators are analogous to the target stores, non-target stores, and buildings in the current experiment, respectively. The non-target stores in our experiment are meant to encourage the activation of a discrimination mechanism and thus are being compared in this thesis to the target stores.

Another way to analyze EEG data is by looking at the spatial distribution of activity across the scalp. It worthy of note that in Figure 10 over half of the topographic plots for individual participants show significant activity in the right parieto-occipital area around 300 ms. Areas of significant activity are seen on an individual basis at the times when the P1 and P300 components would be seen in an ERP, though not all participants show this effect. In addition, central activation is seen in participant 14 and Klimesch et al. (2000) saw a positive wave in the midline electrode positions around 200 ms. The fact that the backwards flow of activation is seen in Figure 13, combined with the grand average topographic plots above in Figure 9, provides reinforcement for the theory that the P1 and P300 belong to part of the same underlying neural activity that occurs in a visual recognition task.

We did not perform any oscillatory analyses in this study. Experiments involving navigation are difficult to design because synchronization and desynchronization of θ oscillations, which can create components in the ERP waveform, can be brought about by a number of tasks for which we did not specifically control (O'Keefe & Burgess, 1999).

Future considerations

Experimental improvements may well produce better results in future studies. A number of different methods could be implemented to more accurately record the occurrence of behavioral events – e.g., use of an eye-tracker, which would record data for exactly what a participant is looking at on the computer screen. Eye-trackers also allow for online peripheral-blurring or peripheral-blocking so that only the section of the screen at which a participant is looking is in focus or can be seen. Another option is to have the participant press a button on the controller when they see a target store, providing an explicit cue with which to line up the data.

In addition, there are analytical improvements that would allow us to continue using the data that we have collected. We could make better behavioral analyses. For example, we might compute the percentage of each object on the screen at any given time, taking into account variables such as color-contrast between surrounding objects. To this end, we might even be able to use a visual-detection algorithm to give us better information about the spatial threshold at which an object can be seen, thereby allowing us to better estimate at what point a participant will see a target store (or any other object) on the screen. This approach would offer greater accuracy than our current approach based on knowing the percentage of screen occupied by a particular object.

As for electrophysiological analyses, “peak-picking” (lining up ERPs by the latency of a particular component) could be applied to the data (Handy, 2005). Gratton, Kramer, Coles, and Donchin (1989) examine and compare peak-picking and Woody filtering (Woody, 1967). The Woody filter is an adaptive filter that helps to line up temporally variable signals via template-matching, improving latency estimation through cross-correlational analyses, and is computationally simple (van Boxtel, 1998). Criticism of and improvements on the Woody filter have been provided in Möcks, Köhler, Gasser, and Pham (1988).

Also, integrating our scalp EEG findings with those of spatial navigation research conducted with intracranial EEG could lead to the discovery of an interesting relationship between these two kinds of electrophysiological recordings.

In summary, the results of this experiment demonstrate that a significant difference in neural activation is detected at the scalp during viewing of a target store versus a non-target store in a complex navigational task. This is important because the elicited effect, that is, the initial right-frontal activation found during a visual recognition task with the corresponding LPC in the right posterior area, is consistent with related literature. This effect was found both within a single participant and across the average of the majority of participants. The significant differences in ERPs and scalp topographies provide evidence not presented in previous experiments and may help to better understand neurophysiological processes of human spatial cognition.

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