DIFFERENCES IN BRAIN OSCILLATIONS DURING PERCEPTUAL REVERSALS IN YOUNG AND OLDER ADULTS

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ABSTRACT

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Multistable perception was being studied by scientists and philosophers for over 200 years. Wealth of this literature provided many interesting findings, most of which is still to be studied with neuroimaging techniques. One of such findings is the slowing of reversal rates with advancing age. This thesis aimed to identify the changes in theta and alpha frequencies as correlates of top-down and bottom-up processes that are related to this age-related decrease. To this end, electroencephalography (EEG) of young and older adults were recorded during continuous presentation of a stroboscopic alternative motion (SAM) stimulus. A control stimulus was also used to differentiate reversal-related activities from other activities related to increased attention, decision making, and novelty response. Findings replicated the previous EEG literature in young adults by showing increase in frontal theta responses and posterior alpha desynchronization at the time of reversals. For older adults, on the other hand, findings showed significant differences in topography of alpha and theta responses. Occipital

alpha desynchronization of older adults was entirely dimished, instead, a significant increase in anterior alpha desynchronization was observed. At the same time, frontal theta response was entirely diminished and it was shifted to occipital areas. Findings from control task showed that this difference was specific to perceptual reversals. Agerelated changes in topography of oscillatory responses is previously shown to reflect compensation rather than pure deterioration. Our findings agree with previous studies. This thesis provided the first findings of aging-related compensatory actions of multiple oscillatory networks in a multistable perception paradigm.

Keywords: multistable perception, aging, electroencephalography, brain oscillations, alpha, theta.

ÖZET

GENÇ VE YAŞLI YETİŞKİNLERDE DÖNÜŞEN ALGILAMA SIRASINDAKİ BEYİN SALINIMLARI DEĞİŞİKLİKLERİ

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Multistabil algı, bilim insanları ve felsefeciler tarafından 200 yılı aşkın süredir çalışılmaktadır. Bu literatürün zenginliği, daha henüz beyin görünteleme yöntemleriyle incelenmemiş birçok ilginç bulgu sağlamaktadır. Bu bulgulardan bir tanesi de ileri yaşın beraberinde getirdiği algısal dönüşüm yavaşlamasıdır. Bu tezin hedefi, yaşlı katılımcıların teta ve alfa dalgalarındaki değişimi bu yaş etkisine sebebiyet veren aşağıdan-yukarı ve yukarıdan-aşağı süreçlerdeki değişimlerle ilişkilendirmektir. Bu amaçla, genç ve yaşlı katılımcıların elektroensefalografisi (EEG) bir stroboskopik alternatif hareket uyaranının sürekli gösterimi sırasında kaydedilmiştir.Algısal değişimle alakalı aktiviteleri artan dikkat ve karar verme ile alakalı aktivelerden ayırt edebilmek için bir kontrol uyaranı da kullanılmıştır. Bulgular, frontal teta yanıtında artış ve posterior alfa desenkronizasyonu göstererek genç yetişkinlerin önceki EEG bulgularını tekrarlamıştır. Öte yandan, yaşlı yetişkinlere yönelik bulgular teta ve alfa yanıtlarında önemli topografik değişiklikler göstermiştir. Oksipital alfa desenkronizasyonu yaşlı yetişkinlerde görülmemesine rağmen bu katılımcılarda önemli bir frontal alfa desenkronizasyonu gözlemlenmiştir. Aynı zamanda yaşlı yetişkinlerde frontal teta yanıtı görülmezken onun yerine oksipital bölgede bir teta yanıtı bulunmuştur. Kontrol görevinin bulguları bu farkın algısal dönüşüme özel olduğunu göstermektedir. Önceki araştırmalar osilasyon yanıtlarındaki ileri yaşla alakalı topografik değişimlerin salt bozulmadansa telafiyi temsil ettiğini göstermiştir. Bulgularımız önceki çalışmalarla uyuşmaktadır. Bu tez, multistabil algı paradigmasında ileri yaşla beraber görülen çoklu osilasyon ağlarındaki telafi davranışının ilk bulgusunu ortaya koymuştur.

Keywords: multistabil algı, elektroensefalografi, beyin salınımları, alfa, teta.



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PREFACE

When the biodiversity on earth is considered, it becomes difficult to comprehend the variation of sensory systems across species. A logical conclusion of this would be that most organisms sense their environment differently, and that there are fundamental differences in the way organisms behave and process information because of that. It is true that different organisms have different means of behaving and processing information, but it is also true that most organisms have similar perceptual-behavioral (e.g. startle response, exploratory behavior, and mating behavior) patterns towards evolutionarily significant events or objects (e.g. fear, food, and reproduction). In other words, even though the sensory input varies across species, perception allows organisms to construct a framework to survive, reproduce, and thrive. This is why it is important to think of perception as an evolutionary mechanism that creates its own product by using different sensory inputs.

In my mind, multistable perception (MSP) provides a window for examining the workings of perception. It reveals the moment where sensation is transformed into different interpretations of the world. It was humbling to study the immensely complicated web of electrical activity underlying this process. Now it is clear to me that none of us will ever know enough. We may perceive as if we know, that is when we have to contend with our own interpretations of this world.

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LIST OF ABBREVIATIONS

- EEG electroencephalography
- **ERD** Event related desynchronization
- **ITC** Inter-trial coherence
- **ISI** Inter-stimulus interval
- MS milliseconds
- MT Medial temporal lobe
- **SAM** stroboscopic alternative motion
- SNR Signal to noise ratio

CHAPTER 1: INTRODUCTION

Generally, there is enough sensory stimulation and perceptual cues in daily lives of modern healthy humans for predicting the events in their environment and act accordingly. This results in perceiving coherent percepts (i.e. perceptual interpretations) of the environment that do not change rapidly in time. Human perception, however, has the potential of creating rapidly changing percepts when there is not enough sensory evidence or prior expectations. For instance, couple of cracking sounds during a pitch-dark night at a remote place could be perceived as many different things, especially if the person is alone. It is easy in that circumstance to see faint movements in the darkness that are not actually there. It does not matter whether the sound was created by a little falling branch or a pine cone. Perceptualbehavioral system has to fixate to the sensory evidence at hand and come up with possible explanations that best serves the organism depending on the context. To do this, perception has to be flexible in situations where there is not enough sensory evidence or prior information about the sensation to construct a stable percept. Also, perception has to be coherent and stable in situations where there is enough sensory evidence and clear contextual cues about the perceptual event. If any of these two conditions are not met, organism would fail to execute required patterns of behavior to adapt to its environment. Because lack of flexibility of perception can lead to unrecognized novel threats and lack of stability in perception would impede any sort of goal directed behavior.

1.1. Multistable Stimuli

Above mentioned dynamic property of perception is well observed in multistable perception experiments. Since mid-1800s, experiments on multistable perception used specific sorts of stimuli to elicit perceptual changes without any physical change in the stimuli themselves (Necker, 1832; Long, and Toppino, 2004). This, in turn, allowed researchers to separate sensation from perception in a unique way. These stimuli have been called with different terms such as reversible figures, ambiguous figures/stimuli, bistable or multistable stimuli (Strüber et al., 2000; Kornmeier, Hein, and Bach, 2009; Strüber, and Herrmann, 2002). However, for convenience, these stimuli will be called as multistable stimuli in this work. A key property of multistable stimuli is that they have more than one perceptual interpretation even though the stimulus itself is physically unchanging (e.g. Necker cube) or has only one pattern but perceived to have two or more patterns (e.g. stroboscopic alternative motion). For instance, when an observer starts to look at a multistable stimulus he or she perceives one stable shape or movement direction at first, depending on the stimulus (Figure 1). After some time of observation, this perception spontaneously changes without any change on the stimulus itself. Shape or the movement in the perceptual awareness becomes another interpretation of the same stimulus. These spontaneous reversals occur as long as observation continues. In short, multistable stimuli induce spontaneous perceptual changes between its perceptual interpretations¹.

First formal example of these class of stimuli was the Necker cube (Necker, 1832) (Figure 1). Most commonly used version of Necker cube have two perceptual interpretations that are related to the cube's spatial orientation. In one of these interpretations cube's front face appears to be oriented towards bottom-left side of the cube (Fig 1B). In the other interpretation cube's front face is oriented towards top-right side of the cube (Fig 1C). It has to be emphasized that descriptions of the perceptual interpretations may vary across studies even though researchers describe the same depth perception (Kawabata, and Yamagami, 1978; Kornmeier, and Bach, 2004).

There are different multistable stimuli that have similar characteristics. Figure 1 shows some of these stimuli used in experiments. All these examples demonstrate only the visual multistability. However, perceptual reversals are also observed with tactile and auditory multistable stimuli (Gregory, and Warren, 1958; Carter et al., 2004; Denham et al. 2014). Interestingly enough, observing multistability in different sensory modalities indicates to a global mechanism rather than a modality specific sensory phenomenon.

¹ In order to avoid confusion, it is important to note that perceptual reversal is also called as perceptual switching or perceptual alternation by other researchers. There are no functional differences between these terms.



Figure 1. Multistable stimuli. Figure shows Necker cube (left), vase-face (middle), and duck-rabbit (right) stimuli. On continuous observation, orientation of the front face of Necker cube spontaneously changes to either bottom-left or top-right. Similar effect is observed in vase-face illusion where spontaneous changes occur between either a vase percept or a percept with two face with black background between them. This effect is observed between a duck image and a rabbit image for the duck-rabbit illusion.

1.2. Theoretical Approaches to Multistable Perception

Since Necker's discovery of the Necker cube in 1832, researchers aligned themselves with different explanations for the possible causes of perceptual reversals. Due to such long history of theorizing and hypothesizing, there are several review papers that categorize the hypotheses and theoretical frameworks within which multistable perception is studied. One of the early reviews was written by Vicholkovska (1906), where the author classifies explanations for perceptual reversals under three categories: psychological, physiological and psycho-physical. A recent review by Long and Toppino (2004) classified the terminology of different sides of the debate depending on the era of researchers, which is more convenient for the current study. To categorize early explanations around 1900s authors used the terms central (cortex) vs peripheral (afferent sensory pathways) processes; while for the recent explanations, these authors used the terms top-down and bottom-up processes which are frequently used in cognitive science literature. Regardless of the terminology of the times, central processes, top-down processes, and psychological explanations dwell on the concepts such as attention, learning, and volition while emphasizing the role of non-sensory/higher-order brain areas on perceptual reversals.

At the same time explanations that use peripheral processes, and bottom-up processes emphasized the importance of sensory input, early sensory processing, and neural adaptation/satiation processes. In this work, the terms top-down and bottom-up processes will be used as umbrella terms that encompass the related past concepts in spite of the differences and nuances that were established by the recent literature of neuroscience.

1.2.1. Bottom-up Approaches

Researchers that hold bottom-up processes as the cause of perceptual reversals generally manipulate stimulus characteristics (e.g. changing the luminance or the size of the stimulus), use sensory adaptation (e.g. adapting neurons in retina or early visual cortex with a stimulus before testing) and manipulate the type of stimulus presentation (e.g. presenting stimuli with brief inter-stimulus intervals instead of continuous presentation) to support their hypotheses. Because they argue that the cause of perceptual reversals stem from low-level sensory processes such as retinal input; or basic physiological processes such as neural satiation where excitability of neural groups decreases after continuous stimulation. It must be emphasized that researchers that study bottom-up processes are not strictly adhered to the bottom-up explanations. Especially after 1960s, most of the researchers were proponents of explaining multistable perception with both of the approaches.

Initially L. A. Necker, argued in a letter that perceptual reversals are related to a percept's proximity to fovea (Boring, 1942; Long, and Toppino, 2004). This, in turn, meant that the observer is more likely to be aware of a percept if its features (e.g. edges) are close to fovea. This thinking suggests that the feature of the multistable stimulus that is focused by the eye should be the most prominent. Consequently, this view gives great emphasis on eye movements and fixation. In later years, this idea was tested and results were supportive. One study found that eye movements and perceptual reversals were associated (Ellis, and Stark, 1978). Another study found similar results, where it was more likely to see a certain percept of a multistable stimulus if eyes were fixated on certain locations (Ruggieri, and Fernandez, 1994). However, other studies showed that eye movements and fixation are associated to reversal but they are not necessary for the reversal per se. Specifically, studies that used eye movement recordings showed that reversals are not preceded by eye movements (Pheiffer et al., 1956). A recent study also showed similar results where reversals were found to be independent of eye movements (Aydin, Strang, and Manahilov, 2013).

One of the other bottom-up process is the bias in perceiving certain percepts of a multistable stimulus due to prior stimulation. Studies that investigate the bias effect use unambiguous versions of multistable stimuli to bias the perception towards one interpretation. These unambiguous versions look nearly identical to percepts of the multistable stimuli. However, unambiguous versions of percepts are created such that observation does not cause perceptual reversals. Short exposure to (e.g. 30 seconds) unambiguous version of a percept bias participants to perceive the other interpretation of multistable stimulus (Toppino, and Long, 1987; Long, Toppino, and Mondin, 1992). Researchers argued that this effect is caused by neural satiation hypothesis that was put forward by Köhler in 1940 (Long, and Toppino, 2004). Köhler (1940) found a steady increase in perceptual reversal rates if participants continuously observed multistable stimuli. He suggested that if participants observe a multistable stimulus, underlying neuronal groups that represent individual percepts satiate due to continuous excitation. When these neural groups are excited for a period of time, it becomes difficult to maintain similar levels of excitation within these groups. As a result, excitation of the neural group that represent the current percept becomes stagnant and other neural group that represent the alternative percept dominates the perceptual awareness of the observer. This hypothesis is still one of the most prominent explanations of perceptual reversals. I would further argue that most experimental effects that are considered to be aligned with the bottom-up tradition result from the simple but powerful idea of neural adaptation/satiation hypothesis. Whether the manipulation is biasing, implementing different stimulus durations or inter-stimulus intervals (ISI), or changing the stimulus strength; these all act on the rate of adaptation of neural groups to specific visual input.

Initially Orbach, Erlich, and Heat (1963) tested the adaptation/satiation hypothesis by using intermittent presentation of multistable stimuli. They hypothesized that discontinuous presentation would prevent full satiation of neural groups that represent a percept and would result in decreased perceptual reversals. Authors successfully found that increasing the interval between successive presentations lowered; and further increases prevented perceptual reversals. Results showed a steep decline in the rate of perceptual reversals when the duration of interstimulus interval (ISI) raised above 400 milliseconds (ms). Interestingly, most participants did not experience perceptual reversals in the 1,300 ms ISI condition. Authors argued that neural satiation was subject to decay when ISIs were long enough. Specifically, it was suggested that, on average, an ISI duration around 800 ms was enough for a complete decay of neural satiation. Neuron groups thought to regain their baseline excitability after that duration; therefore, no perceptual reversals occurred due to continuous activity of the neurons groups that represent one of the percepts. Recent studies also used discontinuous presentation procedure and found similar results (Leopold, 2002; Kornmeier et al., 2007). Kornmeier et al. (2007) used 4 different ISIs and found that gradual increase ISIs from 0 (continuous presentation) to 400 milliseconds (steps of: 13 ms, 43 ms, 130 ms, 390 ms) results in gradual increase in reversal rates.

Another bottom-up factor that influence perceptual reversals is the stimulus strength, specifically, the stimulus intensity (i.e. luminance for visual stimuli). Cipywynk (1959) used three different luminance conditions (bright, medium, and dim) while presenting the Necker cube. He found that higher luminance increased the perceptual reversal count. Author argued that low luminance was linked with the longer satiation durations of the sensory brain areas compared to higher luminance conditions. Consequently, it took longer to initiate perceptual reversals in dim light condition because neuron groups that represent each of the percepts remained active for longer durations.

Overall, bottom-up explanations largely rest on the argument of satiation (or adaptation) of sensory brain areas. Many studies used different techniques to manipulate the satiation process and successfully showed its effect on perceptual multistability.

1.2.2. Top-down Approaches

Other hypotheses on the cause of perceptual reversals involved top-down processes. For instance, Helmholtz (1910/1962) argued that even though reversals appear as involuntary, there is a sense that they can be trigger via desire. In today's terminology, his "desire" is called as volitional control. According to Long and Toppino (2004), volitional control experiments date back to work of Mull, Arp, and Carlin (1952). It appeared that participants had the ability to speed up or slow down

the rate of perceptual reversals just by mental effort (Toppino, 2003). Generally, there are three experimental conditions in volitional control experiments: switching, passive and hold. In switching condition, participants are asked to try to change the percept to the other interpretation as soon as they perceive an interpretation. Passive conditions are used as control conditions and participants are asked to observe the multistable stimuli without any effort to change its percepts. In hold conditions, contrary to switching conditions, participants are asked to hold the current percepts as long as possible. All conditions require participants to report, usually with button presses, whenever they experience a perceptual reversal. This procedure showed that switching condition resulted in higher reversal rate than passive condition. Also, reversal rates in hold condition was decreased compared to the passive condition. Strüber and Stadler (1999) also found that strength of volitional control was increased when participants exerted control on meaningful multistable stimulus (e.g. duck-rabbit) compared to an abstract multistable stimulus (e.g. Necker cube). It was suggested that volitional control, in general, could be a process where attention is selectively focused to intended spatial locations of the desired percept. Authors also argued that memory representation of a meaningful stimulus would be more accessible, and therefore volitionally control would be easier to implement.

It was shown that knowing the reversibility of multistable stimuli influence whether participants would experience perceptual reversals or not. Rock and his colleagues conducted a study where one group of participants received instructions about the reversibility of stimuli and another group received instructions with no information of reversibility. Authors used four different trial durations (e.g. 30 s, 60 s, 120 s, 180s) to ensure that this effect persists regardless of duration. They've shown that only about half of the participants in the no information group reported perceptual reversals, regardless of trial duration. On the other hand, all participants reported perceptual reversals in the other group, again, regardless of trial duration. Authors argued that this effect contradicts with the neural satiation model in which it is assumed that the reversal process is automatic.

Familiarity effect aside, another learning effect is observed in participants who participated to multistable perception experiments more than once. It was found that once participants learn about the reversibility and report their reversals in one experiment, they report increased reversal rates if they participate the same experiment once again (Long, Toppino, and Kostenbauder, 1983). Given that satiation is also thought to effect reversal rates through continuous observation of one figure in short periods of time; researchers used one-week intervals between four experiments to eliminate the effects of satiation (Donahue, and Griffits, 1931; Long, Toppino, and Kostenbauder, 1983; Long, and Toppino 2004). Regardless of the weekly intervals, there was a gradual increase in reversal rates in each subsequent experiment. Once again, these results showed that perceptual reversals are not caused solely by bottomup processes.

1.3. Aging and Multistable Perception

Aside from these experimentally manipulated factors, aging is another factor that influence perceptual reversal rates of humans. Several studies showed significant variations in perceptual reversals in participants with different age groups. One of the earliest of such studies used binocular rivalry task² to investigate effects of aging on perceptual reversals (Jalavisto, 1964). Jalavisto (1964) found that participants who are older than 60 years old experienced significantly fewer perceptual reversals compared to participants below that age. Kondo and Kochiyama (2018) employed two different multistable stimuli to measure age-related changes in perceptual reversals in auditory and visual modalities. Visual stimuli were visual plaids where participants could see either a "single plaid moving upward or two different plaids moving sideways in opposite directions". Auditory stimulus was the auditory streaming stimuli that is constituted of repetition of tones in two different frequencies (e.g. A and B) in A-B-A pattern. When auditory streaming stimulus is continuously played, participants could hear either a pattern with a galloping rhythm that belongs to one perceptual stream or two tones that belong to two different perceptual streams. Similar to visual multistable stimuli, participants occasionally experience perceptual reversals between the interpretations of this auditory stimulus. Authors found marginally significant differences in reversal rates between participants in their 50s (n = 6) and participants in their 20s (n = 11) for both stimuli. It was also shown that there were significant

 $^{^2}$ Binocular rivalry is a task where each eye receives different stimuli simultaneously, as a result, participants either see one or the other stimulus. Similar to other multistable stimuli, participants experience spontaneous reversals on which stimulus they see. Even though the task is different than, say, a Necker cube task where input to both eyes are the same; researchers argue that underlying mechanism that causes perceptual reversals are related across different stimuli (Leopold, and Logothetis, 1999).

negative correlations between age and reversal rates in both sensory modalities. A possible explanation for the marginal significance between groups could be explained by unequal and small sample sizes of groups. It is a well-known finding that reversal rates have high inter-individual variability, therefore, analyzing reversal rates in small and unequal sample sizes can yield unreliable results in multistable perception experiments. Another factor could be the upper threshold of age in older adult group which was maximum of 60 years. Most findings that show age related differences in perceptual reversal rates had either 55 or 60 years of age as the lower age threshold for the older adult group (Aydin, Strang, and Manahilov, 2013; Patel, and Reed 2016).

For instance, Aydin, Strang, and Manahilov (2013) used Rubin Face-Vase stimulus to examine age related differences in perceptual reversal rates. Authors sampled 20 younger adults ($M_{age} = 24.4$, $SD_{ag} = 4.12$ years) and 16 older adults (M_{age} = 69.2, SD_{age} = 6.90 years) and found that older adults reported significantly lower perceptual reversals than younger adults in passive viewing condition. Interestingly, Aydin, Strang, and Manahilov (2013) also found that older adults could increase their reversal rate in switching condition as much as younger adults, but unlike younger adults; older adults failed to slow down their reversal rates in hold condition. This result indicates separate brain networks that are responsible for holding and switching perceptual interpretations. Diaz-Santos et al., (2017) employed Necker cube as the multistable stimulus and found significantly lower numbers of perceptual reversals in older adults ($M_{age} = 65.9$, $SD_{age} = 5.6$ years, n = 24) compared to younger adults (M_{age} = 19.4, SD_{age} = 1.5 years, n = 20) in passive viewing. Authors of the latter study also used a set of cognitive measurements that included processing speed, inhibition, verbal fluency and set-shifting to examine whether cognitive performance measurements are related to multistable perception or not. However, results showed that cognitive performance measures are not related to perceptual reversal rates. Diaz-Santos et al., (2017) also found that perceptual reversal rates between younger and older adults only differed in passive and hold conditions but not in the switching condition. These studies also used eye tracking devices to examine whether eye movements were related to perceptual reversals (Aydin, Strang, and Manahilov, 2013; Diaz-Santos et al., 2017). Both of the studies failed to find a significant relationship between eye movements and perceptual reversals.

In short, a clear decline in reversal rates after the ages of 55 to 60 is shown by several studies that use different multistable stimuli and experimental designs. Therefore, it is plausible to assume that decreased reversal rates are independent of stimuli and caused by age-related changes in the brain that also effect perceptual processing. However, the lack of relationship between cognitive performance measures and perceptual reversal rates makes it difficult to explain age-related decrease solely with top-down explanations. Regardless, it was also shown that top-down control on perceptual reversals are impaired in older adults in hold condition. These findings indicate that the underlying reasons for age related decline in perceptual reversals cannot be explained by isolated factors. It is likely that age related decrease in reversal rates is caused by changes in both bottom-up and top-down processes. Drawing from brain imaging studies can help us better understand the age-related decline in perceptual reversals.

1.4. Electroencephalography (EEG)

EEG is a method of measuring brain activity by recording electric dipoles. These dipoles are produced by the electrical currents that result from changes in postsynaptic potentials of pyramidal neurons in cortex. Post-synaptic potentials change whenever a pre-synaptic neuron excites or inhibits it by means of releasing positively (e.g. Na+, K+, Ca++) or negatively (Cl-) charged ions into the synaptic cleft (Obermaier, Müller, and Pfurtscheller, 2003; Sanei, and Chambers, 2007). However, EEG can only capture synchronous activity of many pyramidal neurons due to weakness of the signals produced by single neurons. Additionally, these neurons have to be parallel to each other and perpendicular to the skull. Otherwise positive and negative currents cancel each other. Fortunately, most of the pyramidal neurons in human cortex are in parallel to each other and perpendicular to skull. The synchronous activity of many pyramidal neurons is picked up by electrodes that consist of silversilver chloride (Ag-AgCl) disks placed on human scalp with help of an electrode cap. Placements of these electrodes are decided on 10-20 electrode placement system where distances between electrodes are proportionally divided based on skull landmarks (Figure 2). Electrode labels carry the names of most proximal brain regions; odd numbers that follow these labels represent left hemisphere and even numbers represent right hemisphere (Sanei, and Chambers, 2007).



Figure 2. International 10-20 electrode placement system from (a) sagittal and (b) horizontal (b) perspectives (Source: Sanei, and Chambers, 2007)).

1.5. Neuroscience and Multistable Perception

In a seminal review, Leopold and Logothetis (1999) argued that perceptual reversals are caused by synchronized activation of different neuron groups that are distributed across the brain. Authors' interpretation was that perceptual reversals are not caused by low-level sensory areas but they result from synchronized activity of different neuron groups with different sensory and perceptual functions. Importantly, authors suggested that high-level brain areas modulate the activities in low-level sensory areas to trigger perceptual reversals. A similar line of thinking was prevalent among the members of a prominent team that study electrophysiological correlates of cognitive processes using electroencephalography (EEG) since 1970s (Başar, 1972; Başar-Eroğlu, and Başar, 1991; Başar et al., 2011; Başar, and Güntekin, 2013). Their main focus was to identify functional correlates of brain oscillations in different frequency bands in sensory and cognitive processing. The hypothesis was that complex brain functions, such as cognitive processes, result from synchronized activity of selectively distributed delta, theta, alpha, beta, and gamma oscillations (Başar et al., 2001). Instead of assigning single functional role for a given oscillatory activity of one frequency range; Başar et al. (2001) argued that cognitive and sensory

processes are governed by superimposed oscillations with different amplitudes, durations and delays. This framework provides a convenient tool for analyzing fastpaced-parallel brain activities that give rise to changes in perceptual awareness. Therefore, this study will use oscillatory activities in theta and alpha frequency ranges to identify underlying alterations in oscillatory networks that are related to decreased perceptual reversal rates in older adults.

1.5.1. Neural Correlates of Top-down Processes

In 1993, Başar-Eroğlu and her team conducted the team's first experiment in multistable perception paradigm. Researchers used stroboscopic alternative motion (SAM) stimulus to induce perceptual reversals and asked participants to press a button whenever they experience a perceptual reversal (see Methods section, Figure 4). Authors have found a slow positive wave (0.5 to 4 Hz; delta frequency), approximately 250 ms before the button press. It was argued that this slow wave was a result of an endogenous cognitive process where perceptual mechanism shifts from one stable brain state to another. Later research also discussed this finding as the marker of "conscious realization of the perceptual reversal", also called as perceptual closure (Mathes et al., 2006; Mathes et al., 2014). Therefore, it was concluded that the activity in the delta frequency during perceptual reversals reflected a top-down process. This conclusion was in parallel with the previous notion that delta frequency reflects cognitive processes such as decision making, and signal detection (Başar-Eroğlu et al., 1992; Başar et al., 2001).

Another frequency band that was thought to reflect top-down processes during perceptual reversals is the theta frequency band (4-8 Hz). A previous study showed an increase in theta response during perceptual reversals of SAM stimulus (Mathes, et al., 2014). It was also shown that maximum theta response was found at frontal area and that here was a linear decrease in amplitude towards posterior areas in healthy young subjects (Mage = 23.20, SD = 3.50). Researchers argued that frontal maximum of theta activity reflects a combination of processes such as expectation and prior experiences. These processes is thought to ensure coherent perception when the sensory information is ambiguous and leads to conflict between interpretations of the stimulus. A subsequent study published by the same group compared reversal related theta activity between healthy controls and patients with schizophrenia (Mathes, et al., 2016). It was found that theta increase during perceptual reversals was absent in

patients with schizophrenia. Authors argued that this indifference in theta activity reflects deficits in spatio-temporal integration of neural information transfer in patients. However, there was no difference in perceptual reversal rates between controls and patients.

These studies are in line with previous findings related to theta activity in other paradigms such as oddball or go/nogo tasks. More generally, theta response is related to processes such as conflict resolution, expectancy states, and memory processes (Mathes et al., 2014; Mathes et al., 2016). Inadequate stimulation also induces theta response which is thought to serve an associative function in that context (Başar, 1998; Başar, 1999). Taken together, it is apparent that theta response reflects top-down processes such as information transfer and conflict resolution also in multistable perception. More specifically, anterior theta activity modulates the activity in posterior areas using prior experiences and expectations in situations where there is perceptual ambiguity. It is plausible to assume that disturbances in this network possibly leads to poor conflict resolution capabilities of the whole brain network.

Interestingly, Cohen (1959) recruited participants with lesions at right frontal areas to examine changes in reversal rates compared to healthy participants. He found that participants with frontal lesions experienced significantly lower perceptual reversals compared to healthy participants. Windmann et al. (2006) also showed decreased reversal rates and decreased ability to control reversal rates in frontal lesions patients. In line with these findings, Brascamp et al. (2018) reported reliable activations in right frontal and right parietal areas during perceptual reversals. These results support the assumption that disturbance in fronto-parietal networks would cause impairments in generating and switching between coherent percepts.

1.5.2. Neural Correlates of Bottom-up Processes

We encounter with Köhler's (1940) neural satiation hypothesis whenever we discuss bottom-up processes in multistable perception. Even though his original hypothesis is not empirically plausible anymore, the idea that lead to his hypothesis is still applicable. In todays terms, argument was that perceptual reversals are an indication of the changes in underlying brain states. These brain states, according to Köhler, were changing due to the transient dominance periods of specific neural groups. These dominance periods were transient because the neural groups satiated

over time due to continuous activation. Fortunately, we now have tools to test this idea with EEG. It is a very-well known finding that spontaneous activity in alpha frequency range (8-14 Hz) increases when participants close their eyes, and decreases whenever they open their eyes (Başar et al., 2000). Another important finding is that alpha activity decreases during cognitive and sensory events (Klimesch, 1999; Başar et al., 2000). This reduction in alpha amplitude is also called as alpha desynchronization which was derived from the term event related desynchronization (ERD). A deduction from the findings would be that alpha activity is decreased whenever the brain is in an active state. However, behavior of alpha frequency is far more complicated. Başar and his coworkers (2000) provided a clear depiction of various alpha response patterns in various cognitive and perceptual processes. Authors outlined that alpha activity can be decreased and enhanced at different areas of the brain at the same time during a cognitive task (Başar et al., 1997). It is also possible for alpha activity to increase in one cognitive task and decrease in another. Therefore, defining a general function for alpha frequency range is not helpful. It is more productive to discuss alpha frequency both in the context of multistable perception and in relation to activities in other frequency bands that is observed during perceptual reversals.

Initially, İşoğlu-Alkaç et al. (2000) found a global reduction in alpha frequency amplitude within the same time window (-440 to -80 ms before button press) of the slow positive wave. Authors argued that parallel activities in alpha and delta frequencies represent two different processes that in combination lead to the perceptual reversals. A magnetoencephalography (MEG) study also found a slow and steady decline in alpha amplitude that took around 1 seconds, which rebounded at the time of button press (Strüber, and Herrmann, 2002). Similarly, maximum desynchronization of alpha frequency was within same time window with the delta response that reflects conscious awareness of reversals. Interestingly, there was no slow and steady decline during a control task (exogenous task) where reversals are initiated by changes in the actual stimulus. Instead, alpha activity during exogenous reversals decreased very briefly and quickly around 300 ms before the button press and then rebounded. Authors argued that slow decline in alpha activity in endogenous task, where reversals are initiated by the brain, reflects the bottom-up process of slow destabilization of current perceptual interpretation. Findings indicate that destabilization is a passive process and it is not reflected to the conscious awareness

of participants. Strüber and Herrmann (2002) suggested that this slow destabilization is followed by a sudden change in visual awareness; which is reflected in P300-like delta response. İşoğlu-Alkaç and Strüber (2006) reached to similar conclusions about the function of alpha activity during perceptual reversals. They argued that alpha desynchronization reflects an automatic arousal reaction that initiates attentionnal processes in a bottom-up manner. Başar-Eroğlu et al., (2016) investigated differences in alpha activity between patients with schizophrenia and healthy controls in a multistable perception task. Patients showed higher alpha activity during no reversal periods. However, slow decline of alpha was observed in patients as well. Authors interpretation was that patients compansated attenuated theta response, which reflects imparied spatio-temporal integration, with additional recruitment of alpha networks to further stabilize internally generated percepts. This, in turn, points to the conclusion that bottom-up and top-down processes work in combination to create coherent perceptual interpretations. Whenever an alteration occurs in one of the oscillatory networks; others adapt to the alteration by changing their own responses.

1.6. Neuroscience and Aging

To our knowledge, this is the first study that investigate brain oscillations of older adults in a multistable perception paradigm. However, drawing from studies that use other cognitive paradigms and different neuroscientific methods an help us understand what sorts of changes we can expect from an aging brain. First and foremost, it is important recall that participants experience significantly lower perceptual reversals during passive viewing after around 60 years of age (Jalavisto, 1964). Another important behavioral finding was that older participants were able to speed up their perceptual reversal rates, but they cannot slow down the rate of reversals. Former finding hints to impairments in both bottom-up and top-down processes. Latter finding indicates an alteration specific to top-down processing. Therefore, we should look for age-related changes in brain activities that reflect both of these processes.

One single neuron study on young and older macaque monkeys investigated differences in neural responses to simple visual stimulation over multiple trials (Yang et al., 2009). Older neurons in V1 and medial temporal lobe (MT) showed marked increases in response variability. It was also shown that signal-to-noise ratio (SNR) of these neurons was lower. Meaning that difference between spontaneous brain activity

and brain activity in response to an external stimulus was lower for older neurons. Another study showed that these alterations in response variability and SNR cause impairments in stimulus selectivity of older neurons (Schmolesky et al., 2000). In other words, neural groups that primarily respond to specific stimuli lose their response specificity and start to respond to other stimuli as well. Identical age related impairments were also found in neurons of older cats (Hua et al., 2006). Authors concluded that age-related decrease in SNR and increase in response variability reflects an impairment of retrieving signals from noisy backgrounds in older cells. Interestingly, Kolev et al. (2002) found that middle-aged participants ($M_{age} = 53.6$ $SD_{age} = 2.2$ years) showed decreased phase locking and amplitude in occipital fast alpha (10-15 Hz) in response to simple visual stimulation. However, phase locking and amplitude of frontal fast alpha was increased in middle aged participants. Authors suggested that visual information may be communicated to associative frontal areas by occipital-frontal fast alpha networks as a compensatory action. But what if visual information is inconclusive? Impaired stimulus selectivity of older neurons is a more severe problem if stimulus have more than one perceptual interpretation. Because any feature of the stimulus can be interpreted as either of two percepts. This, in turn, would cause increased uncertainty about what the percept is and higher conflict between possible percepts. An intuitive conclusion for multistable perception would be that, low SNR of older neurons in occipital area would cause disturbances in gradual destabilization of percepts which is reflected in alpha frequency. Furthermore, increased response variance would most likely impede gradual destabilization. Because process of destabilization cannot be isolated to one percept if response specificity of neural groups is compromised.

However, previous studies provide mixed results for alpha responses in cognitive tasks where the stimulus is not ambiguous (e.g. not endogenous). Schmiedt, Mathes, and Başar-Eroğlu (2009) showed that alpha activity during sensory, sensory-motor, and cognitive processing in a Go/NoGo task are not affected by age. Authors also discussed that literature does not provide a clear difference in alpha activity in early visual sensory processing between older and young participants in similar cognitive tasks (e.g. oddball task). However, stimulus discrimination and decision making processes in the former study is not comparable to multistable perception paradigm. Because interpretations of a multistable stimulus are not exogenously

generated (e.g. by stimulus); rather, internally generated interpretations of the same stimulus are made conscious by interactions of different neural populations in different time scales and in different locations. This difference is outlined in Strüber and Herrmann's (2002) MEG study where alpha decrease was long and gradual during endogenous reversals; while the decrease was sudden and very brief for the exogenous reversals. The former represents gradual destabilization of endogenously generated percepts; where the latter represents stimulus-driven alpha ERD. Therefore, it is likely that occipital alpha desynchronization during endogenous reversals is going to be effected by age. In theory, this would cause a shift in priority of the brain networks to resolve the increased perceptual interpretations; how would synchronized activity distributed networks can make unresolved perceptual interpretations conscious? Would selectively distributed networks in theta frequency help to resolve the conflict in low-level areas as we would expect from a dynamic compensatory system?

Recalling the partial impairment of volitional control of older participants would provide a proper context for relating upcoming literature to multistable perception. Those studies showed that top-down processes are somewhat impaired in older adults, but not in every aspect. Schmiedt-Fehr and Başar-Eroğlu (2011) investigated theta and delta responses of older ($M_{age} = 63 SD_{age} = 7$ years) and young adults ($M_{age} = 23 SD_{age} = 3$ years) in a visual Go/NoGo task. Older adults had decreased power and inter-trial coherence (ITC) in late theta response (200 to 600 ms post stimulus) at central areas during NoGo trials. Authors argued that altered responses in older adults reflect an attenuated long range information transfer function to inhibiting the anticipated response. A very similar study examined age related changes in an auditory Go/NoGo task; and results conflicted in the visual Go/NoGo study (Schmiedt-Fehr, Dühl, and Başar-Eroğlu, 2011). Older adults showed stronger ITC in early theta response (0 to 200 ms post stimulus) both in Go and NoGo trials at central locations. Interpretation was that these differences might reflect top-down enhancement of auditory processing and age-related stabilization of neural connections that process auditory information. They concluded that observing contradictory theta responses in visual and auditory Go/NoGo paradigms possibly reflect different age-related changes between these sensory modalities.

1.7. Present Study

Before outlining the aim and the reasoning behind this study, a clarification about the data is needed. Present study used two datasets, one from Germany and the other from Turkey. Dataset from Germany was used to investigate our main questions, which are about age-related differences in oscillatory networks in multistable perception. Dataset from Turkey was used to explore reversal characteristics of three different multistable stimuli: Necker cube, Necker lattice, and SAM. Further details are presented in Methods section.

Literature points to alterations in top-down and bottom-up processes as the causes of age-related decrease in reversals (Jalavisto, 1964; Aydin, Strang, and Manahilov, 2013). These processes can be represented in terms of selectively distributed networks in different frequency bands (Başar et al., 2001). For instance, increased theta activity at frontal areas reflect the process of resolving perceptual conflict by using prior experiences and expectations (Mathes et al., 2014). Gradual decrease in alpha activity, on the other hand, reflects gradual destabilization of conscious percepts mainly at occipital area; where representations of percepts are maintained in a bottom-up manner. Previous studies showed frontal shift of alpha networks in response to simple visual stimulation with advancing age, but not in response to cognitive events (Kolev et al., 2002; Schmiedt, Dühl, and Başar-Eroğlu, 2009). Authors argued that this was a compensatory action where impairments at occipital area is compensated anterior shift of alpha networks. Frontal theta response of older adults also found to be impaired in a visual task that require behavioral inhibition, but not action (Schmiedt-Fehr, and Başar-Eroğlu, 2011). This finding paralells with the behavioral findings where older adults could speed up reversals (action) but could not slow down/hold conscious percepts.

This study is aimed to identify the alterations in selectively distributed networks that contribute to decrease in perceptual reversal rates after the ages of 55 to 60. A control task (exogenous task) is included to compare effects of aging between changes in endogenous perception and perception of changes in external stimuli. Alterations in bottom-up processes such as neural satiation and cortical excitability is measured by activity in alpha frequency range. Theta frequency was measured for examining alterations in top-down processes such as resolution of perceptual conflict by using expectations and prior experiences. We expect that there would be significant

changes in alpha response of older adults, especially at occipital areas. Because both human EEG studies and animal single neuron studies show clear alterations in simple stimulus processing at occipital areas (Kolev et al., 2002; Yang et al., 2009). Furthermore, a shift in location of alpha desynchronization is also expected due to previously observed compensatory action of frontal alpha networks in middle aged subjects (Yordanova, Kolev, and Başar, 1998; Kolev et al., 2002). Specifically, alpha desynchronization at posterior locations will be higher in young adults compared to older adults; but the desynchronization will be higher at anterior locations for older adults. We do not expect to observe differences in alpha activity between young and older adults in control task.

Previous studies that used external visual stimuli (e.g. Go/NoGo task) to induce cognitive oscillatory responses already showed decreased central theta responses in older adults (Schmiedt-Fehr, Başar-Eroğlu 2011). We expect that this alteration will be observed during perceptual reversals by diminished frontal theta responses in older adults. It is also expected that activations in distinct theta networks will compensate impaired function of frontal networks. Specifically, we expect to observe: (1) lower theta responses in older participants in both tasks, especially at frontal areas; (2) frontal theta response at frontal areas will be lower than

Additionally, reversal rate of SAM was compared between young and older participants across all participants in both countries. We expected to observe agerelated decreases in reversal rate regardless of participants' country. As part of the experiments in Turkey, exploratory analyses were conducted on reversal characteristics of Necker cube, Necker lattice, and SAM stimuli.

CHAPTER 2: METHODS

2.1. Participants

115 participants have participated in this study. 30 of those have participated in Bremen, Germany. 85 of the participants have participated in Izmir, Turkey. For convenience, I will call German sample/participants to former and Turkish sample/participants to latter group. German participants' data were collected in Bremen University, Germany by Prof. Dr. Canan Başar-Eroğlu (my supervisor) and her team. German data were never published in previous studies. Turkish participants' data were collected in Izmir, Turkey by the author of this thesis.

German sample consisted of two age groups, namely older (M_{age} = 61.8 SD_{age}= 3.81) and young (M_{age} = 23.93 SD_{age}= 2.52) groups. 2 German participants were lefthanded, and 6 participants were male (%20). Mean years of education was 15.66 for older and 14.23 for young group. Turkish sample consisted of psychology students in Izmir University of Economics (M_{age} =20.34 SD_{age}= 1.67). There were 10 male (%16.6) participants in Turkish sample. Students were informed prior to participation that they will receive an extra credit for Introduction to Psychology I class if they participate in the experiment. 25 Turkish participants were excluded due to prior head trauma, psychiatric diagnoses, psychiatric medicine use, and invalid data. Three of the remaining participants in Turkish sample were left-handed. Raw data from Germany did not include participants with head trauma, psychiatric diagnoses, or psychiatric medicine use. All participants in both countries had normal or corrected to normal vision.

2.2. Apparatus and Material

2.2.1. Stimuli

Total of four stimuli were used in the experiments in Turkey, and two stimuli were used in experiments in Germany. Necker cube, Necker lattice, SAM, and exogenous stimulus was used in Turkey; whereas only SAM and exogenous stimulus were used in Germany. All stimuli were created using Microsoft PowerPoint 2016 and then exported as image files for presentation for Turkish sample.

Necker cube and Necker lattice stimuli are shown in Figure 3 alongside their disambiguated percepts. Width-height-depth ratio of Necker cube was 1:1:0.6 $(7.3 \times 7.3 \times 4.8 \text{ cm})$. Cube was drawn on a black screen with white lines on a computer

screen. Vertical and horizontal visual angle of the cube were both 3.21° . A red fixation point was placed at the top right vertex of the cube's front face (if perceived as such). Lattice was created with nine small Necker cubes with width-height-depth ratio of 1:1:0.2 ($9.2 \times 9.2 \times 2.1$ cm). Rotation of the small cubes were rotated 90° counterclockwise to prevent possible adaptation effects that are related to previous or future exposures to Necker cube. A red fixation point was also placed at the middle of Necker lattice. Lattice stimulus was a version of the Necker lattice presented in Kornmeier and Bach (2006). It was drawn on a black background with white lines and displayed on a computer screen. Vertical and horizontal visual angle of the lattice were 3.43° and 3.72° , respectively.

Depiction of SAM and exogenous stimuli are presented in Figure 4. A black rectangle on a white background with a width-height ratio of ~0.7:1 (7.6×10.9 cm) was created and centered on the computer screen. A small white fixation rectangle was placed at the center of black rectangle. Then, two additional black rectangles with the same properties and fixation point were created. Two small white dots were placed at one of the opposite corners (top left, bottom right) diagonally of one of the rectangles. Same was applied to the second rectangle but white dots were placed at the other opposite corners (i.e. top right, bottom left) Rectangles with dots at the corner are defined as double-dot displays, and the rectangle with fixation point is defined as fixation display. SAM was created by repeated and subsequent presentation of double-dot and fixation displays. Sequence of display presentation was in the following order and repeated throughout the experiment: fixation, double-dot, fixation, double-dot. Durations of double-dot displays were ~165 ms and the duration of the fixation display were ~85 ms. Therefore, duration of each sequence was approximately 500 ms.

A slightly modified version of the SAM rectangles was used to create the exogenous stimulus. Double-dot displays were placed at either horizontal or vertical corners instead of diagonal corners for this version. Sequence of stimulus presentation and durations of double-dot and fixation displays were identical. Properties of SAM and exogenous stimulus were the identical in experiments in Germany and Turkey.


Figure 3. Necker cube and Necker lattice stimuli. (A) Necker cube and its bottomleft and top-right interpretations. (B) Necker lattice and its top-left and bottom-right interpretations. Interpretations (percepts) are named according to the orientation of their front faces.



Figure 4. Presentation sequence of SAM (left) and exogenous stimulus (right). Only the horizontal motion of exogenous stimulus is shown. Sequence of its vertical motion is identical, but the dots are placed at the top and bottom corners horizontally.

2.2.2. Stimulus Presentation

These images were presented via custom scripts written in MATLAB 2018a (prior version for the German sample) using Psychophysics Toolbox extensions (The MathWorks Inc., MA, USA; Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Two different display devices were used for samples in Turkey and Germany. A PC controlled 60 Hz 19" Acer V195WL computer monitor with 1440x900 pixel resolution was used for experiments in Turkey. On the other hand, a 19" CRT (Cathode-Ray Tube) monitor was used for the experiments in Germany. CRT monitor was controlled by a PC.

2.3. Tasks

2.3.1. Stroboscopic Motion Tasks

SAM and exogenous stimuli were used in two separate tasks: endogenous and exogenous tasks. Schematic illustration of both tasks and each of the perceived motions are presented in Figure 5. Endogenous task employed stroboscopic alternative motion (SAM) and participants reported internally generated spontaneous reversals of motion perception. There are two visual illusion are at play in endogenous task: (1) one is the illusion of *stroboscopic motion* where participants perceive as if the dots move from one point to another, and (2) the other is the illusory *alternation of the motion direction* due to the diagonal positioning of the dots (Mathes et al., 2016). Participants either experience vertical or horizontal motion during continuous observation.

Exogenous task used the modified version of SAM where the motion reversals were externally (by stimulus change) triggered (Mathes et al., 2016; Başar-Eroğlu et al., 2016). Similar to SAM, perceived stroboscopic motion of exogenous stimulus was either vertical or horizontal. This task was used as a control measure for SAM. In other words, it was possible to check that participants understood the perceptual reversal instructions by monitoring which buttons they pressed for which motion reversals. It was also possible to measure reaction time in exogenous task which provided an approximation for the reaction times in SAM. Number of reversals within a minute was set to 8 for exogenous stimulus. Previous studies used ~9.5 exogenous reversals per minute in accordance with the results of healthy young participants (Mathes et al., 2016). However, it was decided to lower the exogenous reversal rate for this study.

Because number of endogenous reversals reported by older participants are significantly lower than young participants (Jalavisto, 1964; Aydin et al., 2013).

Instructions were different for experiments in Germany and Turkey. Instructions for Turkish sample are explained in this paragraph, and instructions for the German sample are explained in the next paragraph: Participants were asked to indicate changes in motion with a keyboard button press. Reversals to horizontal motion were reported with "8" and reversals to vertical motion were reported with "7" on the numpad of a computer keyboard. On very rare occasions, some participants may experience clockwise or counterclockwise rotations in endogenous task. They were informed on this issue and asked to indicate clockwise rotation with "8" and counterclockwise rotation with "7" if they ever experience that motion. This information was only given verbally to avoid biasing participants towards clockwise percepts by showing it visually.

Participants in German sample were asked to press a hand-made button press device whenever they experience a perceptual reversal. There was no keyboard or mouse presses during EEG recording. This way, participants did not hear a sound when they pressed a button and this prevented possible signal distortions caused by an auditory stimulus. There was no indication of the rotation of perceptual reversals, participants only reported the reversal itself.

2.3.2. Necker Tasks

Unlike stroboscopic motion tasks, Necker tasks did not have an exogenous condition. Necker lattice and Necker cube were continuously shown to participants via a computer screen. They were asked to press a keyboard button as soon as they experienced a perceptual reversal and indicate which of the percepts they see after the reversal. Participants were asked to indicate changes in orientation (perceptual reversal) with a button press. Reversals to rightward orientations were reported with "8" and reversals to leftward orientations were reported with "7" on the numpad of a computer keyboard (Figure 3).



Figure 5. Endogenous and exogenous stimuli and percepts. (A) Vertical motion of exogenous stimulus is generated by repeated subsequent presentations of Vert1 and Vert2. Repeated subsequent presentations of Horz1 and Horz2 results generates horizontal motion. Repeated subsequent presentations of Amb1 and Amb2 results in either horizontal or vertical motion perception, both of which are generated internally. (B) Depicts the relationship between stimulus presentation and the perceived motion. (left) Perceived motion direction is dependent on the change of presented stimulus (exogenous reversal) in exogenous task. (right) In contrast, change in perceived motion is internally generated (endogenous reversal) and stimulus presentation remains the same in endogenous task (Source: Mathes et al., 2016).

2.4. Procedure

2.4.1. Turkish Sample

Participants were invited to two separate experimental sessions that were at least two hours and at most 1 week apart from each other. Participants' perceptual reversals were measured with Necker cube and Necker lattice stimuli in one of the sessions. The other session used SAM for measuring perceptual reversals and exogenous stimulus for measuring reaction times. Participants who initially participated in the session with Necker stimuli were defined as Necker-first group. Participants that initially participated to the session with SAM and exogenous stimuli were defined as SAM-first group. Assignment to session groups was pseudorandomized across participants and number of participants in the Necker-first and SAM-first groups were equal.

Participants were invited to the Neuroscience of Mind and Behavioral Research Laboratory in Izmir University of Economics on a date and hour that they have decided. They sat 100 cm away from a computer monitor in a dimly lit room. Initially, all participants are handed an informed consent form to ensure that their participation is voluntary and that they understand that they can quit participating in the experiment whenever they desire. Then they have filled out a demographic information form where they state their age, sex, education level, handedness in addition to stating any previous diagnoses including psychiatric and chronic conditions, any medication use, or previous head traumas. They were also asked about their state of hunger, coffee and alcohol consumption, and amount of sleep they had at the day of experiment. Participants were briefed about perceptual reversals and perceptual interpretations of the stimuli in the experiment. Then experimenter instructed them to observe the multistable stimulus and report whenever they experience the reversals. After participants experience perceptual reversals under the supervision of experimenter, they were informed about which button presses they should perform to indicate which perceptual reversal. Participants were also informed about the effect of volitional control and asked not to implement control on perceptual reversals. Fixation points for each stimulus was shown to participants and they were asked to fixate their eyes on those points. Because eye blinks can cause reversals themselves, they were asked to prevent eye blinks as much as they can. After these verbal instructions, participants are left alone in the room and a set of visual

instructions were presented on the computer monitor. Visual instructions were nearly identical to the verbal ones and were presented before each trial for each stimulus separately.

After the instructions, 90 seconds length training trials for each stimulus in the experiment has started. There were inter-trial intervals of 30 seconds between training trials. Therefore, a training block with minimum of 210 seconds (aside from the time that participants spent on visual instructions) was created. Another 30 second inter-trial interval was initiated when the training block was finished. Then two separate test trials with 240 seconds duration initiated. These trials were separated with a 120 seconds inter-trial interval. As a result, a test block with a minimum of 600 seconds (aside from to the time that participants spent on visual instructions) duration was created. As a consequence, duration of a session was around 15 to 20 minutes. After the test block is finished, a screen appeared stating that the experiment is finished and asked participant to call in the experimenter.

Exogenous task was always the first test trial in SAM sessions. The order of Necker cube and Necker lattice test trials were counterbalanced across participants in Necker sessions.

2.4.2. German Sample

Participants were seated in a dimly lit, sound proof, electromagnetically shielded room. All participants gave informed consent. Initially, participants were briefed about perceptual reversals and perceptual interpretations of the SAM. They were asked to look at the central white dot of the SAM throughout the experiment. First, eyes closed and eyes open spontaneous EEG was recorded, with duration of 100 seconds in each condition. Subsequently, a training session of approximately 100 seconds ensured that participants are able to perceive reversals and also report them. Then, participants started with the exogenous task. After that, they started the endogenous task and completed the experiment. Both exogenous task and endogenous task lasted approximately 10 minutes each. Consequently, duration of EEG recording was around 25 minutes without counting the preparations before and after the experiment.

2.5. EEG Recording

The EEG was recorded using Ag-AgCl electrodes at F3, F4, C3, C4, P3, P4, T5, T6, O1, and O2 locations according to the 10-20 system (Jasper, 1958). Earlobe electrodes were used as reference electrodes. Electrode impedance were below 5 k Ω for all electrodes. EOG from medial-upper and lateral-orbital rim of the right eye was also recorded. The EEG was amplified with a Nihon Kohden (EEG-4421 G) EEG device with band limits 0.1-70 Hz. The EEG was digitized on-line with a sampling rate of 500 Hz. Digitized EEG was stored within a hard disc of a computer for offline EEG analysis. A 50 Hz Notch filter was applied to remove the mains interference. For the recording of EOG, the time constant 0.3 s with a low pass filter at 70 Hz was used. All channels were displayed by a computer monitor to observe EEG activity during the recording.

2.6. Definition of Epochs and Artifact Rejection

Segmentation of unstable and stable epochs are depicted in Figure 6A.

2.6.1. Definition of Unstable Epochs

Unstable epochs are the time windows where there is only one button press indicating a perceptual reversal. Length of the unstable epochs were 5 seconds with 3 seconds before and 2 seconds after the button presses. These epochs are named as unstable because either stimulus (exogenous) or perception (endogenous) of the stimulus changes in these epochs. All demarcations of exogenous unstable condition were then adjusted for the time of stimulus change. This created additional set of epochs with identical data but demarcated with stimulus change onsets instead of button press onsets (Figure 6B). Epochs with false positive reports of perceptual change in exogenous task was discarded.

2.6.2. Definition of Stable Epochs

Onset of each double-dot display of SAM and exogenous stimulus was used for creating artificial markers on continuous EEG signal. This resulted in stimulus markers with 250 ms intervals throughout the signal in both tasks. Time windows that without a button press and also surround 3 seconds before and 2 seconds after these artificial markers were used to create stable epochs. Epochs are discarded if data points from another unstable or stable epoch was included in the same time window. Stable epochs do not include the perceptual reversal event and therefore the perception of the stimulus is stable during these epochs.





Figure 6. Depiction of data segmentation from continuous EEG. (A) Illustrates the segmentation of stable and unstable epochs using button presses: presses are indicated with small button pushing icons on short red bars. Presses indicated change in motion direction. 3000 ms before and 2000 ms after the button presses are segmented for unstable epochs. Stable epochs were the same duration but did not include button presses. (B) A depiction of button press (top) and stimulus change (bottom) demarcations on the same trial of an exogenous unstable epoch of an older participant. Red vertical lines indicate epoch demarcations (t=0) which is button press for top and stimulus related motion change for bottom figure. Black vertical lines show motion change onset for top and button press for bottom figure (Source: Mathes et al., 2016).

2.6.3. Artifact Rejection

Epochs with more than one button presses are excluded from analyses for all conditions. This prevented possible distortions of perceptual reversal related activity by eliminating post-motor activity of that response. Visual inspection of each trial in *unstable epochs* of all tasks provided the following exclusion procedure for the time window of -1500 ms to 200 ms around the button press demarcation: All epochs with eye movement or other artefacts were manually excluded from analyses. Large drifts and spikes that could result from muscle activity, sweating, and changes in conductance were excluded from analyses. Large ocular artefacts were also discarded. This procedure was repeated for stimulus demarcated unstable exogenous epochs within the time window of 500 ms before and 1200 ms after the stimulus demarcation. Same exclusion procedure was applied to stable epochs but only for time window of 1000 ms before and 100 ms after the demarcations of stable epochs.

Due to unbalanced number of epochs between participants and groups, a random exclusion procedure was conducted. This procedure ensured that all participants had 30 epochs at maximum with the minimum of epoch count of 15. Table 1 shows mean number of analyzed epochs for each group and condition.

Table 1. Mean number of epochs across conditions* and participant groups. Standard deviations are shown in parentheses.

	Unstable Epo	ochs	Stable Epochs		
Groups	Endo	Exo Button	Exo Stimulus	Endo	Exo
Older	26.5 (5.50)	30 (0)	28.67 (4.62)	30 (0)	30 (0)
Young	29.67 (1.15)	29.5 (1.45)	29.58 (1.00)	30 (0)	29.83 (.58)

*Note 1. Endo = Endogenous epochs, Exo = Exogenous epochs, Button = Button press demarcated epochs, Stimulus = Stimulus onset demarcated epochs.

2.7. Time-Frequency Decomposition

Figure 7 shows both grand averaged delta responses and participant averages for endogenous reversals, stimulus locked exogenous reversals and response locked exogenous reversals. However, activity in delta frequency was not investigated with statistical analyses. It was used for defining time windows for the analysis of other frequency bands. Details of the window selection process are described in the next section (i.e. *Selection of Time Windows*).

Time-frequency decomposition of the EEG data was conducted via wavelet convolution in frequency domain (Cohen, and Donner, 2013). Main idea of the convolution in frequency domain is to multiply power spectrums of both the signal and the wavelet and then take the inverse fast Fourier transform (iFFT) of this multiplication. Convolution theorem suggests that this method yields the same results with time domain convolution, but with shorter computation duration (Cohen, 2014). The transformation procedure was conducted mainly with custom scripts and some built-in Matlab 2018a functions, therefore a clear presentation of the process is required to avoid vague definitions. There were several critical steps for the transformation, namely: placing all available EEG data one after another to create one continuous signal (i. e. signal concatenation), frequency domain transformation of signal and wavelet, multiplication of transformed signal and wavelet in frequency domain, time-domain transformation of multiplied spectra via inverse fast Fourier transform, reshaping signal into original format, power and phase extraction, normalization of data using stable epochs as baseline, and trial based averaging of the normalized epochs. Three separate wavelet convolutions were conducted to transform signal into delta (1 - 4 Hz), theta (4 - 8 Hz), and alpha frequencies (8 - 14 Hz). All of the above steps mentioned were applied separately for delta, theta, and alpha wavelet transformations.

Initially, all artifact free epochs from all conditions of each participant were individually concatenated as if they consist a continuous signal. Selected regions of interest (ROI) were F3, F4, C3, C4, P3, P4, O1, and O2 for theta and alpha; and only P4 for delta band transformation. Then complex wavelets were constructed and scaled for each frequency by:

$$\psi(t) = (e^{2\pi i f/t})(e^{-t^2/2\sigma^2})$$
(1)

$$\sigma = \frac{n}{2\pi f} \tag{2}$$

Where *t* is time, *f* is frequency, σ^2 scales the gaussian window of the complex wavelets according to *n*, which is the number of wavelet cycles. Frequencies ranged

from 1 to 4 Hz in 0.5 Hz steps for delta; and ranged from 4 to 8 Hz in .25 steps for theta; and 8 to 14 Hz in .25 steps for alpha frequency. Number of wavelet cycles were set to n=3 for delta, n=6 for theta, and n=7 for alpha frequency transformations. Centre-frequency for delta band was 2.5 Hz for older group and 3.5 Hz for young group. Using the toolbox of Torrence and Compo (1998), %95 of the activity reflected within the centre frequencies were.75 to 4.25 for older, and 1.05 to 5.95 for young group. Centre frequency for theta band was 5.5 Hz for all participants (Mathes et al., 2014; Mathes et al., 2016). %95 of the activity reflected within this centre frequency was ranged from 3.7 to 7.3 Hz (Torrence, and Compo, 1998). Furthermore, centre frequency for alpha band was 11 Hz for all participants, and 95% of its activity included the activity between 7.87 and 14.13 Hz for this centre frequency. This range was defined as two standard deviations of the wavelet in the frequency domain. Complex wavelets were normalized to have unit energy. The concatenated signals and the complex wavelets were then transformed into frequency domain (i.e. power spectrum) using the built-in fast Fourier transform (FFT) algorithm in Matlab 2018a (Frigo, and Johnson, 1998). FFT algorithm in Matlab 2018a is defined for vector x and *n* sampling points by:

$$y_k = \sum_{j=1}^n \left(\omega_n^{(j-1)(k-1)} x_j \right)$$
(3)

Where $\omega = e^{-2\pi i/n}$ is one of n complex roots of unity and *i* is the imaginary unit. Resulting power spectrums of the signal and the complex wavelets were then multiplied. Result of this multiplication was transformed into time domain using the built-in inverse FFT (iFFT) algorithm in Matlab 2018a. Using the same definitions above, with vector *x*, *n* sampling points, and ω ; iFFT is defined by:

$$x_{j} = \sum_{k=1}^{n} \left(\omega_{n}^{(j-1)(k-1)} y_{k} \right)$$
(4)

Resulting complex signal was then reshaped into a format where conditions, trials, and time points are separated, similar to the signal format before concatenation.

Then frequency-band specific power *A* was calculated for each participant at each time point, and averaged over trials in each condition using:

$$A(t) = \sum_{k=1}^{n} |Z(t)_k|^2$$
(5)

Where Z is the complex signal, t is time, and n is the total number of trials of a participant in a given condition.

To illustrate the changes in oscillatory activity in unstable epochs relative to stable epochs, baseline normalization was conducted *only for theta frequency* separately for each participant, each task, and channel. In accordance with previous studies, it was decided to take averaged values of stable epochs as the baseline activity instead of using remote time points within the unstable epochs (Mathes et al., 2014; Başar-Eroğlu et al., 2016; Mathes et al., 2016). Baseline windows started 700 ms before the epoch marker (0 ms) and ended at the zero-time point. This resulted in extraction of the time window 700 ms before the demarcation of stable epochs for each task. Power values within the baseline time window were averaged across time points for each frequency, resulting in one mean value for each frequency (Cohen, 2014). Each of the baseline values were then log transformed and subtracted from each log transformed spectral estimate of averaged unstable epochs for each task and participant (6). This procedure created baseline normalized time-frequency power values for each participant and task. Relative change in activity in unstable epochs was represented in decibels (dB):

$$dB = 10 \times \log_{10}(power/baseline) \tag{6}$$

Normalized theta power values were then averaged within the specified time windows in the centre frequency for all participants. These averaged power values were then used in statistical analyses.



Figure 7. Participant and group averages of delta responses. Figure shows 0.5 to 4 Hz bandpass filtered single participant averages and grand averages across stimulus (top) and response (middle) locked exogenous conditions; and also response locked endogenous condition (bottom). Vertical dashed line at time zero marks the stimulus onset in stimulus locked condition and it also marks button presses for the two response locked conditions.

2.8. Selection of Time Windows

2.8.1. Background

Most of cognitive neuroscience experiments use an external stimulus to locate the exact onset of a cognitive event. A commonly used example is an oddball task. Oddball task generally consists of two different stimuli; one stimulus is presented more frequently (non-target) than the second stimulus (target stimulus) (Wienke et al., 2018). In cited version of the task, participants are asked to press a button whenever they see the target stimulus. This allows to locate the exact time of the target stimulus that marks the onset of the subsequent cognitive event (forward averaging). This results in well-defined time windows for specific cognitive processes that are represented by EEG activity. However, selection of time windows in multistable perception experiments are of special difficulty due to the endogenous nature of the perceptual reversal event. Reason is that the perceptual event is endogenous, in other words, there is no external stimuli that one can clearly assign the perceptual reversal event. Because of that researchers used different methods for reliably defining time windows in this paradigm.

One of the most prominent analysis window definition method is backwardaveraging using the button press demarcation (Başar-Eroğlu et al., 1993). Participants press a button to indicate whenever they experience a perceptual reversal. Exact timing of this button press is then used to create the time point zero (t_0) . Depending on the parameters of specific studies, a time window before (e.g. 1500 ms) and/or after (e.g. 1000 ms) the button press is used for creating epochs of perceptual reversals. Because participants press the button to indicate the experienced perceptual reversals, brain activity related to perceptual reversals fall behind the t₀. Researchers use the t₀ and an additional point in time to create time windows for analyzing specific brain activities (Strüber, and Herrmann, 2002; Mathes et al., 2014). However, defining fixed time windows (e.g. starting from button press to 500 ms before button press) across different studies with different participants also poses a problem. Because the reaction time of participants could vary, and this could potentially result in excluding brain activities of slow responders from the analyses. Phase coherence measures would also suffer from the reaction time jitter and consequently this would reflect on the power measures of EEG signals.

Researchers overcome this problem by employing a task that use a stimulus with comparable properties to its multistable counterpart but induce exogenous reversals (stimulus pattern is changed externally) instead of endogenous reversals (Figure 5). Similar to the demarcation of target stimulus in oddball paradigm, exogenous reversals are marked by the change of the stimulus itself. This allows researchers to estimate mean reaction time that is in parallel to reaction time in endogenous reversals. Defining a window that starts from t₀ and extends backwards to somewhere around the mean/median reaction time is one of the best options to locate the perceptual reversal related brain activity (Başar-Eroğlu et al., 1996; Mathes et al., 2014; Başar-Eroğlu et al., 2016; Mathes et al., 2016). However, if reaction time variability of participants is not comparable as it is in this study; it is problematic to use estimates of reaction time for defining the windows. In line with this issue, one study clearly showed that using response locked averaging of exogenous reversals results in remarkably different waveforms than the stimulus locked averaging of the same signal (Strüber, and Herrmann, 2002). This difference is inherent to the response locked averaging due to variability of reaction times across trials and participants.

A method that is more robust against reaction time variability was first introduced in 1998 (İşoğlu-Alkaç et al., 1998). Researchers used WT on artifact free single sweeps to obtain frequency coefficients of the time series. Then authors averaged these coefficients to define the dominant coefficient which was reported to be in the delta range (0.5 - 4 Hz). 1998 study of İşoğlu-Alkaç et al., used this method to select single sweeps with the same polarity and latency estimates with the dominant coefficients. Reason was to increase signal to noise ratio by selecting those sweeps and obtain consistent peak and latency values. Unfortunately, current study cannot benefit from that method due to small number of trials of older participants as a consequence of lower reversal rates of the age group. However, following studies of the same group used a similar method with additional estimates for defining time windows (İşoğlu-Alkaç et al., 2000; İşoğlu-Alkaç, and Strüber, 2006). These studies estimated mean latencies of wavelet transformed (WT) delta (0.5-4 Hz) peaks obtained from averages of single sweeps, and used the resulting standard deviation to create a range around the mean latency to define time windows for analyses. For the sake of simplicity and readability, this method is referred as latency-based selection.

It was decided to use latency-based selection method in delta frequency for definition of the analysis time windows for alpha, and theta frequencies (İşoğlu-Alkaç, and Strüber, 2000; Mathes et al., 2006). Primary reason is that the method is robust against the high reaction variability reported in older participants in this study.

2.8.2. Definition of Time Windows for Analyses

Main conception of the reversal related positivity is that it reflects the conscious awareness of the perceptual reversal (Başar-Eroğlu et al., 1993; Mathes et al., 2016). Because of that, the time window selection for analyzing the peak power and latency of the RRP cannot exceed the time of button press. Because activity after that window do not include perceptual reversal related activity. Accordingly, it was decided to use the time window that ranges from button press ($t_0 = 0$ ms) down to 1000 ms before the button press (Strüber, and Herrmann, 2002) for extracting mean latency parameters of delta frequency. First, maximum power and its corresponding latency in delta frequency were extracted from group-averaged wavelet transformed signals for each group (İşoğlu-Alkaç et al., 1998; İşoğlu-Alkaç, and Strüber, 2006). This resulted in separate centre frequencies with power and latency values for each group. Maximum group-averaged delta power was observed in 2.5 Hz for older group and 3.5 Hz in young group. These frequencies were then used to extract maximum delta power and its latency for individual participants in each group. Participants' power and latency extraction was conducted on trial-by-trial averages of wavelet transformed single sweeps. Then latency of maximum delta power was averaged across all participants and a grand average of latency was computed. However, obtaining common time windows using the latencies of all participants resulted in heterogeneity of variance in theta and alpha power values. Therefore, it was decided to define only the low-cutoff point via latency extraction and then extend the window until zero-time point. Therefore, M_{latency} - (1.96 \times SE_{latency}) was defined as the low cut-off point for the *late* window (late window = -.520 to 0 ms). An earlier time window with identical duration preceding the late window (early window = -1.04 to -.520 ms) was defined as the early window (Figure 8).



Figure 8. Illustration of analyzed time windows. Group averages of baseline normalized **theta** power at F4 electrode. Windows are separated by dashed vertical blue lines; transparent light orange (left) and transparent red (right) sections highlight early and late windows, respectively. Solid and dashed horizontal red lines show the %95 CI of reaction times ($RT_{mean}\pm1.96\times RT_{SE}$) of younger and older groups, respectively.

2.9. Statistical Analyses

2.9.1. Goodness of Fit Analyses of Dwell Times

Percepts that were more likely to appear first and have longer dwell times were defined as *dominant percepts*. These were left-oriented percept for Necker cube, rightoriented percept for Necker lattice, and vertical apparent motion for SAM. Dwell times of dominant percepts were extracted using the time intervals between button presses that indicate the perceptual reversals to the dominant percept, and the subsequent button press that indicate perceptual reversals to the other percept. This extraction was applied to each multistable stimulus and participant in Turkish sample. It was previously suggested that using time series with low number of data points is not acceptable for goodness of fit analyses (Kang, and Blake 2010). Therefore, it was decided to pool all dwell times of all participants separately for each dominant percept. Due to high inter-individual and intra-individual variance of dwell times, all dwell times were divided by the median dwell time separately for each dominant percept and each participant. This resulted in median normalized dwell times for all stimuli and participants. These normalized dwell times were then pooled separately for each dominant percept. As a result, total of three dwell time pools were created for left-cube percept (N = 1163), right-lattice percept (N = 1170), and vertical SAM percept (N =936).

The built-in function, *fitdist()*, of MATLAB 2018a was used for obtaining parameters of lognormal (1) and gamma (2) distribution of each dwell time pool. Then, probability density functions of gamma and lognormal distributions were created using the parameters obtained from the pooled dwell times. Finally, six separate chi-square goodness of fit analyses (two distributions and three dwell time pools) were employed to assess fitness of three dwell time pools into lognormal and gamma distributions.

$$f(x|a,b) = \frac{1}{b^{a}\Gamma(a)} x^{a-1} e^{\frac{-x}{b}} : \Gamma(a) \text{ is the gamma function at } a:$$
(1)

a is the shape parameter and *b* is the scale parameter.

$$f(x|\mu,\sigma) = \frac{1}{x\sigma\sqrt{2\pi}} exp\left\{\frac{-(\ln x-\mu)^2}{2\sigma^2}\right\} ; \quad x > 0.: \text{ Pdf of log-}$$
(2)

normal distribution. μ is the mean of logarithmic values and σ is the standard deviation.

2.9.2. Reversal Rate Comparisons Across Turkish and German Samples

To obtain unbiased results for reversal rate comparison analyses across different samples, it was decided to pseudo-randomly select four samples (n=15) from the Young Turkish Sample (N=60) instead of one. To create samples with pseudo-randomly selected participants, each participant in Turkish sample was assigned a random number that was generated in Excel 2016. Then, samples of 15 participants were selected in ascending manner according to the size of the random number participants were assigned. This resulted in total of six samples with four young Turkish sample, one young German sample, and one older German sample all with sample sizes of 15.

Due to differences in task durations across samples, reversal rate counts were divided by the number of minutes for tasks. This resulted in reversal rate per minute measure of reversal rates. However, heterogeneity of variances was observed and this was corrected by log₁₀ transformation of all the scores. A One-way ANOVA was used to compare log-transformed reversal rate per minute across six samples.

2.9.3. Theta Frequency Analyses

Two separate mixed design ANOVAs were performed on endogenous and exogenous tasks to investigate modulations in theta power: Three-way mixed design ANOVA analyses were employed using age group (young and older) as betweensubjects factor, eight locations (F3, F4, C3, C4, P3, P4, O1, and O2), and two time windows (early and late) as within-subject factors. All main and interaction effects were reported using Greenhouse-Geisser correction for violations of the assumption of sphericity. Partial eta squared values were reported as estimations of effect size of main and interaction effects. Post-hoc comparisons were reported using Bonferroni correction (p = .05/n of tests) when there were any significant main or interaction effects. Additionally, three sets of planned comparisons were conducted to investigate: (1) between group differences at each time window and each electrode; (2) theta activity differences from early to late window at each electrode separately for both groups. Bonferroni correction was applied only to second planned comparisons. When expected results are also found significant, results of planned comparisons were reported instead of post-hoc comparisons.

2.9.4. Alpha Frequency Analyses

Two separate mixed design ANOVAs were performed on endogenous and exogenous tasks to investigate modulations in alpha power: A three-way mixed design ANOVA was performed with age group (young and older) as between-subjects factor, four locations (mean of F3/F4, C3/C4, P3/P4, and O1/O2) and two time windows (early and late) as within-subjects factors. Greenhouse-Geisser correction was reported to correct for violations of sphericity. Partial eta squared values were reported as estimations of effect size. Post-hoc comparisons were reported using Bonferroni correction (p = .05/n of tests) when there were any significant main or interaction effects. Additionally, two sets of planned comparisons were conducted to investigate: (1) alpha activity differences between early and late windows separately for both groups; (2) whether temporal modulation (*i.e.* early to late) of alpha activity at different electrodes differ between older and young groups. When expected results are also found significant, results of planned comparisons were reported instead of post-hoc comparisons.

CHAPTER 3: RESULTS

3.1. Behavioral Findings

3.1.1. Goodness of Fit Analyses of Dwell Times of SAM, Cube, and Lattice Stimuli in Young Turkish Sample

Six separate chi-square analyses were conducted to investigate whether the distribution of dwell times of SAM, lattice, and cube stimuli would fit either to lognormal or to gamma distribution (Figure 9). Results showed that dwell times of left-oriented cube percept was not significantly different than lognormal distribution $\chi^2(1, N = 1163) = 1.935$, p > .05, but it was significantly different than gamma distribution $\chi^2(1, N = 1163) = 41.877$, p < .0001. Distribution of dwell times for right oriented lattice percept also was not significantly different than lognormal distribution $\chi^2(1, N = 1170) = 7.601$, p > .05, but it was significantly different than gamma distribution $\chi^2(1, N = 1170) = 43.978$, p < .0001. However, results showed that distribution of dwell times of SAM stimulus was significantly different than both lognormal $\chi^2(1, N = 936) = 8.337$, p > .05 and gamma $\chi^2(1, N = 936) = 57.639$, p > .05 distributions.

Overall, chi-square goodness of fit analyses has shown that dwell times of cube and lattice stimuli had lognormal distributions. However, distribution of dwell times of SAM stimulus did not fit to either lognormal or to gamma distribution.



Figure 9. Distribution of observed dwell times and corresponding lognormal and gamma distributions of Necker cube (**A**), lattice (**B**), and SAM (**C**) stimuli. Probability density of observed durations are shown with **bars**; expected lognormal (**dashed**) and gamma (**solid**) distributions are shown by lines. Calculations were conducted on the dwell times of the shown percepts under each letter (i.e. A, B, and C).

3.1.2. Reversal Rate Correlations of Three Multistable Stimuli in Young Turkish Sample

Two separate Spearman Rho correlation analyses were conducted to investigate the relationship between reversal rates of SAM, cube and lattice in Necker first and SAM first conditions. One additional analysis also was conducted on aggregate reversal rates across all conditions (Table 2). Result of correlation analysis on aggregate reversal rates showed a moderate significant positive correlation between cube and lattice stimuli r = .629, p < .01. Significant moderate positive correlation between cube and lattice stimuli r = .629, p < .01. Significant moderate positive correlation between first r = .679, p < .01, and SAM first r = .544, p < .01 conditions. However, reversal rate of SAM was not correlated with reversal rates of cube (r = .142, p > .05) and lattice (r = .249, p > .05) stimuli in Necker first condition. There were no significant correlations between reversal rates of SAM and cube (r = .003, p > .05), and SAM and lattice (r = .024 p > .05) in SAM first condition either. Aggregate reversal rate of SAM also was not correlated with aggregate reversal rates of cube (r = .100, p > .05.) and lattice (r = .097, p > .05).

Results indicated that cube and lattice stimuli are related in their perceptual reversal counts regardless of experimental conditions. On the other hand, reversal rates of SAM found to be unrelated with reversal rates of cube and lattice stimuli across all conditions.

Table 2. Spearman Rho correlation coefficients of reversal rates between SAM, cube, and lattice stimuli in aggregate reversal rate, SAM first and Necker first conditions for young Turkish sample (N=60). Mean reversal rates (**bold**)and standard deviations (*SD*) are presented in a separate column.

Stimuli	Mean Reversal Rates <i>(SD)</i>	Cube	Lattice	SAM
<u>Aggregate</u> <u>Reversal Rates</u>				
<u>(N=60)</u>				
Cube	39.45 (<i>16.44</i>)	1		
Lattice	38.90 (15.10)	.629*	1	
SAM	34.10 (<i>16.50</i>)	.100	.097	1
SAM First Condition				
<u>(IN=50)</u>				
Cube	41.36 (<i>15.47</i>)	1		
Lattice	42.90 (<i>14.82</i>)	.544*	1	
SAM	36.3 (20.33)	.003	024	1
<u>Necker First</u> Condition				
<u>(N=30)</u>				
Cube	37.53 (<i>17.39</i>)	1		
Lattice	34.90 (<i>14.53</i>)	.679*	1	
SAM	31.90 (<i>11.42</i>)	.142	.249	1

Note 2. *s denote significance at p < .01.

3.1.3. Reversal Rate Differences Across Young Turkish, Young German, and Older German Participants

To compare reversal rates across different age groups and countries, a one-way ANOVA was conducted with the sampling condition. Sampling condition included four young Turkish samples that were randomly drawn from the whole Turkish young sample in addition to the young German and older German samples, creating a factor with 6 levels. Results showed that there was a significant effect of sampling on mean reversal rates per minute F(5, 89) = 5.529, p < .001 (Figure 10). To investigate the differences between individual samples, Bonferroni correction was employed to compare group means and also to control for multiple comparisons. Results of multiple comparisons showed that mean reversal rate per minute of DE_older sample was significantly lower than mean reversal rates of DE_young, TR_young1, TR_young2, TR_young3, and TR_young4 samples: %95 CIs [-0.486, -0.046], [-.535, -.095], [-.535, -.095], [-.535, -.095], and [-.499, -.058], respectively. Additionally, it was shown that mean reversal rate per minute was not significantly different between DE_young sample and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young1, TR_young2, TR_young3, and TR_young4 samples %95 CIs [-.270, .171], [-.269, .171], [-.244, .197], [-.233, .237], respectively.



Figure 10. Mean perceptual reversals per minute of one older German sample (DE_Older), one younger German sample (DE_Young), and four younger Turkish samples (TR_1, TR_2, TR_3, TR_4). Errors bars indicate 95% CI. Sample sizes for all samples were n = 15.

3.1.4. Reaction Time Comparison Between Younger and Older German Participants

Initially, a one-way ANOVA was conducted to investigate mean reaction time differences between younger and older German participants. However, Levene's test showed that reaction time of older participants (SD=.194) had higher variability than that of young participants (SD=.085). Therefore, a Mann-Whitney U test was employed to control for the violations. Results showed that the mean rank of reaction time for younger group (Mdn = .611 ms) was significantly higher compared to older group (Mdn = .771 ms) U (N_{older} = 15, $N_{younger}$ = 15) = 44.000, p < .01 (Figure 11).



Figure 11. Mean reaction times of older and younger German participants. Error bars show 95% between subjects CI.

3.2. Electrophysiological Results

3.2.1 Overview

Figure 12 shows theta modulation in unstable windows relative to stable windows in exogenous and endogenous tasks. Similarly, relative alpha modulation during unstable windows for both tasks is depicted in Figure 13. Visual depiction of the theta frequency in endogenous task show that frontal theta activation is impaired in older group relative to young group. However, occipital theta of older group seems to have increased activity relative to young group, especially in the left hemisphere. Results for exogenous tasks does not show such topographical differences. However, older group seems to have decreased theta response over all locations relative to young group. Results for theta and alpha frequency activities are reported in separate sections. Visual inspection of alpha activity in endogenous task also shows marked differences between groups. Most apparent one is the frontal alpha desynchronization at frontal locations for older group in endogenous task, which does not exist in young group. Importantly, posterior alpha desynchronization seems to be decreased in older group relative to young group. Alpha desynchronization, at least in the specified time windows, does not seem to exist in exogenous task for both groups. However, there is a marked unresponsiveness of alpha activity for older group over frontal and central areas; whereas young group show slight increases in activity around -500 to -200 ms followed by a short desynchronization around the button press. Overall, visual inspection suggests that there are topographical differences in brain responses between older and young participants. These topographical differences seem to increase in endogenous task compared to exogenous task.



Figure 12. Theta modulation in endogenous (top) and exogenous (bottom) tasks. Activity at eight ROIs are shown for young (left) and older (right) groups. Frequencies are indicated at vertical axis, time is shown by the horizontal axis. Button press is indicated by the black vertical line at zero point. Colors show increases (red) and decreases (blue) in theta activity during unstable windows relative to stable windows (baseline) in decibel (dB) units.



Figure 13. Alpha modulation in endogenous (top) and exogenous (bottom) tasks. Activity at eight ROIs is shown for young (left) and older (right) groups. Frequencies are indicated at vertical axis; time is shown by the horizontal axis. Button press is indicated by the black vertical line at zero point. Colors show increases (red) and decreases (blue) in theta activity during unstable windows relative to stable windows (baseline) in decibel (dB) units4

3.2.2. Theta Activity During Endogenous Reversals

Theta activity within late window in endogenous task was significantly higher compared to early window (main effect of time: F[1, 22] = 5.085, p < .05, $\eta^2 = .188$). Age group did not have a significant effect on theta activity F(1, 22) = .413, p > .05. Also, there was no interaction of time and age group F(1, 22) = 1.873, p > .05. Bonferroni corrected planned comparisons showed that theta activity was significantly increased at F3, F4, C3, C4, and P3 locations at late window compared to early window in young group (p < .006), there was no significant increase in remaining electrodes (p > .006 all comparisons) (Figure 14A). On the contrary, modulation in theta power from early to late window was not significant at any of the ROIs in older group (p > .006 all comparisons) (Figure 14B). A set of planned comparisons was conducted to assess theta activity differences at each electrode between the two groups, separate comparisons was conducted for each time window. Only the activity within same time periods and same electrodes were compared between groups. None of the locations showed significant differences in theta activity between groups within early window (p > .05 all comparisons). Similarly, results for the comparisons of theta power at late window showed no significant differences between young and older groups (p > .05 all comparisons). Results also showed that interaction effect of time and location was not significant F(3.123, 68.704) = 1.473, p > .05.

Location did not have a significant effect on theta activity F(3.425, 75.341) =.748, p > .05. However, an interaction effect of location and group was found F(3.425,75.341) = 3.492, p < .05., $\eta^2 = .137$ (Figure 15). Another group difference was found for the theta activity difference between F3 and P3 electrodes F (1, 22) = 5.161, p < .05. This was also true for theta activity difference among C3 and P3 ROIs between groups F(1, 22) = 6.274, p < .05. Simple effect analyses were employed to investigate differences between electrode locations separately at each group (Figure 14). Comparisons showed that theta activity at F4 was significantly lower compared to O2 ROI in older group (MD = .49, SE = .21), p < .05; this comparison was not significant for young group (MD = .30, SE = .33), p > .05. Also, theta activity at F3 electrode was significantly lower compared to activity at P3 for older group (MD = .55, SE = .23), p < .05, while there was no significant difference between these locations for the young group (MD = .15, SE = .21), p > .05 (Figure 17B). Similarly, theta activity at C3 was significantly lower than P3 for older group (MD = .41, SE = .18), p < .05. Activity between C3 and P3 ROIs was not significantly different for the young group (MD = .17, SE = .17), p > .05. Finally, there was no three-way interaction effect of group, time, and location F(1.875, 41.248) = 1.405, p > .05.





Figure 14. Figure shows theta activity within early (-1040 to -520 ms) and late (-520 to 0 ms) windows of endogenous task for young (**A**) and older (**B**) groups. Vertical axis represents activity in unstable windows relative to stable windows in decibels. Error bars show 95% within-subjects CI.



Figure 15. Figure shows theta activity at early (-1040 to -520 ms) and late (-520 to 0 ms) windows, all electrodes (F3, C3, C4, P3, P4, O1 O2) and two groups (older, young). Vertical axis represents activity in unstable windows relative to stable windows in decibels Error bars show 95% within-subjects CI.

3.2.3. Theta Activity During Exogenous Reversals

Results showed that theta activity within late window was significantly higher compared to early window in exogenous task F(1, 22)73.444, p < .0000001, $\eta^2 = .769$. Even though the effect of time was consistent across groups (time x group interaction: F[1, 22] = 2.497, p > .05, and locations (time x location interaction: F[1.630, 35.859] = 1.989, p > .05); young group had higher overall theta activity compared to older group F(1, 22) = 4.766, p < .05, $\eta^2 = .178$. Results also showed that the main effect of location was significant $F(3.385, 74.472) = 2.855, p < .05, \eta^2 = .115$. Regardless, there was no interaction effect of location and group F(3.385, 74.472) = 1.214, p > 1.214.05). Planned comparisons was conducted to investigate theta activity differences between ROIs averaged over groups and time windows. Results showed that highest mean theta activity in the whole sample was observed in F4 (M = 1.03, SD = 1.18) and lowest activity was observed in O2 (M = .40, SD = .79); and that difference in activity between these areas was significant F(1, 22) = 8.310, p < .05. Remaining comparisons across electrodes were not significant (p > .05). Set of bonferroni corrected planned comparisons were conducted to investigate theta modulation from early to late window at each individual location separately for two groups (Figure 16). Additionally, a set of planned comparisons was conducted to investigate between group differences of theta power at each electrode within late time window (Figure 17). Results showed that young group had higher late theta activity at F4 (MD = 1.24, SE = .55, C4 (MD = 1.38, SE = .54), P4 (MD = 1.12, SE = .47), and O2 (MD = 1.02, SE = .30) locations (p < .05 all comparisons). Difference of mean theta power between early and late windows was significant at F3, C3, C4, P3, P4, O1, and O2 ROIs in young group (p < .006 for all comparisons) (Figure 16). Yet the difference at F4 was not significant for young group (p = .008). Results for older group showed that only the modulation at F4 and O2 electrodes were not significant (p > .006), and O1 was only marginally significant (p = .0067). However, theta activity at F3, C3, C4, P3, and P4 electrodes showed significant increase at late window compared to early window for older group (p < .006 for all comparisons) (Figure 17). Additionally, three-way interaction effect of location, group, and time was not significant F(3.196, 70.310) =.393, *p* > .05.


Figure 16. Figure shows theta activity at early (white: -1040 to -520 ms) and late (gray: -520 to 0 ms) windows of exogenous task for young (**A**) and older (**B**) groups. Vertical axis represents activity in unstable windows relative to stable windows in decibels. Error bars show 95% within-subjects CI.



Figure 17. Figure shows theta activity at early (-1040 to -520 ms) and late (-520 to 0 ms) windows and two groups (older, young). Vertical axis represents activity in unstable windows relative to stable windows in decibels. Error bars show 95% within-subject CI for the two groups.

3.2.4 Alpha Activity During Endogenous Task

Results showed alpha activity was significantly decreased at late window compared to early window F(1, 22) = 16.376, p < .01, $\eta^2 = .427$. Early to late decrease in alpha activity was significant for the older group (MD = .60, SE = .22) as well as the young group (MD = .60, SE = .21), all p's < .05 (Figure 18). However, group x time interaction was not significant F[1, 22] = .000, p > .05), also main effect of group was not significant F(1, 22) = .873, p > .05. A trend to significance was found for the effect of location on alpha activity F(1.998, 43.958) = 2.898, p = .066. Location and group interaction was not significant as well F(2.229, 49.044) = 2.432, p > .05.

However, the three-way interaction of time, group, and location was found significant F(2.229, 49.044) = 5.906, p < .01, $\eta^2 = .212$ (Figure 19). Planned within subjects contrasts were employed to further investigate the three-way interaction. Results showed that alpha modulation from early to late window was significantly different between groups at frontal area F(1, 22) = 5.678, p < .05. There was also a trend to significance for the temporal alpha modulation at occipital area between the groups F(1, 22) = 4.068, p = .056. Simple effect analyses were conducted to delineate temporal modulation of alpha activity within all electrodes separately in both groups (Figure 19). Results showed that the alpha power decrease at frontal area was significant for older group (MD = -.67, SD = .46) with p = .0003; however, no significant difference was found for the young group (MD = -.08, SD = .72) with p =.706. There was also a significant decrease in alpha power at central area for older group (MD = -.78, SD = .96) with p = .017. No such decrease was observed for the young group (MD = -.66, SD = 1.15) with p = .071. Conversely, a significant alpha decrease at occipital area was found for young group (MD = -.91, SD = .52) p =.00009. This comparison was not significant for the older group (MD = -.24, SD =1.01) with p = .421. Additionally, late alpha decrease at parietal area was significant for young group (MD = -.74, SD = .71) p = .004. Similarly, a significant temporal alpha modulation at parietal area was found for the older group (MD = -.71, SD = 1.03) with p = .035.



Figure 18. Figure shows alpha activity at early (white: -1040 to -520 ms) and late (gray: -520 to 0 ms) windows of endogenous task for young (**A**) and older (**B**) groups. Vertical axis represents alpha activity in unstable windows relative to stable windows in decibels (values are in reverse order). Error bars show 95% between-subjects CI.



Figure 19. Figure shows alpha activity at early (-1040 to -520 ms) and late (-520 to 0 ms) windows and two groups (older, young). Vertical axis represents activity in unstable windows relative to stable windows in decibels (values are in reverse order). Error bars show 95% within-subject CI for the two groups.

3.2.5 Alpha Activity During Exogenous Task

Analyses showed that none of the main effects had significant effects on alpha power during exogenous task. Alpha activity during exogenous task was not significantly different between groups (F[1, 22] = 2.160, p > .05) or between locations (F[2.391, 52.612] = 1.208, p > .05). There was no main effect of time as well F(1, 22)= 2.935, p > .05. Planned comparisons also showed that neither the alpha activity of the older group (MD = .36, SE = .22) nor the young group (MD = .15, SE = .20) were significantly different between time windows (Figure 20). However, an interaction effect of location and time was found $F(1.941, 42.703) = 4.276, p < .01, \eta^2 = .163$. Bonferroni corrected post-hoc comparisons showed that occipital alpha activity was significantly lower at late window when compared to early window (p = .0124). However, there was no significant temporal modulation in alpha activity at the rest of the locations (p > .0125 for all comparisons).

The three-way interaction of group, time, and location was not significant F(1.941, 42.703) = .193, p < .05 (Figure 21). Set of planned comparisons were employed to investigate whether temporal modulation (early to late) of alpha activity within electrode locations (F, C, P, O) varied between young and older (Figure 20). None of the electrode locations showed different alpha modulations from early to late window when compared between the groups (p > .05 all comparisons).



Figure 20. Figure shows alpha activity at early (white: -1040 to -520 ms) and late (gray: -520 to 0 ms) windows of exogenous task for young (**A**) and older (**B**) groups.. Vertical axis represents activity in unstable windows relative to stable windows in decibels (values are in reverse order). Error bars show 95% between-subjects CI.



Figure 21. Figure shows alpha activity at early (-1040 to -520 ms) and late (-520 to 0 ms) windows and two groups (older, young). Vertical axis represents activity in unstable windows relative to stable windows in decibels (values are in reverse order). Error bars show 95% within-subject CI for the two groups.

CHAPTER 4: DISCUSSION

This thesis investigated alterations in brain oscillations that underlie age related decreases in endogenous perceptual reversals. EEG recordings of young and older adults in endogenous and exogenous tasks were analyzed. Results from both tasks are discussed in comparison to each other. Alterations in oscillatory networks in both tasks are discussed in relation to age. Activity in theta and alpha frequencies were examined to identify underlying brain activities that are related to top-down and bottom-up processes, respectively.

There were remarkable differences in topography of theta and alpha responses between young and older adults in endogenous task. Young adults showed maximum theta responses at anterior areas, but it was shifted to posterior areas in older adults. This relationship was reversed for alpha frequency. Young adults showed highest alpha desynchronization at posterior areas while it was shifted to anterior areas in older group. These topographical shifts in theta and alpha frequencies were not observed during exogenous reversals; however, young group showed stronger theta activation in exogenous task. This shows that lack of sensory evidence in endogenous task resulted in recruitment of compensatory alpha and theta networks for older adults. Anterior shift in alpha networks shows that perceptual interpretations are now represented in anterior areas. Posterior shift of theta response in older adults indicates a switch to stimulus-driven strategy for initiating reversals. In other words, whole brain network shifts available resources to occipital areas to enhance visual attention for gathering any sensory cues that could help initiate perceptual reversals.

4.1. Behavioral Findings

SAM, Necker cube, and Necker lattice was used to investigate whether there are different perceptual reversal characteristics between these stimuli. Results from Turkish young adults showed that perceptual reversal rates obtained from Necker cube and Necker lattice stimuli were related. Also, distribution of dwell times of both Necker stimuli were lognormal. This indicates a shared mechanism that underlie perceptual reversals of Necker stimuli. On the contrary, perceptual reversal rates obtained from SAM was not related to the ones obtained with the two Necker stimuli. It was also shown that distribution of dwell times of SAM was not lognormal. Interestingly, distributions of dwell times were significantly different than gamma distribution for all stimuli. Levelt (1965) was the first researcher to our knowledge that used statistical properties of dwell time distributions as a tool for representing underlying brain activity. He showed that dwell times of different stimuli are distributed similar to that of a gamma distribution. Initial interpretation, which is still widely accepted, was that duration of dwell times were defined by a stochastic process in the brain that produce excitation spikes (Levelt, 1965; Brascamp, Klink, and Levelt, 2015). However, his arguments were based on the findings from binocular rivalry tasks. Regardless, later researchers found that dwell times mostly constitute gamma distributions even in different multistable stimuli like Necker cube, Rubin's face-vase, and stroboscopic alternative motion (Murata et al., 2003). Still, there are other studies that also show that dwell times fit to distributions other than gamma, such as lognormal and beta prime distributions (Zhou et al., 2004; Brascamp, Klink, and Levelt, 2015). Considering the prominence of gamma distributions across different multistable stimuli, our results seem to contradict with some of the previous studies. However, there are important differences in methodologies between this study and studies that report best fits to gamma distribution (Murata et al., 2003; Murata et al., 2004). Most importantly, these studies used experimental designs where each multistable stimuli was observed as long as 1 hour, with prior training durations of 15 minutes. Whereas we used four minutes of observation time for each stimulus, with only 90 seconds of training durations. It is also notable that SAM stimulus used in Murata (2003) did not have a fixation display, instead double-dot displays were presented without an interval between them. These two factors could radically change the overall durations and therefore distributions of dwell times. Mostly because reversal rates gradually increase in the course of continuous observation (Köhler, 1940). Remarkably, a study used several different multistable stimuli and investigated relationship between their reversal rates using 60 seconds of observation durations for each stimulus (Cao et al., 2018). Authors reported that reversal rate of Necker cube was not related to reversal rates of motion-related multistable stimuli such as motion induced blindness, biological motion, and Lissajous-figure. Therefore, careful comparison of literature with our results indicate different reversal characteristics between SAM and the two Necker stimuli. Investigating this difference with older participants would lead to important clues on causes of age related decrease in perceptual reversals.

Another important finding of this study was that the reversal rates of SAM across four Turkish and one German young samples were the same. Furthermore, all young samples had higher reversal rates than older German participants (n = 15). These results are in line with previous studies that show decrease in reversal rates after the ages of 55 to 60 (Jalavisto, 1964; Aydin, Strang, and Manahilov, 2013). Additionally, our results showed that using the same multistable stimulus leads to consistent reversal rates within different age groups, even in different experimental settings and in different countries. A study by Kondo and Kochiyama (2018) observed age related decrease in reversal rates also with an auditory multistable stimulus. Therefore, there is a hint that age-related decrease in reversal rates are independent of type of multistable stimulus, experimental environment, sensory modality, and participants' country. However, there was no older Turkish participants in our analysis to fully confirm the latter assumption.

In addition to reversal rates, reaction time measurements were also different between young German and older German participants. Older participants reacted slower to changes in motion direction exogenous task. Also, variability of reactions times was higher in older adults. These findings are in line with previous studies that report age related increase in reaction times (Yordanova et al., 2004; Schmiedt-Fehr, Mathes, and Başar-Eroğlu, 2009; Schmiedt-Fehr, and Başar-Eroğlu, 2011). However, Yordanova et al. (2004) pointed out that reaction time increases are specific to cognitive tasks and they are not observed in simple reaction time tasks. This finding was consistent across auditory and visual modalities. Furthermore, evidence points to alterations in top-down networks instead of impairments in motor cortex as the cause of age-related differences in reaction times (Yordanova et al., 2004; Schmiedt-Fehr et al., 2011).

4.2 Electrophysiological Findings

4.2.1. Theta (4-8 Hz) Activity

Previous literature shows clear involvement of frontal theta networks in largescale information transfer, expectation, and conflict resolution (Cohen, and Cavanagh, 2011; Karakaş, 2020). Başar-Eroğlu and Demiralp (2001) investigated theta networks by comparing findings of studies on humans and cats. Their investigation showed that similar pattern of frontal theta activation in response to various cognitive events was apparent in both cats and humans (Başar-Eroğlu, and Başar, 1991; Başar-Eroğlu et al., 1991; Başar-Eroğlu et al., 1992). Furthermore, single neuron recordings of monkeys showed activation in same frontal networks in response to anticipated stimulus (Fuster, 1997). Above mentioned human-subject studies employed tasks that require focused attention, signal detection, matching for target recognition, and expectation. In a multistable perception experiment on the other hand, additional top-down and bottomup processes are required to generate, maintain, and switch between multiple percepts (Başar-Eroğlu et al. 1993; Leopold, and Logothetis, 1999; Mathes et al. 2006). Mathes et al. (2014) reported the first perceptual reversal related theta response in humans using SAM stimulus. However, theta response was observed also for SAM's exogenous counterpart. Distinctness of perceptual reversal related response was the difference between anterior (e.g. frontal and central) and posterior (e.g. parietal and occipital) areas. There was a marked anterior dominance of theta response during endogenous reversals that did not exist to the same degree in exogenous reversals. Following studies also showed the same topographical difference in theta responses between exogenous and endogenous reversals (Mathes et al., 2016; Rürup et al., 2020). Authors argued that this difference reflects additional recruitment of top-down processes to resolve perceptual conflict that is specific to endogenous reversals. Specifically, increased anterior theta response reflects the employment prior experiences and expectations to resolve perceptual conflict. The notion that endogenous reversals result from feedback loops between high-level associative areas and low-level sensory areas is prevalent among many researchers (Leopold, and Logothetis, 1999; Brascamp et al., 2017).

Current findings on endogenous reversals showed early to late increase in overall theta amplitude only for young group. Furthermore, this increase was observed at every location except right parietal and both occipital areas. On the contrary, theta response was not increased at any of electrode locations for older group. Interestingly, highest overall theta activation for older group was found at parietal and occipital locations. Regardless of the differences in topography, there were no differences in theta activity between young and older adults even in frontal locations. This was still true when theta activity at individual electrodes was compared separately within early and late time windows. Some of our findings show similarities between two recent studies that compared theta response of healthy controls and schizophrenia patients in multistable perception paradigm (Mathes et al., 2016; Rürup et al., 2020). Both of those studies showed diminished frontal and central theta activations in addition to weak parietal and occipital theta responses in patients. Also, healthy controls had significantly higher theta responses than patients during endogenous reversals. This indicates impaired top-down processes in schizophrenia patients which is only partially observed for older adults in this study. This difference in functionality of theta networks between patients and older adults cannot be explained by reaction time variability. Because behavioral findings between schizophrenia patients and healthy controls are similar to behavioral findings in this study: older adults had higher reaction time variability and slower reaction times than young adults. However, it is likely that our analyses suffered from this issue. Increased reaction time variability might have caused wider theta responses and prevented obtaining significant differences between the two time windows. This problem is further complicated by the lack of distance between analyzed time windows. This complication stems from the computation of wavelet convolution that partially extends to both windows and cause slight confounds to time resolution of computed theta amplitude (Cohen, 2014).

Findings on exogenous reversals depict a different picture for age related differences. Increase in theta activity from early to late windows was observed for young and older adults during exogenous reversals. Topography of theta responses were also similar between groups. Both groups showed highest activity at frontal areas and lowest activity at occipital areas. Older adults had lower theta amplitude when compared to young adults within late window of exogenous task. This difference was true for all locations on right hemisphere and also at left parietal area within late window. Schmiedt-Fehr and Başar-Eroğlu (2011) showed age-related alteration of theta networks only during NoGo trials in a visual Go/NoGo task. That result reflects differences in response inhibition which is not required in exogenous task. They also reported comparable levels of theta activation between young and older adults during Go trials. This activation, on the other hand, reflects stimulus matching and memoryrelated operations to execute button presses. Cognitive processes required to execute a Go trial is more relevant to exogenous reversals than the ones in NoGo trials. However, current study showed remarkable aging effects in theta activity during exogenous reversals that does not exist in Go trials of a Go/NoGo task (Schmiedt-Fehr, and Başar-Eroğlu, 2011). There are two important differences between Go trials and exogenous reversals that possibly caused the difference between this and the

mentioned study (Schmiedt-Fehr, and Başar-Eroğlu, 2011). The most probable explanation of differences between these findings is the differences in novelty in two tasks. Schmiedt and Başar-Eroğlu (2011) used visual cues that warned participants about which of the trials they are about to encounter. This eliminates the factor of novelty which is partly present in exogenous reversals due to slight randomization of durations of each percept. Also, exogenous stimulus induces perception of apparent motion (e.g. dots moving vertically or horizontally). Importantly, Mathes et al. (2014) argued that theta activity induced by exogenous reversals represented object binding processes that is also shared with endogenous reversals. Therefore, it is also possible but less likely that creating the perception of new apparent motion demanded more resources than perceiving a simple dot stimulus and that this was reflected in decreased theta responses (Schmiedt-Fehr, and Başar-Eroğlu, 2011). Comparing our findings with findings of Go/NoGo studies indicates to the possible contribution of novelty effect to theta amplitude both in endogenous and exogenous reversals. This conclusion is supported by previous literature that show age-related alterations in theta range during novelty processing (Polich, 1997; Yordanova et al., 2004). On the other hand, Aktürk et al. (2020) used a facial expression recognition paradigm and found increased frontal theta response and phase locking in older participants. Authors argued that frontal theta networks compensated the impaired occipital delta activity in older participants. Once again, variety of findings across different tasks show that it is crucial to investigate each frequency in relation to others and also to a given task. Remarkably, observing age related theta amplitude decrease in exogenous reversals but not in endogenous reversals further proves that there are separate theta networks responsible for endogenous reversals.

4.2.2. Alpha (8-14 Hz) Activity

Activity in alpha frequency range is related to various sensory, motor, and cognitive processes (Başar et al., 1997; Klimesch et al., 1998; Başar et al., 2000). One of the most reported functional correlates of alpha is its blocking due to simple sensory stimulation (Niedermeyer, 1993; Başar, and Schürmann 1996). Another well-established finding is alpha desynchronization during and/or in anticipation to various tasks (Klimesch, 1997; Babiloni et al., 2004). As Başar et al. (1997) and many other prominent researchers pointed out, there is no single and general pattern of alpha activity that correlates with all the different cognitive processes (Klimesch, 1999;

Başar-Eroğlu et al., 2016). Instead, there are distinct and distributed alpha networks that respond to specific events in different alpha sub-bands (Klimesch, 1999; İşoğlu-Alkaç, and Strüber, 2006). For example, ERD in upper alpha band (10-12 Hz) is associated with memory performance while ERD in lower alpha band (6-10 Hz) is associated with attention and arousal (Klimesch et al., 1998; Klimesch, 1999). However, findings on perceptual reversal related correlates of alpha activity narrow down the scope of investigation for this study. Primarily, alpha desynchronization is thought to represent destabilization of conscious percepts in multistable perception experiments (Strüber, and Herrmann, 2002). This interpretation is presented in various studies that used various multistable stimuli, data analysis methods, and brain imaging techniques (Strüber, and Herrmann, 2002; Mathes et al., 2010; Başar-Eroğlu et al., 2016). For the first time, İşoğlu-Alkaç and Strüber (2006) differentiated functions of alpha sub-bands in a ~70 minute Necker cube task and came up with further conclusions. They argued that desynchronization in lower-1 alpha (6-8 Hz) reflected a bottom-up arousal reaction that in turn triggers attentional processes. They also discussed a possible top-down function for lower-2 alpha as a correlate of expectation of upcoming reversals. This distinction provided another evidence towards the multifold functionality of alpha networks (Başar et al., 1997).

This study did not differentiate between sub-bands of alpha activity. However, our findings replicated earlier finds of alpha activity in endogenous reversals in young adults, and also found noteworthy aging effects on topography of alpha desynchronization. We found that previously described posterior-dominance of alpha desynchronization was shifted towards anterior areas with advancing age. Remarkably, early to late alpha desynchronization at occipital area was entirely diminished for older group. Older group also showed strongest desynchronization at frontal and central areas; areas where no desynchronization was observed for young group. Interestingly, Kolev et al. (2002) used a simple visual stimulation experiment and reported age-related increase in alpha (7-15 Hz) amplitude and phase-locking at frontal and central areas. In line with our study, they also reported decreased upper alpha (10-15 Hz) phase-locking and amplitude at occipital location. Similar findings were obtained in another study showing age-related increase in alpha phase-locking and enhancement to simple auditory stimulus (Yordanova et al., 1998). Kolev et al. (2002) argued that sensory information transferred to associative areas to compensate

for reduced functionality of sensory brain areas. At this point of the discussion, it is important to recall aging studies with single cell recordings and interpret their results in relation to our study. Single neuron studies on cats and monkeys showed clear reduction in signal to noise ratio of visual brain areas in addition to increases in response variability of aged neurons (Schmolesky et al., 2000; Hua et al., 2006; Yang et al., 2009). Shared conclusion of those studies was that aging decreased stimulus selectivity of older neurons due to reduced ability to retrieve sensory signals out of noisy ongoing activity. Remarkable similarities between previous human EEG studies, animal single cell studies and findings of current study are in line with our expectations: (i) age-related deterioration of visual areas are reflected in diminished occipital alpha responses; (ii) representation of perceptual interpretations are adopted by compensatory alpha networks in anterior areas.

Findings of exogenous task showed a general alpha desynchronization at occipital area. Young and older groups showed comparable levels of alpha desynchronization in both time windows and across all areas. Previous studies also showed alpha desynchronization during exogenous reversals but the reduction was steeper and more brief compared to endogenous reversals (Strüber, and Herrmann, 2002). Our findings are in line with that description. On the other hand, Başar-Eroğlu et al. (2016) did not find significant alpha desynchronization during exogenous reversals. However, this difference can be explained by different lengths of analyzed time windows between studies. Başar-Eroğlu et al. (2016) analyzed time windows with 200 ms durations whereas current study used time windows with 500 ms durations. Importantly, high cut off of their late window was at 100 ms before the button press. Consequently, large portion of sharp and brief alpha desynchronization was not included in that study (Başar-Eroğlu et al., 2016). Overall, our findings are in line with previous studies that show stimulus-driven alpha responses to exogenous reversals. However, it is plausible to ask why exogenous reversals did not activate frontal alpha networks just as previous simple visual stimulation studies showed (Kolev et al., 2002). Two important distinctions have to be emphasized: (i) exogenous reversals result from small changes in continuous sequence of visual stimulation; (ii) these small changes in sequential stimuli are followed by motor responses that require involvement of cognitive processes. Therefore, it is likely that exogenous reversals induce alpha responses that are similar to ones induced by an oddball stimulus (Yordanova, Kolev, and Polich, 2001). Unfortunately, stimulus locked exogenous reversals are not statistically analyzed in this study. This prevents making valid comparisons of our response locked alphas to stimulus locked oddball alphas in Yordanova et al. (2001).

4.2.3. Integrative Function of Alpha and Theta Frequencies

Frontal theta networks of young adults are shown to contribute to resolution of perceptual conflict by means of expectation and prior experiences (Mathes et al., 2014; Mathes et al., 2016). Posterior alpha networks, on the other hand, has the function of maintaining representations of perceptual interpretations (Strüber, and Herrmann, 2002, İşoğlu-Alkaç, and Strüber 2006; Başar-Eroğlu et al., 2016). Once again, these findings were replicated in this study. However, older adults showed severe alterations in both networks. Posterior shift of theta activity combined with frontal shift of alpha desynchronization in older adults is explained by the following: (i) decreased ability of occipital areas to distinguish between perceptual interpretations are compensated by increased visual attention and signal detection by recruiting occipital theta networks (Başar et al., 1997; Kolev et al., 2002); (ii) frontal theta networks, which are known to have diminished functionality in older individuals, are further deactivated for maximizing efficiency of frontal alpha networks (Schmiedt-Fehr, and Başar-Eroğlu, 2011); (iii) perceptual representations within frontal alpha networks are continuously communicated with posterior theta networks; (iv) when destabilization exceeds a threshold within frontal areas, posterior theta networks resolve the perceptual conflict by assembling external visual signals and internal signals coming from most active neural groups in frontal areas.

Overall, age-related changes in endogenous task reflect compensatory activations that interact between different frequency bands. As a result, role of bottomup processes is increased and role of top-down processes are decreased during the resolution of perceptual conflict. This, in turn, resulted in decrease of reversal rates in older participants. Specifically, diminished frontal theta activity led to decreases in ability to detect and decide one or the other perceptual interpretations for older adults. Instead, this was compensated by occipital theta networks that facilitated visual attention to external stimuli for triggering perceptual reversals. However, at the same time, recruitment of occipital theta networks resulted in increased matching between external information with the current perceptual interpretation. Due to continuous communication between theta and alpha networks, representations in alpha networks are continuously fortified by pieces of external sensory information that relate to the current percept. This, in turn, resulted in longer dwell times for each interpretation due to external stimulation of relevant neural populations. This resulted in passive and automatic type of volitional holding effect where, in the original effect, perceptual reversals are slowed down by increased attention to one interpretation with conscious effort (Mathes et al., 2006). Interestingly, this explains decreased ability of older adults to hold their percepts as well as their intact ability of increasing reversals in volitional control experiments (Aydin, Strang, and Manahilov, 2013).

These findings are in line with many other studies where age-related changes are related to compensation instead of deterioration (Başar et al., 1997; Kolev et al., 2002; Schmiedt-Fehr et al., 2009; Schmiedt-Fehr et al., 2016).

4.3. Limitations

Initially, study started with a stage with purely behavioral experiments on Turkish participants. Aim was to investigate whether age-related changes apply similarly to Necker cube, Necker lattice, and SAM stimuli. However, experiments were put on halt at March 21 2020, due to COVID-19 pandemic. As a result, it was not possible to gather desirable amount of data from older participants in Turkey. Therefore, we have proceeded with a raw dataset of Prof. Dr. Canan Başar-Eroğlu and her team which they recorded in University of Bremen, Bremen, Germany. Another limitation of this study is our sample size. Future studies should include more participants to obtain more representative samples for each age group. At the same time, future studies should investigate participants within the age range of 65 to 75. This would help further delineate effects of healthy aging. Also, male and female participants were not equal in this study. This is another important factor that should be controlled in future studies.

Even though there were visually apparent hemispheric differences between groups, hemispheres were not included in statistical models as factors. Because including them in combination with all regions of interests would result in including same variances multiple times within the same model. Using advanced statistical models can help to overcome this problem in future studies. We also did not use other advanced data analyses methods such as inter-trial coherence and phase coherence. Using these methods would provide better understanding of the relationship between multiple oscillatory networks, perception, and healthy aging.

4.4. Conclusion

This study provided the first examination of age related alterations in multiple oscillatory networks in a multistable perception paradigm. Effects of healthy aging on brain oscillations were different between exogenous and endogenous tasks. Findings of exogenous reversals indicate age-related impairments in top-down processes such as large-scale information transfer and signal detection. More importantly, endogenous generation and maintenance of percepts as well as resolving the perceptual conflict between these interpretations required drastic changes in oscillatory networks in aged participants. However, integrative function of multiple oscillatory networks remained intact even after those changes. This indicates that agerelated alterations in oscillatory networks represent compensation rather than deterioration. Furthermore, in a counter-intuitive way, our conclusions suggest that performance decreases in behavioral measurements might not always reflect impairments.

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APPENDIX A



İzmir Ekonomi Ünivesitesi Sosyal Bilimler Enstitüsü Den eysel Psikoloji Bölümü

BİLGİLENDİRİLMİŞ ONAM FORMU

Sevgili katılımcı,

<u>Araştırmanın Amacı</u>

Bu araştırma İzmir Ekonomi Üniversitesi Deneysel Psikoloji programına bağlı olarak yürütülmektedir. Prof. Dr. Canan Başar'ın danışmanlığıyla psikoloji bölümünde yüksek lisans yapan Kurtuluş Mert Küçük tarafından yürütülen bu araştırma görmenin nasıl gerçekleştiğini size bazı görseller göstererek incelemektedir.

Deneyde Yapacaklarınız

Bu çalışmada bilgisayar üzerinden size aşağıdakilere benzer, iki farklı yorumu olan şekiller gösterilecek ve bu şekillerin görünümü değiştiğinde klavye yardımıyla rapor etmeniz istenecektir. Deney süresince fiziksel ya da ruhsal durumunuzu kötü etkileyecek herhangi bir işlem gerçekleştirilm emektedir.





Bu şekilde ortada beyaz bir vazo görünmektedir. İki kenardaysa birbirlerine dönük siyah suratlar görünmektedir. Bu şekilde bir genç kadın suratı arkaya dönük şekilde görünmektedir. Yaşlı bir kadın da suratının yarısı gözükür halde görünmektedir.

Gönüllülük Esası ve Bilgilerinizin Gizliliği

Çalışmadaki katılımınız tamamıyla gönüllülük esasına dayalıdır. Haliyle eğer katılımayı bırakmak isterseniz, istediğiniz an bırakabilirsiniz. Eğer bırakmayı seçerseniz, sizin aleyhinize herhangi bir sonuç olmayacaktır. Bireysel bilgileriniz sadece araştırmayı yürütenler tarafından görülecek ve araştırmayla ilişkisi olmayan kimseyle paylaşılmayacaktır. Diğer bir deyişle bu çalışmadan elde edilecek bilgiler tamamen araştırma amacı ile kullanılacak olup kişisel bilgileriniz gizli tutulacaktır.

Araștım a ile ilgili ek sorularınız var ise bunları <u>kurtulusmertkucuk@gmail.com</u> adresinden sorabilirsiniz.

Yukarıdaki bilgileri dikkatli bir şekilde okudum, anladım ve çalışmada yer almayı kendi rızamla kabul ediyorum.

Tarih

//___

İmza

APPENDIX B



İzmir Ekonomi Ünivesitesi Sosyal Bilimler Enstitüsü Deneysel Psikoloji Bölümü

DEMOGRAFİK BİLGİ FORMU

•Yaşınız : _____ • Cinsiyetiniz:

• Kalemle yazarken hangi elinizi kullanıyorsunuz? 🗆 Sağ 🗆 Sol

• Aldığınız en son diploma ya da bitirdiğiniz okul seviyesi nedir? Eğer şu an okuyorsanız içinde olduğunuz öğrenim seviyesini belirtiniz.

🗆 İlkokul 🗆 Lise 🗆 Lisans 🗆 Yüksek Lisans 🗆 Doktora veya sonrası 🗆 Hiçbiri

• Bugün kaç saat uyudunuz?: _____ • Bugün saat kaçta uyandınız?: ____

• Sigara kullanıyor musunuz? 🗆 Evet 🛛 Hayır

Günde ortalama kaç paket sigara içiyorsunuz:

• Alkol kullanıyor musunuz? 🗆 Evet 🛛 Hayır

Haftada kaç gün alkol kullanıyorsunuz: ____

• Kahve tüketiyor musunuz? 🗆 Evet 🛛 Hayır

Günde ortalama kaç bardak kahve içiyorsunuz:

• En son kaç saat önce yemek yediniz?: _____ • Kendinizi aç hissediyor musunuz?: _____

• Herhangi bir kronik hastalığınız var mı? Varsa belirtiniz

• Daha önce kafa travması geçirdiniz mi (düşüp kafanızı çarpmak, trafik kazası geçirmek vb.)?

• Daha önce herhangi bir psikolojik/psikiyatrik hastalık tanısı aldınız mı? Varsa belirtiniz.

• Herhangi bir ilaç kullanıyor musunuz?

Evet I Hayır İlaç adı: ______

Araştırmanın ikinci aşamasına çağırabilmemiz için iletişim bilgilerinizi yazınız.

Telefon:

E-mail adresi:	
	이 가지 이번 것이 있는 것이 같이 했다.

Tarih: __/__/ Saat: