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Age-Related Changes in the Neural Correlates of Interval Timing

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Age-Related Changes in the Neural Correlates of Interval Timing

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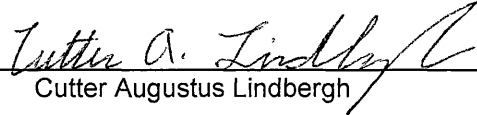of the College of William and Mary in Candidacy for the Degree of
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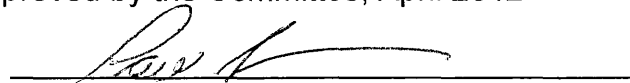
APPROVAL PAGE

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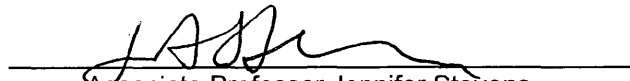
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COMPLIANCE PAGE

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ABSTRACT PAGE

It is well established that older adults exhibit deficits in interval timing. The mechanisms underlying these deficits, however, remain a subject of debate. The present study sought to shed light onto the nature of age-related timekeeping distortions using a duration bisection paradigm and electroencephalography (EEG). The duration bisection paradigm is a classic timekeeping task in which participants make judgments about whether a series of "probes" are closer in duration to "short" or "long" anchor durations. 24 young and 17 older adults volunteered to participate in the study. Event related potentials (ERPs), including the Contingent Negative Variation (CNV), were examined during temporal accumulation and bisection categorization. Results indicated that the point of subjective equality (PSE), or some value near the PSE, is among the critical information drawn from memory for the categorization decision, regardless of age. A shallower CNV amplitude observed in older adults during temporal accumulation indicates that fewer pulses were amassed in the accumulator than in young adults. The most probable culprit for this observation is an age-related decline in attentional performance, which may be a primary factor in producing age-related timing distortions. Behaviorally, older adults performed similarly to young adults, suggesting that to preserve timing abilities during the aging process, older adults may recruit additional neural resources through a process of cognitive scaffolding.

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Acknowledgments

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Age-Related Changes in the Neural Correlates of Interval Timing

The importance of mental timekeeping in our daily lives cannot be overstated. For example, timing is necessary for movement coordination, driving, listening to and producing music, localizing sound, conversing with others, and planning actions (Clynes & Walker, 1986; Macar & Vidal, 2004; Matell & Meck, 2000; Roberts, 1998). Of particular importance is the timing of durations in the seconds-to-minutes range, referred to as interval timing (Matell & Meck, 2000). Interval timing plays a role in such a wide range of behaviors—from determining whether a busy street can be safely crossed to returning to the stove just as a pot of water begins to boil—that it has been described as "essential" to everyday functioning (Block, Zakay, & Hancock, 1998; Matell & Meck, 2000; Zakay & Block, 1997). More broadly, interval timing is necessary for anticipation, expectation, attention, perception, and cognition (Carroll, Boggs, O'Donnell, Shekhar, & Hetrick, 2008; Macar & Vidal, 2004).

Interval timing abilities have been shown to decline as a person ages (e.g., Block et al., 1998; Craik & Hay, 1999; Wearden, Wearden, & Rabbitt, 1997). Considering the wide range of behaviors in which timing plays a role, studying the nature of these deficits is important in and of itself (Block, Zakay, & Hancock, 1998). Moreover, because timing and time perception require a multitude of cognitive operations, including attention, memory, and decision

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processes, researchers have begun to employ timing paradigms to shed light onto the cognitive aging process more generally (Lustig & Meck, 2001).

Despite the fact that researchers have been investigating timekeeping deficits in older adults for over a century, there is still considerable debate surrounding the precise nature of these deficits (Block et al., 1998; Lustig, 2003). For example, some researchers have found older adults to underestimate and overproduce temporal intervals compared to young, healthy controls (e.g., Craik & Hay, 1999). Others have observed the aging process to distort time in the exact opposite direction, with older adults overestimating and underproducing temporal intervals (e.g., Block et al., 1998). Others, still, have found an absence of any age-related timing distortions (e.g., McCormack et al., 1999; Wearden et al., 1997). In addition, measures of timing variability—that is, how precise or consistent one is at timekeeping—have yielded mixed results (Lustig, 2003). Some researchers (e.g., Block et al., 1998) have found older adults to display increased timing variability compared to young controls, while others (e.g., Rammsayer, 2001) have observed no such differences between age groups.

One approach that has proven helpful in making sense of these conflicting findings is to examine age-related timing deficits within the context of Scalar Expectancy Theory (SET). SET, originally proposed by Gibbon, Church, and Meck (1984), is arguably the most widely accepted psychological model of interval timing. According to SET, a continuously

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running pacemaker-like mechanism in the brain generates neuronal pulses. At the beginning of a to-be-timed interval, an attention-modulated switch is opened so that an accumulator-like mechanism can begin counting the number of pulses that are emitted by the pacemaker. The current pulse count in the accumulator is stored in working memory and compared to a value stored in reference memory corresponding to the target duration. When the pulse count held in working memory is equivalent to the value stored in reference memory, a decision is made that the duration being timed is over.

Many researchers have attempted to link timing deficits in older adults to one or more of the cognitive components implicated by SET. One component in particular that has gained considerable attention as a potential culprit for producing age-related timing distortions is the internal pacemaker mechanism (e.g., Block et al., 1998; Vanneste, 2001; Zakay & Block, 1997). Accordingly, temporal estimation and production errors in older adults are thought to arise from changes in the rate at which the pacemaker emits pulses. Most theorists who hold this view aver that the pacemaker systematically slows down with age, such that fewer pulses are emitted than necessary during the timing of a given interval (Block et al., 1998). In support of this view, Vanneste (2001) found spontaneous tapping rates in older adults to be significantly slower than spontaneous tapping rates in young adults. This provides evidence for a slower pacemaker rate because spontaneous tapping directly indexes one's "internal tempo," which, in turn, has been shown to

reflect internal clock speed (Denner, Wapner, & Werner, 1964; Vanneste, 2001). The notion of a decreased pacemaker rate in older adults is in agreement with earlier claims made by Surwillo (1968), who posited that age-related decreases in perceptual-motor speed result from the slowing of a central timing mechanism. It is also in agreement with subjective reports made by older adults that time passes more rapidly than it did during their younger years (e.g., Baum, Boxley, & Sokolowski, 1984). From a biological perspective, an age-related reduction in clock speed is plausible considering that the speed of the pacemaker has been shown to depend upon variables such as metabolic rate and body temperature (Block et al., 1998). During the aging process, basal metabolism and brain temperature decrease, which would theoretically lead to reductions in clock speed, as observed by Vanneste (2001) and others (Altman & Dittmer, 1968; Kadlub, 1996).

Age-related timing deficits have also been attributed to the deterioration of the memory processes outlined in SET. It has been found that the aging process is accompanied by a reduced ability to remember information, particularly from the beginning of an event (Inglis, 1965). Older adults would thus be expected to under-reproduce previously learned temporal intervals due to a loss of pulses from memory, particularly from the beginning of the interval (Block et al., 1998). Moreover, one would expect this effect to be most exaggerated when reproducing longer intervals, as more pulses would be lost overall. Several studies have since demonstrated that older adults do in

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fact under-reproduce temporal intervals, and that these under-reproductions are greatest for longer temporal intervals (e.g., Kelley, 1980; Perbal et al., 2002; Vanneste & Pouthas, 1995). In addition, timing abilities in older adults have been correlated with scores on working and long-term memory tests (Perbal et al., 2002).

Another popular view is that timekeeping distortions in older adults result from age-related declines in attention. Indeed, research has demonstrated that aging is accompanied by changes in attentional performance (e.g., Hasher & Zacks, 1979; Jennings & Jacoby, 1993). These changes are most pronounced among "controlled" aspects of attention—that is, those aspects of attention that require awareness and intention (Hasher & Zacks, 1979; Jennings & Jacoby, 1993; Lustig, 2003). Within the context of SET, age-related deficits in controlled attention are thought to cause a "flickering" of the attention-modulated switch, thereby intermittently interrupting the flow of pulses from the pacemaker to the accumulator (Lustig, 2003). The consequence of this flickering is a slower clock because fewer pulses are able to pass into the accumulator than necessary when timing a given interval (Lustig, 2003).

The strength of the attention hypothesis arises from its ability to account for the conflicting findings in the literature regarding the nature of the observed timekeeping deficits in older adults. A recent meta-analysis of interval timing revealed that older adults have increased internal clock speed

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relative to younger adults (Block et al., 1998). Although at first this finding may seem to contradict the attention hypothesis, it actually provides support. As Lustig (2003) noted, nearly every experiment included in the meta-analysis employed absolute time judgment paradigms. Absolute time judgments refer to when participants are asked either to estimate how much time has passed during an interval of an unknown length or to produce an interval of a specified length (Lustig, 2003). According to the attention hypothesis, an older adult's clock speed is slowed during everyday life because already limited attentional resources must be divided among a multitude of distractions arising from the surrounding environment (Lustig, 2003). The reference value an older adult learns for a given duration in everyday life is therefore based upon a slowly operating clock (Lustig, 2003). By contrast, in an experimental setting in which a participant's sole task is to estimate or produce a given duration, older adults can focus their full attention upon timing (Lustig, 2003). The consequence of this attentional discrepancy is that absolute time judgments in experimental settings are based upon reference values obtained from a slowly operating, everyday clock (Lustig, 2003). Behaviorally, this discrepancy translates into overestimations and underproductions—that is, an apparently accelerated internal clock (Lustig, 2003). In an absolute time judgment task in which older adults were forced to divide their attention between timekeeping and some other task, such as making judgments about randomly presented visual stimuli, older adults

showed shifts in the opposite direction, underestimating and overproducing intervals (Craik & Hay, 1999). The fact that manipulating the attentional demands placed upon older adults can reverse clock speed direction further supports an attention-based hypothesis (Lustig, 2003).

Seeing as explanations based upon changes in pacemaker rate, memory processes, and attentional mechanisms have all gained empirical support, it seems likely that age-related timing deficits are the result of a complex interaction of these factors and possibly others. In an attempt to better understand this interaction, the present study employed electroencephalography (EEG) to illuminate age-related changes in the neural mechanisms underlying interval timing. EEG is an excellent candidate for timing research because of its high temporal resolution, which enables information to be obtained about cognitive processes that cannot be obtained through the use of behavioral measures alone (Luck, 2005; Ng, Tobin, & Penney, 2011). As examples, studies examining event related potentials (ERPs), such as the Mismatch Negativity (MMN), Omitted Stimulus Potential (OSP), and Error Negativity (Ne), have supplemented behavioral measures to reveal critical information about human timing mechanisms (Bertoli, Heimberg, Smurzynski, & Probst, 2001; Bullock, Karamuursel, Achimowicz, McClune, & Basar-Eroglu, 1994; Luu, Flaisch, & Tucker, 2000; Macar & Vidal, 2004). The inclusion of the MMN, OSP, and Ne in timing-based paradigms have enabled researchers to: (1) gain physiological evidence for the

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existence of timing mechanisms in the human brain; (2) demonstrate the reliability and sensitivity of the human timing system; (3) shed light onto temporal expectation and learning processes; and, (4) illuminate a hierarchical organization of the human timing system, which necessitates attention at higher and more complex levels of temporal processing (Bertoli et al., 2001; Bullock et al., 1994; Luu et al., 2000; Macar & Vidal, 2004).

Another ERP that has proven particularly useful in shedding light onto mental timekeeping processes, and was a focus of analyses in the present study, is the Contingent Negative Variation (CNV). The CNV is a negative going waveform that occurs during the actual timing of an interval, and has thus been referred to as an "on-line" index of temporal encoding (Macar & Vidal, 2004). Interestingly, the amplitude of the CNV corresponds to the subjective experience of the duration being timed, such that larger amplitudes are associated with subjectively longer passages of time and vice versa (Macar, Vidal, & Casini, 1999). This was demonstrated in a task in which participants were instructed to reproduce a 2500 ms interval by placing it between two button presses (Macar et al., 1999). The behavioral responses of the participants were divided into 3 categories, each with a 200 ms range (short: 2200-2400 ms; correct: 2400-2600 ms; and long: 2600-2800 ms). Although participants were always attempting to reproduce the same 2500 ms interval, the amplitude of the CNV depended upon the response category: short

responses produced the smallest CNV amplitude; long responses the greatest; and correct responses somewhere in between.

Birbaumer, Elbert, Canavan, and Rockstroh (1990) aver that slow, negative-going waveforms, such as the CNV, result from excitatory postsynaptic potentials at apical dendrites in the underlying cortex. Within the context of SET, the neuronal activation associated with the CNV may be due to the steady accumulation of temporal units or "pulses" (Macar & Vidal, 2004). This relationship between CNV amplitude and neuronal activation due to pulse accumulation provides electrophysiological evidence in favor of timekeeping models, like SET, that include an accumulator mechanism (Macar & Vidal, 2004). In addition, it has allowed researchers to gain information about the accumulation process, including when it begins, the rate at which it occurs, and when it ends (e.g., Macar et al., 1999; Ng et al., 2011).

Recently, Ng et al. (2011) studied the CNV in a group of group of healthy, young adults while they performed the duration bisection task. The duration bisection task is well established, and has been used to explore time perception in humans and animals (Ng et al., 2011). In a typical duration bisection task, participants learn a "short" anchor duration (e.g., 1 s) and a "long" anchor duration (e.g., 9 s). Subsequently, participants are asked to classify intermediary "probe" durations (e.g., 2, 3…8 s) as closer to the short or long anchor.

The inclusion of the CNV in the duration bisection paradigm marks a

novel approach to understanding the memory and decision processes associated with interval timing. This is particularly relevant because there has been considerable debate surrounding what information is drawn from memory during temporal decision-making. This debate is perhaps most evident within the context of the duration bisection task, which requires participants to compare values held in working memory to values held in reference memory, and then make decisions based on these comparisons. Wearden (1991) proposed a similarity difference rule in which participants decide how to respond by subtracting the probe duration from each of the two anchors. In this way, the participant responds "short" if the probe duration is closest to the short anchor and "long" if the probe duration is closest to the long anchor. Gibbon (1981) similarly proposed that the short and long anchors are used in duration categorization, but that the decision is based on a ratio comparison of how similar the probe is to the two anchors rather than a difference comparison. In contrast to Wearden (1991) and Gibbon (1981), Wearden and Ferrara (1995) claimed that some point other than the anchor durations is used to categorize the probes, likely the arithmetic mean. The basis for this claim arose from observing performance on a novel bisection task, which required participants to categorize probes as "short" or "long" in the absence of anchor durations (Wearden and Ferrara, 1995). In other words, participants classified probes on the basis of any criteria they chose. The novel bisection task yielded a psychophysical function that was identical to the

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psychophysical function yielded in a classic bisection task (i.e., with anchor durations) with the same probes. Finally, Wearden (2004) proposed that the decision process involves normalizing the difference between the probe and the anchor durations, and then comparing this difference to a threshold to determine the nature of the response.

Ng et al. (2011) found the CNV elicited by the bisection task probes to: increase in amplitude until the short anchor duration; remain constant until approximately the geometric mean (GM) of the short and long anchors; and then begin to return to baseline. Given that the CNV is an "on-line" index of temporal accumulation, the observed electrophysiological response pattern suggests that a critical value near the GM is among the information drawn from memory during the categorization decision (Ng et al., 2011). This is because temporal accumulation is no longer necessary beyond when this critical value is reached. If a later value were necessary for bisection categorization, such as the long anchor duration, one would expect temporal accumulation to continue until that later value was reached rather than to cease well beforehand.

Taken together, Ng et al.'s (2011) findings provide support for Wearden and Ferrara's (1995) claim that a value roughly halfway between the short and long anchor durations is among the critical information for bisection categorization. These findings also refute the notion that the bisection decision is based upon a similarity difference rule or a ratio comparison because both

of these theories imply that temporal accumulation would be necessary

throughout the entire duration of every probe (Gibbon, 1981; Wearden, 1991).

The present study incorporated ERP measures into the duration

bisection paradigm to add to the findings of Ng et al. (2011) and further

illuminate the cognitive processes underlying age-related deficits in interval

timing. The duration bisection paradigm was chosen due to its heavy emphasis

on cognitive operations suspected to affect timekeeping abilities in older

adults, including attention, memory, and decision processes (Lustig & Meck,

2001). The major goals of the present research were twofold. First, to resolve

the controversy surrounding the cognitive processes responsible for producing

age-related timing distortions. Second, to determine whether older adults use

the same criteria as young adults during bisection categorization. To achieve

these goals, accuracy, variability, and response latencies were recorded to

assess for age-related differences in behavioral measures of timekeeping. In

addition, the CNV and ERPs time-locked to probe offset were analyzed to

shed light onto age-related changes in temporal encoding and decision

processes. To the author's knowledge, the analysis of offset-locked ERPs in

the duration bisection task was an unprecedented approach to the investigation

of temporal decision processes, and was undertaken to supplement

conclusions drawn from examining the CNV alone.

Given Ng et al.'s (2011) findings that a value roughly halfway

between the short and long anchor durations is among the critical information

for the categorization decision, it was hypothesized that "long" responses would be associated with significantly faster response times than "short" responses. This is because the critical information for the bisection decision was expected to have been obtained prior to the offset of "long" probes, such that a motor response would be the only action necessary following "long" probe offset. By contrast, bisection categorization was expected to be incomplete prior to the offset of "short" probes due to a lack of critical information. Accordingly, a decisional process was expected in addition to a motor response following "short" probe offset, which would contribute to greater response latencies on these trials. In addition, it was hypothesized that the extra decisional process following "short" probe offset relative to "long" probe offset would be reflected by differences in ERPs time-locked to probe offset based upon response category.

Method

Participants

23 young adults (M=20.17 years; 16 females) and 17 older adults (M=75.65 years; 6 females) participated in the experiment. The young adults participated in exchange for course credit, while the older adults were recruited from the community via flyers and received $10/hour as compensation. 20 of the young adults and 16 of the older adults were right-handed. All of the participants had normal or corrected to normal vision, and none had a history of neurological diseases or psychiatric disorders. Data from

5 of the young adults and 3 of the older adults were excluded from analyses due to a failure to follow task instructions. In addition, data from 1 of the young adults was excluded due to excessive artifact in the EEG data. This study received approval from the Institutional Review Board (PHSC-2011-02-11-7139-pdkieffaber) and adhered to the guidelines set forth by the Protection of Human Subjects Committee. Written informed consent was obtained from every participant.

Neuropsychological Tests. The Saint Louis University Mental Status (SLUMS) Examination and a digit span test were administered to determine whether cognitive status correlated with any of the timekeeping measures.

The SLUMS is an 11-item, 30-point test that assesses such cognitive abilities as orientation, attention, memory, and executive functioning (Tariq, Tumosa, Chibnall, Perry, & Morley, 2006). It is similar in format to the Mini-Mental State Examination (MMSE), but is considered a more sensitive detector of mild neurocognitive disorder (MNCD) (Tariq et al., 2006). The average score for the older adult group was a 26.67 (SD=2.35); the average score for the young adult group was a 27.40 (SD=2.46).

The digit span test was similar in structure to the Digit Span subtest of the Wechsler Adult Intelligence Scale-III, which is a widely accepted and effective measure of short-term memory (Richardson, 2007; Wechsler, 1997). Participants were presented with computerized, audio recordings of digit sequences and asked to recall each sequence verbatim by entering the digits

on a keyboard. Digit sequences began at a length of 2 digits, and gradually increased in length to a maximum of 8 digits. 5 different sequences were presented at each sequence length. Based upon the scoring criteria set forth by Wechsler (1997) and used elsewhere (e.g., Woods et al., 2011), digit span scores were calculated as the maximum sequence length reached for which less than two sequences of that length were incorrectly reported. The average digit span for the older adult group was a 6.09 (SD=1.22); the average digit span for the young adult group was a 6.2 (SD=1.23).

Stimuli

Stimuli were comprised of blue squares that were presented on a computer screen against a black background. The short and long anchor stimuli had durations of 1250 and 3000 ms, respectively. The intermediary, "probe" stimuli had durations that were linearly spaced from 1425 to 2825 ms at 175 ms intervals (i.e., 1425, 1600, 1775, 1950, 2125, 2300, 2475, 2650, and 2825 ms).

Procedure

The duration bisection task was programmed in E-prime (Psychology Software Tools, USA). During the initial training block, the short and long anchor stimuli were each presented 3 times. Participants received feedback prior to each of these presentations about whether the subsequently presented anchor would be "short" or "long" (i.e., "Next is an example of the short/long stimulus"). The intermediary, "probe" stimuli were presented in 2 testing

blocks separated by a "refresher" block in which the short and long anchors were again presented 3 times each. Each of the 2 testing blocks consisted of 12 presentations of each of the 9 probes. The probes were presented in a randomized order within each block.

Participants were comfortably seated facing a computer monitor in a dimly lit, electrically shielded booth. Participants were instructed to indicate on a color-coded response pad whether each of the probes was closer in duration to the short or long anchor. Participants pressed a pink button with their left index finger if they felt the probe was closer to the short anchor or a green button with their right index finger if they felt the probe was closer to the long anchor. Participants were told to make their best guess if they were unsure about whether a probe should be classified as short or long.

EEG Recording

A DBPA-1 Sensorium bio-amplifier (Sensorium Inc., Charlotte, VT) was used to continuously record EEG data at 2000 samples per second. Brain activity was monitored from 72 scalp sites using Ag-AgCl sintered electrodes mounted in a fabric cap. The reference electrode was positioned on the tip of the nose and the ground electrode was positioned on the forehead. Horizontal eye movements, vertical eye movements, and blinks were monitored by electrodes placed above, below, and on the outer canthus of each eye.

Data Analysis

Behavioral Data. A psychophysical response function was created for each participant by calculating the probability of responding "long" for each of the probes. The point of subject equality (PSE) was calculated for each participant using the process laid forth by Maricq, Roberts, and Church (1981). Accordingly, the method of least squares was used to fit a straight line to the probability of responding "long" for every 3 adjacent probes. The line that yielded the greatest slope was then selected to find the duration associated with a probability of 0.5 of responding "long." This duration was reported as the PSE. A grand average psychophysical response function was created for both the young adults and the older adults.

Response latencies were calculated as the length of time from probe offset to when a response was made. Outlier responses were defined for each participant as those that were more than twice the inter-quartile range below the 25th percentile or above the 75th percentile and were excluded from analyses. With the remaining values, two sets of response latencies were created for each participant: one that included an average response latency for every trial on which the participant responded "short" and one that included an average response latency for every trial on which the participant responded "long." The resulting "short" and "long" response latencies were averaged across participants in each of the age groups to produce grand average response latencies. In turn, these grand average response latencies were submitted to a two-way mixed (between-within) ANOVA with age group

(young vs. old) as the between-subjects factor and bisection categorization (short vs. long) as the within-subjects factor.

EEG Data. EEG data were analyzed using a set of customized routines written in MATLAB. Raw data were visually inspected and extreme artifacts were rejected. Independent component analysis was used to identify and remove ocular artifacts due to blinks and eye movements (Stone, 2002).

Probe Offset ERPs. Epochs time-locked to probe offset were created with a window from 200 ms pre offset to 1000 ms post offset. Baseline corrections were achieved by subtracting the average voltage of the 200 ms window prior to probe offset from each epoch. Epoched data were smoothed with an IIR Butterworth band-pass filter from 0.1 to 20 Hz and any segments containing values in excess of +/- 100 μV were omitted from further analyses.

Based on the topographical distribution of brain activity at probe offset as revealed in a grand average scalp plot, electrodes CPz, Cz, C1, C2, CP1, and CP2 were selected as the focus of further analyses. Macar and Vidal (2003) and others (e.g., Pfeuty, Ragot, & Pouthas, 2003) have also found temporal decision-making to occur in this midline centro-parietal location, though previous analyses have focused on CNV peak rather than ERPs at stimulus offset.

Collapsing across these electrodes of interest and averaging across participants for the timeframe of 200 to 700 ms post probe offset produced two grand average ERPs for each age group: one for trials on which

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participants responded "short" and one for trials on which participants responded "long." The average amplitudes of each of these waveforms were calculated and submitted to a two-way mixed (between-within) ANOVA with age group (young vs. old) as the between-subjects factor and bisection categorization (short vs. long) as the within-subjects factor.

CNV. Independent component analysis (ICA) was used to identify and analyze the CNV (Makeig et al., 1999). ICA has been established as an effective means of analyzing the CNV in several studies (e.g., Jervis et al., 2007; Klein & Feige, 2005).

Rather than calculating a CNV for each of the probes, the data were analyzed in terms of eleven 250 ms temporal windows, which began at 75 ms (i.e., 75-325, 325-575…2575-2825 ms). The first 75 ms segment of each trial was excluded from analyses due to previous findings that the beginning of a CNV waveform is often adulterated by other early components, such as the P2 (e.g., Ng et al., 2011; Pfeuty, Ragot, & Pouthas, 2005).

Importantly, each window included trials from any probe whose duration fell within that window. For example, the first 5 windows (75-1325ms) included data from the first 1325 ms of every probe, regardless of probe duration, because none of the probes offset prior to the end of the fifth window (the shortest probe was 1425 ms). It was thus assumed that EEG activity would be the same on every trial throughout this timeframe as participants had no way of knowing when a probe would offset before the fact.

By contrast, the last window (2575-2825 ms) only included trials from the second longest and longest probes because trials from all of the other probes had offset prior to the beginning of this window. This method of creating temporal windows and averaging across probes was used by Ng et al. (2011), but only for the first 800 ms of their paradigm. The advantage of averaging across probes throughout was that the maximum amount of data was incorporated into the analyses for each window.

Grand average CNV waveforms were then created for both the young adults and the older adults. For both age groups, average amplitudes were calculated for each of the 11 windows. The resulting values were submitted to independent samples (old vs. young) t-tests.

Results

Behavioral Data

Psychophysical Response Functions. The psychophysical functions for the young and older adult groups demonstrated that the probability of responding "long" increased as the probe duration increased (Figure 1). The grand average PSE for the young and older adult groups were 2013.39 and 1979.32 ms, respectively. To provide points of reference, the arithmetic mean (AM) of the short and long anchors was 2125 ms and the GM was 1936.49 ms. An independent samples t-test revealed that the PSE for these two groups did not significantly differ from one another, $t(29)=.369$, $p=.715$.

Response Latencies. The mean "short" response latencies for the young and older adult groups were 747.11 (SD = 95.15 ms) and 643.24 ms (SD = 66.70 ms), respectively. The mean "long" response latencies for the young and older adult groups were 706.32 (SD = 133.69 ms) and 579.38 ms (SD = 119.29 ms), respectively. Response latencies for both age groups are depicted in Figure 2. A two-way mixed ANOVA revealed main effects for age group, $F(1,29)=9.74$, $p=.004$, and bisection categorization, $F(1,29)=18.89$, $p=.000$, but no interaction $F(1,29)=.92$, $p=.346$. Surprisingly, the age group main effect indicated that the older adults were significantly faster to respond than the young adults. Planned comparison, paired samples t-tests demonstrated that both the young adults, $t(16)=3.20$, $p=.006$, and the older adults, $t(13)=2.96$, $p=.011$, were significantly faster to make "long" responses than "short" responses. This finding supports the hypothesis that more time would be required to make "short" responses (relative to "long" responses) due to the presence of a decisional process following the offset of "short", but not "long" probes.

EEG Data

Probe Offset ERPs. The mean ERP amplitude associated with the "short" responses for the young and older adult groups were 7.28 (SD = 6.25 μV) and 6.43 μV (SD = 3.91 μV), respectively. The mean ERP amplitude associated with the "long" responses for the young and older adult groups were 3.74 (SD = 6.55 μV) and 6.52 μV (SD = 4.46 μV), respectively. A two-

way mixed ANOVA revealed an interaction between age group and bisection categorization, $F(1,29)=4.43$, $p=.044$, but no main effects for age group, $F(1,29)=.286$, $p=.597$, or bisection categorization, $F(1,29)=4.01$, $p=.055$. Planned comparison, paired samples t-tests demonstrated that young adults had a significantly greater ERP amplitude for the "short" responses than the "long" responses, $t(16)=3.02$, $p=.008$. This difference in offset-locked ERPs is consistent with our predictions and supports the notion that a decisional process followed the offset of "short" probes, but not "long" probes. By contrast, the ERP amplitudes corresponding to the "short" and "long" responses did not significantly differ from one another in the older adult group $t(13)=-.07$, $p=.946$.

These probe offset ERPs are depicted in Figure 3. Figure 4 provides scalp plots of the differences in ERP amplitudes between the "short" and "long" responses for each age group, including their topographical distribution.

CNV. When averaged across all 11 temporal windows, neither the amplitudes (Young: -1.09 μV; Old: -.56 μV) nor the slopes (Young: .04 μV/ms; Old: -.09 μV/ms) of the CNV waveforms were significantly different between age groups [Amplitude: $t(29)=-1.34$, $p=.189$; Slope: $t(29)=1.96$, $p=.60$] (Figure 5). However, significant age-related differences in CNV properties were present when certain portions of the waveform were examined in isolation. Young and older adults had significantly different slopes when averaged across the first 7 temporal windows (Young: .09 μV/ms; Old: -.15

$\mu V/ms$), t(29)=3.05, p=.005. Similarly, young and older adults had significantly different CNV amplitudes when averaged across these same windows (Young: -1.14 μV; Old: -.41 μV), t(29)=-2.119, p=.043. The fact that these differences occurred during the first 7 temporal windows was particularly noteworthy because the PSE for both age groups was located within the 8th temporal window. From the 8th temporal window onward, CNV slopes for young and older adults were not significantly different, t(29)=.093, p=.927; in fact, they closely paralleled one another (Young: -.05 $\mu V/ms$; Old: -.07 $\mu V/ms$). This was also true of CNV amplitudes during this timeframe (Young: -1.01 μV; Old: -.82 μV), t(29)=-.324, p=.748.

Correlational Analyses With Neuropsychological Variables

In order to determine how behavioral and EEG measures of timekeeping were associated with neuropsychological measures of cognitive functioning, correlational analyses were conducted between SLUMS scores, digit span scores, response latencies, probe-offset ERP amplitudes, and CNV properties (i.e., amplitude and slope). The only significant correlation found between timekeeping measures and neuropsychological test performance was between digit span scores and probe-offset ERP amplitudes corresponding to "short" responses. This correlation was significant in both the young adult group, r=.880, p=.001, and the older adult group, r=.639, p=.034.

Discussion

Behavioral Data

As expected, the psychophysical response functions for both age groups revealed that the probability of responding "long" increased with probe duration. Although the response functions failed to yield slopes as steep as is generally obtained in duration bisection paradigms, this may have been due to the large ratio of the short anchor to the long anchor in comparison to other studies (e.g., McCormack et al., 1999; Ng et al., 2011; Wearden et al., 1997). In addition, the shorter relative distance between the shortest probe and the longest probe, which was exaggerated by the fact that probes equivalent to the anchor durations were excluded from test trials, likely further limited the resolution of the psychophysical response function at either end.

Young and older adults had nearly the same bisection point, which is not uncommon in duration bisection paradigms (e.g., McCormack et al., 1999; Wearden et al., 1997). The similarity in slope of the response functions indicated that both age groups exhibited comparable levels of precision and accuracy. The lack of an age difference on these measures has been obtained previously on the bisection task (e.g., Wearden et al., 1997).

The similarities in performance observed between the young and older adult age groups may be due to the fact that the duration bisection paradigm is a relative time judgment task (Lustig, 2003). As Lustig (2003) noted, the performance of young and older adults on relative time judgment tasks is often quite similar (e.g., McCormack et al., 1999; Rammsayer, 2001; Wearden et al., 1997). By contrast, significant age-related differences in performance

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are common on absolute time judgment tasks (e.g., Block et al., 1998).

In order to understand why age-related timing distortions tend to be present on relative time judgment tasks but not on absolute time judgment tasks, it is helpful to examine how these two tasks differ in design. Relative time judgment tasks are comprised of exposure to an unspecified critical duration in an initial training phase. In a subsequent testing phase, participants are asked to make temporal judgments relative to the critical duration learned during the training phase. This is in contrast to an absolute time judgment task, in which participants either assign a verbal label to some unspecified duration or produce some specified duration. An important distinction between relative time judgment tasks and absolute time judgment tasks is that, in the former case, reference memory values for the critical duration are learned within the context of the experiment (Lustig, 2003). By comparison, in an absolute time judgment task, reference memory values are learned within the context of everyday life (Lustig, 2003).

Lustig (2003) attributed age-related discrepancies in performance on relative versus absolute timing judgment tasks to attention. On a relative time judgment task, the attentional demands under which the reference memory value is acquired (training phase) and the accumulator value is acquired (testing phase) are equivalent. Therefore, the internal clock can be said to operate at roughly the same speed between the training phase and the testing phase. By contrast, on an absolute time judgment task, the reference values

are obtained in the hustle and bustle of everyday life. The high attentional demands of everyday life may interrupt the flow of pulses from the pacemaker to the accumulator, resulting in a more slowly operating clock. These reference values are then used as a point of comparison for temporal judgments made in the quiet experimental setting, in which a participant's sole task is timekeeping. Accordingly, a relatively faster clock produces the accumulator values obtained in the experimental setting because extra attentional demands do not interrupt pulse accumulation. The consequence of this attetnional discrepancy between everyday and experimental settings is that accumulator values produced by a more rapidly operating clock (experimental setting) are compared to reference values produced by a more slowly operating clock (everyday life). One would expect this to result in underproductions and overestimations, and a meta-analysis revealed that it does (Block et al., 1998).

The attentional hypothesis proposed by Lustig (2003) has been supported by timing studies that systematically manipulate the attentional demands placed on participants. For example, Vanneste and Pouthas (1999) incorporated a divided attention task into the training trials of a relative time judgment task, but allowed participants to utilize full attentional resources during testing trials. As expected, this led to under-reproductions. Older adults under-reproduced to a significantly greater degree than young adults, suggesting that older adults are more susceptible to increased attentional

demands due to their already limited attentional resources (Vanneste &

Pouthas, 1999). It has also been demonstrated that timing is distorted in the

exact opposite direction when increased attentional demands are placed on

participants during testing trials, but not training trials (Lustig & Meck, 2002).

Probe Offset ERPs

In the young adult group, probe offset ERP amplitudes were

significantly greater for "short" responses than "long" responses. According to

SET, responses are preceded by a memory stage, in which the current

accumulator value is compared to a reference memory value, and a decision

stage, in which participants decide how to respond on the basis of this

comparison. The greater amplitude associated with the "short" responses, then,

may be an electrophysiological index of these memory comparison and

decision processes. The strong correlation found between "short" response

ERP amplitude and digit span scores (for both age groups) supports this view.

The relative reduction in ERP amplitudes for "long" responses likely reflects

that the memory comparison and decision processes necessary for bisection

categorization had already occurred on these trials, well before probe offset.

The lack of a correlation between digit span scores and "long" response ERP

amplitudes supports the notion that memory process were not involved on

these trials.

If, as Ng et al.'s (2011) findings suggest, the critical information for

the categorization decision—which Ng et al. (2011) hypothesized to be the

short anchor and a value near the GM—is acquired prior to the offset of "long" probes, then participants need only respond following "long" probe offset. By contrast, participants would still need to engage in memory and decision processes at "short" probe offset because bisection categorization would be incomplete due to a lack of critical information. The observed difference in offset-locked ERPs between "short" and "long" responses provides support for this logic.

This explanation is corroborated by the greater response latencies associated with the "short" responses relative to the "long" responses. On "short" probes, participants likely engaged in memory and decision processes prior to making a response. On "long" probes, by contrast, participants had presumably already engaged in these extra cognitive processes and made their decision about how they intended to respond at probe offset. Consequently, the only action left at "long" probe offset was to make a response. One would thus expect the "short" probe response latencies, which required cognitive processes in addition to a motor response, to be longer than the "long" probe response latencies, which only required a motor response. This is precisely what was observed.

Probe offset ERPs showed a different pattern in the older adult group. While the ERP amplitude corresponding to the "short" responses were comparable between age groups, the older adults did not show the same reduction in amplitude on "long" responses relative to "short" responses.

Instead, the older adults showed a "long" response ERP amplitude that was nearly identical to their "short" response ERP amplitude. One possible explanation for this age-related difference is that older adults employ different information than do young adults to make their bisection categorization. Perhaps, due to the deterioration of various cognitive processes (e.g., attention, memory, etc…), older adults cease to rely on the PSE during bisection categorization because its computation becomes increasingly difficult and/or unreliable. To compensate, older adults may adopt one of the decision-making strategies described previously that do not rely on the PSE, such as the similarity difference rule or the ratio comparison (Gibbon, 1981; Wearden, 1991). Regardless of whether older adults base their decision upon a subtraction of the probe duration from the short and long anchor (similarity difference rule) or a division of the short and long anchors by the probe duration (ratio comparison), the same cognitive operations could be expected to occur at probe offset for both "short" and "long" probes. Accordingly, one would expect the same neural activity at probe offset regardless of probe type, as observed.

The problem with this explanation arises when the response latency data is considered. Like young adults, older adults completed their bisection categorization significantly faster for "long" probes than "short" probes. If the same cognitive processes were occurring at probe offset regardless of probe type—as both the similarity difference rule and ratio comparison imply—the

same response latencies would be expected for both "short" and "long" probes. The fact that older adults, like young adults, responded faster on "long" probes indicates that a decision about bisection categorization had already been completed on these trials prior to probe offset. This also seems to contradict any explanation that does not include the PSE as among the critical information used during bisection categorization.

A more probable explanation, which reconciles the apparent contradiction between the electrophysiological and behavioral data, involves the Scaffolding Theory of Aging and Cognition (STAC) (Park & Reuter-Lorenz, 2009). With age, the brain has been shown to suffer various structural and functional changes, such as volumetric loss, reductions in white matter density, and the formation of neurofibrillary plaques and tangles (Head et al., 2004; Park & Reuter-Lorenz, 2009; Raz et al., 2005). According to the STAC, the brain is a highly adaptive organ that attempts to preserve cognitive function in the face of these changes by reorganizing existing neural connections and recruiting additional neural circuitry (Park & Reuter-Lorenz, 2009). This process has been referred to as "cognitive scaffolding" or "compensatory recruitment" (Cabeza et al., 1997; Park & Reuter-Lorenz, 2009). Several neuroimaging studies have provided support for the STAC, demonstrating that older adults show increased activation in various brain regions during task performance relative to young adults (Park & Reuter-Lorenz, 2009). For example, Nielson et al. (2006) found older adults to

display significantly more activation than young adults in 15 out of 20 observed brain regions on a semantic memory task. Similar patterns have been observed in episodic memory, working memory, perception, and inhibition tasks (Cabeza et al., 1997; Grady et al., 1994; Nielson, Langenecker, & Garavan, 2002; Reuter-Lorenz et al., 2000). Interestingly, higher levels of activation have been associated with superior task performance, suggesting that compensatory recruitment is a normal and healthy characteristic of the aging process (Cabeza et al., 2002; Sugarman et al., 2012).

When applied to the present experiment, the STAC suggests that the greater ERP amplitude produced by older adults relative to young adults on "long" responses was reflective of compensatory recruitment. More specifically, older adults recruited additional neural resources to execute the memory and decision processes necessary for bisection categorization on these trials. Yet despite this difference in neural activity, the behavioral data (i.e., response latency and accuracy) of older adults on "long" responses was similar to that of young adults. This is not surprising considering that behavioral performance between age groups is often analogous when compensatory recruitment is observed (e.g., Nielson et al., 2006). In fact, by definition, the observed recruitment could not truly be described as "compensatory" if task performance was not similar.

CNV

Within the context of SET, it has been suggested that the amplitude of the CNV is related to the number of pulses that amass in the accumulator, with more accumulated pulses leading to greater CNV amplitudes and vice versa (e.g., Macar et al., 1999). Accordingly, the age-related difference in CNV amplitude observed across the first 7 temporal windows likely reflects a difference in the number of accumulated pulses. More specifically, the reduced CNV amplitude in the older adult group indicates that fewer pulses were accumulated during this timeframe than in the young adult group.

One explanation for this observation is that aging leads to a systematic reduction in the rate at which the pacemaker mechanism emits pulses. As previously noted, however, the problem with this explanation is that a recent meta-analysis showed older adults to exhibit timing distortions in the exact opposite direction (Block et al., 1998). Accordingly, if age-related timing distortions do result from changes in pacemaker rate, the present findings would contradict a significant body of previous research about the nature of those changes.

A more probable explanation, which, as articulated above, can be seen to provide support rather than opposition to the majority of previous research, is that age-related changes in attention were responsible for the observed reduction in CNV amplitude. Lustig (2003) argued that attentional deficits in older adults lead to a "flickering" of the gate between the pacemaker and the accumulator, such that fewer pulses are accumulated than necessary. The

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reduced CNV amplitude in the older adult group, then, may have been a consequence of such "flickering," which would have reduced the number of pulses flowing into the accumulator. If this interpretation is correct, the present findings provide physiological evidence for age-related reductions in accumulated pulses due to attentional decline.

From the 8th temporal window onward (1825-2825 ms), neither the slope nor the amplitude of the CNV was significantly different between age groups. The fact that CNV characteristics became similar somewhere within the 8th temporal window (1825-2075 ms) is particularly noteworthy because the PSE for both age groups fell within this window. According to Ng et al. (2011) and based on the findings of the present study, probe durations that exceeded the PSE no longer required memory and decision processes for bisection categorization. This is because the critical information necessary for the categorization decision had already been obtained prior to the offset of probes judged to be "long." Ng et al. (2011) concluded that the resolve of the CNV following a value near the GM indicates that the GM is among the critical information drawn from memory to make the categorization decision. The present findings support the notion that a value near the GM is among the criterion used in probe categorization because age-related differences in the neural correlates of temporal accumulation ceased once this value was reached. Moreover, the content of the information used during categorization does not

seem to change with age, as evidenced by the near identical CNV between age groups from the 8th window onward.

It is unclear from the data, however, whether the target criterion is the GM or some other target duration, such as the PSE. This is because the GM (1936.49 ms) and the PSE for both age groups (Young: 2013.39; Old: 1979.32) fell within the 8th temporal window. Yet this may become a moot point when one considers that the location of the PSE has been shown to depend upon the spacing of the probes. Wearden and Ferrara (1995) demonstrated that when probe durations are spaced geometrically, the PSE tends to be near the GM; when spaced linearly, the PSE is near the AM; and when spaced reverse geometrically, the PSE is above the AM. In Ng et al. (2011)'s design, the probes were spaced geometrically, which may account for their finding that the CNV begins to resolve after a value near the GM. In the present experiment, the probes were spaced arithmetically, which may imply that the target criterion is greater than the GM and closer to the AM. In any case, it seems more useful to speak of the target criterion in terms of the PSE rather than the GM because the PSE shifts according to probe spacing and is therefore sensitive to the design of the experiment.

The fact that the CNV slope for both age groups remained negative from the 8th window onward is consistent with findings that suggest participants continue to acquire information until the end of even the longest probes (Brown et al., 2005). Continued attention throughout long probes may

serve to enable participants to "fine-tune" their target criterion if necessary (Brown et al., 2005; Ng et al., 2011).

Conclusion

The present experiment shed light onto the mechanisms underlying age-related changes in interval timing through the inclusion of electrophysiological measures into the duration bisection paradigm. Results indicated that the PSE, or some value near the PSE, is among the critical information drawn from memory during the categorization decision. This holds true regardless of age. Behaviorally, older adults were able to perform very similar to younger adults—something that is often observed on relative time judgment tasks (e.g., Lustig, 2003; McCormack et al., 1999; Wearden et al., 1997). To preserve timing abilities during the aging process, older adults may recruit additional neural resources through a process of cognitive scaffolding, as evidenced by the heightened amplitude of the probe offset ERP on "long" probes. The shallower CNV amplitude in older adults during temporal accumulation seems to indicate that fewer pulses were amassed in the accumulator than in young adults. The most probable culprit for this observation is an age-related decline in attentional performance, which may be a primary factor in producing age-related timing distortions. Future research should incorporate electrophysiological measures into timing paradigms that systematically manipulate the attentional demands placed on

the participant to better determine whether attention truly is at the root of

timing deficits in older adults.

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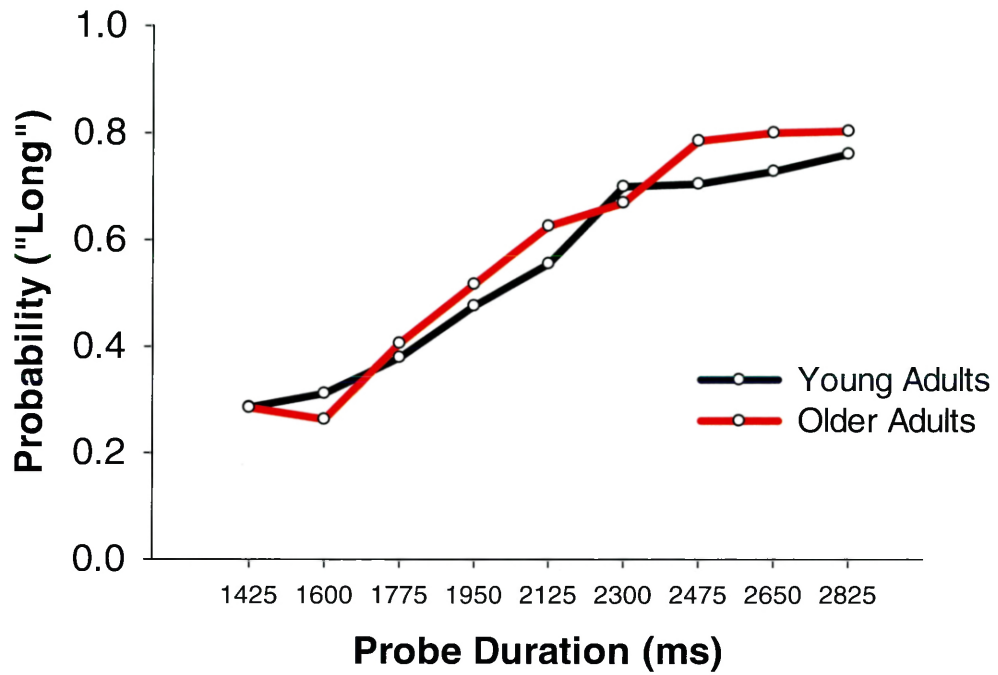
Psychophysical Response Functions

Figure 1. The probability of making a "long" response for each probe duration
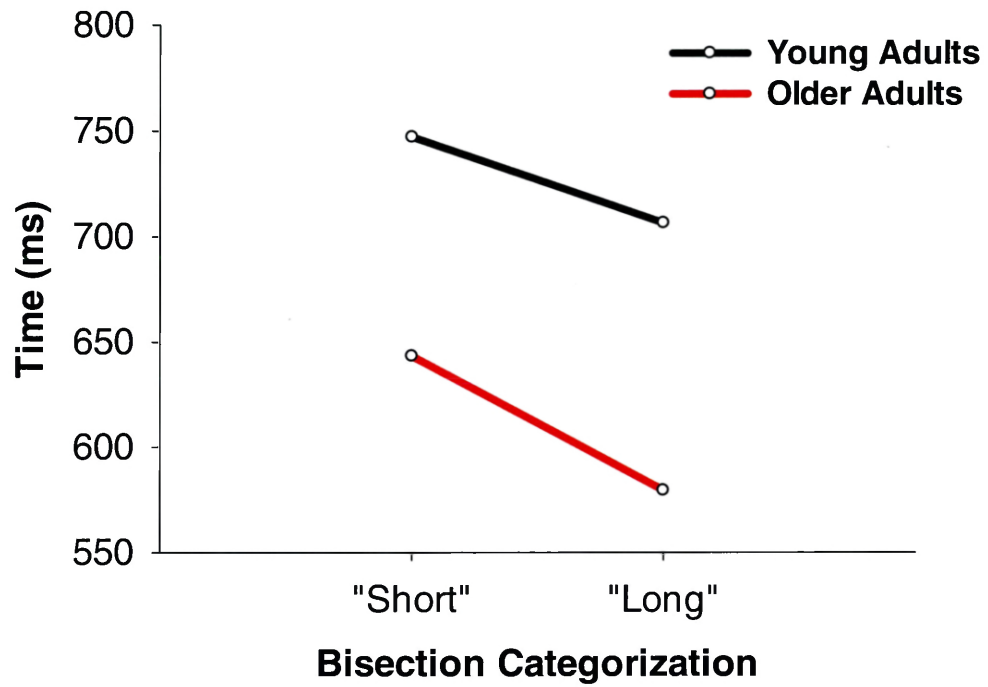
averaged across each of the age groups.

Figure 2. Response latencies for the "short" and "long" bisection categorizations averaged across each of the age groups.
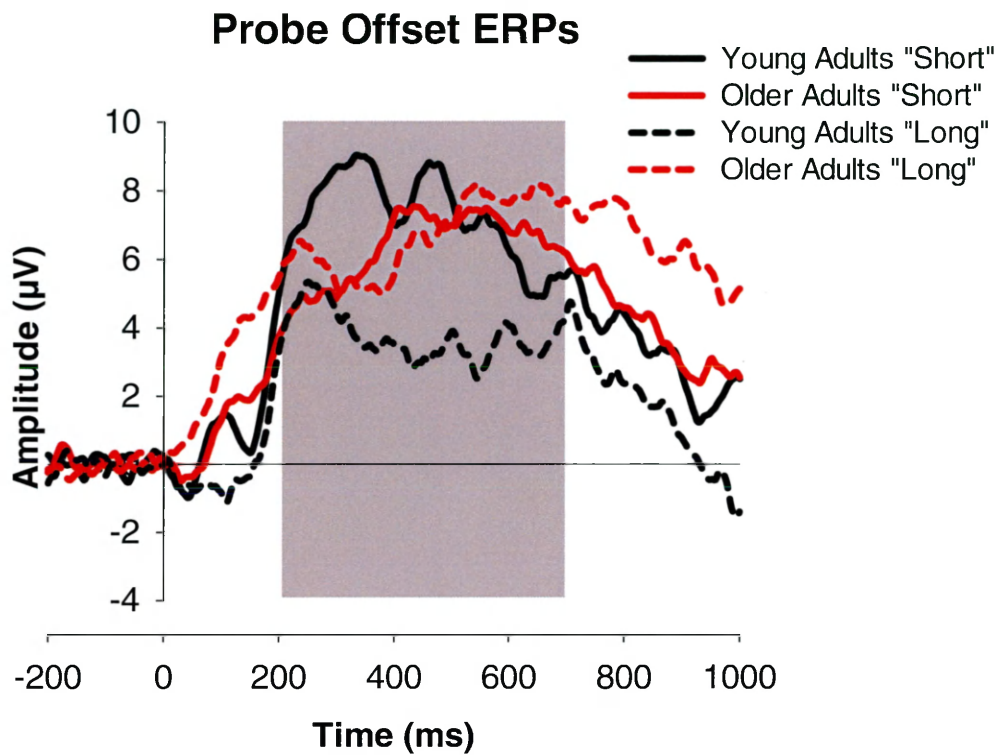
Probe Offset ERPs

Figure 3. The grand average ERP waveforms for the "short" and "long"

responses for each of the age groups. These waveforms were calculated by

time locking to probe offset (0 ms) and collapsing across the 6 midline centro-

parietal electrodes of interest (i.e., CPz, Cz, C1, C2, CP1, and CP2).
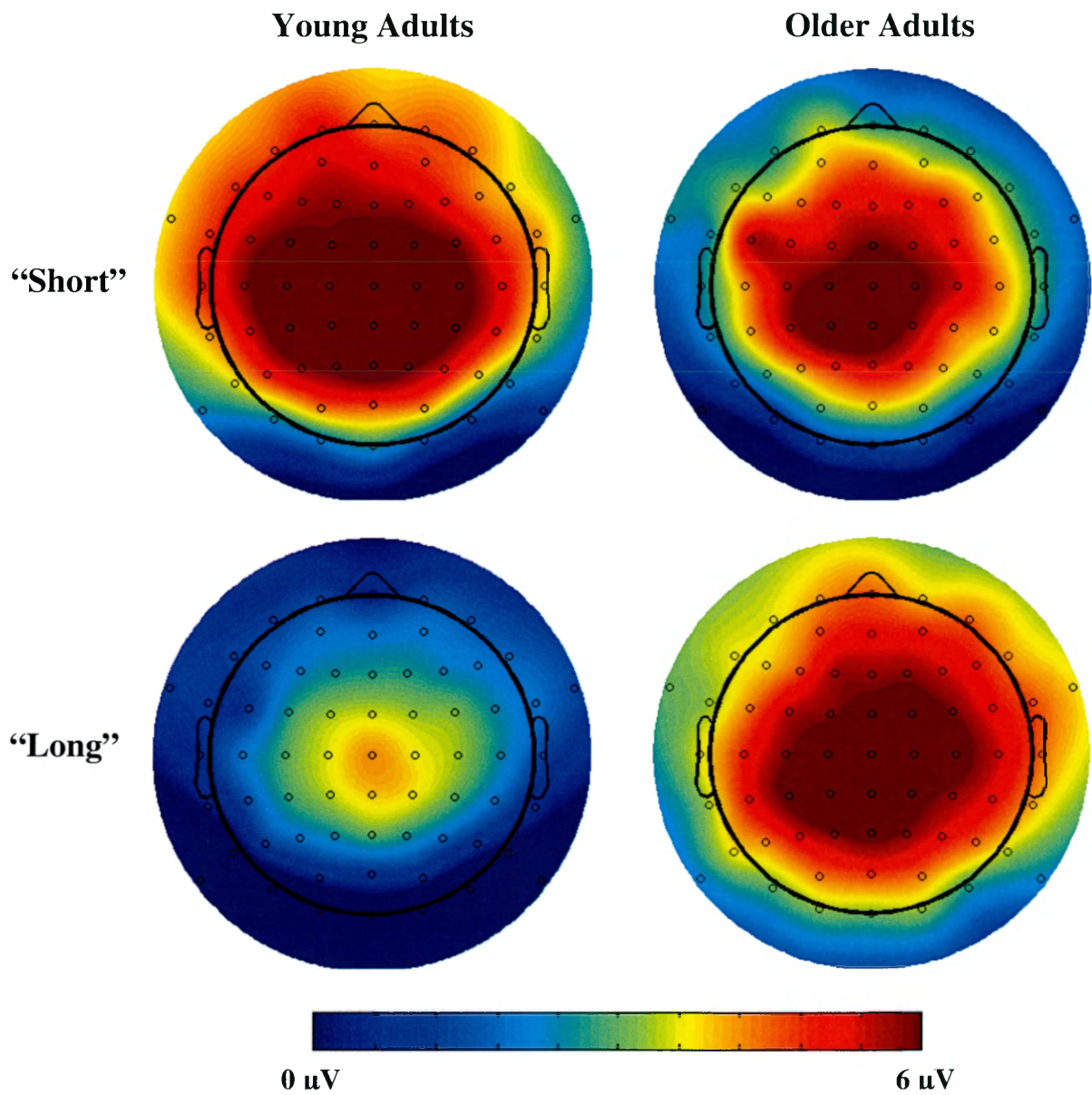
Scalp Plots

Young Adults   **Older Adults**

"Short"

"Long"

0 µV   6 µV

Figure 4. Scalp plots of brain activity averaged across the 200-700 ms time

window post probe offset for "short" and "long" responses.
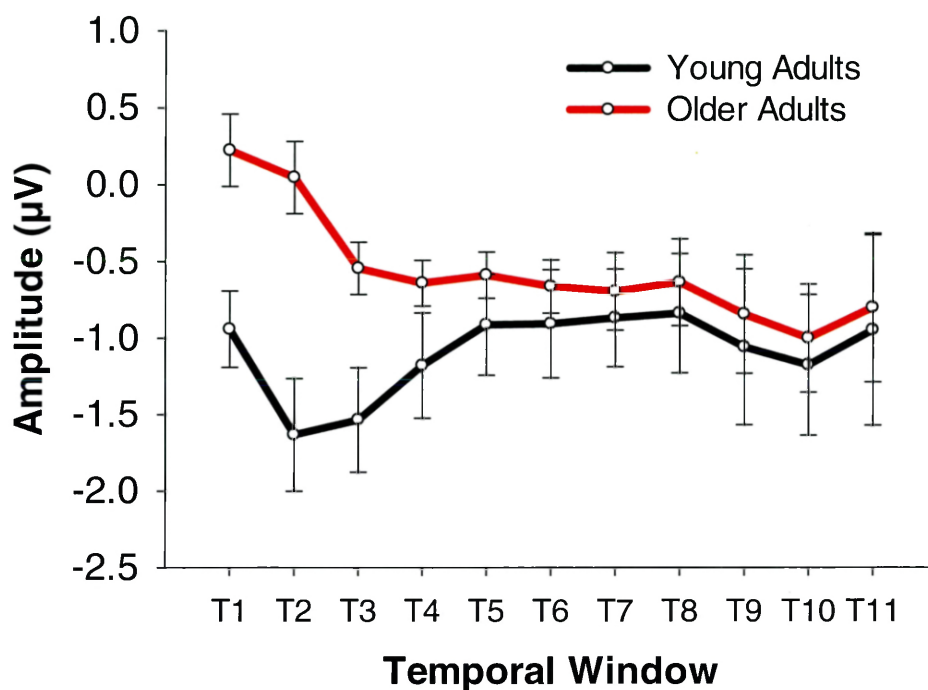
49

CNV Amplitudes

Figure 5. CNV amplitudes for each of the age groups, averaged across probes

to create eleven 250 ms temporal windows, beginning at 75 ms post probe

onset (i.e., 75-325, 325-575…2575-2825 ms).