

Transcranial Magnetic Stimulation Investigation of Time Dilation

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DEDICATION

This is dedicated to my loving parents for their unwavering support, my lab mates for helping me stay sane and my cat Sasha for being my constant companion.

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I would like to thank my family, my friends and the members of my lab that helped me throughout my degree as well as with my research. I would also especially like to thank my advisor, Dr. Martin Wiener for both supporting me with this thesis and my previous studies as well as pushing me to become a better researcher.

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LIST OF ABBREVIATIONS

Analysis of Variance	ANOVA
Behavioral Theory of Timing	BET
Functional Magnetic Resonance Imaging.....	fMRI
Bilateral Human Motion Complex.....	hMT
Inferior Parietal Cortex.....	IPC
Middle Temporal/Visual Area Five.....	MT/V5
Point of Subjective Equality.....	PSE
Random Dot Motion.....	RDM
Ratio of Estimation.....	RO
Repetitive Transcranial Magnetic Stimulation (theta burst)	rTMS
Standard Stimulus/Comparison Stimulus.....	S1/S2
Scalar Expectancy Theory.....	SET
Supplementary Motor Area.....	SMA
Transcranial Electrical Stimulation.....	tES
Transcranial Magnetic Stimulation.....	TMS
Transcranial Random Noise Stimulation.....	tRNS
Visual Cortex.....	V1

ABSTRACT

TRANSCRANIAL MAGNETIC STIMULATION INVESTIGATION OF TIME DILATION

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Time perception has long been a focus among cognitive neuroscientists. An abundance on research on time perception and the underlying theories has demonstrated that subjective judgments of time can be significantly distorted based on various physical properties of a stimulus. One of the areas of time perception research that has garnered attention is the perception time dilation, in which the perception of time can expand, or contract based on the motion and velocity of a stimulus. However, the understanding of the underlying neuronal mechanisms of time dilation remain controversial. To that end, this study utilized a discrimination task using random dot motion stimuli along with transcranial magnetic stimulation to induce the effect of time dilation as well as inhibit the regions of the brain associated with time perception and motion based on previous literature. The results found that TMS to MT/V5 reduces accuracy for speed while TMS to the SMG slightly reduces accuracy for time. Additionally, we found that while motion impacts the perception of time, time does not impact motion.

LITERATURE REVIEW

Introduction

Time perception has long been a major focus among researchers, and while an abundance of models for timing have been proposed, only a few concrete theories of subjective time have survived over the decades. These theories include Scaler Expectancy Theory (SET) which proposes an internal pacemaker and accumulator (Gibbon, Church, & Meck, 1984; Treisman, 1963), and change based theories such as Behavioral Theory of Timing (BET) which suggests that time perception is calculated based on the number of changes in space (Brown, 1995; Poynter, 1989; Bizo & White, 1994; Fetterman & Killeen, 1992).

Further, the counter model theory proposes that attentional shifts underlie temporal distortion, and that instead of an internal clock, the brain simply records the approximate rate of its own information processing (Eagleman, 2005; Tse' et al 2004). Despite the abundance of previous research on time perception and time dilation, in which the subjective judgments of duration can be significantly distorted (i.e. increased) based on the various physical properties of a stimulus, an understanding of the underlying neuronal mechanisms of time dilation have yet to be elucidated. It has been well established that physical properties such as size, saliency, luminosity, complexity,

coherence, depth, motion and speed have been found to alter time perception (Gavazzi, Bisio & Pozzo, 2013; Gorea & Kim, 2015; Kanai et al., 2006; Karşılar & Balci, 2016; Mathews, 2011; ; Morrone, Ross, & Burr, 2005; Schubotz, 2011; Tomassini et al., 2011; Xaun et al., 2007; Yamamoto & Miura, 2012). However, studies that have investigated the property that is critical for inducing time dilation and in turn, the underlying neuronal processes, are still highly debated, with much research offering conflicting findings; specifically, regarding the induction of time dilation by motion, speed and temporal and spatial frequency.

Behavioral Findings

Various methods have been employed to measure time perception, with the three most commonly used methods being temporal discrimination/comparison, temporal bisection and temporal reproduction. In discrimination tasks, subjects are presented with stimuli consecutively with varied physical properties and are required to discriminate between the stimuli and indicate, for example, if one stimulus was presented with a longer or shorter duration than another stimulus. Similarly, in a temporal bisection task, subjects' judgments when comparing two stimulus durations indicates a subject's perception of the midpoint between two stimulus durations. Another method for evaluating subjective time perception is through temporal reproduction tasks in which subjects are presented with a stimulus for different temporal intervals and are then asked to reproduce the temporal interval, usually via a key press. These popular methods have allowed researchers to successfully measure subjective time perception and the relationships between time perception and motion, velocity, temporal frequency, and

distance as well as a number of additional physical properties. To that end, a number of studies have sought to investigate these relationships, such as a study conducted by Au, Ono, and Watanabe (2012) that probed whether time dilation depends on the actual physical motion of an object, or its relative motion with respect to the retina. The researchers conducted two experiments in which subjects were presented with a moving stimulus and static reference stimulus for different temporal intervals. Subjects were asked to judge which stimulus had a longer duration. In experiment one, the subject's eyes were fixated while viewing the stimuli. In experiment two, the subject's eyes moved in conjunction with the stimulus at the same velocity, determined using an eye tracker. Results showed that stimulus duration was perceived as longer when the object was physically moving as opposed to relative retinal motion. This provides evidence that the time dilation effect by object motion is not induced by retinotopic coordinates, but instead by spatiotopic coordinates.

In turn, there may be a spatiotopic neuronal mechanism that links space and time in the brain and that exists in areas beyond the primary visual cortex (V1), representing higher-level processing (Morrone, Cicchini, & Burr, 2010). Another area of interest within time dilation is the difference in time perception between implicit motion and non-implicit motion in static images. To address this, Yamamoto and Miura (2012) investigated whether implicit motion information from static images would influence the perceived duration of image presentation through four separate experiments. In experiment one, subjects were presented with two static images. The first image was of a person with their body positioned in a running stance (implied motion) and a second

image of a person standing (little implied motion). The researchers also presented this condition using an image of an animal instead of a human. In the third experiment, the researchers replicated the physical position of the person in the images using blocks. In one condition, the subjects were told the blocks were supposed to represent an onion (no implied motion).

The study found that implied motion (running posture) for the human, animal, and block images were perceived as being of longer duration. However, this effect was diminished for the block condition when participants were told the blocks were an onion. These results, in agreement with the previous study, indicate higher order motion processing beyond the visual cortex as the primary source of time dilation effects for visual stimuli.

Another area of debate within the time perception literature is in the effect of motion coherence on time dilation. A number of studies have looked at motion coherence versus incoherence (Karşılar & Balci, 2016). For example, Yamamoto and Miura (2016) looked at the effect of motion coherence on perceived duration as it is related to perceived speed. The researchers used a temporal bisection task as well as a modified version of the diamond display.

In their first experiment, results showed that moving stimuli were perceived as having a longer duration for circular coherent motion than incoherent linear motion. In experiment two, the researchers found duration was perceived as shorter for coherent than for incoherent stimuli when both stimuli moved linearly. The researchers also looked at speed and found that perceived differences in velocity were consistent with the

results of experiments one and two in that perceived speed was faster for experiment one and slower in experiment two when the actual speed remained constant across both experiments.

As in the study conducted by Yamamoto and Miura (2016), these results suggest that coherence of local motion signals influences time perception, and this effect may reflect the changes in perceived speed rather than motion coherence which would indicate later stage global motion processes in areas such as the middle temporal visual area (MT/V5) (Kanai et al., 2006). While motion coherence did affect perceived duration, this effect was largely mediated by perceived speed.

The impact of speed on time dilation is perhaps the physical property that has been studied most extensively. Multiple studies have solidified the overarching impact of speed on time dilation, such as work conducted by Gorea and Kim (2015) in which they found that time dilates more with induced speed, i.e. the perception of an object's motion in relation to background movement (Zivotofsky, 2004) than with the absolute physical speed of an object using a random-dot-motion stimulus.

Additionally, Mathews (2011) further demonstrated that changes in stimulus speed influence subjective duration using temporal judgment and reproduction tasks. Mathews used moving and rotating shapes in three different conditions: constant speed, decelerating motion, and accelerating motion, and found that subjects perceived the stimuli moving at a constant speed to have a longer duration than decelerating speed but a shorter duration than accelerating speed. In addition, decelerating speed was perceived to

have a longer duration than accelerating speed. However, this effect disappeared during the reproduction task.

Tomassini and colleagues (2011) investigated the impact of speed on perceived duration of visual and tactile stimuli. In this study, participants reproduced the duration of visual and tactile gratings separately as well as combined visuo-tactile gratings moving at a variable speed for three different durations. The results were that the apparent durations of the stimuli increased with increasing speed. This effect was more pronounced for tactile than for visual stimuli, although visual stimuli were perceived to last 200 ms longer than tactile stimuli. However, in a cross-modal speed-matching task, visual stimuli were perceived as faster than tactile stimuli. Despite these conflicting results, for both vision and tactile stimuli, the perceived duration depended on speed.

While speed and motion have been clearly implicated in time dilation, temporal frequency and its accompanying theories are more highly debated. Temporal frequency can be described as the number of occurrences of a repeating event per unit of time and is closely associated with the change model of time perception. The change model defines time perception as the number of changes during an event where increased velocity leads to more changes in space, which in turn lengthens duration perception. (Brown, 1995; Kanai et al., 2006; Poynter, 1989). Through a series of studies, Kanai and colleagues (2006) sought to determine the critical property for the induction of time dilation by conducting separate experiments that evaluated speed, distance traveled and temporal and spatial frequency. The five experiments were conducted as follows: experiment one had subjects reproduce stimulus durations using a moving or stationary black square

presented for varied durations. In experiment two, subjects viewed a random dot motion (RDM) stimulus that was presented at varied durations and speeds.

Experiment three's stimuli consisted of a concentric sinusoidal grating that was expanding for speed and temporal frequency. Experiment four followed the same protocol as experiment three, but instead manipulated spatial and temporal frequency independently. Finally experiment five used a Gaussian luminance blob modulated with temporal frequency. The researchers performed a set of three-way repeated measures ANOVA and found that motion coherence did not affect perceived duration and did not interact with stimulus duration or stimulus speed. However, the speed of individual dots had a significant effect where perceived stimulus duration increased with the increasing speed of individual dots. Here, the researchers suggested that coherent motion is not necessary for induced time dilation.

The researchers then conducted another set of ANOVAs to evaluate stimulus duration, speed and temporal frequency and found that speed was not a critical factor in inducing time dilation and that time dilation was induced by increasing temporal frequency of the stimulus. Lastly, this study found that time dilation is limited when the stimuli was moving at a lower velocity and had lower temporal frequency. In contrast, stimuli with a high temporal frequency and increased velocity resulted in increased time dilation. The results of this study agreed with previous work showing that increased velocity leads to increased perception of duration.

Additionally, based on these results, Kanai and colleagues (2006) suggest that temporal frequency is the primary determinant for the magnitude of the perception of

time dilation, and other physical properties such as speed, coherence, and spatial frequency are of little importance for inducing time dilation. To that end, the researchers concluded that because temporal frequency as opposed to speed is responsible, time dilation is a function of early stage processing.

In agreement with these findings, prior research conducted by Brown (1995) also showed that stimulus movement alters temporal perception by lengthening duration perception through a series of reproduction and production experiments. In experiment one, Brown (1995) asked participants to reproduce a temporal interval of moving and stationary stimuli and found that moving stimuli were perceived as lasting longer than stationary stimuli. In another task, participants reproduced temporal intervals of a moving stimulus with increasing velocity. In contrast to previous findings, the author found that increasing speed did not significantly lengthen temporal judgments.

However, an additional task found that when participants were asked to produce a temporal interval (in seconds) by pressing a key while a moving stimulus appeared on the computer screen, increasing velocity of the stimulus did increase temporal judgments. Brown (1995) concluded that these results are in line with the change-based theory of time perception and the role of temporal frequency in time dilation where perception of temporal intervals can be increased based on the number of changes in space, or in this case, a stimulus.

While these studies provide ample evidence of temporal frequency's role in time dilation, these studies only took into account temporal intervals in the suprasecond range as opposed to the subsecond range. To address this issue, Kaneko and Murakami (2009)

conducted a study that measured the perceived durations of moving and static stimuli in the subsecond range using two different methods. The first experiment used the matching method while the second used the reproduction method. For the first experiment, Kaneko and Murakami (2009), using a Ratio of Estimation (RO) regression analysis as an index of time dilation, showed that while temporal and spatial frequency did increase the RO, speed was the major determinant of RO in that as speed increased, the RO increased proportionately with log speed. In experiment two, a similar effect of speed was observed where the magnitude of time dilation relied most heavily on speed. The results of this study, in contrast with the previous studies, suggests that time dilation critically depends on speed, rather than temporal frequency, indicating that the space-time mechanism responsible for time dilation takes place at a higher stage of processing in the brain where properties of speed are represented.

Among all of the previously discussed studies, two main ideas of time dilation have emerged. The first is that the primary physical property critical for inducing the illusion of time dilation is temporal frequency, suggesting that the neuronal regions responsible for producing time dilation for visual stimuli exist in lower levels of the visual hierarchy and do not extend far beyond the primary visual cortex. The second proposes that time dilation does not depend on temporal frequency, but instead depends primarily on speed, which implicates higher-level, extrastriate regions of processing in the brain. However, due to the behavioral nature of these studies, these assumptions are somewhat speculative.

fMRI Findings

To disentangle the processing stage of visual time dilation, a number of functional magnetic resonance imaging (fMRI) studies have sought to identify the specific brain regions responsible for distortions in subjective duration. A study conducted by van Wassenhove and colleagues (2011) utilized a temporal discrimination task in which subjects viewed a stream of five visual events. All of the events were static with the exception of the fourth event in which the stimulus was presented as looming or receding. Subjects were required to make a judgment as to whether the looming or receding target stimulus was presented for a longer or shorter duration than the standard stimuli. The behavioral findings showed time dilation for looming stimuli relative to receding stimuli.

The fMRI results revealed that the looming stimulus engaged brain regions involved in self-referential coordinates such as mid- and posterior cingulate regions of the left hemisphere including the left-medial cingulate, precuneus regions, and small left superior frontal and middle frontal activation. These posterior midline cortices have been shown to be associated with the default network which is thought to be activated during the resting state or during self-relevant thoughts (Lombardo, 2010; Raichle, 2001).

The researchers also revealed that similar brain regions were activated for both looming and receding stimuli, including the insular cortex, anterior cingulate cortex, basal ganglia, and the right and left dorsolateral prefrontal cortices. Differential activation was also found for looming and receding targets, including the mid and posterior cingulate regions in the left hemisphere for looming targets. In contrast, stronger activation was seen in the left anterior insula, left dorsal thalamus and anterior cerebellum

for receding stimuli than looming stimuli. van Wassenhove and colleagues (2011) suggests that these results are in favor of the internal clock theory of time perception due to the looming target's inducing time dilation where the looming target increases the rate of the pacemaker.

Additional work conducted by Assmus and colleagues (2003) investigated whether the left inferior parietal cortex integrates temporal and spatial information in the absence of a required complex task using fMRI. Subjects completed a collision judgment task in which they were presented with the black outline of a square and two moving dots of the same or different size, moving at the same or different constant speeds. The participants made a judgment as to whether or not the dots would collide behind the square or whether or not the dots were the same size. The researchers reached a number of conclusions: first, when evaluating collision and size relative to baseline (blank screen), the occipital temporal junction, bilateral human motion complex (hMT), right parietal cortex and the left premotor cortex were activated. When the researchers evaluated collision judgments versus size judgments, they found left inferior parietal activation. In conclusion, Assmus and colleagues (2003) found direct evidence that the left supramarginal gyrus integrates temporal and spatial information.

Additional fMRI studies have further implicated the roles of the basal ganglia, SMA, human motion complex (hMT) (Takemura et al., 2012) and the right frontal cortex in duration estimation (Wiener, et al. 2010). Ferrandez and colleagues (2003) utilized two visual discrimination tasks in which the relevant discrimination dimension was either stimulus duration or intensity. Subjects were asked to indicate whether the current

stimulus was equal to or different in duration or intensity from the previously shown stimulus. The results showed that for intensity-minus-duration, activation was seen in the right occipital gyrus, fusiform gyri, hippocampus, precuneus and the intraparietal sulcus. Alternatively, for duration-minus-intensity, activation was seen in the basal ganglia, SMA, ventrolateral prefrontal cortex and the temporal cortex. Based on these findings, the researchers concluded that the SMA and basal ganglia are especially relevant for the possible internal clock mechanism while the frontoparietal areas may be associated with time dilation based on attentional orienting.

In support of the previous fMRI studies, an additional study conducted by Pouthas et al., (2005) administered a duration discrimination task with long and short intervals, and also found that the preSMA, anterior cingulate, prefrontal and parietal cortices, as well as the basal ganglia, were similarly activated regardless of the estimated duration. However, the findings also showed that the preSMA, anterior cingulate, the right inferior frontal gyrus, bilateral premotor cortices and right caudate nucleus showed increased activation with increasing duration estimation.

In line with previous research, this supports the idea that the caudate-preSMA circuit, anterior cingulate and premotor inferior frontal regions comprise the internal clock mechanism responsible for temporal duration estimation and induction of time dilation. Pouthas and colleagues (2003) also report that, based on their results, the preSMA may receive output signals from the internal clock mechanism located in the striatal structures through striatal efferent pathways.

Brain Stimulation Findings

Finally, a small subset of Transcranial Magnetic Stimulation (TMS) and Transcranial Electrical Stimulation (tES) studies have attempted to disentangle the brain regions involved in aspects of duration estimation by temporarily disrupting regions frequently cited as involved with time perception, motion and visual processing. Dormal and colleagues (2016) used transcranial random noise stimulation (tRNS) to stimulate the right parietal cortex and the SMA while subjects completed a series of behavioral tasks that measured numerosity and duration as well as sequential or simultaneous presentation of a stimulus. They found that performance was enhanced for the duration estimation task but not for the numerosity task for right parietal stimulation but not SMA, showing that duration estimation for subsecond time depends on the right parietal lobe.

Bueti, Bahrami & Walsh (2008) presented similar findings through a series of experiments that utilized temporal discrimination tasks for moving stimuli, static stimuli and auditory stimuli while subjects underwent rTMS over the right or left parietal cortex and left MT/V5. In experiment one, subjects completed a discrimination RDM task with 100% motion coherence. The second experiment utilized the same task paradigm, but the stimulus was static. In experiment three, participants discriminated between two dot arrays that varied in the number of dots as well as the duration displayed.

Participants were asked to indicate using a key press whether a previously-presented dot array (target stimulus) was shown in the first or second dot array. Experiment four followed the same task as in experiment three but with the presented durations played through an auditory tone. Finally experiment five further used this task

but varied the durations more widely. The researchers found that for experiments one and two, TMS to the right IPC and area MT/V5 significantly impaired temporal discrimination of moving and static stimuli, suggesting that both areas are independently important.

Additionally, experiment three showed no impairment in task performance. Experiments four and five, which utilized an auditory tone for duration, only showed task impairment when subjects underwent TMS to the right IPC. Given these findings, Buetti, Bahrami & Walsh (2008) concluded that the MT/V5 is relevant for spatial and temporal processing, specific to the visual modality. In addition, they also concluded that the right posterior parietal cortex is important for time perception and estimation, rather than the left posterior parietal cortex.

Lastly, Salvioni et al., (2013) used paired-pulse TMS across a series of five discrimination experiments and indeed found that both V1 and area MT/V5 are involved in encoding time in memory and that this encoding is independent from low-level processing. Experiments 1 and 2 used a classic discrimination paradigm that consisted of light blue disks as stimuli. Participants were presented with two temporal intervals, one as the standard duration and the second was a comparison duration. Participants indicated which interval lasted longer using a key press. In experiment three, the interval length was held constant and instead, the brightness of the stimuli was manipulated, and participants decided which pair of disks was brighter. In the final experiment, participants were shown two sequential flashing stimuli and had to decide whether the stimuli flashed once or twice.

Additionally, the researchers found that brightness discrimination was not affected by TMS to either stimulation site. Even more interesting, their results suggest that temporal discrimination performance increased after TMS to area V1 but not MT/V5. In summary, Salvioni et al., (2013) findings conclude that when estimating duration, areas V1 and MT/V5 function simultaneously, but function independently while encoding temporal information into memory.

The totality of these studies has provided some insight into the neuronal mechanisms behind time dilation, especially as it relates to the parietal regions and area MT/V5. However, more research is needed to fully addresses the underlying nature of the perception of time dilation. Therefore, this study will examine time dilation using transcranial magnetic stimulation (TMS). Specifically, the primary purpose of this study is to investigate whether inhibiting the areas of the brain involved in time perception and motion affects time dilation or if a separate space-time mechanism in the brain is responsible, distinct from those regions associated with time and motion. Repetitive TMS was administered to two sites involved in timing and motion, area MT/V5 as well as the inferior parietal cortex.

METHOD

Participants

The current study was constrained by six subjects who were recruited from the graduate and undergraduate student population of George Mason University. The subjects were compensated with \$15 per hour for each experimental session. Subjects were between 18 and 35 years old and included four females and two males. Subjects were also right-handed and had no reported history of psychiatric or neurological illness. Additional exclusionary criteria included: any previous history of head injury, seizures, migraine, neurological or psychological disorders, and alcohol or drug abuse. Subjects also could not be pregnant, nursing, or possibly pregnant. Informed consent was obtained from all subjects before the experiment.

Materials

This study used a classic comparison/discrimination task such as the one used in Schlichting, Jong, and van Rijn (2017). In this task, participants were instructed to compare two sets of random-dot-motion (RDM) stimuli and make a judgment as to whether the comparison stimulus was presented for a longer or shorter duration than the standard stimulus, or whether the comparison stimulus was moving at a faster or slower speed than the standard stimulus. RDM stimuli were comprised of 100 white dots, sized at 20 pixels, presented in a central field size of 15cm diameter. The dots were displayed

on a grey background and appeared at random locations within the field. Each dot lasted until they passed the field border at which point a new dot appeared at another random location.

The study was divided into two sessions. Prior to starting the first session, participants underwent repetitive transcranial magnetic stimulation (rTMS) to one of the two stimulation sites including area MT/V5 or the inferior parietal cortex. Participants viewed the stimuli on a Dell Gaming LED Monitor, running at 100Hz refresh rate and indicated their judgments regarding the stimuli using a CHERRY MX Red STRAFE Mechanical Gaming Keyboard.

Green and white stickers were placed over keys 'F' and 'J'. Subjects indicated their response to the stimuli by pressing the 'green' key for shorter duration or slower speed and the 'white' key for longer duration or faster speed. The colored stickers were placed over the response keys in order to avoid the subject associating the 'F' key with the response "faster".

Procedure

Participants completed one iteration of the discrimination task per session. The two sessions took place on separate days. Participants were seated in front of the Dell Gaming LED Monitor, and completed an eligibility questionnaire and consent form. After completion of these forms and prior to starting the task, subjects completed a set of practice trials consisting of one sub block of each time and speed to ensure the subject fully understood the task instructions. Participants then underwent rTMS to one of our two stimulation sites.

Immediately following the stimulation, the first trial of the task began with the presentation of the standard stimulus (S1) followed by a brief blank interval. The participant was then presented with one of eight comparison stimuli before pressing a key to indicate whether the comparison stimulus (S2) was presented for a longer or shorter duration than the standard stimulus (S1) or whether the RDM stimuli was moving at a faster or slower rate than S1. A white fixation cross was solely present on the screen immediately following S2. The word “Respond” then appeared on the screen with a response window lasting four seconds. The S1 for time trials remained constant at 500ms and comparison stimuli for time trials had four shorter durations (0.33s, 0.37s, 0.41s, 44s) and four longer durations (0.56s, 0.59s, 0.63s, 0.67s) with each comparison duration presented eight times for a total of 64 temporal discrimination trials per task.

For motion trials, S1 remained constant at 20 cm/s and also had four faster speeds (0.24cm/s, 0.28cm/s, 0.32cm/s, 0.36cm/s) and four slower speeds (0.04cm/s, 0.08cm/s, 0.12cm/s, 0.16cm/s) Each of the 8 velocities were also presented 8 times, with a total of 64 trials per block. Time and speed were alternated in sub blocks of eight trials each and the first sub block (time or speed) was counterbalanced between subjects. All RDM stimuli had 100% motion coherence, moving from left to right. Participants were cued at the start of each sub block as to whether they were to be comparing velocity or duration. The RDM experimental task was programmed and presented using PsychoPy (Peirce, 2007).

Following the first session, participants were scheduled for the second session. The second session was identical to the first with the exception of the stimulation site.

Participants underwent rTMS to the second stimulation site which depended on the first session per each participant.

Transcranial Magnetic Stimulation

TheBrainsight Stereotaxic system (Rogue Research) was used to set up each participant for TMS. The TMS administered for this study was theta burst stimulation/repetitive TMS (rTMS) as demonstrated by Huang, and colleagues (2005). Each participant was scanned or required to provide MRI T1 structural images. A Polaris infrared tracking system was used to measure the position of the participant's head and Brainsight to register and align the subject's brain to their MRI T1 structural image scan. The two stimulation sites included the right inferior parietal cortex (rIPC) and area MT/V5. The rIPC Talairach coordinates (55, -30, 40) were taken from Wiener et al. (2012) and the MT/V5 MNI coordinates (-52, -71, 0) were used from the study conducted Bosco et al. (2008). Additionally, the MT/V5 region was only stimulated in the left hemisphere as previous research has shown that left hemisphere stimulation is more instrumental in inhibiting motion perception and more likely to reduce phosphenes than right hemisphere stimulation (Stewart, Battelli & Cowey, 1999).

RESULTS AND DATA ANALYSIS

To analyze the data, we first examined behavioral performance by calculating the proportion of trials in which subjects judged S2 as “longer” for both the attended and non-attended dimensions, within and across subjects to establish whether or not we induced the effect of time dilation. Here we found that subjects were more likely to perceive the durations as lasting longer when the speeds were faster while subjects were attending to the time trials (Fig 1A). This time dilation effect was observed regardless of the TMS stimulation condition. Also, no corollary effect was seen for speed, i.e. longer durations did not shift the perception of speed when subjects were attending to the speed trials. We conclude from this behavioral analysis that while longer durations do not affect perception of speed, speed does impact time perception (Fig 1B).

Additionally, we conducted a repeated measures ANOVA for performance accuracy to investigate the effects of task (speed or time) as well as the interaction between stimulation site and task. A significant main effect for task, $F(1, 5) = 90.497, p < .001, \eta^2 = 0.948$, was seen, specifically showing that subjects were overall more accurate when judging speed than time. Additionally, there was no significant main effect for stimulation site, $F(1, 5) = 1.00, p = 0.36, \eta^2 = 0.167$ and there was no significant interaction between task and stimulation site, $F(1, 5) = 1.189, p = 0.325, \eta^2 = 0.192$.

Additional analysis did reveal that while the TMS effect was not significant to either stimulation site, the effect was in the hypothesized direction for each site. TMS to area MT/V5 was also marginally significant as revealed by a paired-samples t-test comparing SMG stimulation and MT/V5 stimulation while subjects attended to time, ($M = 0.77, SD = 0.03$) - ($M = 0.80, SD = 0.07$), $t(5) = -0.255, p = 0.809$, Cohen's $d = -0.10$), and SMG and MT/V5 stimulation while subjects attended to speed, ($M = 0.96, SD = 0.02$) - ($M = 0.93, SD = 0.03$), $t(5) = 2.423, p = 0.060$, Cohen's $d = 1.10$. (Fig. 1C)

However, further analysis conducted by looking at the proportion of subjects responding, “faster” (for speed trials) or “longer” (for time trials) through a 2 (stimulation site) x 2 (task) x 8 (interval, time/speed) repeated measures ANOVA found a significant interaction between task and time/speed interval, $F(7, 35) = 20.972, p < .001, \eta^2 = 0.807$ and as well as a significant interaction between stimulation site, task and interval, $F(7, 35) = 2.287, p = 0.05, \eta^2 = 0.314$. The main effect of task was significant, $F(1, 5) = 12.158, p < .05, \eta^2 = 0.709$ as was the effect of interval, $F(7, 35) = 178.681, p < .001, \eta^2 = 0.9$. The main effect of stimulation site was not significant, $F(1, 5) = 0.455, p = 0.530, \eta^2 = 0.083$, nor was the interaction between stimulation site and task, $F(1, 5) = 0.486, p = 0.517, \eta^2 = 0.089$. The interaction between stimulation site and interval was also not significant, $F(7, 35) = 1.895, p = 0.100, \eta^2 = 0.275$.

We also conducted another 2 (stimulation site) x 2 (task) x 8 (interval, time/speed) repeated measures ANOVA to look at the proportion of subjects responding “longer” for time for the *unattended* dimension. Here again we did not find a significant main effect for stimulation site, $F(1, 5) = 0.455, p = 0.530, \eta^2 = 0.083$. The interaction between site

and task was not significant, $F(1, 5) = 0.486$, $p < 0.517$, $\eta^2 = 0.089$ and the interaction between site and interval was also not significant, $F(7, 35) = 1.221$, $p = 0.318$ $\eta^2 = 0.196$. There was a significant main effect of task $F(1, 5) = 12.158$, $p < 0.05$ $\eta^2 = 0.709$ as well as a significant main effect of interval $F(7, 35) = 10.844$, $p < .001$, $\eta^2 = 0.684$. In addition, a significant interaction was seen for task and interval $F(7, 35) = 11.857$, $p < .001$, $\eta^2 = 0.703$ as well as a significant interaction between task, interval and stimulation site, $F(7, 35) = 2.333$, $p < .05$, $\eta^2 = 0.318$, indicating that, following SMG stimulation, subjects became less influenced by motion on time.

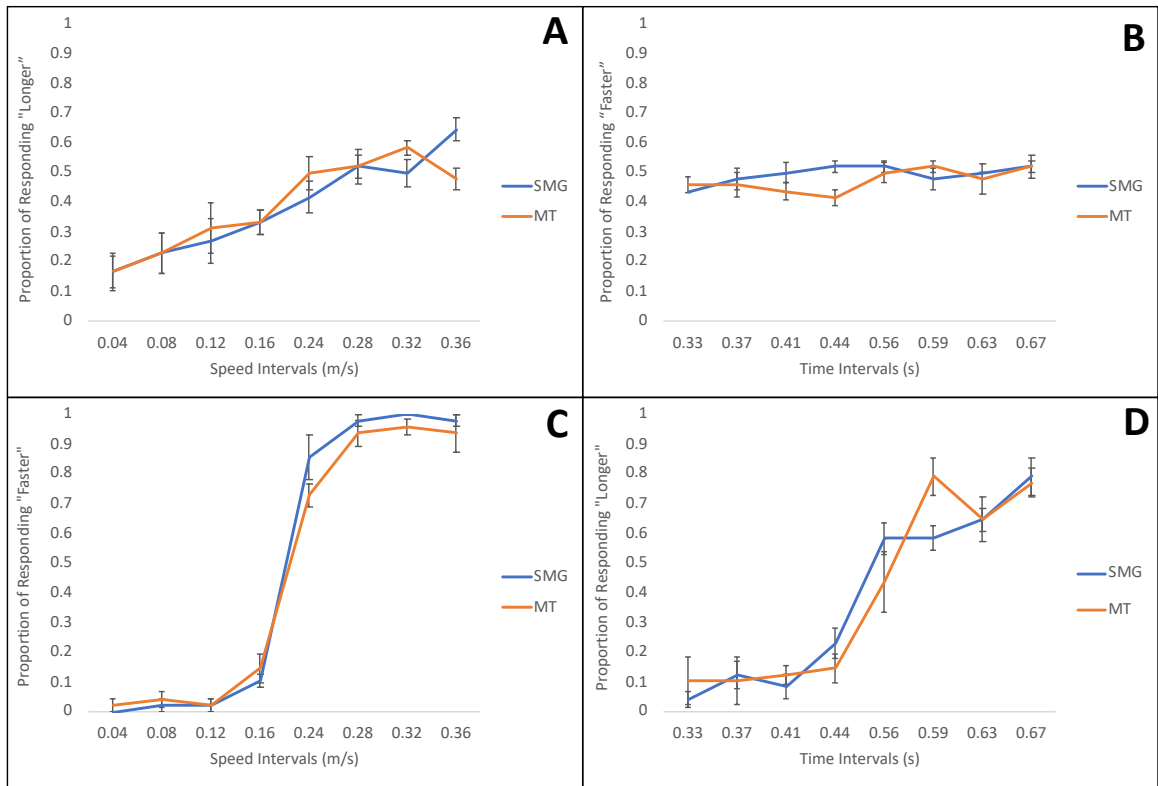


Figure 1. Showing the mean values across subjects. For all figures, error bars denote standard error. (A) shows the time dilation affect in which subjects perceived the temporal durations as lasting longer when the speed of the stimuli was moving faster. (B) No effect on time perception was seen when with manipulation of speeds. C. TMS to MT/V5 resulted in decreased performance in which subjects perceived the speed as moving slower while attending to the speed trials. (D) TMS to the SMG decreased performance. Subjects perceived temporal intervals to have longer durations when attending to the time trials following SMG stimulation.

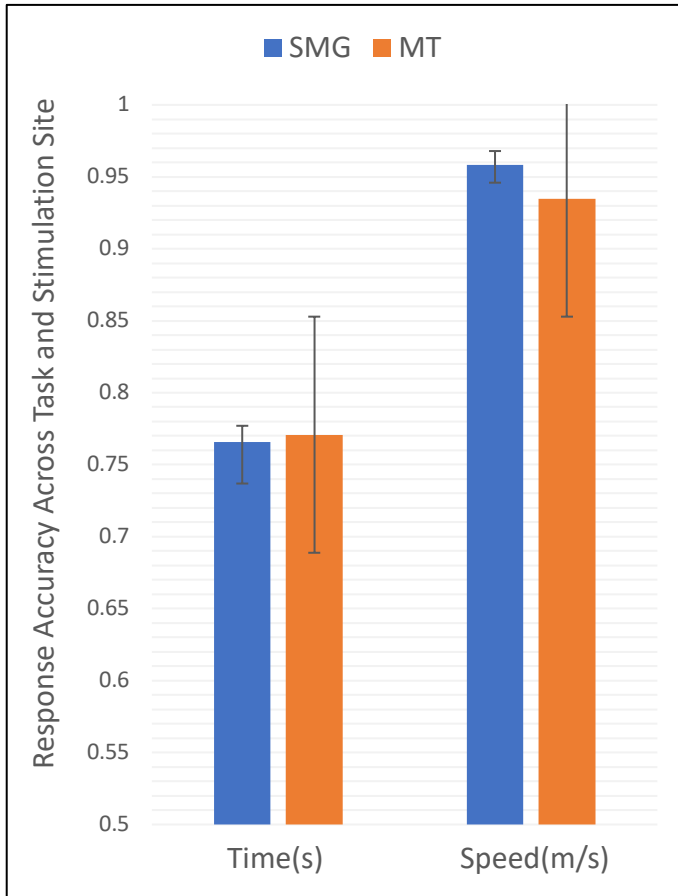


Figure 2. Mean values for accuracy for attended and non-attended dimensions across SMG and MT stimulation. Time bars show that SMG stimulation slightly reduced accuracy for time while MT stimulation slightly increased accuracy performance. The speed bars show that accuracy for SMG stimulation when attending to speed was higher than accuracy for speed following MT stimulation. Error bars denote standard errors.

DISCUSSION

The purpose of this study was to delineate between the brain regions associated with time and motion to better understand the neuronal mechanisms behind time dilation. One of the main controversies in time perception research and specifically time dilation, is whether the perception of time dilation, where time may expand depending on the physical properties of a stimulus, is representative of lower or higher levels of visual processing. From the first perspective, the primary source of time dilation takes place in area V1 and may depend on retinotopic coordinates as opposed to spatiotopic coordinates (Kanai and colleagues, 2006).

On the other hand, a more extensive amount of previous studies has implicated higher-level, extrastriate regions of processing in the brain, indicating higher order motion processing beyond the visual cortex as the primary source of time dilation (Au, Ono, & Watanabe, 2012; Yamamoto & Miura 2016). Specifically, the inferior right IPC and area MT/V5. Another primary purpose of this study was to further dissociate between motion and time for time dilation behaviorally and ideally, provide additional research showing that velocity is critical for inducing time dilation.

This study combined rTMS and a comparison task to induce the effect of time dilation by presenting RDM stimuli in which subjects were asked to make a judgment as to whether stimulus S2 was presented for a longer duration than S1 or was moving at a faster speed than S1. Subjects completed the task following stimulation to either the rIPC

(SMG) or area MT/V5, dependent on the session. The results revealed a number of significant and trending findings. First, the effect of time dilation was seen in which faster speeds lead to longer perceived durations when subjects were attending to time. This effect was seen regardless of TMS.

Additionally, TMS to area MT/V5 appeared to reduce accuracy when subjects were making judgments regarding the speed of the stimulus in that subjects were more likely to perceive the stimuli as slower. On the other hand, TMS to the SMG appears to somewhat reduce accuracy when subjects were attending to time and thereby, decrease the effect of time dilation. Interestingly, TMS to area MT/V5 appeared to increase the effect of time dilation consistently across subjects suggesting that subjects are more impacted following MT/V5 stimulation.

While the decrease in time dilation following SMG stimulation may be unexpected, a precedence for this effect was set by Hayashi et al. (2013) where, through a series of TMS experiments using duration and numerosity in a comparison and reproduction task, stimulation to the rIPC impaired accuracy for both numerosity information and temporal information. These results by Hayashi et al. (2013) and the current results indicate that the rIPC and MT/V5, while being a part of the same multimodal circuit used in processing a variety of magnitudes, may serve different functions. Specifically, for processing time and speed. Lastly, no effect was seen on speed perception depending on time, suggesting that while speed impacts perception of time, time does not appear to impact perception of speed.

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Eva Robinson received her Bachelor of Arts in psychology from the University of North Florida in 2017. She went on to a Master of Arts program in psychology with a concentration in Cognitive and Behavioral Neuroscience at George Mason University and will graduate in 2019. She will begin working towards her Doctor of Philosophy in Cognitive Neural Systems at the University of Arizona in Fall 2019.