MANIPULATION OF SPACE AND TIME IN THE TACTILE UNIVERSE

MANIPULATION OF SPACE AND TIME IN THE TACTILE UNIVERSE

BY
AKASH DEEP, HON. B.SC.

A Thesis Submitted to the Department of Psychology, Neuroscience & Behaviour
in Partial Fulfillment of the Requirements
for the Degree Masters of Science

McMaster University MASTERS OF SCIENCE (2018) Hamilton, Ontario
(Psychology, Neuroscience & Behaviour)

TITLE: Manipulation of space and time in the tactile universe

AUTHOR: Akash Deep, Hon. B.Sc. (McMaster University)

SUPERVISOR: Dr. Daniel Goldreich

NUMBER OF PAGES: ix, 93

Abstract

The study of tactile illusions like visual illusions can reveal the brain's processing strategies. A famous tactile illusion is the cutaneous rabbit illusion. Fundamental to this illusion is the perceptual length contraction phenomenon: two taps that occur in rapid succession on the forearm are perceived as occurring closer together than they were physically placed. Our lab previously proposed a Bayesian probabilistic model that views perception as a compromise between expectation (prior experience) and sensation (likelihood of sensorineural data given hypothesized tap locations). The model proposes a low-speed prior, an expectation based on experience that objects tend to be stationary or to move slowly on the skin. When the sensation of space is unclear (e.g., taps are weak), the model predicts that expectation will strongly influence perception. Consistent with this prediction, our lab previously showed that the use of weaker taps causes more pronounced perceptual length contraction. Here we report psychophysical tests on 64 participants, which confirmed this finding. Our study also used stimulus sequences consisting of a weak and a strong tap, for which the Bayesian model predicts an asymmetric perceptual length contraction, such that the weaker tap location will be perceived to shift more than the stronger tap. The experimental results confirmed this prediction, providing further support for our Bayesian probabilistic model as an explanation for perceptual length contraction. However, our results revealed a discrepancy in the data at the smaller SOAs, which showed less length contraction than predicted. We hypothesized that participants might overestimate the smaller SOAs, an effect our lab defines as time dilation. Accordingly, in a second study we investigated the effects of varying SOA and lengths on perceived SOA. The model predicts more pronounced time dilation at smaller SOAs and larger lengths. The psychophysical data from 37 participants confirmed the trends predicted by the model.

Acknowledgements

I would like to extend my greatest gratitude towards all the individuals that have provided me with the support to successfully complete my Masters.

First and foremost, I would like to acknowledge my supervisor Dr. Daniel Goldreich for giving me the great opportunity to research in his lab and instilling in me his passion for research. He is a phenomenal mentor with a vast amount of knowledge and patience. It is because of these qualities combined with his love for learning and teaching that I was able to accomplish such a feat as this thesis. I am grateful for his guidance and continuous support all these years. From all of our interactions, I will cherish the memories from our our weekly meetings the most. Although, we both went on many interesting tangents about American politics, our meetings were still just as productive as they were entertaining. Thank you for being an amazing teacher and supervisor for the past three years.

I would like to further thank all the lab members part of the tactile acuity lab for creating such a great environment where help is always given even when it's not asked for. Specifically, I would like to thank my two thesis students Umangjot Kaur Bharaj and Farah Hassan, who’s tremendous hard work allowed us to accomplish two projects in two years. I wish the best for the both of you and hope you both find happiness and success wherever you go. Next, I would like to thank Keon Allen for being a strong support system and an amazing friend during the two years of my Masters. It has been an incredible journey and I wouldn’t ask for a better dance partner. I would also like to thank Lux Li, Kyle Gauder, Jo Spyra, Mike Wong, Jonathan Tong, Nina, and the rest of the tactile lab for their tremendous support and phenomenal attitude in the lab.

I wish to acknowledge all the people that made the long and gruelling days running experiments and working on my thesis at the Psychology building enjoyable and productive; you have created for me a home away from home: Zeeshan Haqqee, Rob Valdizon, Hasan Siddiqui, Laagi Yoganathan, Sumeet Farwaha, Carmen Tu, and Kiran Matharu.

Next I would like to thank all my friends who have been there before I began my Masters. Whether it was teen problems in high school, getting through exam season during undergrad, stress from research during my masters, helping me solve my girl problems, or figuring out my path in life, you have seen it all and have helped me make it through. I wouldn’t be

who I am without any of you, thank you: Devan Singh, Evan Amalfitano, Natasha Chandarana, Erica Huynh, Lorenzo Rosas, Jordan Ho, Patrick Te, Alicia Serrano, Rohoma Zakir, Carina D’Souza, Daaksh Bharat, and Savreet Boparai.

Last, but not the least, I would like to thank my family. Saleena, we may not have had the greatest sibling relationship growing up, but in the past couple years you have become not only the greatest sister that anyone in the world could ever have, but also an amazing best friend. I am proud to be your brother and lucky to have a wise and caring sister as you. You are going to achieve great things in your life and I can not wait to be there with you when you do. Mom and Dad, none of this would be possible without either of you supporting me as you have. You both have worked incredibly hard and have sacrificed a tremendous amount in order for Saleena and I to have the amazing life that we do. I am the luckiest son on the planet, and I hope I can someday repay both you for everything you have done for me.

Table of Contents

Chapter 1: Introduction 1
- 1.1 The Senses 1
- 1.2 Perceptual Inference 3
- 1.3 Cutaneous Rabbit Illusion 7
- 1.4 Bayesian Inference 8
- 1.5 References 11

Chapter 2 — Stronger is Weaker: Manipulation of Sensation of the Cutaneous Rabbit Illusion 14

Chapter 2.1: Introduction 14
- 2.1.1 Previous Cutaneous Rabbit Research 14
- 2.1.2 Bayesian Inference 16
- 2.1.3 The Low-Speed Prior 18
- 2.1.4 Previous Experiment 20
- 2.1.5 Current Experiment 21

Chapter 2.2: Methods and Materials 22
- 2.2.1 Participants 22
- 2.2.2 Apparatus 22
- 2.2.3 Sensory Testing Procedure 24
- 2.2.4 Perceptual Length Contraction 25
- 2.2.5 Tactile Acuity Testing σ_s 26
- 2.2.6 Statistical Analysis 27

Chapter 2.3: Results 29
- 2.3.1 Weaker taps elicit more perceptual length contraction 29
- 2.3.2 Both SS and WW taps elicit symmetric perceptual length contraction 29
- 2.3.3 The perceptual midpoint is stationary in SS and WW (symmetric), but shifts in the mixed condition (asymmetric) 32

Chapter 2.4: Discussion 37
- 2.4.1 Comparison to previous studies 37
- 2.4.2 Experimental results support the model 40
- 2.4.3 The model may generalize to other sensory modalities 42

2.4.4 Future directions 44

Chapter 2.5: References 48

Chapter 3 — Are we there yet: Time Dilation in the Tactile Space 52

Chapter 3.1: Introduction 52
3.1.1 Neurophysiology of time perception 52
3.1.2 Time dilation 54
3.1.3 Bayesian approach to time dilation 55

Chapter 3.2: Methods and Materials 58
3.2.1 Participants 58
3.2.2 Apparatus 58
3.2.3 Sensory Testing Procedure 59
3.2.4 Tactile Temporal Acuity Testing (σ_t) 60
3.2.5 Time Dilation Percent Determination 62
3.2.6 Tactile Spatial Acuity Testing (σ_s) 65

Chapter 3.3: Results 66
3.3.1 Time dilation is significantly increased at shorter SOAs and non-significantly increased at greater lengths 66
3.3.2 Individuals eliminated from the study had worse temporal and/or spatial acuity 67
3.3.3 Median graphs illustrate a strong length effect. 68

Chapter 3.4: Discussion 72
3.4.1 Comparison to previous studies 72
3.4.2 Experimental results support the model 75
3.4.3 Future directions 77

Chapter 3.5 References 90

Figure Captions

Chapter 2 — Stronger is Weaker: Manipulation of Sensation of the Cutaneous Rabbit Illusion

Figure 1. Perceived Position, Distance, and Midpoints of the Weak-Weak and Strong-Strong Conditions 34

Figure 2. Perceptual Midpoints of the Mixed Conditions 36

Figure 3. Length Contraction Discrepancy: Possibility of Time Dilation at Small SOAs 47

Chapter 3 — Are we there yet: Time Dilation in the Tactile Space

Figure 1. Group A and B Time Dilation (Average Values) 69

Figure 2. Group A and B Time Dilation (Median Values) 70

Figure 3. Combined Group A and B (Average and Median Values) 71

Figure 4. Sigma T vs Sigma S 85

Figure 5. Sigma T vs Most Time Dilation a Participant Perceived Regardless of Condition 86

Figure 6. Sigma S vs Most Time Dilation a Participant Perceived Regardless of Condition 87

Figure 7. Light From Above Illusion 88

Figure 8. Bayes Factor Distribution 89

Chapter 1 — Introduction

1.1 The Senses

Our senses are vital to our ability to interact with the world. Each sense has a variety of sensory receptors that are exclusive to that sense. Humans have the ability to sense odours, taste, touch, sound, and light. These are the five traditional senses that are commonly known; however, humans have the ability to also sense pain, temperature, balance, body position, and other physical stimuli. The acuity of these senses vary from one organism to another. Compared to humans, dogs have fewer cones and significantly more rods in their eyes; dogs then have better visual acuity during the night, but poorer acuity during the day (Coren, 2005). There are also stimuli in the world that humans are unable to detect with their senses. Certain species of fish have the ability to detect change in water pressure and currents, while others have the ability to detect magnetic and electrical fields (Albert & Crampton, 2005). There are two categories of senses: exteroceptive and interoceptive. Exteroceptive senses deal with the body's external state and encompass the five traditional senses, while the interoceptive senses focus on the state of the internal organs. Common interoceptive senses include sensations of hunger, swallowing, vomiting, acid reflux, stretch receptors located in the lungs to regulate respiratory rate, and many more (Farr et. al., 2016). All of these senses provide valuable data of the world around us, which forms our perception.

One of the most fascinating yet least understood senses is the sense of touch. The skin is the largest sensory organ of our body. During prenatal development in animals, the skin is the first sense organ to emerge and grow (Field, 2014). It consists of several components containing a high abundance of cells, sweat glands, and nerve endings, with a wide variety of receptors underneath. The density of these components will differ from one location of the body to another. Areas with a high density of receptors (e.g. finger tip) would have higher tactile acuity than areas with a lower density of receptors (e.g. back). The skin relays a multitude of essential sensory information that allows for safe and meaningful interactions with the world. Mechanoreceptors found underneath the epidermis layer of the skin react to stimuli that cause a change in skin shape and activate Aβ fibers. From here, the action potential travels through the spinal cord, brainstem, and thalamus. This pathway terminates in the primary somatosensory cortex (S1) and is known as the dorsal medial lemniscus (DCML) pathway (Sullivan & Schmitz, 2007).

There are four types of mechanoreceptors: Merkel, Meissner, Ruffini, and Pacinian. These mechanoreceptors differ in their receptive field size and the type of stimuli they respond to. Meissner and Pacinian both respond to vibrations (low frequency and high frequency vibrations respectively), while Merkel responds to static indentation, and Ruffini responds to skin stretch (McNulty & Macefield, 2001). Having different mechanoreceptors with specialized sensitivities allows individuals to perceive a variety of physical characteristics, such as texture, orientation, pressure, and edge. With these complex abilities, the skin has the power to convey language to individuals who lack the ability to see. Braille is a language created for blind individuals to read text by moving their fingers over cells of raised dots (Braille, 1829). Alongside mechanoreceptive (touch) information, the skin also continuously communicates proprioception (body positioning), nociception (pain), and thermorecepetion (temperature) information (Purves, at al., 2001). The skin is therefore a jack of all trades, while also being the master of those trades. The sense of touch is a valuable sensory system that has been relatively understudied by the scientific community.

Despite the precision of its receptors and their connections in the central nervous system, the interpretation of tactile input—and indeed input through all the senses—is an uncertain inference process, as explained below.

1.2 Perceptual Inference

All of our senses, including the sense of touch, are imprecise—their neural activity varies from moment to moment. Therefore, a repeated identical stimulus will evoke varying neural responses with each iteration.

Research indicates that, in order to perceive in the most accurate way possible, the brain does not solely rely on neural responses to stimuli, but also on prior knowledge (Sumner & Samuel, 2009). Our perception is comprised of two components—the sensory input received from our sensory receptors and our previous experiences with the stimulus (Bernstein, 2010; Clark, 2013; Seriès & Seitz, 2013).

In the first component, a physical stimulus interacts with our body and sends neural signals down the nervous system to the cortex. For example, when we view a rose, the light bouncing off it travels to the back of the retina, which sends signals down the retinal ganglion cells, which in turn results in a signal sent to the occipital lobe of the cortex. This visual signal of the rose then interacts with the signals being sent from the olfactory sense and other senses—allowing for a fuller sensory perception of the rose. As previously stated, this step is subject to neural variability. This component of perception can be considered a bottom-up approach to processing of a stimulus.

The second component involves a top-down approach, where our attention, prior experiences, and learning shape the interpretations of the signals being received in the cortex. An increasing amount of research indicates that our perception may be influenced by our prior experiences (Bernstein, 2010; Clark, 2013; Seriès & Seitz, 2013). In other words, the brain utilizes prior knowledge in conjunction with what we sense in order to make a quick probabilistic conclusion about our surroundings. These conclusions are probabilistic in the sense that the brain infers, based on all prior experiences and the current stimuli, which perception is most likely to be true among the many possibilities.

Numerous experiences over time lead to learning and the development of categories and higher perceptual thresholds. To a child, a majority of the objects in the world are novel; therefore, there are hardly any expectations and minimal categorizations. As experience is gained, there are more expectations, and finer predictions. An incorrect prediction leads to new predictions and hypotheses, which results in learning. This learning and gaining of perceptual acuity applies to all sensory systems, whether that be by gaining a higher taste acuity to recognize different forms of wine or increasing tactile acuity to read braille. Prior experiences therefore allow for more efficient interactions in the real world. They are highly advantageous because they reduce the cognitive load the brain would experience if it were to fully decode every piece of sensory information. In all these scenarios it can be argued that the brain is doing predictive coding where the brain produces numerous hypotheses and continually updates them to make predictions about the incoming sensory input (Clark, 2013). Predictive coding diverges from the view that the brain is integrating sensory signals with little to no feedback from the cortex and the accumulated prior experiences. This theory implies a strong impact of expectation on perception, which means our perception is never truly unbiased.

One method to understand the impact of biases on our perception is by studying illusions. Illusions provide a sneak peak into how the brain decodes incoming sensory information. They are distortions of the world being represented by our perception. Interestingly, illusions are common experiences shared among many individuals. As stated previously, much research indicates that the brain infers the most accurate perception based on prior knowledge in conjunction with the current stimuli (Knill & Richards, 1996). Illusions may therefore be the result of this inference. For example, a classic visual illusion, known as the duck-rabbit illusion, involves looking at an ambiguous drawing which can be perceived either as a duck or a rabbit (Brugger, & Brugger, 1993). The animal that we perceive is affected by the time of the year. When viewing the picture around Easter, people tend to perceive it as a rabbit, while during October they tend to perceive it as a duck (Seriès & Seitz, 2013). This inference occurs because the brain utilizes prior (yet very recent) experiences of rabbit images during Easter, and ducks migrating south in October to find the optimal hypothesis that explains the current data in accordance with prior experiences.

If priors make perception optimal, then how can they also cause illusions? When a prior reflects the statistics of the environment, it causes perception in that environment to become more accurate. This is presumably the case in much real-world perception. However, the advantage of priors begins to break down when the statistics of the environment no longer match the prior, such as might occur in viewing illusions or studying priors in a laboratory setting. In such cases, priors can cause illusions. Indeed, the study of illusions is a means by which to investigate the brain's priors. Despite their apparently general importance to perception, most documented research in priors and perceptual illusions are in the visual modality; studies in the tactile modality remain sparse.

1.3 Cutaneous Rabbit Illusion

One well-known perceptual illusion in the tactile modality is the cutaneous rabbit illusion (aka sensory saltation) (Goldreich, 2007). The cutaneous rabbit illusion illustrates how the brain interprets tactile stimuli on the skin. The original illusion involves 5 taps given at three different locations across the forearm (15 taps in total) (Geldard, 1982). When the time between taps is small, the individual perceives the taps as occurring between the three actual tap locations. Although the areas between the three locations are never stimulated, the brain perceives the taps "hopping" along the arm. Interestingly, the illusion persists even when the intervening skin area is anesthetized. This provides evidence for the idea that the illusion is not produced in the peripheral nervous system, but rather in the central nervous system (Goldreich, 2007). Here, we focus on a variation of the rabbit illusion that involves just two taps along the forearm. When these two taps occur sequentially with a short inter-stimulus interval, they are perceived as being closer together than they actually were, which our lab defines as length contraction (Goldreich & Tong, 2013). To explain this phenomenon, a Bayesian probabilistic model is proposed.

1.4 Bayesian Inference

$$P(H_i|D) = \frac{P(D|H_i)P(H_i)}{\sum P(D|H_k)P(H_k)}$$

Posterior Probability ∝ Prior x Likelihood

(Perception) ∝ (Expectation) x (Sensation)

(Equation 1)

The Bayesian probabilistic model (equation 1) incorporates prior knowledge to determine the most probabilistic outcome for what is perceived. This is similar to the idea of the brain utilizing prior knowledge of the natural world in order to interpret incoming sensory information. This leads us to the question, what prior experiences with the natural world would lead to an illusion such as the cutaneous rabbit? The Bayesian model proposes a “low-speed” prior (Goldreich & Tong, 2013). This means the accumulation of prior knowledge from experiencing tactile stimuli on our body has shaped our expectation for stimuli to move slowly on the skin. This is because whenever we experience any form of a tactile stimulus in the world, it tends to move slowly (i.e. the movement of clothing while walking, shaking someone’s hand, playing a sport, etc.). The low-speed prior, however, only explains part of the illusion. The Bayesian model also proposes a uniform-motion prior—the expectation for a single object to move in a steady and fixed direction (Goldreich & Tong, 2013). When experiencing two sequential stimuli with a short delay, our brain tends to infer that the stimuli are one object moving a shorter distance than what physically occurred. In addition to an individual’s prior knowledge, the Bayesian probabilistic model also utilizes the sensations (i.e. neural signals) that an individual receives, referred to as their likelihood. The Bayesian probabilistic model calculates posterior probability (i.e. our perception) which is proportional to the product of the prior and the likelihood. The posterior probability tells us the probability of a hypothesis being correct, having considering the observed evidence. Therefore, in scenarios where there is a broad likelihood function (i.e. taps are weak, or one is stimulated in a region with low acuity), the prior (i.e. expectations) would have a larger influence on the posterior probability. On the other hand, having a sharper likelihood function (i.e. strong taps, or one is stimulated in a region with high acuity) would cause the prior to have less of an influence on the posterior probability.

Previous research has shown the effect of manipulating the perceived distance between taps by manipulating the time between the taps, or the stimulus onset asynchrony (SOA). A smaller SOA leads to a stronger effect of length contraction (Geldard, 1982; Tong et al., 2016); our Bayesian model explains this effect as the result of a change to the prior over length, which is the product of the low-speed prior standard deviation and the SOA (Tong et al., 2016). However, what happens when the likelihood or the sensation is manipulated? In addition, the illusion has only been studied using experiments that focus on participants' perception of the location of the taps. Another essential component to touch and to understanding this illusion is time. By asking individuals how they perceive the time that passes between the taps, we can get a better understanding of how the brain processes time and its influence on touch. This thesis will outline experiments that manipulate the likelihood (Chapter 2) and investigate participants' perception of the time that passes between taps (Chapter 3).

1.5 References

Albert, J. S., & Crampton, W. G. R. (2005). Electroreception and electrogenesis. The physiology of fishes, 3, 431—472.

Bernstein, D. A. (2010). Essentials of Psychology. Cengage Learning, 123–124. ISBN 978-0-49590693-3.

Braille, L. (1829). Method of writing words, music and plain songs by means of dots for use by the blind and arranged for them. Paris, France: l'Institution Royale des Jeunes Aveugles.

Brugger, P., & Brugger, S. (1993). The Easter bunny in October: Is it disguised as duck?. Perceptual and motor skills, 76(2), 577—578.

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behavioral and brain sciences, 36(3), 181—204.

Coren, S. (2005). How dogs think: understanding the canine mind. Simon and Schuster.

Farr, O. M., Chiang-shan, R. L., & Mantzoros, C. S. (2016). Central nervous system regulation of eating: Insights from human brain imaging. Metabolism Clinical and Experimental, 65(5), 699—713.

Field, T. M. (Ed.). (2014). Touch in early development. Psychology Press.

Geldard, F. A. (1982). Saltation in somesthesis. Psychological Bulletin, 92(1), 136.

Goldreich, D. (2007). A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. PLoS ONE, 2(3). Doi: 10.1371/journal.pone.0000333

Goldreich, D. & Tong, J. (2013). Prediction, postdiction, and perceptual length contraction: A Bayesian low-speed prior captures the cutaneous rabbit and related illusions. Frontiers in Psychology, 4. doi: 10.3389/fpsyg.2013.00221

Knill, D. C., & Richards, W. (1996). Perception as Bayesian inference. Cambridge University Press.

McNulty, P. A., & Macefield, V. G. (2001). Modulation of ongoing EMG by different classes of low-threshold mechanoreceptors in the human hand. The Journal of physiology, 537(3), 1021—1032.

Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, A. S., McNamara, J. O., & Williams, S. M. (2001). The somatic sensory system. Neuroscience. 5th ed. Sunderland, MA: Sinauer Associates.

Seriès, P., & Seitz, A. (2013). Learning what to expect (in visual perception). Frontiers in human neuroscience, 7, 668.

Sullivan, O., & Schmitz, T. J. (2007). Physical rehabilitation. FA Davis Company, Philadelphia, PA, 385.

Sumner, M., & Samuel, A. G. (2009). The effect of experience on the perception and representation of dialect variants. Journal of Memory and Language, 60(4), 487—501.

Tong, J., Ngo, V., & Goldreich, D. (2016). Tactile length contraction as Bayesian inference. Journal of neurophysiology, 116(2), 369—379.

Chapter 2 — Stronger is Weaker: Manipulation of Sensation in the Cutaneous Rabbit Illusion

2.1 Introduction

In the cutaneous rabbit illusion, individuals perceive two rapidly successive taps as closer together in space than they were physically placed. A related phenomenon is the the tau effect, in which a pair of stimuli separated by a small time interval is perceived as shorter in distance than a pair with the same spatial separation but a larger time interval (Helson, 1930; Helson & King, 1931). Interestingly, Helson and King (1931) found that the effect of the illusion persists even when the participants are made aware of conditions responsible for it. Both of these effects are instances of what our lab defines as tactile length contraction (Goldreich, 2007). Interestingly, perceptual length contraction has also been experienced in vision and audition. Furthermore, the effects were not only unimodal, but also crossmodal. For instance, time discrepancy in auditory beeps affect the perceived distance between visual flashes of light (Kamitani & Shimojo, 2001; Shams et. al., 2004); similarly, visual flashes placed along the skin affect the perceived locations of tactile stimuli in the rabbit illusion (Asai & Kanayama, 2012).

2.1.1 Previous Cutaneous Rabbit Research

Geldard and Sherrick (1972) discovered the cutaneous rabbit illusion; the original rabbit illusion consisted of 15-taps, but later they discovered the illusion was still possible with just 3-taps. They believed the subsequent tap worked as an attractant, which shifted the perceived location of the previous tap towards itself. This theory would mean that the rabbit illusion is asymmetrical in the sense that the perceived location of the previous tap moves towards the subsequent tap, while the perceived location of the subsequent tap remains stationary. Their research showed how a smaller time or stimulus onset asynchrony (SOA) between two taps can lead to more pronounced length contraction. The illusion has also been shown to occur at different areas of the body; areas of lower tactile acuity (i.e. back and forearm) experience a more pronounced illusory effect, whereas areas of higher tactile acuity (i.e. hand and fingers) experience a weaker effect.

Later, Kilgard and Merzenich (1995) found evidence against Geldard and Sherrick’s theory of an asymmetrical length contraction. Using a 4-tap configuration instead of the 3-tap version preferred by Geldard (1982), they discovered that the illusion was indeed symmetrical in nature: the perceived location of the taps approached one another equally as the SOA decreased. They further discovered that the illusion can be manipulated by attention. When the researchers asked the participants to direct their attention to either the proximal or distal region of the forearm, the perceived location of the taps shifted towards the attended location. Attention therefore has the same effect as changing the acuity of the attended region. The attended area represents an area of high acuity; therefore, the effect of the illusion is weaker here, meaning the perceived tap location shifts less. The unattended area is the opposite, representing an area of low acuity; therefore, the effect of the illusion is stronger, meaning the perceived tap location shifts more. Consequently, directed spatial attention results in an asymmetrical length contraction.

2.1.2 Bayesian Inference

As described in chapter one, according to the Bayesian framework, perception is influenced by prior probabilities and likelihoods. When tactile acuity is manipulated by changing body areas or the area to which an individual is attending, the likelihood or the sensation is affected. This can be illustrated through the length contraction equation below.

$$l^* = \frac{l_m}{1 + 2\left(\frac{\sigma_s}{\sigma_v t}\right)^2}$$

(Equation 1)

Equation 1 is the perceptual length contraction formula proposed by Goldreich (2007). In this equation, l^* represents perceived length and l_m represents measured length (i.e. a random sample drawn from a Gaussian distribution centred on the actual length). The perceived length is affected by the interaction between the likelihood distribution (σ_s), prior distribution (σ_v), and SOA (t). The formula shows that, as t approaches infinity, l^* approaches l_m; conversely, as t approaches zero, l^* approaches zero. Previous empirical findings of the cutaneous rabbit illusion follow these trends (Geldard, 1982; Kilgard & Merzenich (1995); Tong et al., 2016). The formula also predicts that, when the likelihood distribution broadens (larger σ_s), the perceived length will diminish. A larger likelihood distribution — i.e., an unreliable neural signal — can be achieved by changing the location of the taps to a low acuity area or tapping in an unattended area. These trends, too, have been observed empirically (Tong et al., 2016).

However, Equation 1 by itself cannot explain the asymmetrical effects of the attention experiment of Kilgard & Merzenich (1995). When σ_s differs at the two tap locations, the Bayesian model (Goldreich, 2007; Goldreich & Tong, 2013) predicts that the midpoint of the perceived tap locations will shift towards the attended location:

$$\Delta_{midpt} = \frac{l_m}{2}\left(\frac{\sigma_{s1}^2 - \sigma_{s2}^2}{(\sigma_v t)^2 + \sigma_{s1}^2 + \sigma_{s2}^2}\right)$$

(Equation 2)

Equation 2 is a change in midpoint formula. Here, we see the parameters of l_m, σ_s, σ_v, and t as found in the length contraction formula (Eq. 1). There are, however, two different σ_s values in the equation; when the two taps are administered at two different conditions (i.e. an attended tap location and an unattended tap location), the σ_s values for the two conditions will differ. Two differing σ_s values will then result in a shift in the midpoint towards the location with the smaller of the two σ_s values, thus meaning an asymmetrical length contraction. A smaller σ_s is an area of high tactile acuity or an attended tap location. The formula shows that, as t approaches zero, if σ_s at one location greatly exceeds that at the other, the midpoint shift approaches l_m divided by 2 (i.e., the perceived midpoint approaches one of the actual stimulus locations). Conversely, as t approaches infinity, the midpoint shift approaches zero. Similarly, when the two σ_s values are the same, the midpoint shift is zero, which means length contraction is symmetrical.

2.1.3 The Low-Speed Prior

In both of the equations the low-speed prior (represented by σ_v) plays a crucial role. We hypothesize that each person has a set low-speed prior that is unique to them, with little variation across individuals (Goldreich, 2007). The low-speed prior is a sharp distribution centered at zero, which allows for some speeds greater than zero to occur. It is this set low-speed prior that causes the illusion to take place. However, alternate explanations for the illusion, such as the constant velocity prior, exist. In the constant velocity prior the distribution is not as sharp as the low-speed prior, which means it allows for a wider range of speeds (Jones & Huang, 1982). Here, the assumption is that the velocity generated from a prior stimulus will carry over and effect the perception of a subsequent stimulus. Although the constant velocity prior might plausibly explain the effects observed in multiple sequence stimuli (i.e. the tau effect and Geldard's 15-tap rabbit), it does not explain the effects seen in two stimuli paradigms (i.e. Kilgard and Goldreich's two tap rabbit). In the two stimuli paradigms, there is no prior stimulus to generate a velocity to manipulate the perception of the current stimuli. The low-speed prior on the other hand provides a strong explanation for both the multiple sequence stimuli and the two stimuli paradigms (Goldreich, 2007).

Another explanation for the illusion is the low-acceleration prior. The low-acceleration prior is a generalization of the constant velocity prior, where the distribution allows for moderate forms of acceleration to occur. The implication to the brain is that it expects tactile stimuli to move at constant velocity or to accelerate only moderately. Compared to the low-speed prior model, the low-acceleration model does not follow the trend seen in Geldard's participants and actually underestimates the perceived location of the first tap and overestimates the perceived location of the last tap (Goldreich and Tong, 2013). The purpose of any model is to find a coherent way to fit data; to accommodate for low acceleration, the first perceived tap location must be located before the actual first tap location to allow the later taps to be located in accordance with low-acceleration movement. As any accelerating object requires time to decelerate and stop, the last tap is perceived past the actual last tap location to accommodate this idea.

2.1.4 Previous Experiment

A past study in our lab has shown the effect of having a larger likelihood distribution (σ_s), or an unclear sensation of space. The study focused on providing either weak or strong taps to the skin in a two interval forced choice experiment. Participants compared two stimuli of differing lengths and were asked which length was larger. The first stimulus length and time were held constant at 3cm and 1000 ms, while the length and time for the other stimulus varied. We predicted that weak taps should elicit an unclear sensation of space, and thus cause the likelihood function to broaden, while a strong tap would elicit a clearer sensation of space, or a sharper likelihood function. The study supported our hypothesis; weaker taps resulted in a greater σ_s and elicited a more pronounced perceptual length contraction than stronger taps (Tong et. al., 2016).

2.1.5 Current Experiment

Our current study focuses on observing the effects of a mixed tap condition (i.e. one weak and one strong tap) in addition to verifying the same strength (strong-strong versus weak-weak) effects seen in the previous study. Unlike the previous study, this study implements a pointing paradigm, where the participant indicates on a computer monitor where they perceived the tap locations on their forearm. This is different to our previous study, where the participant simply indicated which of the two stimuli was longer. Furthermore, the tests are done at the standard 10 cm length, rather than the 3 cm length in the previous study. The study also tests the symmetrical nature of the illusion to test the theories by Geldard and Kilgard & Merzenich. According to the Bayesian model, we expect a symmetrical perceptual length contraction when observing taps of the same strength and an asymmetrical perceptual length contraction when observing a mixed tap condition. In the mixed tap condition, the model predicts the weaker tap shifts more than the stronger tap.

2.2 Material and Methods

2.2.1 Participants

Sixty four undergraduate participants (18-27 years old, with a median age of 20; 43 females) were recruited from McMaster University. The study protocol was approved by the review board of McMaster University. Prior to beginning the experiment, the participants read through an exclusion criteria list which included the following: diabetes, dyslexia, attention deficit, learning disability, neurological disorders, carpal tunnel, arthritis, hyperhydrosis, low vision, and any left arm damage (cuts, scars, callouses, or nerve damage). If the participant indicated experiencing anything on this list, their participation was ended. Participants were also excluded if they were from the program of Psychology, Neuroscience & Behaviour (PNB) at McMaster. The majority of PNB students have learned of the cutaneous rabbit illusion, and by having knowledge of the illusion the participant may be biased to respond in a certain way during the experiment. Each participant read and signed a consent form.

2.2.2 Apparatus

The tactile stimuli were sub-millimeter mechanical pulses on the skin of the forearm, delivered via two cylindrical motors (Tactile Stimulator MkII; Fong Engineering; Oakland, CA, USA). These motors were positioned orthogonally to the skin and were controlled by a National

Instrument board (PCIe-6259; 16 bit analog output resolution, 2.8 MHz). The board was programed using LabVIEW running on a Macintosh MacPro 3.1 computer. The cylindrical motors were held in place by mechanical micro-manipulators (Eric Sobotka Co.), which allowed the experimenter to adjust the angle, forward-backward, right-left, and upward-downward movements of the motors. Both motors were equipped with a rounded stainless-steel pinhead probe tip (1 mm diameter), which contacted the skin. Real time displacement of the probes was measured via a linear variable displacement transducer (LVDT) inside of the motor. Using LVDT, the stimulators were lowered into the skin to a baseline indentation of 0.5 mm (i.e. 500 μm). Two tap strengths were used in the experiments: the strong tap had a pulse amplitude of 150 μm; the weak tap had a pulse amplitude of 75 μm. In both cases the taps were administered as a single-period sine wave, which lasted for 10 ms. Prior to beginning the experiment, the participant was tapped by each stimulator in order to test the strength of the taps. Both stimulators during this test were set to provide strong taps to the skin (i.e. a pulse amplitude of 150 μm). If the participant felt one tap to be weaker than the other, then the weaker probe's baseline indentation was increased by 0.1 mm (i.e. 100 μm) increments until the taps felt subjectively the same.

2.2.3 Sensory Testing Procedure

Participants were asked to wash their left forearm prior to beginning the experiment. After washing, the forearm was measured from wrist to elbow. The length was recorded and measurements were drawn on the forearm using a washable-ink pen. A visible ruler was drawn at 0.5 centimeter increments down the forearm. The purpose of the lines was to aid the experimenter in placing the stimulators on the forearm. The stimulators were hidden from the participant's view behind an opaque black curtain. The participant was seated in a way that allowed them to comfortably see the computer monitor on which they indicated their responses. The participant's arm was placed palm side up, behind the curtain and under the stimulators. The arm comfortably rested on a piece of foam padding which formed an L shape, supporting the arm both underneath and on the right side. This ensured the participant was comfortable and minimized movement. The stimulators were placed on the lateral forearm skin, specifically in the region innervated by the lateral antebrachial cutaneous nerve; we took care to avoid placing the stimulators over the flexor carpi radialis tendon running down the middle of the forearm (Agur & Dalley, 2009). During the experiment participants were given periodic 2-min breaks approximately every 50 trials, with the option to take a longer break if needed. They were also recommended to get up and walk around during the break. This was done to ensure that the participants did not feel exhausted after sitting in one spot for a lengthy period of time.

2.2.4 Perceptual Length Contraction

Stimulators were placed 10 cm apart from each other, centred on the middle of the forearm. Participants were tapped four times on their forearm. Taps one and two were reference taps, separated by 1000 ms and paired with a beep sound. Taps three and four were not paired with a beep sound, and the time between these taps varied. In front of the participant was a computer screen with a grey bar running down the middle of the screen. On the grey bar were two arrows indicating the locations of tap one and two. The participant was asked to imagine the grey bar as their arm, and to indicate on the bar where they felt taps three and four in reference to taps one and two. The experiment followed a 2 (spatial order) x 2 (strength order) x 2 (SOA order) design. The timing between taps, referred to as the SOA, was counterbalanced across participants. The participant experienced 1000 ms, 200 ms, 100 ms, 50 ms, and 25 ms. After each participant experienced the 1000 ms SOA, they were given the other SOAs in either ascending or descending order. The 1000 ms SOA has been well established in the literature as producing little to no length contraction. By starting with this SOA, participants were able to become familiar with the stimulus without affecting the results. In addition, the study contained three varying conditions of tap strength: a weak-weak, a strong-strong, and a mixed condition. The order in which these conditions were given was counterbalanced, so that the participant either experienced the weak-weak condition (WW) or the strong-strong condition (SS) first. Regardless of the order of the weak or strong condition, they were always followed by two mixed tap conditions. During the mixed tap condition, the order in which the strong tap came was pseudo-randomized; within a set of 20 trials of one SOA, half were randomly strong tap first, while the other half were weak tap first. Lastly, the spatial order of the taps was also counterbalanced. The participant either experienced the proximal (closer to the elbow) or distal (closer to the wrist) tap first.

2.2.5 Tactile Acuity Testing (σ_s)

Stimulators were placed 2 cm apart and centered on the middle of the forearm. Unlike the previous experiment where the distance was set, in this experiment the distance varied according to the participant's performance on a two-interval forced choice test. After every twenty trials (for a total of 120 trials) the bayesian adaptive method would provide a distance based on the previous performance of the participant that would gain the most knowledge of their tactile acuity. The experimenter would then adjust the distance between the probes accordingly. The possible distances the participant could experience varied from 1 cm to 8 cm with 0.5 cm increments. The participant experienced two taps at varying lengths and was asked to determine whether the first tap they felt was closer to the wrist or the elbow. They would indicate their response by pressing the left (wrist) or right (elbow) key on a Kensington 33374-P presentation pointer. Like the previous experiment, the Marsona 1288A Marpac sound conditioner played white noise throughout the experiment to mask any auditory cues that may be experienced by the participant from the movement of the stimulators. Throughout the experiment the program is also monitoring the consistency of the responses the participant is providing by a guessing Bayes Factor (BF). The more inconsistent or random the responses are, the higher the BF will be. A high BF is indicative of either a lack of focus, guessing, or a participant that belongs to a population that is unable to determine the correct response to the trials. This population may just have some differences in their sensory system or tactile perception that prevents them from perceiving the taps normally. If a high BF results, then the experiment is run again. If on the second try the experiment results in a high BF again, then the participant is not included in the study.

2.2.6 Statistical Analysis

The participant data were analyzed using IBM SPSS Statistics 25. The statistical method used is specified in the results section below. In some cases the repeated measures analysis of variance (ANOVA) statistical method is used and the Mauchly’s sphericity test was carefully observed in these cases. Here, if the sphericity is violated, we used a correction method based on the epsilon value; if the epsilon value is <0.75 or the value is not known, then the Greenhouse-Geisser correction is applied, whereas if the epsilon value is >0.75, then the Huynh-Feldt correction is applied (Girden, 1992). When Bonferroni correction was used for multiple comparisons, the reported p-values are multiplied by the number of comparisons.

2.3 Results

2.3.1 Weaker taps elicit more perceptual length contraction

Figure 1a and 1b illustrate the magnitude of length contraction in SS and WW respectively. Both conditions show more length contraction as time decreases; however, WW shows a greater degree of length contraction than SS. A two-way repeated measures ANOVA on the magnitude of length contraction was conducted with tap strength (SS or WW) and SOA (25 ms, 50 ms, 100 ms, 200 ms, and 1000 ms) as within-subject factors. Both strength and SOA showed significant main effects (strength: ($F(1, 63) = 52.753$, $p < 0.001$); SOA: ($F(2.464, 155.212) = 127.945$, $p < 0.001$)), whereas the interaction of strength and SOA did not ($F(2.518, 158.660) = 1.084$, $p = 0.351$). These results indicate that weak taps elicit significantly more length contraction than strong taps, as predicted by the Bayesian observer model.

2.3.2 Both strong-strong (SS) and weak-weak (WW) taps elicit symmetric perceptual length contraction

Both the SS and WW conditions found in figure 1c and 1d respectively, show the perceived location of the taps symmetrically approaching one another as the SOA decreases; we define this perceptual displacement of each tap towards the location of the other as “inward” displacement. Two separate three-way repeated measures ANOVA were conducted for SS and WW on the perceived migration of each tap with tap position (proximal or distal) and SOA (25 ms, 50 ms, 100 ms, 250 ms, 1000 ms) as within-subject factors and stimulus order (proximal to distal (P-D) or distal to proximal (D-P)) as a between-subjects factor. Tap migration is calculated as the distance between the actual tap location and the perceived tap location (with inward displacement defined as positive). The effect of SOA was significant in both the strong and weak conditions (strong: F(2.885, 178.897) = 109.229, $p < 0.001$; weak: F(2.196, 136.123) = 62.613, $p < 0.001$).

Importantly, the tap position had no significant effect in either the strong or the weak condition (strong: (F(1, 62) = 1.673, p = 0.201); weak: F(1, 62) = 0.000, p = 0.999), and furthermore the interaction between tap position and stimulus order was not significant in either condition (strong: F(1, 62) = 1.543, p = 0.219; weak: F(1, 62) = 1.004, p = 0.320). This strongly indicates that the perceptual migration of the two taps occurred symmetrically.

To confirm the symmetrical nature of length contraction, we compiled the data into either first tap migration or second tap migration, regardless of whether the individual experienced the P-D or D-P condition. Here, we conducted two separate two-way repeated measures ANOVA for SS and WW on perceived migration of each tap with tap temporal position (1st tap or 2nd tap) and SOA as within-subject factors. In the SS condition

SOA showed a significant main effect, whereas tap temporal position did not (SOA: F(2.889, 182.029) = 106.287, $p < 0.001$; tap temporal position: F(1, 63) = 1.526, $p = 0.221$). The interaction of SOA and tap temporal position was not significant (SOA*tap temporal position: F(2.624, 165.308) = 1.661, $p = 0.183$).

The WW condition showed similar main effects to SS (SOA: F(2.880, 181.463) = 38.742, $p < 0.001$; tap temporal position: F(1, 63) = 1.756, $p = 0.190$). In the case of the WW condition, the ANOVA additionally showed a marginally significant interaction of SOA and tap temporal position (SOA*tap temporal position: F(2.624, 165.313) = 2.830, $p = 0.047$); post-hoc Bonferroni corrected paired t-tests revealed that this marginal interaction was due entirely to a greater migration of the first tap than the second at 200 ms SOA (1st tap migration: M = 25.246 mm, SD = 20.876 mm; 2nd tap migration: M = 34.031 mm, SD = 23.647 mm; t(63) = -2.680, $p = 0.045$). None of the t-tests at the other SOAs were significant (all $p > 0.50$).

The absence of a significant effect of tap temporal position in either the SS or WW conditions, together with the absence of obvious interaction effects, clearly indicates that perceptual length contraction occurred symmetrically for the two tap positions; specifically, the amount of perceptual migration was equivalent for taps on both parts of the arm and for both the first and second tap, as predicted by the Bayesian observer model.

2.3.3 The perceptual midpoint is stationary in SS and WW (symmetric), but shifts in the mixed condition (asymmetric).

The perceptual midpoints for SS and WW in figure 1e and 1f respectively, stay relatively stable at all five SOAs. A one-way repeated measures ANOVA assessed the effect of SOA on the perceptual midpoint. SOA did not have a significant effect on the perceptual midpoints in either the SS or WW conditions (strong: ($F(2.603, 164.019) = 0.179$, $p = 0.887$); weak: ($F(3.090, 194.666) = 1.313$, $p = 0.271$)). These results clearly indicate a stable perceptual midpoint location across all five SOA's for the same tap strength conditions, which illustrates a symmetrical length contraction effect.

In stark contrast to the SS and WW conditions, in the mixed condition illustrated in figure 2, the perceptual midpoint location shifted towards the strong tap position as SOA decreased. We subtracted the perceptual midpoint of the strong proximal weak distal condition (StP-WkD) from that of the strong distal weak proximal condition (StD-WkP) for each participant at each SOA (perceptual midpoint difference scores). A one-way repeated measures ANOVA on these difference scores with SOA as a within-subjects factor indicated a significant main effect ($F(3.332, 209.936) = 8.866$, $p < 0.001$).

These data were also analyzed through multiple Bonferroni corrected paired t-tests to compare tap migration in the mixed condition for the strong versus the weak tap. For this purpose, we took the average migration of the strong tap position (regardless of whether this was from StrP – WkD or StrD – WkP) and similarly the average migration of the weak tap position. Each strong versus weak tap migration was compared within each of the five SOA's. The analysis revealed that there is a significant difference between the strong tap migration and the weak tap migration across all five SOA's (25 ms: $t(63) = 7.356$, $p < 0.001$; 50 ms: $t(63) = 5.825$, $p < 0.001$; 100 ms: $t(63) = 5.274$, $p < 0.001$; 200 ms: $t(63) = 3.732$, $p = 0.002$; 1000 ms: $t(63) = 6.043$, $p < 0.001$). These results are consistent with the trend predicted by the Bayesian observer model.

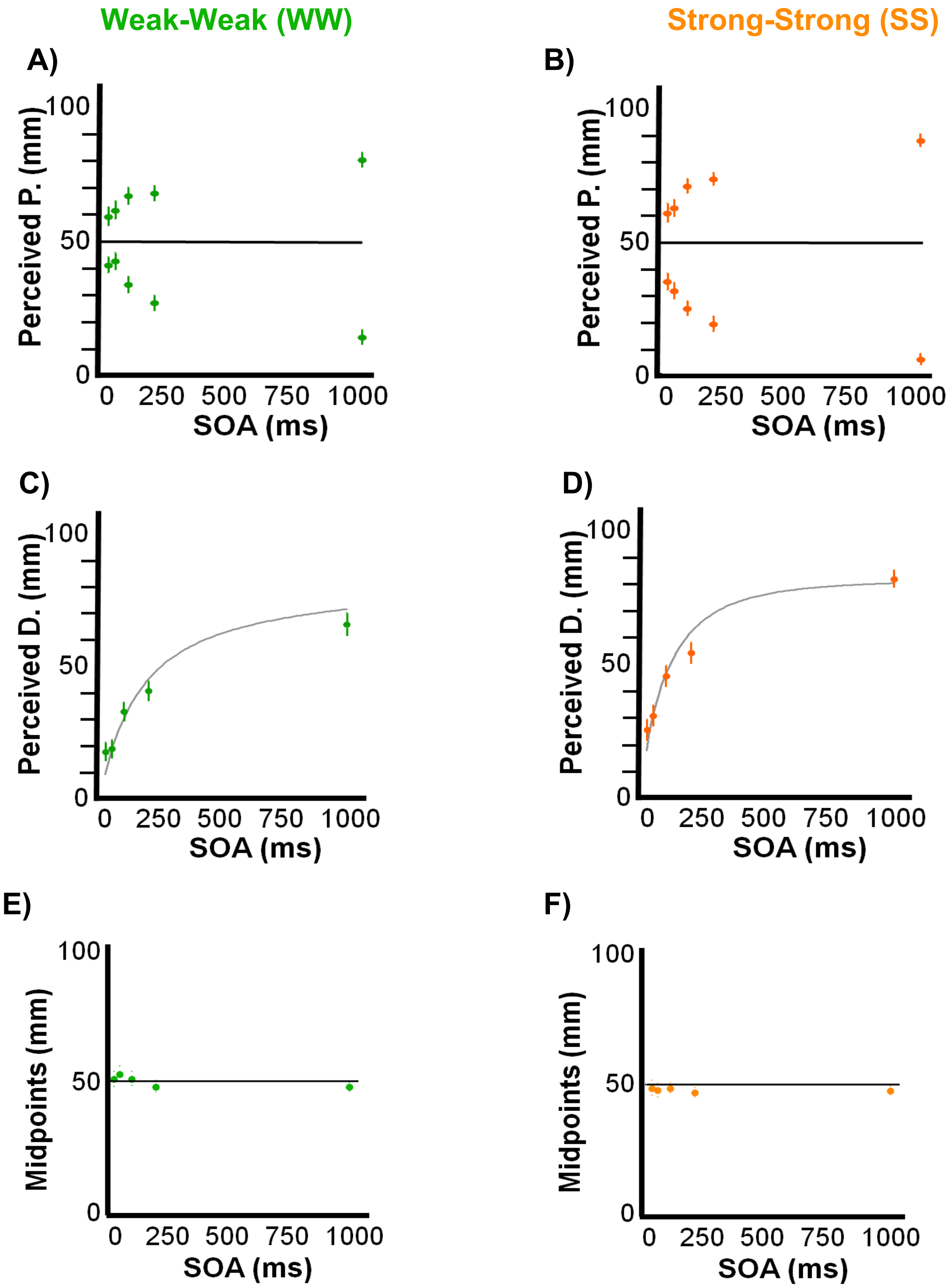


Figure 1. A) and B) show the perceived position (mm) of the taps for the WW (left) and the SS (right) over the five SOAs (ms). The black line through the 50 mm mark indicates the middle position of the two actual tap positions. C) and D) show the perceived distance (mm) of the WW (left) and the SS (right) over the five SOAs (ms). The perceived distance was

achieved by subtracting the distal position by the proximal position illustrated in A) and B). The gray line are the model-fits for each of the conditions. E) and F) show the midpoints (mm) of the WW (left) and the SS (right) over the five SOAs. The black line through the 50 mm mark indicates the middle position of the two actual tap positions.

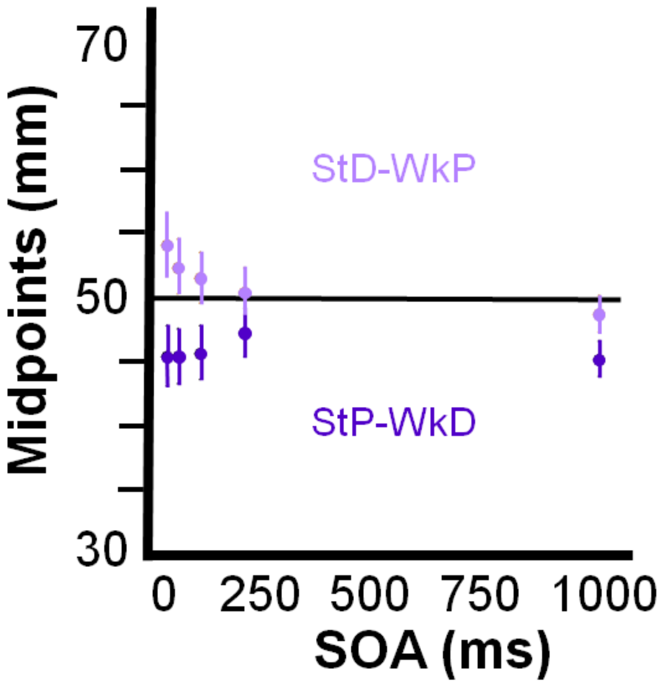


Figure 2. The midpoint positions (mm) of both the mixed conditions of strong distal weak proximal (StD-WkP) and strong proximal weak distal (StP-WkD) across the five SOAs (ms) are illustrated in the graph above. The black line through the 50 mm position indicates the middle position between the two actual tap positions.

2.4 Discussion

Here we have reported the results of tactile spatial perception psychophysical experiments on 64 participants. We have confirmed previous findings of a robust length contraction effect at short SOAs and have extended these findings by exploring the effect of stimulus strength and in particular, the effect on perception of mismatched intensity of the two taps. Our results are consistent with the predictions of a Bayesian observer model previously proposed by our laboratory (Goldreich, 2007; Tong et. al., 2016).

2.4.1 Comparison to previous studies

Many previous studies have investigated the cutaneous rabbit phenomenon (Geldard & Sherrick, 1972; Geldard, 1982; Kilgard & Merzenich, 1995; Kamitani & Shimojo, 2001; Shams et. al., 2004; Flach and Haggard, 2006; Goldreich, 2007; Trojan et. al., 2010; Miyazaki et. al., 2010; Asai & Kanayama, 2012; Goldreich & Tong, 2013; Tong et. al., 2016;). Despite many methodological differences, these studies are in broad agreement in showing the clear effect of SOA on perceived distance on the skin. Nevertheless, previous studies have disagreed with respect to the symmetric or asymmetric nature of the rabbit illusion, and few studies have investigated the effects on the illusion of stimulus strength. Here we consider each of these factors in turn.

Previous studies have reached differing conclusions of the symmetrical nature of the cutaneous rabbit illusion. Geldard (1982) and Trojan et. al. (2010) both provide evidence of an asymmetrical illusion, in which the attractee (prior tap) perceptually shifts towards the attractant (subsequent tap). Conversely, Kilgard and Merzenich (1995) show evidence for a symmetrical illusion, wherein both taps are perceptually shifted towards each other uniformly. Geldard's research, although very influential, has two major flaws as noted by Kilgard and Merzenich (1995): 1. Geldard only used trained subjects, which may have introduced a bias. 2. The majority of his research was on the reduced rabbit, which involved three taps; the first tap was always a reference tap separated by a significant amount of time from the two test taps. A reference tap indicates the beginning of a trial and allows for the participant to use the tap as a comparison point to where they felt the two test taps. Having only a beginning reference tap is problematic, as it is difficult to indicate where two taps were perceived without looking at the arm. Having two reference taps (one in the beginning and one at the end) allows for the participant to better imagine where the taps were perceived. Kilgard and Merzenich (1995) added a fourth tap (i.e. a second reference tap), which then resulted in a symmetrical illusion. Our findings contradict the results of Geldard (1982) and support the results found by Kilgard and Merzenich (1995).

Interestingly, Trojan et. al. (2010) did a single test tap localization experiment, and the results indicated that the more distal a tap was, the more likely it was to perceptually shift proximally. This is surprising as this tap is not manipulated by time. The results imply a perceptual bias of humans perceiving taps closer to their elbows than they actually are. In our experiment, we found a strong effect of symmetrical length contraction for the same tap strength conditions, and an asymmetrical length contraction in the mixed tap condition. Interestingly, both conditions show a small trend towards the proximal condition, which may be in line with the results seen by Trojan et. al. (2010).

A previous experiment in our lab studied the effect of strength on the cutaneous rabbit illusion in a two-interval forced choice (2IFC) design; the participant indicated when a stimulus with a set time (1 s) and set length (3 cm) was perceived to be the same length as another stimulus with varying times and lengths. The strength of both taps was kept the same within a block and the SS and WW conditions were compared to see their effect on perceived distance between the taps. Their results revealed more pronounced length contraction in the WW condition than the SS condition (Tong et. al., 2016). Here, we also study these same strength tap conditions in a pointing task, where the participant indicates by clicking on a computer monitor where they felt the taps on their arm. Unlike a 2IFC design, a pointing task allows us to measure the symmetrical nature of the illusion. Furthermore, the current design is studied at the standard length of 10 cm, rather than the 3 cm length in the previous experiment. Unlike the previous experiment, we run a mixed tap condition in addition to the two same strength tap conditions. In the mixed tap condition the participant experiences one strong and one weak tap. Although the methodologies are significantly different, our results also indicate more pronounced length contraction in the WW condition than the SS condition. This indicates the robustness and generality of the manipulation of strength on the cutaneous rabbit illusion. The results also reveal the magnitude of length contraction in the mixed tap condition to be relatively in the middle of both the SS and WW condition.

2.4.2 Experimental results support the model

The experimental data support the low-speed prior model of tactile perception (Goldreich, 2007; Tong et. al., 2016). The results reported here are broadly consistent with the following predictions of this model: 1) From our prior experiences of receiving tactile stimuli on our skin, we have unconsciously developed a low-speed prior. 2) Weaker taps will induce more pronounced length contraction than stronger taps because they induce a more unclear sensation of space. 3) The weak-weak (WW) condition and strong-strong (SS) conditions will induce symmetrical length contraction, where both taps will perceptually shift towards each other equally, thus also illustrating a stable midpoint. 4) The mixed tap condition will induce an asymmetrical length contraction, where the midpoint will perceptually shift towards the location of the stronger tap. The shift will become more pronounced as SOA diminishes.

Previous findings reveal that perceptual length contraction may be affected by the varying spatial acuity on the body (Geldard, 1982; Weinstein, 1968; Goldreich, 2007). These data support the Bayesian perceptual model's prediction that length contraction will be affected by the manipulation of the sensation of space. The current study controlled for the effect of sensory space by avoiding stimulating other body areas and focusing on the forearm. However, the sensation of space is manipulated by other means. Manipulating the intensity of the tactile stimuli on the same area of the body should lead to varying neural signals to the brain. The model predicts that a high intensity (i.e. strong tap) stimulus sequence should lead to a stronger neural signal enabling greater spatial accuracy, thus inducing less perceptual length contraction than a low intensity (i.e. weak tap) stimulus sequence. As predicted by the model, the WW did elicit greater length contraction than the SS. Furthermore, the model proposes that when applying both a strong and a weak tap on the forearm (i.e. mixed tap condition), the result should be an asymmetrical length contraction. In other words, the weak tap will shift more than the strong tap will, which will result in the midpoint perceptually shifting towards the strong tap location. The results of the current study revealed this trend, thus providing evidence towards a Bayesian perceptual model.

According to the Bayesian perceptual model, providing two successive weak taps has the same effect as having a broad likelihood function. In this case, the posterior probability (i.e. our perception) is now greatly influenced by our prior (i.e. expectation), which the model proposes to be one of low-speed. However, two successive strong taps has the same effect as having a sharp likelihood function, which means our perception is now more influenced by our likelihood (i.e. sensation). In both cases, we should see an equivalent perceptual shift of both points towards the midpoint of the forearm. This pattern is seen in both the SS and WW condition and confirms the model's predictions. In the mixed tap condition, the weak tap is producing a broad likelihood function, while the strong tap is producing a sharp likelihood function. According to the Bayesian model, this asymmetrical pattern is why we see the weak tap shift more towards the midpoint than the strong tap.

2.4.3 The model may generalize to other sensory modalities

Our lab has shown the robustness of the Bayesian perceptual model in the tactile modality, but can it explain the findings in other sensory modalities? The rabbit illusion has been observed in vision (Lockhead et al. 1980) and audition (Getzmann 2009; Shore et al. 1998) as well as in touch. Furthermore, the existence of the low-speed prior is strongly supported in the modalities of vision (Weiss et al. 2002; Welchman et al. 2008) and audition (Senna et al. 2015). These results suggest that our Bayesian model may apply equally to other sensory modalities.

In the case of vision, previous studies have reported the existence of a perceptual length contraction effect only when stimuli are presented in the periphery (Geldard, 1976; Lockhead et al. 1980). In terms of Bayesian inference, a broad likelihood function or a weak sensation can be induced by providing the stimulus in the individual's periphery (i.e. low spatial acuity). Providing such manipulations would lead to a perceptual length contraction effect, as reported in the literature. However, a central visual stimulus (i.e. high spatial acuity) would lead to a sharper likelihood function, thus producing less perceptual length contraction. These results, therefore, are in line with what the Bayesian perceptual model proposes and what is observed in the tactile modality. Furthermore, in keeping with our model's predictions and our tactile experimental results, we hypothesize that manipulation of light intensity would have the same effect in the visual modality as manipulating the strength of taps did for the tactile modality. In particular, we predict that, in peripheral vision, a sequence of dim flashes of light would evoke more length contraction than a sequence of strong flashes. Currently no research exists supporting this theory and we hope this will elicit vision researchers to shed light onto this eye-opening phenomenon.

2.4.4 Future Directions

Several ways of manipulating the sensation of space have been outlined above. One method that has not been outlined is selective attention. Directing one's attention to a particular location on their arm increases spatial acuity in that location (Moore, Partner, & Sedgwick, 1999). According to the Bayesian model, directing one's attention to an area should elicit the same effect as applying a strong tap to that area (i.e. sharp likelihood function). The unattended area can be considered analogous to applying a weak tap (i.e. broad likelihood function). This effect should produce the same asymmetrical perceptual length contraction as seen in the mixed tap condition (Goldreich, 2007; Goldreich and Tong, 2013). This effect has been shown by Kilgard and Merzenich (1995). Their study, however, did not measure each participant's spatial acuity. Furthermore, their study only recorded the participant's perceived tap location after ten repeated trials of the same stimulus, rather than after every trial. As a future study, our lab could measure each participant's spatial acuity by doing σ_s measures on the attended and unattended areas.

Despite the success of our Bayesian model in predicting trends in the behavioural data, some quantitative discrepancies between model predictions and observed data were noted. Figure 1a and 1b illustrate the length contraction magnitude difference between the SS and WW condition. A careful observation of the model fits at the smaller SOAs reveals that the model expects more length contraction than what our experimental data reveal. This observation made us ponder, why that may be. The length contraction equation (Eq. 1) introduced in the introduction is also referred to as the basic observer in our lab—this is because the basic equation perceives time veridically; therefore, it assumes time is processed accurately without the possibility of time perception. The full observer introduces temporal uncertainty and therefore a perceived time between taps, *t**, that does not necessarily equal the veridical SOA, *t.*

$$l^* = \frac{l_m}{1 + 2\left(\frac{\sigma_s}{\sigma_v t^*}\right)^2}$$

(Equation 3)

$$\frac{t^*}{t} = \frac{\sigma_s}{\sigma_v t}\sqrt{\frac{2l^*}{l - l^*}}$$

(Equation 4)

Equation 3 is the full observer model rearranged into equation 4 to equal t^*/t. This equation reveals that if the basic observer model were to be true, then t^* would equal t (i.e. a value of 1), thus revealing accurate time perception. However, the data in figure 3a and 3b intriguingly suggest that participants are overestimating the time between taps especially at the smaller times. Our lab defines this phenomenon as time dilation. Time dilation may be the cause of the observed discrepancy at the smaller SOAs and must therefore be investigated. The model makes two predictions: 1) as SOA decreases, the ratio t^*/t will increase, and 2) weaker taps will elicit more time dilation than stronger taps; this is exactly what is observed in the data.

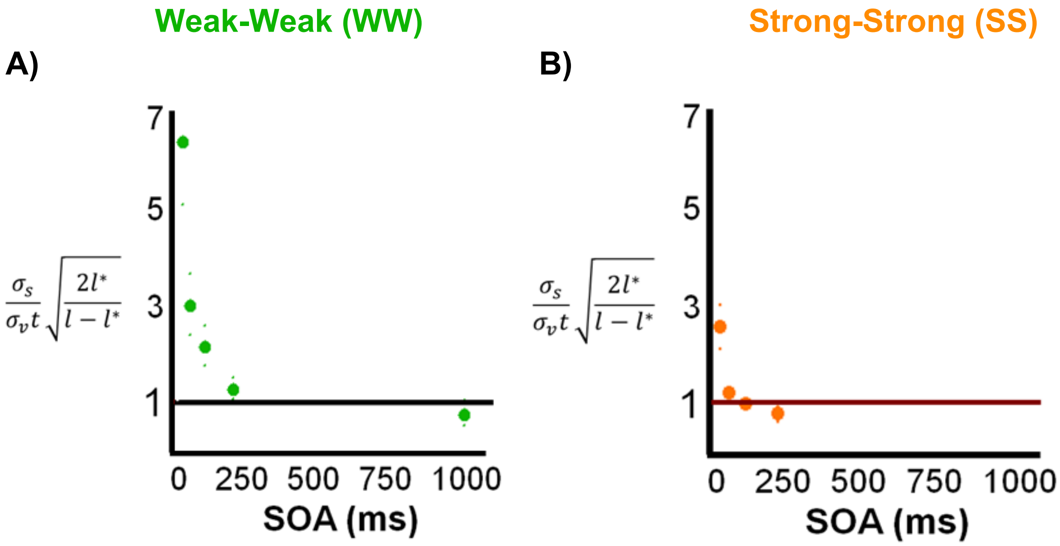


Figure 3. The experimental data from the length contraction experiment was used to graph the time dilation model for both the A) WW and B) SS conditions across the five SOAs. The black line through 1 indicates the ratio of perceived time (*t**) to actual time (*t*) if the basic Bayesian observer model were true. The smaller SOAs are not positioned around 1, thus indicating that time dilation may be involved at the smaller SOAs. The SS graph has a missing data point at 1000 ms, this is because the perceived 1000 ms distance (*l**) from the experimental data was used at the actual distance between the taps (*l*) for both WW and SS.

2.5 References

Agur, A. M., & Dalley, A. F. (2009). *Grant's atlas of anatomy*. Lippincott Williams & Wilkins.

Asai, T., & Kanayama, N. (2012). “Cutaneous rabbit” hops toward a light: unimodal and cross-modal causality on the skin. *Frontiers in psychology*, 3, 427.

Flach, R., & Haggard, P. (2006). The cutaneous rabbit revisited. *Journal of Experimental Psychology: Human Perception and Performance*, 32(3), 717.

Garg, K. (Ed.). (2010). *Human Anatomy: Regional and Applied Dissection and Clinical*. CBS Publishers & Distributors.

Getzmann, S. (2009). Exploring auditory saltation using the "reduced rabbit" paradigm. *Journal of Experimental Psychology: Human Perception and Performance, 35(1),* 289—304.

Geldard, F. A. & Sherrick, C. E. (1972). The cutaneous “rabbit”: A perceptual illusion. *Science, 178,* 178—179.

Geldard, F.A. (1976). The saltatory effect in vision. *Sensory Processes, 1(1)*, 77—86.

Geldard, F. A. (1982). Saltation in somesthesis. *Psychological Bulletin*, 92(1), 136.

Girden, E. R. (1992). ANOVA: repeated measures (No. 84). Sage.

Goldreich, D. (2007). A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. *PLoS ONE, 2(3)*. doi: 10.1371/journal.pone.0000333

Goldreich, D. & Tong, J. (2013). Prediction, postdiction, and perceptual length contraction: A Bayesian low-speed prior captures the cutaneous rabbit and related illusions. *Frontiers in Psychology, 4.* doi: 10.3389/fpsyg.2013.00221

Helson H. (1930) The tau effect-an example of psychological relativity. Science 71: 536–537.

Helson H., & King S.M. (1931) The tau effect: an example of psychological relativity. J Exp Psychol 14: 202–217.

Jones, B., & Huang, Y. L. (1982). Space-time dependencies in psychophysical judgment of extent and duration: Algebraic models of the tau and kappa effects. Psychological bulletin, 91(1), 128.

Kilgard, M.P. & Merzenich, M.M. (1995). Anticipated stimuli across skin. *Nature, 373(6516),* 663.

Kamitani, Y., & Shimojo, S. (2001). Sound-induced visual “rabbit”. *Journal of vision*, 1(3), 478—478.

Lockhead, G.R., Johnson R.C., & Gold F.M. (1980). Saltation through the blind spot. *Perception & psychophysics, 27(6),* 545—549.

Moore, C.E., Partner, A., & Sedgwick, E.M. (1999). Cortical focusing is an alternative explanation for improved sensory acuity on an amputation stump. *Neuroscience Letters, 270(3),* 185—187.

Miyazaki, M., Hirashima, M., & Nozaki, D. (2010). The “cutaneous rabbit” hopping out of the body. *Journal of Neuroscience*, 30(5), 1856—1860.

Senna, I., Parise, C. V., & Ernst, M. O. (2015). Hearing in slow-motion: Humans underestimate the speed of moving sounds. *Scientific reports*, 5, 14054.

Shams, L., Kamitani, Y., & Shimojo, S. (2004). Modulations of Visual Perception by Sound.

Shore, D.I., Hall, S.E., Klein, R.M. (1998). Auditory saltation: a new measure for an old illusion. *The Journal of the Acoustical Society of America*, 103(6), 3730—3733.

Tong, J., Ngo, V., & Goldreich, D. (2016). Tactile length contraction as Bayesian inference. *Journal of neurophysiology*, 116(2), 369—379.

Trojan, J., Stolle, A. M., Mršić Carl, A., Kleinböhl, D., Tan, H. Z., & Hölzl, R. (2010). Spatiotemporal integration in somatosensory perception: effects of sensory saltation on pointing at perceived positions on the body surface. *Frontiers in psychology*, 1, 206.

Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex and laterality. *The skin senses: Proceedings*, 195–222.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature neuroscience*, 5(6), 598—604.

Welchman, A. E., Lam, J. M., & Bülthoff, H. H. (2008). Bayesian motion estimation accounts for a surprising bias in 3D vision. *Proceedings of the National Academy of Sciences*, 105(33), 12087—12092.

Chapter 3 — Are we there yet: Time Dilation in the Tactile Space

3.1 Introduction

How does one perceive time? This perplexing question has left many researchers baffled over the years. An individual who has the ability to perceive time has the ability to define and discriminate temporal intervals between events. Mystery surrounds both the calculations the brain conducts to perceive time and the neural circuitry underlying those calculations. A first step towards understanding the neural circuitry is to identify the cortical areas where time is being processed.

3.1.1 Neurophysiology of time perception

Researchers have found there is no single sensory system in the body that processes time; rather, it is a collection of systems working in tandem (Rao et al., 2001). According to some studies, these systems are dichotic in nature, where cell clusters within the cerebellum, cerebral cortex, and basal ganglia focus on ultradian rhythms (short range; i.e., 1 hr - 24 hrs) (Hobson & Pace-Schott, 2002), while the suprachiasmatic nucleus found in the hypothalamus focuses on circadian (daily) rhythms (Welsh, et al., 2010). Other, complementary studies of time divide time into implicit and explicit time. Here, implicit time refers to the time between one's current state and an expected event in the near future. Explicit time measures the temporal length of a stimulus. An example of implicit time would be wondering if one has enough time to eat breakfast before getting to work on time, whereas explicit time would be processing the temporal duration of breakfast. As with circadian and ultradian time, these two forms of time are also processed in two different regions of the brain, where implicit time is localized in the left premotor cortex, cerebellum, and left parietal cortex, while explicit time involves the right prefrontal cortex and the supplementary motor cortex.

There is a large problem within the neurophysiology of time processing: sense processing. All of our senses have the ability to process miniscule temporal durations on the order of tens of milliseconds; however, the senses process at different speeds (Eagleman, 2009). The brain has to formulate a method to temporally unify all the senses by overcoming this obstacle. An efficient method would be to delay processing until the slowest sense reaches the cortex — a delay of about a tenth of a second (i.e. 100 ms). At first glance, it would seem that the problem of synchronizing sensory processing would magnify in any scenario where one is viewing audiovisual content. However, during the early days of television it was discovered that this is actually not a problem. As long as the two signals are synchronized within the window of 100 ms, the individual viewing the content would perceive the signals uniformly. This discovery implies that our awareness is postdictive in nature.

3.1.2 Time dilation

The second fundamental mechanism of time perception is the calculations the brain is conducting to perceive time. This is the harder of the two mechanisms to directly observe, but we can apply the same method of experimentation as we did to test touch perception in chapter two. To understand how time perception is taking place within the touch modality, we can study stimuli that disrupt normal perception (i.e. illusions). Here, we continue to use the cutaneous rabbit paradigm to now observe the perception of time in touch. A temporal illusion closely related to the cutaneous rabbit is the kappa effect, where a longer spatial separation of two stimuli will alter the perceived time between the two stimuli to be longer (Jones & Huang, 1982). Our lab defines this effect as time dilation (Goldreich, 2007; Goldreich & Tong, 2013; Tong et al., 2016). Time dilation, just like its colleague, length contraction, has also been observed in vision (Chen et al., 2016; Kuroda et al., 2016) and audition (Henry & McAuley, 2009).

Time dilation in touch was first discovered in 1952 by Suto and was originally referred to as the S-effect. Suto utilized a three tap design, which allowed for a comparison between two stimuli. He placed taps one and two on the right forearm and kept the length and time constant; the length and time between taps two and three varied. Interestingly, on some blocks the third tap was placed on the left forearm, where the position of the tap was held constant, but the forearm itself would be adjusted into a variety of different positions. Suto's research revealed that as length increased and SOA (stimulus onset asynchrony) decreased, the effect of time dilation became more pronounced.

3.1.3 Bayesian approach to time dilation

A quantitative approach to understand how time dilation is occurring is by using the Bayesian framework mentioned in chapter one. The length contraction equation (i.e. equation I) from chapter two assumed that time perception was veridical. Here, we continue to use the same likelihoods and priors explained in chapter two, however, we discontinue our assumption of veridical time perception and allow for the model to have temporal uncertainty which can lead to misperceptions of time.

$$l^* = \frac{l_m}{1 + 2\left(\frac{\sigma_s}{\sigma_v t^*}\right)^2}$$

(Equation 1)

Equation 1 is the full Bayesian observer model that allows for temporal uncertainty through t^*. It contains the parameters of l_m, σ_s, σ_v, and l^* as found in the length contraction or the basic Bayesian observer model revealed in chapter two. The advantage to this model to the basic

Bayesian observer model is that it can experience both length contraction and time dilation. The degree to which it will experience one over the other can be better understood by the time dilation formula that relates the real (*t*) and perceived times (*t**) (Goldreich, 2007).

$$\boldsymbol{t = t^{*}\left(1 - 2\left[\left(\frac{\sigma_t}{\sigma_s}\right)\left(\frac{\frac{l}{\tau}}{\left(\frac{t\,*}{\tau}\right)^{2} + 2}\right)\right]^{2}\right)}$$

(Equation 2)

To simplify the equation, we substituted the ratio of σ_s/σ_v with τ. The equation also has a new parameter of σ_t, which accounts for an individual's temporal acuity. We will first focus on the effect σ_s has on perceived time and perceived length. Chapter two revealed that a change in σ_s (i.e. the likelihood distribution) is equivalent to a change in spatial acuity; a large σ_s (i.e. a broad likelihood distribution) means an area of low spatial acuity, whereas a small σ_s (i.e. a sharp likelihood distribution) means an area of high spatial acuity. The model predicts that as σ_s increases perceived length decreases (i.e. more length contraction). Conversely, the model also predicts as σ_s increases, perceived time approaches actual time (i.e. less time dilation). Therefore, an an area of poor spatial acuity would experience more length contraction than time dilation. In regards to length, the model predicts as actual length increases perceived length uniformly increases—neither an increase nor a decrease in length contraction; however, an increase in length does lead to more time dilation. Similarly to length, σ_t will have no effect on length contraction, but a larger σ_t does lead to more time dilation. A large σ_t (i.e. broad temporal distribution) means having poor temporal acuity, whereas a small σ_t (i.e. a sharp temporal distribution) means having high temporal acuity. Unlike the previous three parameters, time is predicted to have the same effect on both l^* and t^*; a decrease in actual time leads to more length contraction and time dilation. Importantly, the length contraction predictions by the full Bayesian observer model were supported by our experimental results in chapter two. However, the magnitude of length contraction at the smaller times did not follow the trend predicted by the model. We believe this may have been due to an influence of time dilation at smaller times. As previously stated, shorter times lead to more pronounced time dilation, which translates to perceiving a larger temporal duration than was provided; a larger perceived temporal duration may cause someone to perceive the length to be longer than it actually is. The current study aims to test the effect of time dilation across varying lengths and times, while also testing an individual's temporal and spatial acuity. We hypothesize that our experimental data will support the previously stated predictions and the findings of Suto (1952).

3.2 Methods

3.2.1 Participants

48 undergraduate students from McMaster University participated in this study. Before the experiment, participants reviewed an exclusion criteria list and self-reported not having any of the listed conditions that might hinder performance on the experiment (e.g. diabetes, dyslexia, attention deficit, learning disability, neurological disorders, carpal tunnel, arthritis, hyperhydrosis, low vision, and any left arm damage—cuts, scars, callouses, or nerve damage). Students from the Psychology, Neuroscience & Behaviour (PNB) program at McMaster were also excluded from participating in the study. These students have learned about the cutaneous rabbit illusion, and thus may be biased in their responses when participating. Participants carefully read the details and possible risks of the experiment outlined in the Letter of Information and Consent and provided signed consent. The McMaster University Research Ethics Board approved the study protocol.

3.2.2 Apparatus

Sub-millimeter mechanical pulses via two cylindrical motors (Tactile Stimulator MkII; Fong Engineering; Oakland, CA, USA) were used to deliver tactile stimuli on the skin of the forearm. Each motor contacted the skin via a rounded stainless-steel pinhead probe (1 mm diameter). A

National Instruments board (PCIe-6259; 16 bit analog output resolution, 2.8 MHz) controlled the motors and was programmed using LabVIEW on a Macintosh MacPro 3.1 computer. Mechanical micro-manipulators (Eric Sobotka Co.) held the probes and allowed the experimenter to adjust their angular, vertical, and horizontal positions. A linear variable displacement transducer (LVDT) was used to measure real time displacement of the probes. The probes were indentated 0.5 mm into the skin using the LVDT program. The taps followed a single-period sine wave pattern for a duration of 10 ms and a displacement amplitude of 150 μm. Before beginning the experiment the perceived strength of each tap was tested by tapping the participant with each stimulator. If the participant indicated that one tap felt weaker than the other, the weaker tap stimulator was lowered into the skin by 100 μm increments until the taps felt subjectively equal.

3.2.3 Sensory Testing Procedures

Prior to beginning the experiment, the participant washed their left forearm. Participants were alternately assigned to either Group A (even number participants) or Group B (odd number participants) (see Time Dilation section below). Using a ruler and a washable-ink pen, the experimenter marked the participant's forearm at 0.5 cm increments. The drawn ruler acted as a guideline for the experimenter in placing the stimulators precisely on the forearm. The stimulators were placed behind an opaque black curtain in order to hide them from the participant’s view. The experimenter helped the participant guide their arm behind the black curtain, to be placed precisely under the stimulators with the palm side up. The stimulators were positioned on the skin of the lateral forearm, which is innervated by the lateral antebrachial cutaneous nerve. This allowed us to avoid positioning the stimulators over the flexor carpi radialis tendon running down the middle of the forearm (Agur & Dalley, 2009). To minimize movement and to increase the participant’s comfort, the arm was placed in a foam padding, which supported the arm from both sides and from the bottom. During the experiments a sound conditioner (Marsona 1288A; Marpac) played white noise to mask any audio cues that might emanate from the motors. 2 minute breaks were periodically provided to the participant. During the breaks they were recommended to get up and walk around and if need be to take a longer break.

Participants undertook a battery comprising three tactile testing procedures to assess their tactile temporal acuity, time perception, and spatial acuity (see below). All testing protocols were conducted with a modified version of the Psi method, a Bayesian adaptive psychophysics procedure (Kontsevich and Tyler, 1999).

3.2.4 Tactile Temporal Acuity Testing (σ_t)

The stimulators were placed 10 cm apart, centered in the middle of the forearm. In a 2-interval forced choice (2-IFC) design the participant received two taps and indicated whether they felt the first tap closer to the wrist or the elbow relative to the second tap. The participant provided their responses by clicking the left (wrist) or right (elbow) key on a presentation pointer (Kensington, 33374-P). The participant underwent a total of 120 trials, where the SOA was adjusted from trial to trial based on the participant's performance. Depending on the participant's performance, they received SOAs ranging from 25 ms to 350 ms. After completing the experiment the participant's Bayes Factor (BF) and σ_t mode was determined. The BF is a likelihood ratio between the probability of the participant's performance given that the participant was randomly guessing on every trial and the probability that their responses followed a best-fit psychometric function. The BF provides a quantitative method to see how consistent the participant's answers were. A low BF factor means that the participant's answers were not random, and implies they understood the task and were performing it to the best of their ability. However, a high BF means that the participant's answers were random, and implies they either did not understand the task, were not paying attention and guessing, or were genuinely unable to do the task. Participants that were unable to do the task may belong to a group of individuals that have natural differences in their tactile acuity and sensory processing that makes completing the task too difficult. Furthermore, since we have a SOA ceiling of 350 ms, participants that have a temporal threshold bigger than this time would find the task difficult, which would result in a high BF. A higher ceiling could have been set; however, 350 ms is already more than double our smallest testing SOA of 150 ms (see Time Dilation section below), which would mean that the individual would have a difficult time responding to the rest of the tasks. Also, we believe that if an individual's performance would result in a temporal threshold bigger than 350 ms, then they are either not focused on the task, or they belong to an extremely small population of individuals that would be unable to do the rest of the experiment due to their natural differences in their tactile acuity and sensory processing. Participants who showed BFs of 0.1 or higher were excluded from further testing and their data are not included in this report. Two participants were excluded for this reason. Each participant's σ_t was taken from the mode of their posterior probability distribution function (PDF). A small σ_t implies that a participant has excellent time perception and is able to discern very short temporal intervals.

3.2.5 Time Dilation Percent Determination

As in the previous task, this task also followed a 2-IFC paradigm; however, in this task instead of experiencing two taps, the individual experienced two pairs of taps. The participant was asked whether the time between the first or second pair of taps was longer. Like the previous task, the responses were recorded via a presentation pointer (Kensington, 33374-P) by clicking the left (1st pair) or right (2nd pair) key.

Depending on which group the participant belonged to, they were tested on either three lengths (i.e. separations) and two SOAs (Group A) or two lengths and three SOAs (Group B). Group A received 5 cm, 7.5 cm, and 10 cm at 150 msec and 600 msec, while Group B received 5 cm and 10 cm at 150 msec, 300 msec, and 600 msec. The participant received the different times and lengths in either ascending or descending order and this was counterbalanced across participants.

Of the two pairs of taps, one pair had a constant SOA and was referred to as the test pair, while the other pair had a varying SOA and was referred to as the comparison pair. The two taps in the test pair were administered via the two separate motors (i.e. at distinct locations), whereas the two taps in the comparison pair were administered by a single motor (i.e. at one location). The test SOA was either 150 msec, 300 msec, or 600 msec, in separate blocks. The comparison SOAs ranged from 25 - 400% of the test SOA and were based on a Bayesian adaptive method. The order in which the test and comparison taps were received was also counterbalanced, as well as whether the first tap was proximal or distal. Stimulus sequences were designed such that three consecutive taps never occurred in one location; i.e., if for a particular participant the test pair preceded the comparison pair, and the test pair was distal followed by proximal, then the comparison location would be distal in order to avoid 3 taps in a row at the proximal location.

The participant experienced a total of six blocks of 50 trials, with each block keeping the test SOA and length constant. At the end of each block, the participant's BF and point of subjective equality (PSE) was determined: the comparison SOA that was perceived to equal the test SOA with 50% probability. The PSE was used determine the participant's percent time dilation, defined as:

$$\%\,Time\ Dilation = \left(\frac{(PSE - Test\ SOA)}{Test\ SOA}\right) x\ 100$$

(Equation 3)

A percent time dilation greater than 0 indicates that a participant perceived the test SOA to be longer than it actually was (i.e. time dilation). Participant's with BFs equal to or greater than 0.1 in any of the six blocks still continued with the experiment; however, their data was not analyzed with individuals with low BFs. 11 of the total 48 participants had a high BF in at least one of their time dilation blocks.

3.2.6 Tactile Spatial Acuity Testing (σ_s)

From the point of view of the participant, the final task is the same as the first task, but in this case length rather than SOA was adjusted. The participant began the task with the two stimulators 2 cm from each other, centered on the middle of the forearm. After every 20 trials (for a total of 120 trials) the length was adjusted using the Bayesian adaptive procedure described below. The total possible distance the participant could experience ranged from 1 cm to 8 cm in 0.5 cm increments. At the end of the task, the participant's BF and σ_s values were determined. If a high BF (i.e., greater than 0.1) occurred, the block was repeated. If on the second try the participant again showed a high BF, their data on this and all tasks were excluded from analysis. Only one participant reached a high BF (the same participant had a high BF on the time dilation task). Each participant's σ_s value was taken from the mode of the posterior PDF for σ_s. A smaller σ_s value implies that a participant has excellent spatial discrimination.

3.3 Results

3.3.1 Time dilation is significantly increased at shorter SOAs and non-significantly increased at greater lengths

Figure 1a and 1b show the average percent time dilation each group (A and B respectively) experienced across the different SOAs. As SOA decreased and length increased the amount of time dilation increased. Two separate two-way repeated measures ANOVA were utilized with length (group A: 5 cm, 7.5 cm, 10 cm and group B: 5 cm, 10 cm) and SOA (group A: 150 ms, 600 ms and group B: 150 ms, 300 ms, 600 ms) as within-subjects variables. Group A showed a significant main effect of SOA and no significant main effect of length (SOA: (F(1, 16) = 5.196, p = 0.037); length: (F(1, 16) = 5.196, p = 0.037)). Group B showed similar results (SOA: (F(2, 34) = 6.586, p = 0.004); length: (F(1, 17) = 0.011, p = 0.918)). The interaction between SOA and length was not significant in either group (group A: (F(2, 32) =0.519, p = 0.600); group B: (F(2, 34) = 0.314, p = 0.733).

We subsequently combined the data from the common conditions in groups A and B (e.g. 150 ms and 600 ms at 5 cm and 10 cm) (Figure 3). Here, there was also a main effect of SOA, no significant effect of length, and no interaction effect (SOA: (F(1, 34) = 15.208, p = 0.000); length: (F(1, 34) = 0.692, p = 0.411); interaction: (F(1, 34) = 0.057, p = 0.813)).

These results indicate that smaller SOAs elicit more pronounced time dilation than larger SOAs; length does not significantly affect time dilation, although the data indicate a nonsignificant trend in this regard; finally, SOA and length do not interact to affect time dilation.

3.3.2 Individuals eliminated from the study had worse temporal and/or spatial acuity

11 of the 48 participants were removed from the experiment due to having a high Bayes factor (BF). Apart from their high BF, these individuals also show a trend of having a higher time and length threshold compared to the individuals with a low BF. We conducted two separate independent samples t-tests comparing both the time threshold (σ_t) and length threshold (σ_s) of the high and low BF populations. For σ_t there was a significant difference between the high BF and low BF populations (high BF: (M = 179.1818 ms, SD = 57.953 ms); low BF: (M = 132.4054 ms, SD = 63.402 ms), t(46) = 2.188, p = 0.034). Similarly, the σ_s thresholds between the two groups were also significantly different (high BF: (M = 5.578 mm, SD = 2.575 mm); low BF: (M = 2.899 mm, SD = 1.419 mm), t(46) = 4.490, p < 0.001). These results indicate that the excluded population had higher spatial and temporal thresholds as well as having a higher BF.

3.3.3 Median graphs illustrate a strong length effect

Figure 2a and b display the median percent time dilation for group A and B respectively, whereas figure 3b displays the median percent time dilation for Group A and B combined. Comparatively, the median graphs illustrate a more pronounced effect of length on perceptual time dilation than their average graph counterparts do. The experimental data have a wide range of data points and outliers that would cause problems when calculating the average. The average is sensitive to outliers, which are not representative of the data set and therefore cause the graphs to be skewed. The median avoids this problem and as a result is not influenced by outliers. Currently the experiment has successfully been run on 37 participants, which is 27 short of our 64 participant goal. We hypothesize the experimental average results will begin to mirror the median graphs as we approach our participant goal—the larger data set will cause the average results to be less sensitive to outliers.

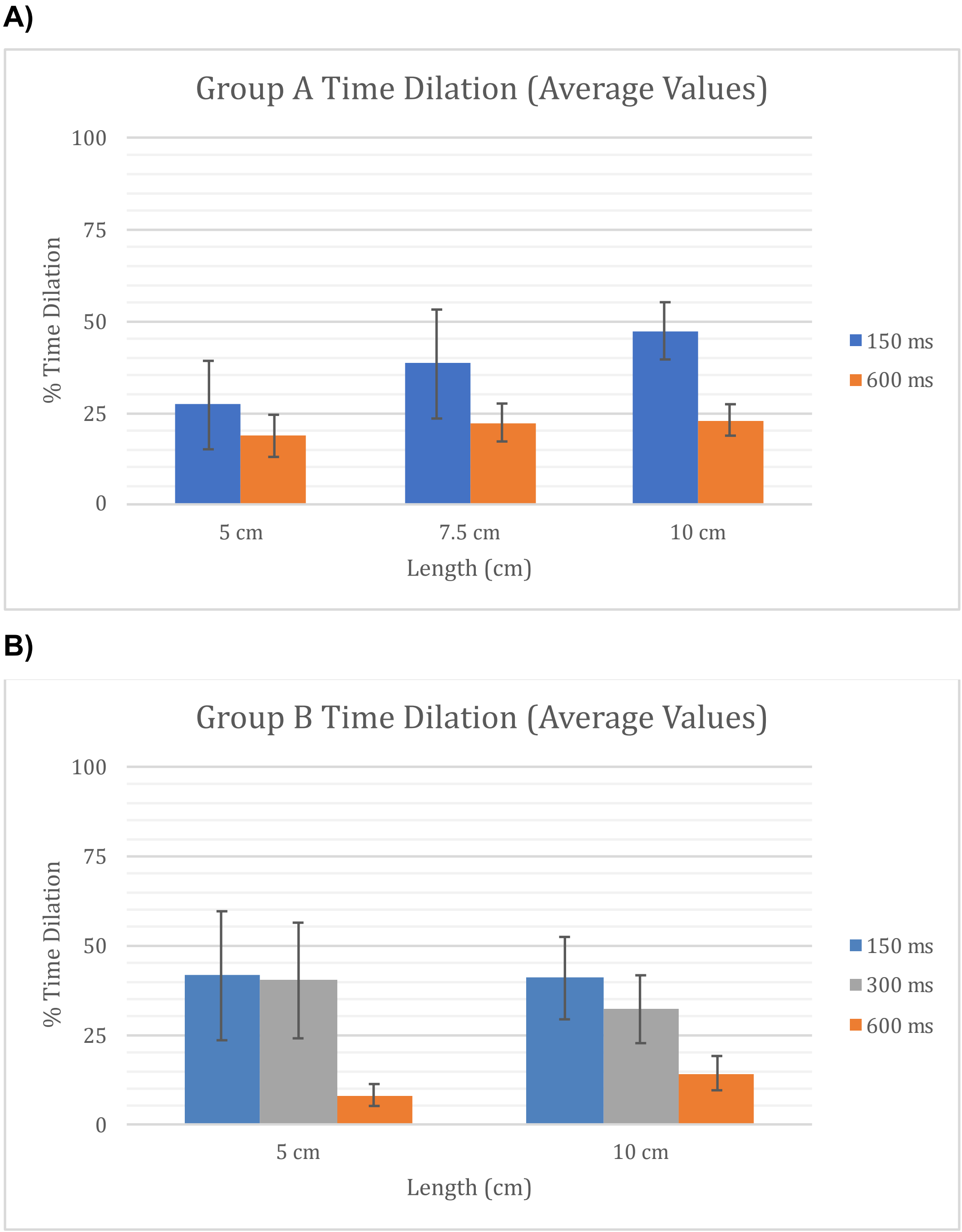
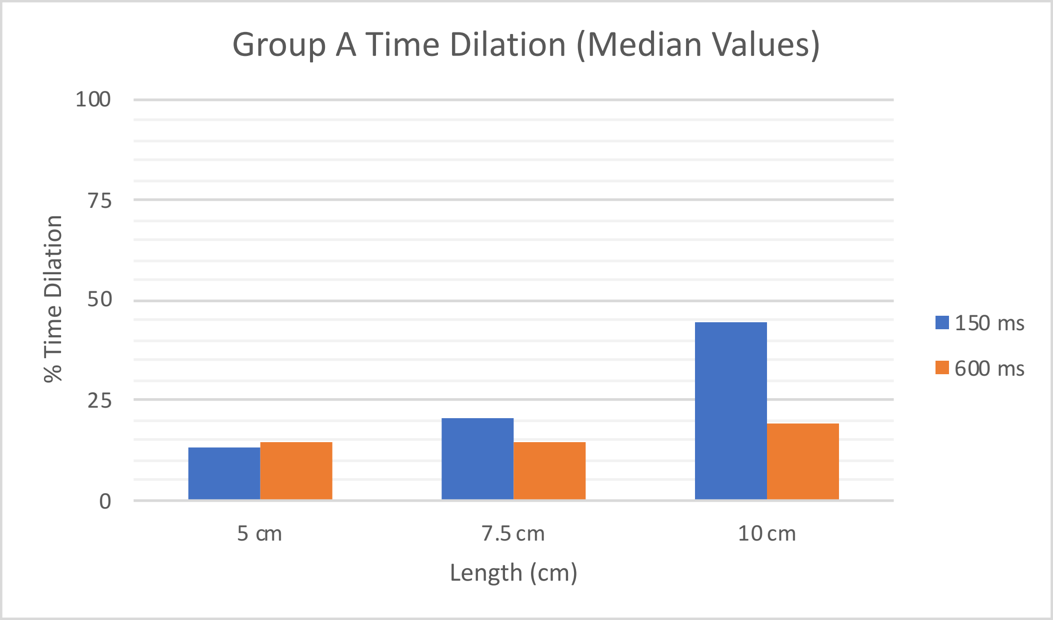


Figure 1. The percent average time dilation across A) three lengths and two SOAs (for Group A) and B) two lengths and three SOAs (for Group B). Both graphs indicate standard error bars for each condition.

A)



B)

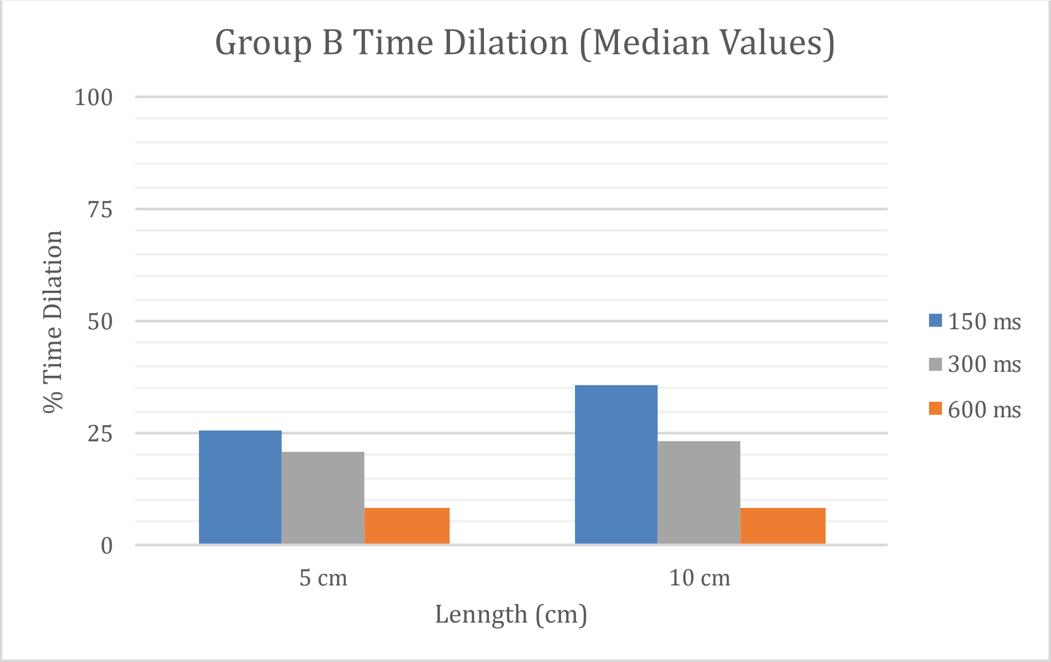
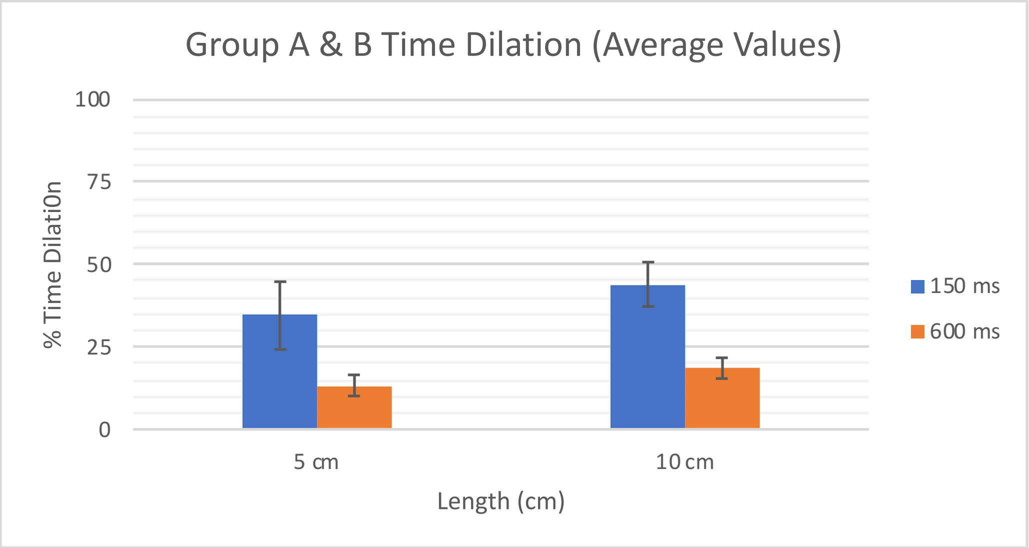


Figure 2. The percent median time dilation across A) three lengths and two SOAs (for Group A) and B) two lengths and three SOAs (for Group B).

A)



B)

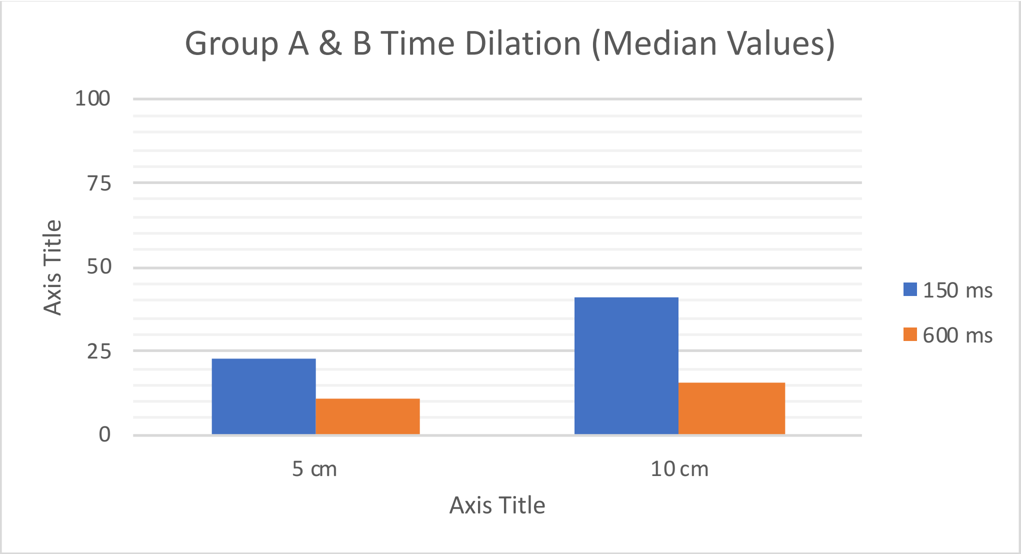


Figure 3. These graphs combine the data for the shared conditions between Groups A and B. A) The graphs reveal the average percent time dilation for 5 cm and 10 cm at 150 ms and 600 ms across both groups. B) The graphs reveal the median percent time dilation for 5 cm and 10 cm at 150 ms and 600 ms across both groups.

3.4 Discussion

The results of 37 participants on tactile temporal perception psychophysical experiments have confirmed the strong effect of time dilation at smaller SOAs than larger ones. Although the results do not indicate a strong effect of length, there is a clear trend towards more time dilation at longer lengths than smaller ones. Furthermore, the 11 excluded participants consistently displayed weaker temporal and/or spatial acuity, thus providing support for the Bayes factor exclusion criterion. Our results, although not all significant, are largely consistent with the predictions of the Bayesian observer model previously proposed by our laboratory (Goldreich, 2007).

3.4.1 Comparison to previous studies

The kappa effect—perceptual time dilation as defined by our lab—is not as well documented as other illusions due to how difficult it is to study and replicate; it is even less documented in the tactile modality. For a participant to compare miniscule differences in time tends to be significantly harder than to compare differences in length, as in the tau effect. Space, unlike time, is easier to interact with (it can be felt and seen) and manipulate. Suto (1952) originally discovered the existence of time dilation. He ran many interesting experiments where three taps were used either all on one forearm, or across two forearms in a variety of positions.

He kept the time and distance between taps one and two the same, while varying the time and distance (or the position of the forearm in the two forearm experiments) of taps two and three. He found consistently that larger distances between taps resulted in more pronounced time dilation.

Suto continued this research to study whether the illusion occurred as well among blind individuals. His results revealed that congenitally fully blind individuals did not experience the illusion, whereas individuals who had sight for a minimum of 10 years experienced the illusion. These results might suggest that although the illusion is occurring in the tactile modality, prior experience with visual stimuli is needed to experience of the illusion (Suto, 1955). An intriguing alternate explanation, however, is that in the absence of vision, blind individuals rely heavily on the sense of touch and develop heightened temporal acuity (small σ_t), leading to a reduction in time dilation as predicted by our model. A previous experiment from our lab revealed a similar result in a vibrotactile masking experiment; congenitally blind individuals who were proficient braille readers showed much less effect of backwards masking than did individuals who were not proficient braille readers (Bhattacharjee et. al., 2010).

Similarly to Suto, our current experiment measured the magnitude of time dilation across different lengths and times; however, in addition to time dilation, we measured each participant's sigma t and sigma s. Having these temporal and spatial threshold data enables us to do deeper analyses, which may shed light on how an individual’s temporal and spatial acuity affect the extent of time dilation they experience. We conducted these analyses and display their results in figure 4, 5, and 6. In figure 4 we compare the sigma t and sigma s data. At first glance, one notices a clear difference in the temporal and spatial acuity of the low BF and high BF groups. During the experiment, the smallest SOA and length that a participant received were 150 ms and 5 cm respectively. A careful observation of the high BF group reveals that, 10 out of the 11 participants in the high BF group have either a high spatial acuity (i.e. >5 cm), a high temporal acuity (i.e. >150 ms), or both. This means that majority of the individuals that received a high BF were unable to properly perceive the stimuli they were provided. Interestingly, there appears to be a positive relationship between sigma t and sigma s—as one increases so does the other. This is true for both the high BF and low BF groups. This indicates that an individual with poor temporal acuity is likely to also have poor spatial acuity, and the same holds true for high acuity. In figure 5 we compare the highest percent time dilation a participant experienced (regardless of block) and compared it to their sigma t. Our model predicts that as sigma t increases, perceptual time dilation increases as well. This trend is clearly seen in the experimental data and therefore it supports the model prediction. Figure 6 compares the highest percent time dilation a participant experienced (regardless of condition) to the participant's sigma s. The model predicts that as sigma s increases, perceptual time dilation decreases. Just as sigma t, the sigma s prediction also holds true in the experimental data and therefore support the model predictions. The additional data of the participant's sigma t and sigma s allowed us to better understand our results and thus, gain a better understanding of the underlying perceptual processing that the brain may be conducting. Although there are differences in methodologies between Suto and our design, the results are very similar; this conveys the strength and generality of the time dilation effect.

3.4.2 Experimental results support the model

Our results are predominantly consistent with the following predictions of the model: 1) Our brain has learned from all the tactile experiences in our life that tactile stimuli tend to move slowly; therefore, we expect objects to move slowly across the skin. 2) As SOA decreases, the effect of time dilation will become more pronounced. 3) As length increases, the effect of time dilation will become more pronounced. 4) At large SOAs, the effect of time dilation will be negligible.

In the current study, we manipulated two variables in order to test perceptual time dilation: length and SOA. Suto's (1952) results revealed more pronounced time dilation at longer lengths and shorter SOAs. This supports our data and the Bayesian perceptual model's prediction for the effect of length and SOA on perceptual time dilation. Although the results for length were not significant, the data reveal a clear trend in that direction. The non-significant result may be attributed to another prediction the model makes: time dilation is more pronounced on body areas of higher spatial acuity. The forearm is an area of low spatial acuity; therefore, the effect of time dilation in this area would be significantly less than an area of higher spatial acuity, such as the finger (Weinstein, 1968). Previous studies of time dilation have also been done on the forearm, which may be why it has been difficult to study and replicate.

Suto's (1955) work on the congenitally blind can also be explained via the Bayesian framework. Congenitally blind individuals have a smaller sigma t and sigma s (i.e. high temporal and spatial acuity respectively), which may be due to a combination of neuroplasticity and training (Goldreich & Kanics, 2003; Goldreich & Kanics, 2006; Bhattacharjee et al., 2010; Wong et al., 2011). Congenitally blind individuals have to depend on their senses of touch and hearing to interact with the world at a very young age. Over time, they gain experience and train these senses to interact with their surroundings as efficiently as possible. Training presumably facilitates a variety of neuroplastic changes both within the the somatosensory and auditory cortical areas, and in other areas. For instance, in congenitally blind individuals, neuroplasticity leads ttouch and hearing to take over the cortical areas normally devoted to vision, thereby causing blind individuals in effect to have larger somatosensory and auditory cortices.

3.4.3 Future Directions

An experiment we have considered doing is testing both length contraction and time dilation on a participant. Testing both phenomenon will provide us with the participant's σ_s, σ_t, l^* and t^* data. The interesting and exciting outcome of this study would be the ability to get a more accurate σ_v of the participant. All of our previous experiments have discussed in great detail the existence of the low-speed prior and how it is the best explanation for the results we and many others have achieved (Goldreich, 2007; Goldreich & Tong, 2013; Tong et. al., 2016). This also extends out to research of length contraction and time dilation in other modalities (Henry & McAuley, 2009; Senna et al. 2015; Chen et al., 2016; Kuroda et al., 2016). A combined length contraction and time dilation study will allow us to thoroughly test our low-speed full Bayesian observer model and analyze how well it is or is not supported by the experimental results.

The next step after doing a thorough low-speed full Bayesian observer model experiment would be to test and manipulate σ_v. In order for us to do so, we must understand priors and the difference between contextual and structural priors. Contextual priors are circumstantial and tend to be relevant for brief situations. They are also easily manipulated, whether that be explicitly or implicitly via “instructions (e.g., Sterzeretal et al., 2008; “the same stimulus will be repeated”), sensory cues (e.g., Posner, 1980; an arrow indicating that a stimulus will appear on the right), or by the spatial, temporal, or stimulus context in which a stimulus is shown (Chun & Jiang, 1998; Haijiang et al.,2006)” (Seriès & Seitz, 2013). Conversely, structural priors are crucial to interacting with the world on a daily basis. They begin forming through a series of interactions with the natural world at a very young age; this usually takes place in the form of implicit learning or they may be priors that are innate and have been passed down from many generations. Unlike contextual priors, structural priors are not easily manipulated; however, in certain scenarios a contextual prior may overpower a structural prior. The light from above prior (Fig. 4) is a strong structural prior, which can be overpowered in a context where light is consistently coming from a different direction. An individual will begin to expect the light to come from that direction in that specific environment, but once the individual leaves the environment, the structural prior remains the primary perceptual influence (Kerrigan & Adams, 2013). We believe that the low-speed prior may be a structural prior built by implicit learning of tactile stimuli from a very young age. The brain has taken all the accumulated experiences of tactile stimuli and formed an expectation to how tactile stimuli will generally interact with the skin, which we believe to be of low-speed centered at 0 m/s.

A method to manipulate σ_v would be to follow the same concept mentioned during the light from above prior example: to create an overpowering contextual prior. All the studies in the past involving the cutaneous rabbit illusion have hidden the stimulators from the view of the participant. This was done to prevent the participant from knowing the actual tap locations. Revealing the stimulators would presumably create an overpowering contextual prior, resulting in a reduced effect of length contraction. The experiment would be done over several days, in which the first few days the participant undergoes length contraction blocks with the stimulators revealed. These are the training days where they are learning a contextual prior of high-speed to overpower the structural prior of low-speed. During the training days, the magnitude of length contraction should reduce to the point where it eventually diminishes. The last day would be the test day, where the participant would still do length contraction blocks, but this time the stimulators would be hidden from view. We believe that training of a high-speed contextual prior would result in the participant experiencing length dilation rather than length contraction on the test day.

During our experiment we utilized the Bayes factor (BF) exclusion criteria as a method to quantitatively estimate the individual’s probability of random guessing. We set the exclusion threshold to 0.1 and if a participant were to receive a BF of 0.1 or higher, their data were excluded from the sample. The reason we chose 0.1 was because the majority of the participants' had BFs that were significantly smaller than 0.1, as can be seen in figure 5. Also, the results revealed a significant difference in the temporal and spatial acuity between the high BF and low BF population. The high BF population revealed a strong trend of having poor temporal and spatial acuity, whereas the low BF population had significantly high temporal and spatial acuity. Therefore, the BF exclusion criterion correctly excluded individuals who showed signs of either low spatial or temporal acuity (10 of the 11 individuals that were excluded), or a lack of attention and/or understanding of the experiment. This demonstrates the utility of the BF exclusion criterion, and we urge other researchers to adopt this quantitative method as an objective way to detect and exclude participants who are unable to perform a challenging perceptual task.

Prior to beginning the finalized time dilation experiment, we ran twelve different iterations of this experiment across 108 participants. One of our later designs involved providing personalized SOAs to each participant in relation to their σ_t mode. Participants received multiples of 0.5, 1, 2, and 4 σ_t. Interestingly, a significant portion of the participants experienced time contraction (i.e. individuals perceived the time to be shorter than the actual time) rather than time dilation at 1σ_t , and especially at $0.5\sigma_t$. Furthermore, time contraction was more pronounced in individuals with a smaller σ_t mode. This is interesting, as the model predicts individuals with a smaller σ_t to have more accurate time perception. I have theorized four possible explanations for this interesting phenomenon: 1) $0.5\sigma_t$ is below the individual's temporal threshold; therefore, it is too difficult a task; 2) the experiment was done on an area of low spatial acuity (i.e. the forearm); 3) time dilation is a difficult task in general, especially at small SOAs; and 4) participants utilize a different strategy to accommodate the difficulty of the task at smaller SOAs. Below, I discuss each of these four explanations in turn, and propose future experiments to further investigate time dilation.

1) σ_t is a representation of an individual's temporal threshold; therefore, if participants were to receive SOAs smaller than their threshold, the task may become too difficult to do. Tong et. al. (2016) experienced a similar problem where their testing length was smaller than some individuals' σ_s mode. This caused them to exclude the data of about a third of their sample, as the results of some of those individuals revealed that the smaller length may have lead to difficulty in properly perceiving the stimuli. Although this explanation may explain the results seen at $0.5\sigma_t$, it does not explain the time contraction at $1\sigma_t$.

2) The model predicts that as σ_s increases (i.e. an area of low spatial acuity) perceived time will approach actual time. Therefore, time

dilation is more pronounced in areas of high spatial acuity, such as the finger, rather than areas of low spatial acuity, such as the forearm. This in turn should lead to less time dilation across all four SOAs, rather than only having an impact on $0.5\sigma_t$ and $1\sigma_t$, which is not the case. Less time dilation in general would also not cause more time contraction at the smaller SOAs.

3) Comparatively, the σ_t experiment is significantly easier than the time dilation experiment—a sentiment also supported by many of the participants. During the σ_t experiment, the participant had to indicate whether they felt the first tap closer to the wrist or the elbow. This is significantly easier than comparing two temporal intervals with a difference in the order of milliseconds and indicating which of the two intervals was longer. Having an easy temporal acuity task may cause an individual to appear to have a higher temporal acuity than they actually do. Furthermore, the current temporal acuity task design is influenced by spatial acuity due to the separation of the two taps by 10 cm and the required spatial location accuracy of the first tap. A method to solve these problems would be to adjust the temporal acuity task to be slightly more difficult and redesign it to strictly measure temporal acuity. I suggest a task involving two pairs of taps, where each pair is administered by two separate motors at two separate locations; i.e. for a particular participant pair one would be administered by motor one and both taps one and two

would occur at the same spot of 5 cm up the elbow, whereas pair two would be administered by motor two and both taps three and four would occur at the same spot of 5 cm down the wrist. Here, the participant would receive two temporal intervals and would be asked which one is longer. This is a very similar task to time dilation, which makes it harder than the current temporal acuity task, while also having a smaller influence of spatial acuity.

4) Some participants revealed strategies they implemented in order to accomplish difficult tasks involving smaller SOAs during time dilation. The most common strategy was if they found focusing on the temporal interval too difficult they would perceive the length difference between the pairs of taps in order to determine which pair had the longer temporal interval. Their logic was that if the taps were perceived further apart, then that must mean they are separated by a longer temporal interval. This was problematic as the participants were told to ignore any effect of length and solely focus on time during this experiment. This strategy would explain why we saw a trend of time contraction at smaller SOAs. In the time dilation task there were two pairs of taps, the test pair had a constant SOA and was separated by a constant length (both were only constant within a block), whereas the comparison pair had a varying SOA and was separated by no length (i.e. both taps were administered at the same location). If at smaller SOAs the participants relied on length, then the test

pair would always be perceived to have a longer temporal interval as these taps are separated by a length, whereas the comparison taps are not, thus resulting in the data showing time contraction. This was a perplexing problem, which is why we decided to implement three set SOAs for the final design of the experiment.

The smallest SOA (i.e. 150 ms) was purposefully chosen to be significantly bigger than the SOAs that more commonly experienced time contraction (i.e. < 80 ms). However, this was a problem in itself as our initial logic of running this experiment was to determine if time dilation was prevalent at smaller SOAs (i.e. <50 ms) to explain the discrepancies seen in the length contraction experiments of chapter two. A future experiment should take into consideration the four points outlined above. A possible design for this experiment would involve the following: 1) comparing time dilation between the finger and the forearm to test the effect of having a small versus a large σ_s; 2) not providing SOAs that are shorter than the individual's σ_t mode; 3) creating a temporal acuity task that is more difficult and requires less spatial acuity in order to find a more accurate σ_t mode (as the one provided above), while also finding the σ_t mode for the finger and forearm separately; and 4) finding a more efficient method that allows participants to better perceive temporal intervals closer to their σ_t mode, which would prevent them from depending on length.

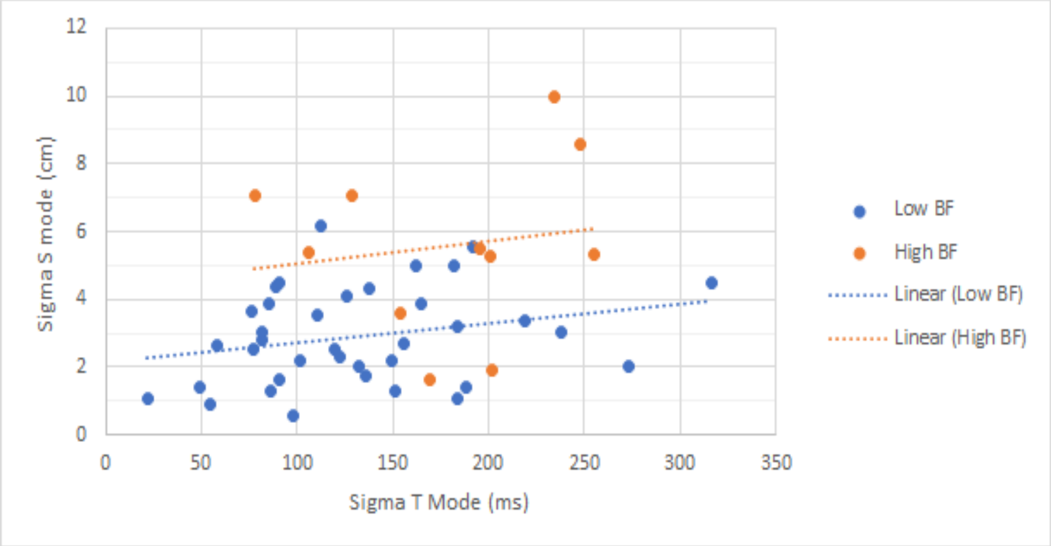


Figure 4. The graph compares all the participants' sigma t mode (ms) to their sigma s mode (cm). These two modes are also between the high BF and low BF groups.

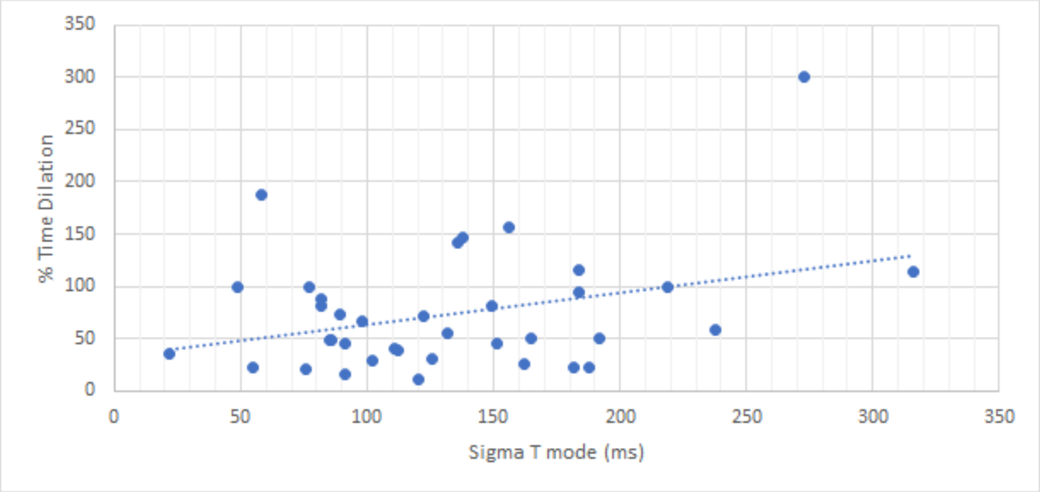


Figure 5. The graph compares all the participants' sigma t mode (ms) to the highest percent time dilation those participants experienced during the experiment. The highest percent time dilation is chosen regardless of the condition the participant experienced it on.

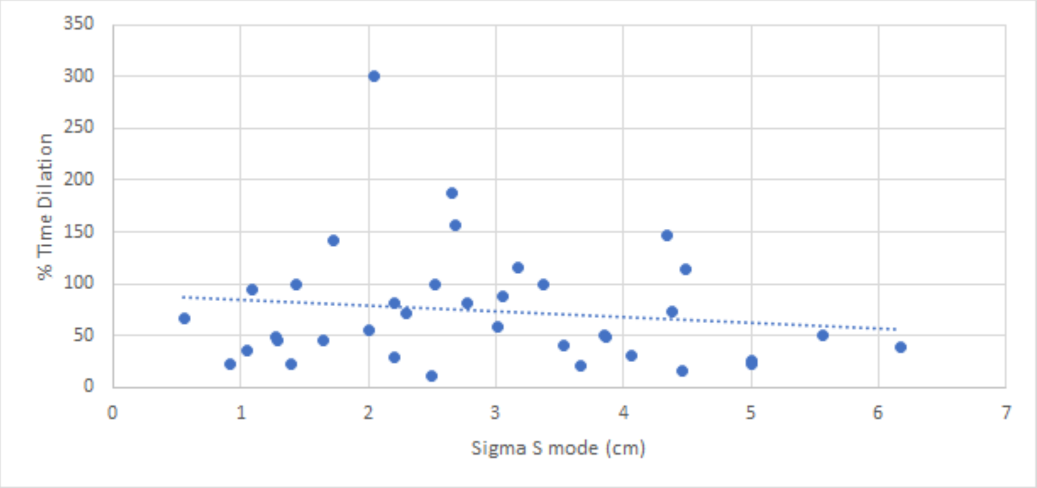


Figure 6. The graph compares all the participants' sigma s mode (cm) to the highest percent time dilation those participants experienced during the experiment. The highest percent time dilation is chosen regardless of the condition the participant experienced it on.

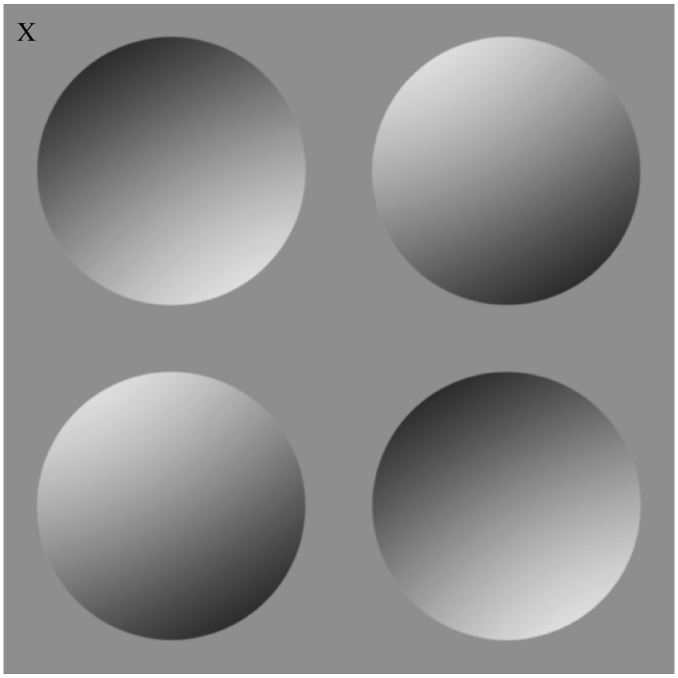


Figure 7. The light from above illusion. Here, the circles from top to bottom have a gradient either going from bright to dark or from dark to bright. This causes the circles to appear convex (bright to dark) or concave (dark to bright). The logic behind this perception is that we have a strong structural prior of expecting light to come from above. This assumption holds true for majority of the situations in the natural world (e.g., the sun and majority of the lights found inside a building tend to be in the ceiling), which is why we have a strong expectation for it. (Stone et al., 2009)

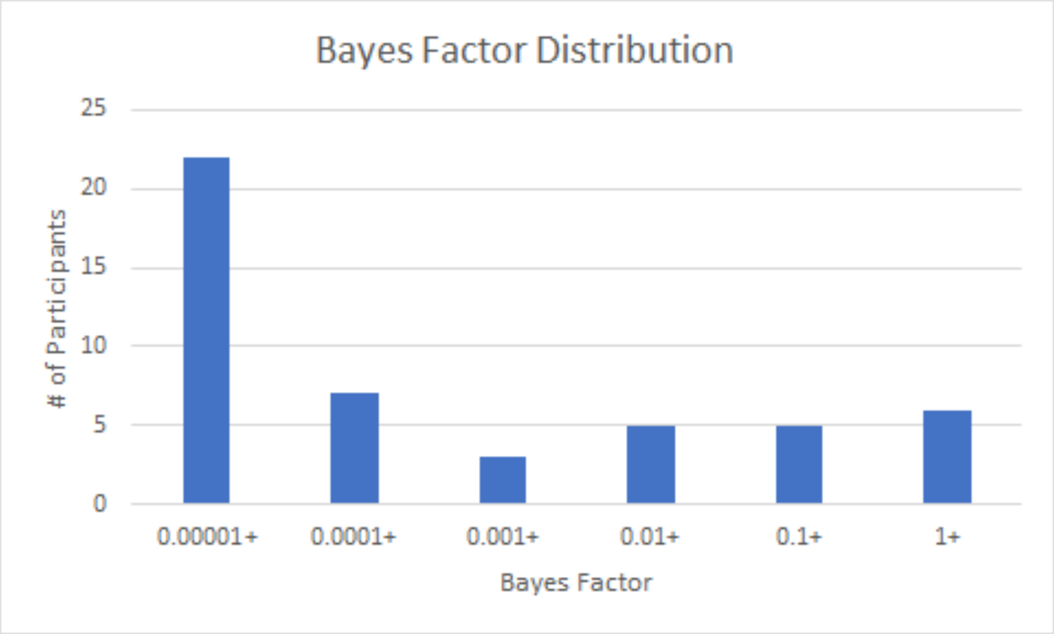


Figure 8. This graph illustrates the highest Bayes Factor (BF) an individual received while running the time dilation experiment, regardless of which block it may be from. The BF data was grouped into discrete logarithmic categories as can be seen above.

3.5 References

Agur, A. M., & Dalley, A. F. (2009). *Grant's atlas of anatomy*. Lippincott Williams & Wilkins.

Bhattacharjee, A., Amanda, J. Y., Lisak, J. A., Vargas, M. G., & Goldreich, D. (2010). Vibrotactile masking experiments reveal accelerated somatosensory processing in congenitally blind braille readers. *Journal of Neuroscience*, 30(43), 14288—14298.

Chen, Y., Zhang, B., & Kording, K. P. (2016). Speed constancy or only slowness: What drives the kappa effect. *PloS one*, *11*(4), e0154013.

Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive psychology*, 36(1), 28—71.

Eagleman, D. M. (2009). Brain time. *What's Next: Dispatches from the Future of Science, edited by M. Brockman. New York: Vintage Books.(Reprinted at Edge. org.)*.

Garg, K. (Ed.). (2010). *Human Anatomy: Regional and Applied Dissection and Clinical*. CBS Publishers & Distributors.

Goldreich, D. (2007). A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. PLoS ONE, 2(3). Doi: 10.1371/journal.pone.0000333

Goldreich, D., & Kanics, I. M. (2003). Tactile acuity is enhanced in blindness. *Journal of Neuroscience*, 23(8), 3439—3445.

Goldreich, D., & Kanics, I. M. (2006). Performance of blind and sighted Humans on a tactile grating detection task. *Perception & Psychophysics*, 68(8), 1363—1371.

Goldreich, D. & Tong, J. (2013). Prediction, postdiction, and perceptual length contraction: A Bayesian low-speed prior captures the cutaneous rabbit and related illusions. Frontiers in Psychology, 4. doi: 10.3389/fpsyg.2013.00221

Haijiang, Q., Saunders, J. A., Stone, R. W., & Backus, B. T. (2006). Demonstration of cue recruitment: Change in visual appearance by means of Pavlovian conditioning. *Proceedings of the National Academy of Sciences*, 103(2), 483—488.

Henry, M. J., & McAuley, J. D. (2009). Evaluation of an imputed pitch velocity model of the auditory kappa effect. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(2), 551.

Hobson, J. A., & Pace-Schott, E. F. (2002). The cognitive neuroscience of sleep: neuronal systems, consciousness and learning. *Nature Reviews Neuroscience*, *3*(9), 679.

Jones, B., & Huang, Y. L. (1982). Space-time dependencies in psychophysical judgment of extent and duration: Algebraic models of the tau and kappa effects. Psychological bulletin, 91(1), 128.

Kerrigan, I. S., & Adams, W. J. (2013). Learning different light prior distributions for different contexts. *Cognition*, *127*(1), 99—104.

Kuroda, T., Grondin, S., Miyazaki, M., Ogata, K., & Tobimatsu, S. (2016). The kappa effect with only two visual markers. *Multisensory Research*, *29*(8), 703—725.

Posner, M. I. (1980). Orienting of attention. *Quarterly journal of experimental psychology*, 32(1), 3—25.

Rao, S. M., Mayer, A. R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature neuroscience*, *4*(3), 317.

Senna, I., Parise, C. V., & Ernst, M. O. (2015). Hearing in slow-motion: Humans underestimate the speed of moving sounds. *Scientific reports*, 5, 14054.

Seriès, P., & Seitz, A. (2013). Learning what to expect (in visual perception). *Frontiers in human neuroscience*, 7, 668.

Sterzer, P., Frith, C., & Petrovic, P. (2008). Believing is seeing: expectations alter visual awareness. *Current Biology*, 18(16), R697—R698.

Stone, J. V., Kerrigan, I. S., & Porrill, J. (2009). Where is the light? Bayesian perceptual priors for lighting direction. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1663), 1797—1804.

Suto Y. The effect of space on time estimation (S-effect) in tactual space.

Shinrigaku Kenkyu 22: 45–57, 1952.

Suto, Y. (1955). The effect of space on time estimation (S-effect) in tactual space (II) the role of vision in the s-effect upon the skin. *Japanese Journal of Psychology*, *26*(2), 94.

Tong, J., Ngo, V., & Goldreich, D. (2016). Tactile length contraction as Bayesian inference. Journal of neurophysiology, 116(2), 369—379.

Welsh, D. K., Takahashi, J. S., & Kay, S. A. (2010). Suprachiasmatic nucleus: cell autonomy and network properties. *Annual review of physiology*, *72*, 551—577.

Weinstein S (1968) Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. *The skin senses : proceedings*. SpringfieldIll.: Thomas. pp 195–222.

Wong, M., Gnanakumaran, V., & Goldreich, D. (2011). Tactile spatial acuity enhancement in blindness: evidence for experience dependent mechanisms. *Journal of Neuroscience*, 31(19), 7028—7037.