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INVESTIGATING THE ROLES OF MECHANORECEPTIVE CHANNELS IN TACTILE
APPARENT MOTION PERCEPTION: A VIBROTACTILE STUDY

By

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THESIS

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Abstract

Tactile apparent motion (TAM) is a perceptual phenomenon in which consecutive presentation of multiple tactile stimuli creates an illusion of motion. Employing a novel tactile display device, the *Latero*, allowed us to investigate this. The current study focused on the Rapidly Adapting (RA) channel and Slowly Adapting I (SAI) channel on the index finger. The experiment implemented vibrotactile masking stimuli to target the mechanoreceptive channels with the goal of gaining better insight into the involvement of mechanoreceptive channels in the perception of TAM. Masking stimuli were used because previous studies have used them to differentiate between different channels; a certain masking stimulus will impact a mechanoreceptive channel more than others. The experiment began by measuring participants' threshold for TAM stimuli by varying the stimulus intensity in a two-choice task (left vs right); participants received test trials consisting of TAM stimuli with 25 Hz and 6 Hz testing for the RA and SAI channels, respectively. Next, participants performed a series of test trials with vibrotactile masking stimuli that preceded the TAM stimuli mentioned above. The vibrotactile masking stimulus varied in duration (4 seconds vs 8 seconds) and intensity (two times vs three times the intensity of the TAM stimuli). The results suggest that there was no difference in accuracy when testing for the RA and SAI channels. The results also showed that the introduction of the masking stimuli significantly lowered accuracy. Overall, neither the RA nor the SAI channel may be uniquely involved in TAM perception. However, further improvement on the current design may aid in isolating each channel to help better understand the channel's role in TAM perception.

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Table of Contents

Title Page.....	i
Abstract.....	ii
Acknowledgements.....	iii
Table of contents	iv
List of Tables	vi
List of Figures.....	vii
List of Appendices	viii
Introduction.....	1
Understanding the Mechanoreceptive Channels and Mechanoreceptors	1
The effects of vibrotactile Masking on Mechanoreceptive Channels	3
Understanding Tactile Apparent Motion.....	6
Current Study and its Rationale.....	10
Method.....	13
Participants.....	13
Material.....	14
Procedure.....	14
Experiment 1: Trials without the masking stimulus.....	14
Experiment 2: Trials with the masking stimulus.....	16
Results.....	16
Discussion	19
Experiment 1: Trials without the masking stimulus.....	19
Experiment 2: Trials with the masking stimulus.....	21
Future Studies and Conclusion.....	24
Tables.	26
Figures.	27

Appendix33

References35

List of Tables

Characteristics of mechanoreceptive channels on the glabrous skin.....	26
Characteristics of masking stimulus used in the experiment.....	26
Counterbalancing of presentation order of the experimental procedure	26
Average number of correct responses and standard deviation in each condition	27

List of Figures

Experimental trial procedure	27
Participant threshold for TAM stimulus in experiment 1	28
The effects of 4 second masking stimulus on participant responses as a function of increasing masking stimulus IV	29
The effects of 8 second masking stimulus on participant responses as a function of increasing masking stimulus IV	30
Comparison of none-masked and masked trials in Mask 1 condition	31
Comparison of none-masked and masked trials in Mask 2 condition	31
Comparison of none-masked and masked trials in Mask 3 condition	32
Comparison of none-masked and masked trials in Mask 4 condition	32

List of Appendices

Appendix A	33
Appendix B	34

Investigating the roles of mechanoreceptive channels in tactile apparent motion perception:

A vibrotactile study

Tactile apparent motion (TAM) can be defined as a perceptual phenomenon when a series of distinct tactile stimuli presented are tied together to create a feeling of motion. Since its discovery, past researchers have investigated the underlying mechanics and characteristics that causes a set of stimuli to be perceived as motion. Furthermore, past research has focused on the behavioural aspect of TAM; there has been very little research done on the neural basis of how such a stimulus is processed. Current research seeks to elucidate which mechanoreceptive channels and their relative receptors are most involved in TAM perception.

Understanding the Mechanoreceptive Channels and Mechanoreceptors

Before discussing TAM perception, it is imperative to understand the function of the mechanoreceptive channels and the corresponding mechanoreceptors themselves. There are four main mechanoreceptive channels: i) Rapidly adapting (RA), ii) Slowly adapting 1 (SAI), iii) Slowly adapting 2 (SAII), and iv) Pacinian (P) channels. These four channels are associated with the Meissner corpuscles, Merkel cell neurite complexes, Ruffini end-organs, and Pacinian corpuscles or paciniform end-organs, respectively (Iggo & Muir, 1969; Chambers, Andres, Duering, & Iggo, 1972; Iggo & Ogawa, 1977; Johansson, 1978). Their respective receptive field and optimal frequency range is shown on Table 1. It is also important to note that the mechanoreceptors are not uniformly distributed across the skin. An example of this is a physiological study by Johansson and Vallbo (1979) that determined the densities of different types of mechanoreceptive units on the hand. The densities of different mechanoreceptive units were measured by stimulating the median nerve and the glabrous skin of the hand and measuring the responses. What was interesting about their findings was that the rate of increase in

mechanoreceptor densities was not linear. Specifically, they had found two points of increase as they measured mechanoreceptor densities from the palm to the fingers: i) between the palm and the base of the fingers and ii) between the most proximal point of the terminal phalanx and the most distal point. Furthermore, this pattern of increase was most exemplified by the densities of the RA and SAI channels, the two mechanoreceptive units with small receptive fields and greater sensitivity to borders (Johansson, 1976) on the index finger. They had near logarithmic increases in mechanoreceptive unit densities between the two points of increase that were mentioned above. This pattern gave insight to the function of the distal phalanx of the index finger; their purpose is to help identify the spatial nature of stimuli. For instance, using the fingertip helps with the understanding of the contour of an object.

Since detection of a tactile motion stimulus could be considered an activity requiring detailed spatial information about the stimulus itself, the two predominant mechanoreceptive units present on the distal phalanx of the index finger are most likely to be involved with TAM. There has also been previous research that suggests that the index finger is one of the most sensitive areas for tactile stimuli (Morioka, 2008). This notion was substantiated by looking at the neural representation of tactile motion stimuli. Both animal and human studies have demonstrated that tactile stimuli are isomorphically represented (Darian-Smith, Davidson, & Johnson, 1980; Johnson & Hsiao, 1992; Johnson & Lamb, 1981). They showed that the SAI channel creates a greater isomorphic representation of tactile motion stimuli than the RA channel. Thus, the function of the SAI channel is to serve as a primary spatial system that translates form and roughness, while the RA channel serves to translate localized tactile events and when the SAI channel is not activated due to small spatial variation of the tactile stimulus (Johnson & Hsiao, 1992). It is possible that the SAI channel could have a more crucial role in

TAM perception due to its higher sensitivity to spatial representation; thus, understanding how the mechanoreceptive channel represents tactile motion stimuli can help to clarify how the mechanoreceptive channels are involved with TAM perception.

The remaining mechanoreceptive channels, P and SAII, are unlikely to be involved in TAM: the former is critical for detecting high frequency vibration, while latter is responsible for detecting skin stretches (Biswas, Manivannan, & Srinivasan, 2015; Olausson & Norsell, 1993). Therefore, the underlying structure of the human hand and the characteristics of the mechanoreceptors themselves gave direction for the current study on deciding on an optimal place to test for the experiment. If the RA channel, SAI channel, and their respective mechanoreceptors are indeed responsible for detecting motion, the distal phalanx of the index finger would be the optimal location for testing.

The Effects of Vibrotactile Masking on Mechanoreceptive Channels

Researchers have also explored thresholds for various tactile stimuli. Notably, research using vibrotactile stimuli shed light on the unique characteristics of different mechanoreceptive channels. This provides an approach to isolating individual channels and their respective mechanoreceptors for the current study.

One interesting area in stimulus detection studies is research involving the use of vibrotactile masking. Gescheider, Bolanowski, and Verillo (1989) investigated the effects of vibrotactile masking on vibrotactile thresholds. Researchers conducted a forced choice task in which participants had to detect the stimulus. The threshold was defined as 75% correct responses. The masking effect, or elevation of threshold, was observed for forward, simultaneous, and backward masking conditions. These conditions differed on the onset of the masking stimulus (before, occur together, after the test stimulus). It was found that: i) the

masking effect was greatest when the test stimuli were in close temporal proximity to the masking stimulus, and ii) the masking effect was greater for forward masking than for backward masking. These findings suggest that the use of a forward mask procedure can result in a reliable masking effect.

A forward mask was also used to differentiate between different mechanoreceptive channels on the hand (Bolanowski, Gescheider, Verillo, & Checkosky, 1988). The authors' hypothesis was that detection of stimuli would become more difficult when the masking stimulus and the test stimulus are concurrently activating the same channel. Past research had uncovered three unique mechanoreceptive channels: Pacinian (P), Non-Pacinian I (NP I), and Non-Pacinian II (NP II) (Gescheider, Sklya, Van Doren, & Verrillo, 1985). Bolanowski et al. (1988) discovered the fourth channel, Non-Pacinian III (NP III), by using a forward mask. They accomplished this by setting up a two alternative, forced choice task experiment in which a participant was presented with a 4 second forward masking vibrotactile stimuli which preceded the test stimuli. They proposed that there was a fourth channel that is sensitive to low frequency vibrotactile stimuli. To demonstrate this, they conducted an experiment with a 40 Hz mask preceding a 0.7 Hz test stimulus. They had also run an identical experiment, except the test stimuli had a frequency of 25 Hz, a frequency that was an optimal vibrotactile stimuli geared towards the NP I channel. For threshold values, they used decibels (dB) referencing a 1 μm peak displacement of the vibrotactile stimulus. The decibel sensation level (dB SL) was used to measure the difference in intensity between the mask and test stimuli; dB SL is a measure indicating the number of dB that one stimuli is above another. Their results showed that the responses to the two experiments differed significantly. In the experiment with the 0.7 Hz test stimuli, no shift in threshold was observed until the mask stimuli was at 10 dB SL (10 μm peak

displacement difference). The relationship between the mask dB SL and the degree in threshold shift was linear with the slope showing a value of 0.46. Meanwhile, the experiment with the 25 Hz test stimuli showed a threshold shift starting when the masking stimuli was at 1 dB SL. The relationship between the mask dB SL and the degree in threshold shift had two distinct relationships depending on the mask dB SL. Mask dB SL 0 to 8 showed a steep linear relationship with a slope value of 0.8. Mask dB SL 8 to 30 showed another linear relationship with a slope value of 0.31. This indicated that the NP I was more susceptible to the 40 Hz forward mask than the NP III channel. Bolanowski et al. (1988) claimed that this stark difference in response between the two conditions was due to the existence of the NP III channel.

Using this method, Gescheider, Bolanowski, Pope, and Verillo (2002) have determined the characteristics of different channels on the fingertip. Using the forward masking procedure, they tested for the vibrotactile thresholds of the P, NP I, and NP III channels. They found that the P channel is responsible for responses at frequencies between 50 to 200 Hz. Meanwhile, the NP I channel and the NP III channel are responsible for ranges between 1.5 to 50 Hz and 0.4 to 1.5 Hz, respectively. Researchers have determined that the P channel is associated with the Pacinian corpuscle. NP I channel (RA) is associated with Meissner corpuscle, and NP III channel (SAI) is associated with Merkel discs.

Another study by Bensmaia, Leung, Hsiao, and Johnson (2005) explored the effects of varying intensity and frequency of the vibrotactile mask on the RA and SAI channels. They found that the RA channel was more susceptible to threshold shift than the SAI channel when increasing the intensity of the masking stimulus. Their results illustrated a linear relationship between threshold shift and masking intensity; the slope was 0.32 and 0.15 for the RA channel and the SAI channel, respectively. However, this relationship was only demonstrated when the

SAI channel was masked by a 30 Hz masking stimulus and the RA channel was masked by a 60 Hz masking stimulus. This result implies that the RA channel may be more susceptible to experience change in threshold compared to the SAI channel. However, the same study found that the SAI channel experiences a greater threshold shift when the masking stimulus increased in frequency. The use of vibrotactile masking illustrates that the RA channel and the SAI channel experience a threshold shift in a complex interplay of masking frequency and intensity.

Past research has shown that each mechanoreceptor has different characteristics when detecting vibrotactile stimuli. This may suggest that perception of TAM using a vibrotactile stimuli will be altered by presenting a forward mask. The underlying concept is that one could differentiate the two mechanoreceptors by presenting them with the optimal tactile stimuli and creating the masking effect. TAM stimuli could be presented after the masking effect has taken place within a single channel. This would provide an opportunity to observe different responses between the channel that has been and has not been affected by the masking stimuli presented before. Research by Bolanowski et al. (1988) was instrumental to the current study because it was the first study to demonstrate a method to isolate the RA and SAI channels.

Understanding Tactile Apparent Motion

One of the earliest studies in apparent motion was examined in the visual system by Korte (1915), in which he established that greater displacement between the stimuli requires greater stimulus onset asynchrony. Lakatos and Shepard (1997) elaborated upon Korte's findings and investigated apparent motion in different modalities. They designed an experiment that implemented a set of 12 stimulators in a circular formation which was presented on the thenar eminence of the participant's hand. They manipulated the number of active stimulators during each trial, which also altered the angular distance between each stimulator. The task of

participants was to determine the direction in which the stimulation was presented: clockwise or counter-clockwise. The results demonstrated that TAM followed Korte's third law: accuracy increased when the increase in distance between stimulus was accompanied with an increase in stimulus onset asynchrony. Their results provided a solid foundation for generating the experimental procedure for the current study.

Kirman (1974a) presented stimulators to simulate apparent motion on the fingertip and manipulated the time of stimulus onset and the duration of the time that the stimulators are active. He showed that as the stimulus duration increased, the overall quality of TAM increased. In addition, his results showed that the optimal interstimulus onset interval (ISOI) of perception of apparent motion was in a J-shaped relationship with stimulus duration. Furthermore, Kirman (1974b) also investigated how the manipulation of the number of stimulators could impact the perception of TAM. It was found that participants reported better perception of TAM for trials with more stimulators active. Kirman (1983) also examined how the shape and type of motion can affect perception of TAM by manipulating seven different pattern types for motion, various ISOIs, and stimulus durations. The results showed that the number of steps involved in a TAM stimulus and the stimulus duration was highly involved in optimal perception of TAM stimulus; however, this was not the case for the pattern types for motion. Kirman's (1983) experiment has shown evidence to suggest that the mechanoreceptive channels may not be partial towards the direction of the TAM stimulus (i.e. up and down vs right and left). Upon further investigation of the relationship between stimulus duration and pattern types, however, Kirman (1983) found that participants' perception of a TAM stimulus with a horizontal line of stimulators moving vertically required longer ISOIs than a TAM stimulus with a pair of stimulators (two dots) moving horizontally to achieve optimal TAM perception. This means that the first pattern

mentioned above required more gap in time between each step of the motion stimulus to be perceived as TAM as stimulus duration increased. They argued that the first pattern would have felt like a square block of active stimulators rather than a wave-like motion with a shorter ISOI; meanwhile, the two dots moving horizontally were more readily accepted as motion despite the shorter ISOI. This is worth taking into consideration because the stimulus duration and ISOI that we use should feel like a wave-like motion when using a vertical line of stimulators moving horizontally. This requires a longer ISOI compared to the stimulus duration of the TAM stimulus.

Sherrick and Rogers (1966) conducted a TAM study similar to Kirman's study (1974a) in the past. They used a 150 Hz vibration of contactors against participants' thighs as their stimuli and varied the ISOIs and stimulus duration. The range of stimulus duration was from 25 to 400 milliseconds. They found a positive linear relationship between the two variables: increases in the stimulus duration required longer ISOIs to be perceived as a good TAM. The slope was approximately 0.65. This relationship contrasted with Kirman's (1974a) results; there was a clear point of decrease and increase of ISOI to create optimal TAM as the stimulus duration increased. Sherrick and Rogers (1966) investigated further and found a similar trend in the lower ranges of stimulus duration. It appears that multiple studies have replicated similar patterns on multiple sites of participants' bodies. Thus, the relationship between stimulus duration and ISOI is thought to be robust. To minimize the time it takes to present the TAM stimulus, ISOI of 70 milliseconds and stimulus duration of 50 milliseconds was chosen from both Kirman (1974a) and Sherrick and Rogers' (1966) study and was implemented in the current study.

There are also studies that have evaluated the neural mechanism behind TAM. Some researchers have used an OPTACON, a specialized braille display apparatus, to investigate the

role of mechanoreceptive channels in TAM perception. Gardner and Palmer (1989) used an OPTACON to present a horizontal TAM stimulus at various speeds. They found that the RA channel was active when the TAM stimulus was presented, but neither SA channels were active. They found that the RA channel was most reactive to the gap of 2.4mm between stimulators and activates in an all-or-none fashion. Their results would suggest that the RA channel is uniquely responsible for TAM perception; however, we believed that the study did not present a fair stimulus for the SAI channel to be represented in the data. The study isolated the SAI and SAI channels as a group using Vallbo and Johansson's (1978) study as a guide. However, previous studies on mechanoreceptive channels demonstrated that the SAI and SAI channels have similar, but distinct characteristics (Bolanowski et al., 1988; Gescheider et al., 2002; Johansson & Vallbo, 1979). Furthermore, the frequency used for the study was based on the frequency of the overall horizontal movement of the OPTACON (25 Hz, 50 Hz, and 100 Hz). Their frequency was based on the ISOI between the stimulators. For example, when the stimulators had a ISOI of 40 milliseconds, the frequency would be 25 Hz. Previous studies by Gescheider et al. (2002) shows that individual channels have optimal frequency to which they respond to; this further shows an unfair stimulus presentation for the SAI system that responds best to a lower frequency. The current study should, therefore, enhance the stimuli presented by vibrating the individual pins at a certain frequency (i.e. lower than 25 Hz). It may be fruitful to employ a new approach to properly isolate the SA channels to determine if there is no TAM perception mediated by the SAI channel. This is especially true knowing the SAI channel's ability to create accurate isomorphic representation of the tactile motion stimulus (Johnson & Hsiao, 1992). Nonetheless, a unique observation into specific channel activation from TAM stimulus presentation is an invaluable resource to reference for the current study as it gives us insight into

physiological responses to TAM stimulus. Using a lower frequency stimulus may shed light into the role of the SAI channel as well.

Studies in the past have manipulated a myriad of variables to observe optimal TAM perception. This yielded several insightful characteristics about TAM perception that translate well into the current study. Previous research and TAM using different modalities has shown similarities (Lakatos & Shepard, 1997). Given that there is a common rule that governs better apparent motion perception for both the visual domain and the tactile domain, there is a need for further investigation in how TAM is perceived. It is possible that TAM perception is mediated by the same processes and show similar neurological responses. The current study will first establish a method for presenting TAM stimuli that corresponds to the optimal frequency range of each channel as this could possibly allude to future studies that can compare the neurological components of how TAM is processed overall.

Current Study and its Rationale

The overall goal of the current study was to gain a better understanding of the involvement of mechanoreceptive channels and the respective mechanoreceptors on TAM perception. TAM was defined as the perceived sense of movement created by a series of onsets and offsets of tactile stimuli. TAM perception has been documented before (Kirman, 1983; Shepard & Lakatos, 1997). By isolating the different mechanoreceptive channels on the fingertip, it is hypothesized that their aptitude for detecting TAM could be demonstrated. The RA channel, known for detecting stimulus displacement (Mountcastle, 2005), and the SAI channel, known for detecting different forms (Johnson & Hsiao, 1992), were the mechanoreceptive channels investigated. These two channels were concentrated on the fingertip in the distal phalanx of the index finger (Johansson & Vallbo, 1979). To isolate the

mechanoreceptive channels in question, a forward masking paradigm was used. Previous research on threshold used this paradigm with the notion that presenting a masking stimulus that is optimal for a certain mechanoreceptor will increase its threshold (Gescheider et al, 2002). In other words, a specific masking stimulus impairs a specific mechanoreceptive type.

With the the *Latero*, a state-of-the-art tactile display apparatus, (see Appendix A) presenting compelling TAM on the finger pad of the index finger was improved upon, as previous methodologies had to resort to using a larger apparatus stimulating larger surface area of the skin with greater distance between test stimuli being presented to test TAM (Zhao, Israr, & Klatzky, 2015; Eid, Korres, & Jensen, 2015). These methodologies would prove to be insufficient in answering the question at hand because mechanoreceptors may not be uniformly situated across the body, as noted by differences in sensitivities of different body parts (Morioka, 2008). Furthermore, studies using the forward masking paradigm only had vibrators that had one point in contact with the skin to isolate mechanoreceptive channels. The apparatuses used in those studies will fail to create a more complicated stimulus. The *Latero* can compensate the losses from methodologies of past research because it delivers a rich, complex tactile stimulus to a focused area of the skin. The device allowed for the experimenter to alter ISOI, stimulus intensity, and length of stimulus displacement by allowing the control of each individual pin. It is the freedom of stimulus-crafting that the *Latero* provides that can help to tackle the research question. Despite the freedom in stimulus-crafting with the *Latero*, there are some limitation present with the current study. For example, when presenting a stimulus for a fraction of a second, there is a limit for the machine to present a low frequency vibration of the pin. For example, a 1 Hz frequency cannot be captured in a 50 milliseconds stimulus duration period. Thus, we need to use a higher frequency if we wish to maintain the integrity of the timing

parameter in creating a TAM with a short stimulus duration (i.e. 6 Hz).

Sherrick and Rogers (1966) and Kirman (1974a) have conducted similar studies, but their results have differed on the values they found for stimulus duration and ISOI. The former used a contactor with a diameter of 0.25 inches and the latter used a contactor with a diameter of 0.025 inches. Kirman (1974a) proposed that the difference originated from the size of the contactors they had used. Since the length column of pins on the *Latero* was closer to that of the contactors used by Sherrick and Rogers (1966), the values from their study was thought to yield more accurate results. Both studies have fortunately found a similar relationship between stimulus duration and ISOI. Thus, the ISOI chosen for the test stimuli was 70 milliseconds and the stimulus duration was 50 milliseconds.

The masking paradigm bore resemblance to Bolanowski et al.'s (1988) experiment; however, we elaborated upon their design by adding a TAM in the mask and test stimuli. Their experiment included a 40 Hz mask stimulus and compared the effects it had on the 0.7 Hz and 25 Hz test stimuli. This method differentiated the two channels in question. The masking stimulus in the current study operated at 30 Hz. The current study used 6 Hz as the low frequency test stimulus and 25 Hz as the high frequency stimulus; the former targeted the SAI channel and the latter targeted the RA channel. Though SAI is optimized for lower frequency than 6 Hz, they are still active at that range (Gescheider et al., 2001; Gescheider, Bolanowski, & Verillo, 2004). 6 Hz was chosen as it was the lowest frequency that adhered to the TAM parameter shown in previous research (Kirman, 1974a; Sherrick & Rogers, 1966) that could be presented within 1 to 2 seconds following the paradigm used by Bolanowski et al. (1988) The masking stimuli were presented for 4 seconds, followed by test stimuli lasting approximately 1 to 2 seconds. Using 40 Hz as a reference, the ISOI for the mask stimuli was 4 milliseconds.

The test stimuli intensity level (IV) ranged from 2 to 30. IV is a degree of intensity that participants can feel from the individual pins from the TAM stimuli. An increase of 1 IV is approximately 1.26 μm increase in displacement from the original pin position (see Appendix B). Bolanowski et al.'s (1998) study using vibrotactile stimuli previously found that at 5 dB SL (5 μm peak displacement difference between mask and threshold), the RA channel was hindered and the SA I channel was not. Though the current study did not follow Bolanowski et al.'s (1998) study exactly, knowing the masking stimulus intensity where the differentiation between the channels occur was crucial.

We hypothesized that the RA channel would be more partial towards TAM. In other words, trials testing the RA channel should yield a lower threshold for participants. This was because of the greater density of RA channels present on the index finger compared to the SAI channel. There was also compelling evidence that the RA channel was more active than the SAI channel when the TAM stimulus was presented (Gardner & Palmer, 1989) and RA channel's role in detection of fine spatial variation (Johnson & Hsaio, 1992). We also hypothesized that, based on the study by Bolanowski et al. (1988), increase in masking stimulus IV should result in evidence of threshold shift in TAM perception. To be more specific, the occurrence of a threshold shift would occur with a lower intensity masking stimulus when testing the RA channel compared to the SAI channel. The results should, therefore, demonstrate a different pattern of threshold shift as a function of masking stimulus intensity in a given vibrotactile frequency of the masking stimulus.

Method

Participants

Forty-one participants were recruited (6 males, 35 females). The average age was 18.85

years ($SD=3.32$ years). Participants needed to be at least 16 years old, right handed, and be without any cortical disorders or persisting body injuries that would interfere with the sensation of the test stimuli. Participants were invited through the Wilfrid Laurier University Psychology Research Experience Program (PREP). Participants received one course credit for each hour they participated.

Material

E-Prime 2.0 was used to conduct the experiment and collect participant responses. The main instrument used in the experiment was the *Latero*. The *Latero* has a 1.2cm^2 display area where the tactile stimuli were presented. The display area consisted of an 8×8 piezoelectric pin array with $1.2\text{mm} \times 1.6\text{mm}$ spacing between them. Though there were 64 pins in total, only the columns were used to create the TAM stimuli. This created a set of eight pins in a column that acted in unison to act as a single stimulator for the experiment.

Procedure

Participants entered a lab and were seated in front of a computer. Their right index finger was placed lightly on top of the display area of the *Latero*. Their left hand rested on a keyboard to control the experiment's progress. Participants were told that they would be given a two-choice task. This meant that the display area presented either a single rightward or leftward moving stimulus on the participants' index fingers at a time; the participants' task was to decide whether the stimulus was moving rightward or leftward by pressing the appropriate keys on the keyboard. Participants pressed "1" for left and "2" for right. The experiment was divided into two parts.

Experiment 1: Trials without the masking stimulus

First, participants received a training session to familiarize themselves with the

experimental procedure. Each session consisted of 10 trials with equal numbers of TAM stimuli moving leftward and rightward directions. The steps of the experimental session are shown in Figure 1. The order of stimuli presentation was randomized by E-Prime 2.0.

This was also the time for the experimenter to assess the participants' threshold for TAM. All TAM stimuli had an ISOI of 70 milliseconds with a stimulus duration of 50 milliseconds (each column vibrated for 50 milliseconds). When testing for the RA channel, participants received 10 TAM stimuli. The vibratory frequency of each stimulator was 25 Hz with approximately 1 second stimulus presentation time. The training session started with an IV of 30. The participants needed to get eight or more correct responses (>80% accuracy) in a session to receive the next session with a lower IV. The IV was decreased by an increment of five until the participant achieved less than 80% correct responses. Then, the IV was increased by an increment of one until the participant achieved 80% correct responses or higher. The process was repeated when testing for the SAI channel, in which the experimental parameters remained the same, except the vibratory frequency of each stimulator was 6 Hz with approximately 2 seconds stimulus presentation time instead. The threshold IV that was identified at this stage was used for the remainder of the experiment.

Once the training session was over, participants received the initial experimental session, which included the non-masked trials. Participants were tested for the RA and SAI channel with their threshold IV. The experimental parameter remained the same as in the training session. Their responses were recorded by E-Prime 2.0 across five repetitions for testing the RA and the SAI channel, totaling 50 trials for each. The experimenter also recorded the participant responses. The experimenter gave short breaks every 10 trials and another break after the participant completed the first experimental session.

Experiment 2: Trials with the masking stimulus

The experimental parameters remained the same except each TAM stimulus was preceded by a masking stimulus (masked trials). The masking stimulus was an oscillation of leftward and rightward movement. The vibratory frequency of the masking stimulus was 30 Hz and the ISOI was 4 milliseconds. The stimulus duration was 10 milliseconds. There were four different conditions created by manipulating the total duration of the masking stimulus and the IV (see Table 2). In each session, there were equal numbers of masking stimuli ending with a leftward movement and rightward movement. The order of the trial presentation was counterbalanced to reduce any order effect that could influence the data (see Table 3). The direction of movement that the masking stimulus ends with had been randomized as well; however, there were equal numbers of masking stimuli that ended with a rightward movement and a leftward movement. Both the experimenter and E-Prime 2.0 recorded participant responses across five repetitions, totaling 50 trials when testing both the RA and the SAI channel for each. The experimenter gave short breaks every 10 trials and the experiment concluded after completing the experimental session. The experimenter debriefed the participants at the end.

Results

One participant was removed from the study because she could not experience the TAM stimuli. Another participant was removed from the Mask 4 condition because the participant's threshold was considered an outlier (z score = 3.74, $p < .05$). Thus, there were 39 participants in total. Participants' threshold for the TAM stimuli are shown in Figure 2. Though both channels were tested for each participant, the threshold found when testing the RA channel and the SAI channel did not differ. To clarify, each individual threshold differed among participants, but the threshold found in an individual did not differ when testing for either channels.

Table 4 shows the average of correct responses out of 50 trials in each experimental condition. We also aimed to observe the effects of increasing masking stimulus intensity and masking stimulus duration on TAM perception. To do this, participant responses were pooled and organized into two categories based on masking stimulus duration (4 seconds vs 8 seconds). The results are shown in Figure 3 and 4. The Y-axis represent the score difference between the masked and the non-masked responses when testing both channels. A greater value on the Y-axis would approximate a greater threshold shift experienced by the participant. The X-axis represents the difference in intensity between the test stimulus and the masking stimulus. For example, a participant who received a 5 IV test stimulus received a masking stimulus with 10 IV and 15 IV in experiment 2; then, the score difference at masking stimulus with 10 IV and 15 IV were plotted. A line-of-best fit is shown for both figures and their respective equation and R^2 values are presented on the figures.

Further analyses were performed on each condition separately to see their effects on TAM perception. A univariate repeated measures ANOVA (type III) was used to examine the participants' performance on the task when they were given the Mask 1 condition. There was an equal of number of observations in each condition; thus, other types of ANOVA would have resulted in a same result as Type III. After data transformation (cube function), Shapiro-Wilk's test revealed that the distribution was normal. The transformation was used to combat the negative skew of the distribution which violates the assumption of normality when using ANOVA. The repeated measures ANOVA showed that there was a significant difference in performances between non-masked and masked trials, $F(3, 27) = 8.045, p < .001$. Post hoc tests using Tukey's HSD revealed that there was a significant difference between non-masked and masked trials testing the SAI channel; participants got 10.4 more incorrect trials when

performing the masked trials than the non-masked trials ($p < .001$). This was not found between the non-masked and masked trials testing the RA channel ($p = .31$). The results are also shown in Figure 5.

When looking at the participants' performances on the task when they were given the Mask 2 condition, the repeated measures ANOVA showed that there was a significant difference in performance between non-masked and masked trials, $F(3, 27) = 43.024, p < .001$. Post hoc tests using Tukey's HSD revealed that there was a significant difference between non-masked and masked trials testing the RA and SAI channels. Participants got 10.9 more incorrect trials when trials when performing the masked trials than the non-masked trials testing the RA channel ($p < .001$); participants got 11.2 more incorrect trials when trials when performing the masked trials than the non-masked trials testing the SAI channel ($p < .001$). The results are also shown in Figure 6.

The repeated measures ANOVA with the Greenhouse-Geisser correction showed that there was a significant difference in performance between non-masked and masked trials when participants were given the Mask 3 condition, $F(3, 27) = 56.675, p < .001$. The correction was used to mediate the violation of sphericity. Post hoc tests using Tukey's HSD revealed that there was a significant difference between non-masked and masked trials testing the RA and SAI channels. Participants got 10.6 more incorrect trials when trials when performing the masked trials than the non-masked trials testing the RA channel ($p < .001$); participants got 14 more incorrect trials when trials when performing the masked trials than the non-masked trials testing the SAI channel ($p < .001$). The results are also shown in Figure 7.

The data was not normally distributed when looking at the participants' performances on the task when they were given the Mask 4 condition. As with Mask 1 condition, the distribution

was negatively skewed. After transforming the data (square function), examining the Shapiro-Wilk's test revealed that the distribution was normal. The repeated measures ANOVA showed that there was a significant difference in performance between non-masked and masked trials, $F(3, 24) = 59.793, p < 0.001$. Post hoc tests using Tukey's HSD revealed that there was a significant difference between non-masked and masked trials testing the RA and SAI channels. Participants got 13.2 more incorrect trials when trials when performing the masked trials than the non-masked trials testing the RA channel ($p < .001$); participants got 13.7 more incorrect trials when trials when performing the masked trials than the non-masked trials testing the SAI channel ($p < .001$). The results are also shown in Figure 8.

Discussion

Experiment 1: Trials without the masking stimulus

The purpose of the current study is to investigate which mechanoreceptive channel is the most involved with TAM perception; we hypothesized that the RA channel would be more involved with TAM perception, resulting in a lower threshold. However, the obtained results indicated that neither channels were partial towards TAM as the threshold remained the same regardless of the channel being tested. This was surprising because past research demonstrated SAI channel's ability to represent tactile motion stimuli (Darian-Smith, Davidson, & Johnson, 1980; Johnson & Hsiao, 1992) and a previous study showing RA channel's excitatory response to tactile motion stimuli (Gardner & Palmer, 1989). We believed that participants would demonstrate a lower threshold for TAM when testing one of the channels. Nonetheless, there may be reasons why the current study could not find a different threshold when testing the RA and SAI channels.

To start, the RA channel's receptive field was most active with 2.4mm stimulator gap

(Gardner & Palmer, 1989) when using TAM stimuli. Meanwhile, the gap between the column of pins of the *Latero* was only 1.2mm. It is possible that the RA channel's activity diminished because our TAM stimuli did not cater to the RA channel like their study. If this was indeed the case, there is a possibility that using the trials targeting the RA channel with a greater pin displacement could have resulted in a lower threshold.

There is also a possibility that other channels were active during the trials. Though the SAI channel was not the focus of the current study, Olausson, Wessberg, and Kakuda (2000) suggest that the SAI channel could be involved in TAM perception by detecting the skin stretches toward the direction of the TAM stimulus. It is possible that the SAI channel mediated the TAM perception in the current study. However, the current study did not employ any tactile stimuli that involved the directionality of the tactile stimuli, meaning that there were no skin stretches to note the direction of the tactile movement. The sense of directionality was derived from the series of consecutive activation of the piezoelectric pins. Thus, we could argue that the SAI channel could have had a lower influence on how the TAM stimuli was perceived.

We could not definitively rule out the possibility that channels other than the RA and SAI channels were not active in the current study. Olausson et al. (2000) suggested the SAI channel may have an active part in TAM perception; there are some who suggest P channel may be involved as well in certain cases (Gardner & Palmer, 1989). However, using lower frequency stimuli should have allowed the RA and the SAI channel to be most active out of the four mechanoreceptive channels. Though there is a reason to believe that the RA and the SAI channel were the only mechanoreceptive channels involved, further discussion on how to eliminate the doubt of contamination in the results should be explored.

Experiment 2: Trials with the masking stimulus

Past research used vibrotactile masking stimuli to see its impact on the mechanoreceptive channels' response to vibrotactile stimuli (Bolanowski et al., 1988; Gescheider et al., 1989; Gescheider et al., 2002). The current study employed a similar methodology for testing TAM perception. Figure 3 shows the impact of the 4 second masking stimulus on participant responses. Previous research on vibrotactile masking demonstrated a greater threshold shift as the masking stimulus intensity increased (Bolanowski et al., 1988); we believed that a greater difference in participant responses between the masked and non-masked trials would indicate a greater threshold shift experienced by the participant. This was demonstrated when we tested the SAI channel. As the masking stimulus IV increased, the general trend indicated that the score difference increased. On the other hand, previous findings on vibrotactile research suggested that the RA channel experiences a sharper increase in threshold shift as masking stimulus intensity increases (Bensmaia et al., 2005). This was not found in here. Instead, the result showed that there is a gradual increase in score difference followed by a decrease in score difference as the masking stimulus IV increased. This could be evidence for a differentiation between the RA and the SAI channel responses in TAM perception. It is worth noting that the R^2 for the trendlines found here are very low. Thus, the results here show some promise as to how the current methodology can show differences in how the channels react to a vibrotactile masking stimuli; however, nothing is conclusive.

Figure 4 shows the impact of the 8 second masking stimulus on participant responses. What was found with a longer duration of a masking stimulus was interesting. Both trendlines for the RA and the SAI channel showed a decrease in score difference until masking stimulus IV of 10 followed by an increase in score difference as the masking stimulus IV increased. The

pattern is reminiscent of a psychophysical tuning curve where there is a clear point of decrease and increase of threshold. However, the current methodology only allowed for a rudimentary form of a psychophysical tuning curve and could not yield a solid evidence for exactly how the masking stimulus IV impacts TAM threshold. It is interesting to find that the trendlines for both the RA and the SAI channel were similar, indicating no differentiation. Thus, further analyses were completed to understand what was happening.

Upon further investigation on individual conditions, the result revealed that the trials testing the RA channel experienced no masking effect in the Mask 1 condition, which included a masking stimulus with the lowest IV and duration. The other trials testing the RA channel demonstrated a significant masking effect. Meanwhile, results from the trials testing the SAI channel demonstrated a significant masking effect on all conditions. The findings are intriguing as there are some evidence of differentiation between the RA and SAI channels. However, the results in the current experiment demonstrated an opposite trend to what Bolanowski et al. (1988) found. The results here would suggest that the SAI channels were more susceptible to a vibrotactile masking stimulus than the RA channels.

Nonetheless, the results with the trials testing the SAI channel parallel what was observed from other previous vibrotactile research. Bensmaia et al.'s (2005) finding on the effects of adapting amplitude on vibrotactile threshold suggests that a threshold shift occurred in the current study. Though the masking effect was shown to be weaker for the SAI channel than the RA channel when the frequency was held constant, there was a significant threshold shift when the masking frequency was 30 Hz. This may be evidence that a similar mechanism from vibrotactile masking is driving the threshold shift in the current study. If true, this would be an interesting discovery as it suggests that the current experimental procedure can serve as a method

for testing differentiation between channels for TAM perception with vibrotactile perception as its foundation. However, if this is true, the result should have indicated a greater masking effect when testing the RA channel. Previous research found that the RA channel quickly experienced a masking effect when exposed to a masking stimulus with greater intensity (Bolanowski et al., 1988; Bensmaia et al., 2005). With no evidence of a masking effect found in the Mask 1 condition for the RA channel, the previous statement regarding the validity of the current study as a mean to use vibrotactile stimulus to investigate the mechanoreceptive channel's role in TAM perception appears questionable.

There are some explanations as to why the current study's result may not have fully paralleled findings from previous vibrotactile research. There was a limitation on the frequency of the test stimuli when translating from a vibrotactile stimulus to a TAM stimulus. It was difficult to recreate a true low frequency (1 Hz and below) TAM stimulus that targets the SAI channel within the current study's parameters. Since we wanted to create a reliable TAM for the participants, we relied on timing parameters from past research on optimal TAM perception (70 msec ISOI and 50 msec stimulus duration) to create the test stimulus (Sherrick & Rogers, 1966). Each pin had only a fraction of a second to manifest a low frequency vibration, which did not allow for a faithful replication of the previous experimental design of other vibrotactile studies. We had to compromise by increasing the frequency of the test stimulus to not jeopardize the other experimental parameters. Since the SAI channel is most active from 0.4 Hz to 1.5 Hz and the RA channel is active from 1.5 Hz to 40 Hz (Gescheider et al, 2002), the current testing trials may not have tested the SAI channel exclusively. It is more likely that the current study experimented on the RA channel only.

This would explain the findings from experiment 1 as there were no difference in threshold between the two channels when tested. This would also explain the results found in figure 4. The trendlines for the RA and the SAI channel was similar to one another. Since the way to differentiate a channel from another channel is to observe the change in threshold as a function of changing masking stimulus intensity, a similar trendlines found in Figure 4 would indicate that only the RA channels were active in the current study. Though it is currently difficult to see the effects of the masking stimulus' effect on the SAI channel, there are some important information on the RA channel obtained from the current study. First, the masking stimulus needs to be approximately 8 seconds long to V-shaped trendline in threshold shift as a function of masking stimulus IV. Second, the change from a decrease in threshold shift to an increase occurs when a participant is given a masking stimulus at approximately 10 IV. The two information are crucial if we want to create a psychophysical tuning curve that helps to represent a characteristic of the RA channel in TAM perception. If we can reliably replicate this for the RA channel and we can find a different trend for the SAI channel, we would be fully capable of answering how to differentiate between mechanoreceptive channels involved with TAM perception.

Future Studies and Conclusion

The findings from the current study are promising for future directions for investigating the mechanoreceptive channels and TAM perception. Firstly, the current study can be revised to rectify the issue of the frequency of trials testing the SAI channel. Future studies can use different timing parameters that can still evoke optimal TAM perception. For example, previous research on TAM showed a linear relationship between ISOI and stimulus duration (Sherrick & Rogers, 1966); a longer ISOI and a corresponding increase in stimulus duaration could create an

optimal TAM perception. This could allow future studies to better translate a low frequency vibration onto the TAM stimulus.

In addition, the study did not investigate EEG/ERP signature for TAM perception with the current experimental setting. The current study cannot determine if the masking effect seen with the TAM stimulus is simply restricted to the changes made to the somatosensory periphery or if there is indeed a change in the somatosensory cortices. A previous study by Pei, Hsiao, Craig, and Bensmaia (2010) investigated the motion direction sensitivity of the somatosensory cortex; their endeavor pointed to the S1 as a good region of interest for our future study to examine with our experimental design. Identifying an EEG/ERP signature for TAM perception when testing each mechanoreceptive channel could be a fruitful endeavor to fully answer the research question at hand.

The current study proposed a unique methodology for examining TAM perception by isolating the mechanoreceptive channels involved. There was evidence that future studies could elucidate how much the RA and the SAI channel, and possibly other mechanoreceptive channels, are involved in TAM perception through improvement of the current design.

Table 1

Characteristics of mechanoreceptive channels on the glabrous skin

	Rapidly Adapting (RA)	Slowly Adapting I (SAI)	Slowly Adapting II (SAII)	Pacinian (PC)
Receptive Field	Sharp, Small (22 mm ²)	Sharp, Small (9 mm ²)	Obscure, Large (60 mm ²)	Obscure, Large (>100 mm ²)
Optimal Frequency	1.5 Hz to 50 Hz	0.4 Hz to 1.5 Hz	Responds to skin stretches	150 Hz to 300 Hz

Note: Receptive field value came from the study by Roudaut, Lonigro, Coste, Hao, Delmas, and Crest (2012) and Vallbo and Johansson (1984). The optimal frequency can vary on the amplitude of the vibrotactile stimulus (i.e. intensity).

Table 2

Characteristics of masking stimulus used in the experiment

	Mask 1	Mask 2	Mask 3	Mask 4
Duration (ms)	4	4	8	8
IV	2	3	2	3

Note: IV for the mask stimulus is X times magnitude of the test stimulus. For example, the mask stimulus IV is 20 if the test stimulus IV is 10 in the Mask 1 condition.

Table 3

Counterbalancing of presentation order of the experimental procedure

	No Mask RA	No Mask SAI	Mask RA	Mask SAI
Order 1	1 st	2 nd	3 rd	4 th
Order 2	1 st	2 nd	4 th	3 rd
Order 3	2 nd	1 st	3 rd	4 th
Order 4	2 nd	1 st	4 th	3 rd

Table 4

Average number of correct responses and standard deviation in each condition

	No Mask RA	No Mask SAI	Mask RA	Mask SAI
Mask 1	43.2 (3.33)	41.9 (3.54)	39.2 (6.60)	31.5 (9.65)
Mask 2	42 (3.20)	40.4 (3.13)	31 (4.16)	29.2 (4.05)
Mask 3	43.1 (4.04)	41.7 (2.50)	32.5 (4.45)	27.7 (4.55)
Mask 4	44.1 (2.69)	40.4 (2.59)	31.4 (6.87)	28.2 (6.16)

Note: Maximum score is 50.

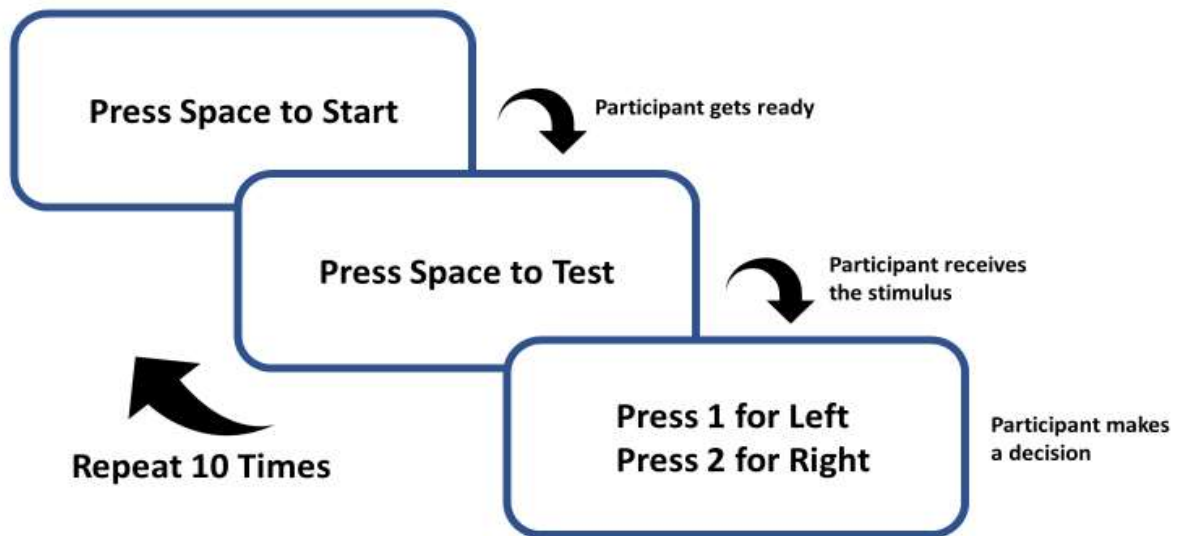


Figure 1. Experimental trial procedure

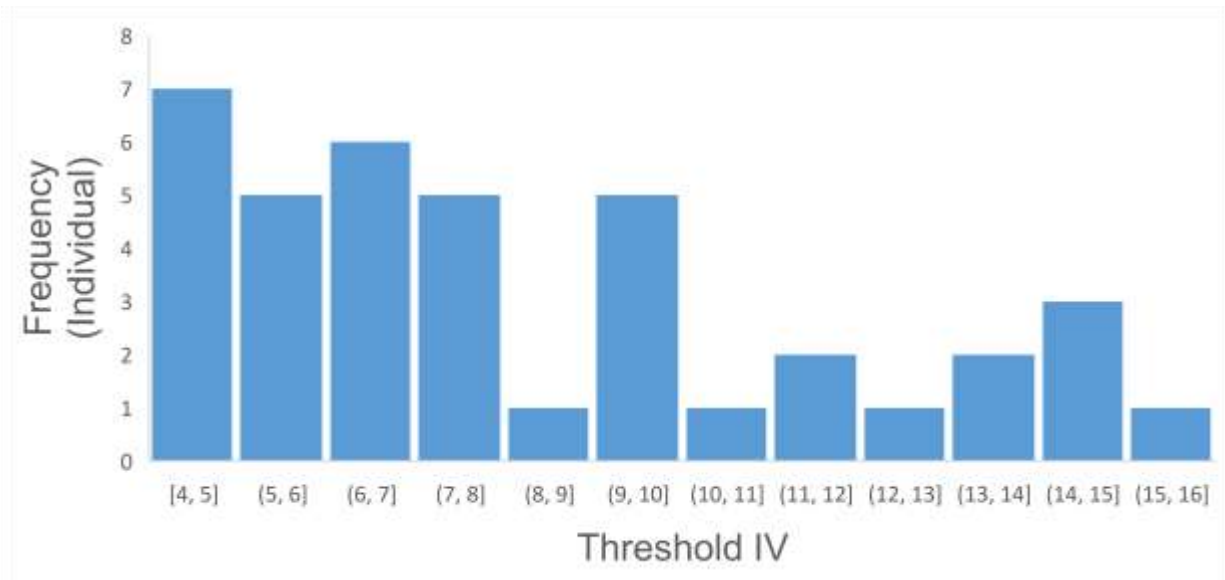


Figure 2. Participant threshold for TAM stimulus in experiment 1. The range is IV 4 to 15. The figure shows results for both the RA and the SAI channel.

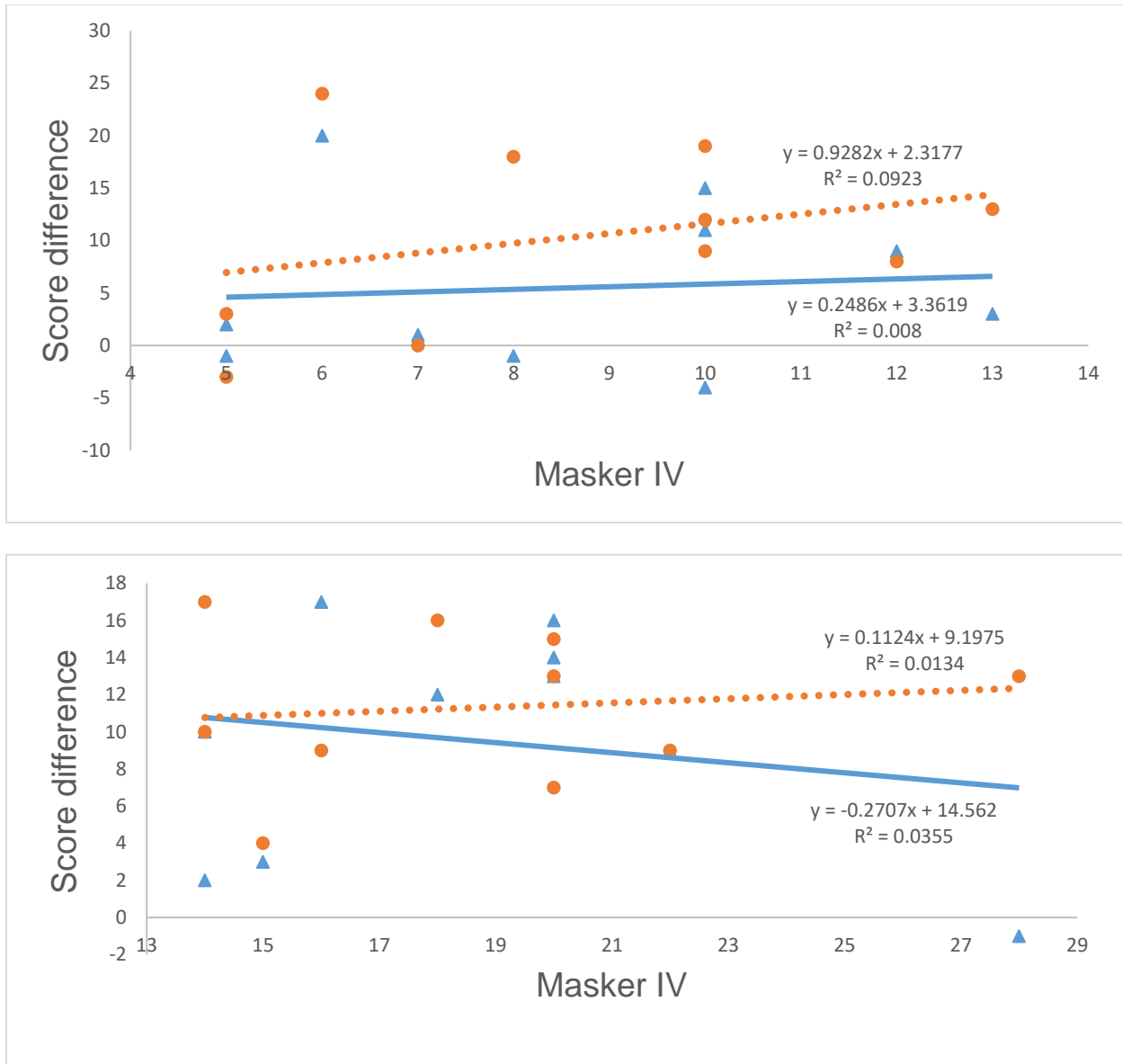


Figure 3. The effects of 4 second masking stimulus on participant response as a function of increasing masking stimulus IV. The triangles represent participant responses when testing the RA channel and the circle represent participant responses when testing the SAI channel. A line-of-best-fit are shown for responses when testing both channels. The solid line represents the line-of-best-fit for the RA channel and the dotted line represent the line-of-best-fit for the SAI channel. The median masking stimulus IV was 13.5.

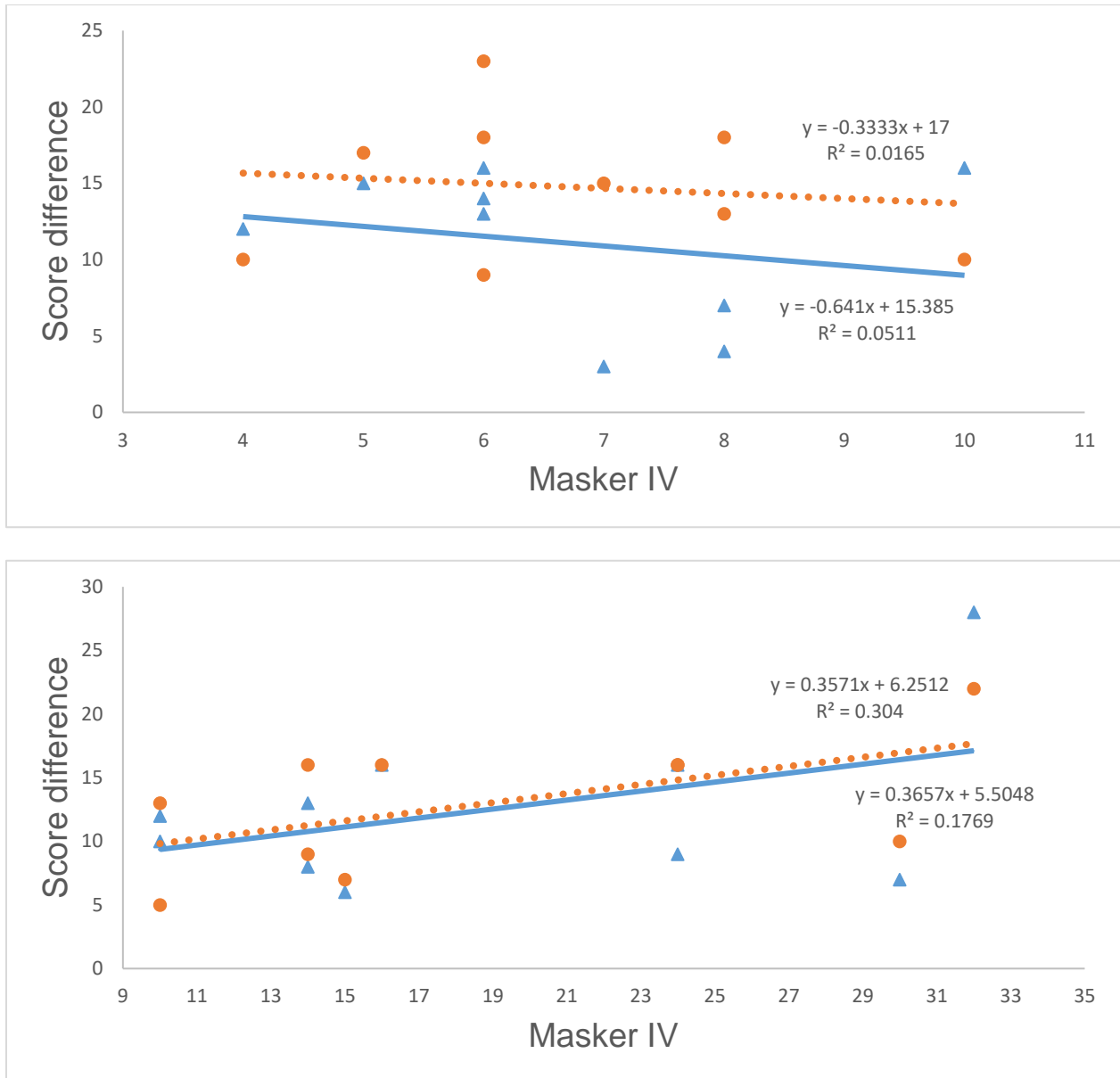


Figure 4. The effects of 8 second masking stimulus on participant response as a function of increasing masking stimulus IV. See Figure 3 for guide. The median masking stimulus IV was 10.

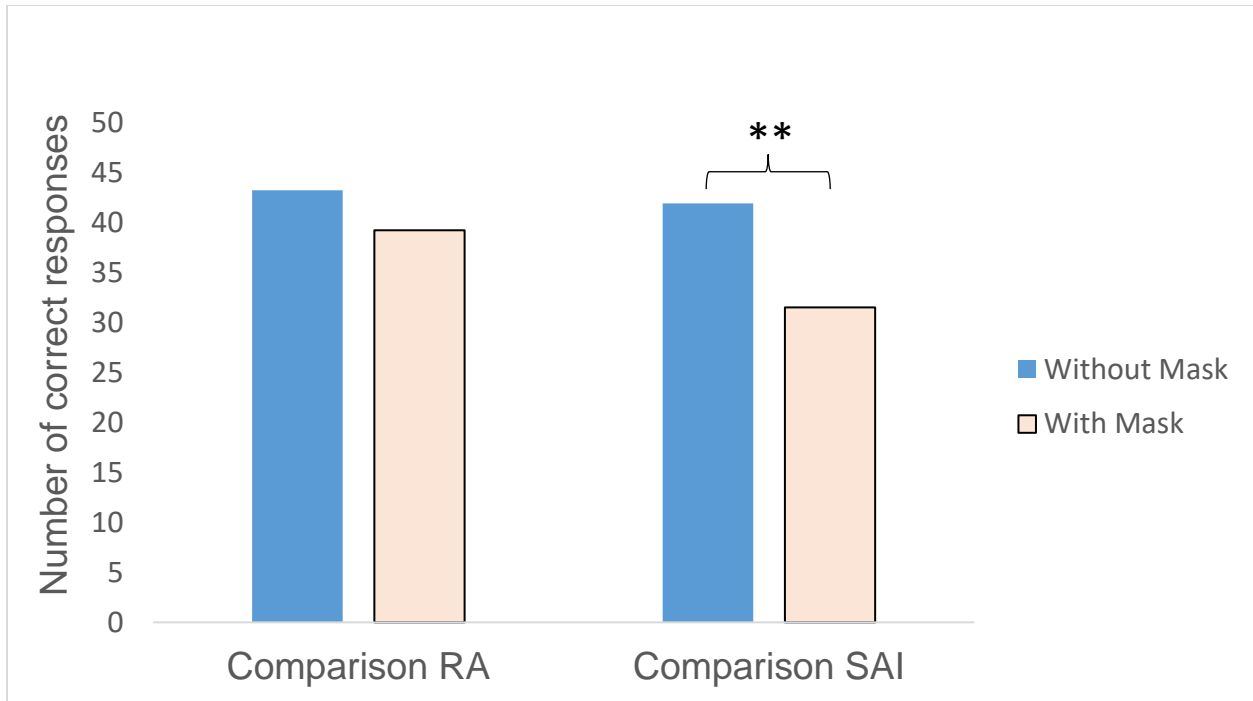


Figure 5. Comparison of non-masked and masked trials in Mask 1 condition

Note. For the following figures, ** means $p < .001$.

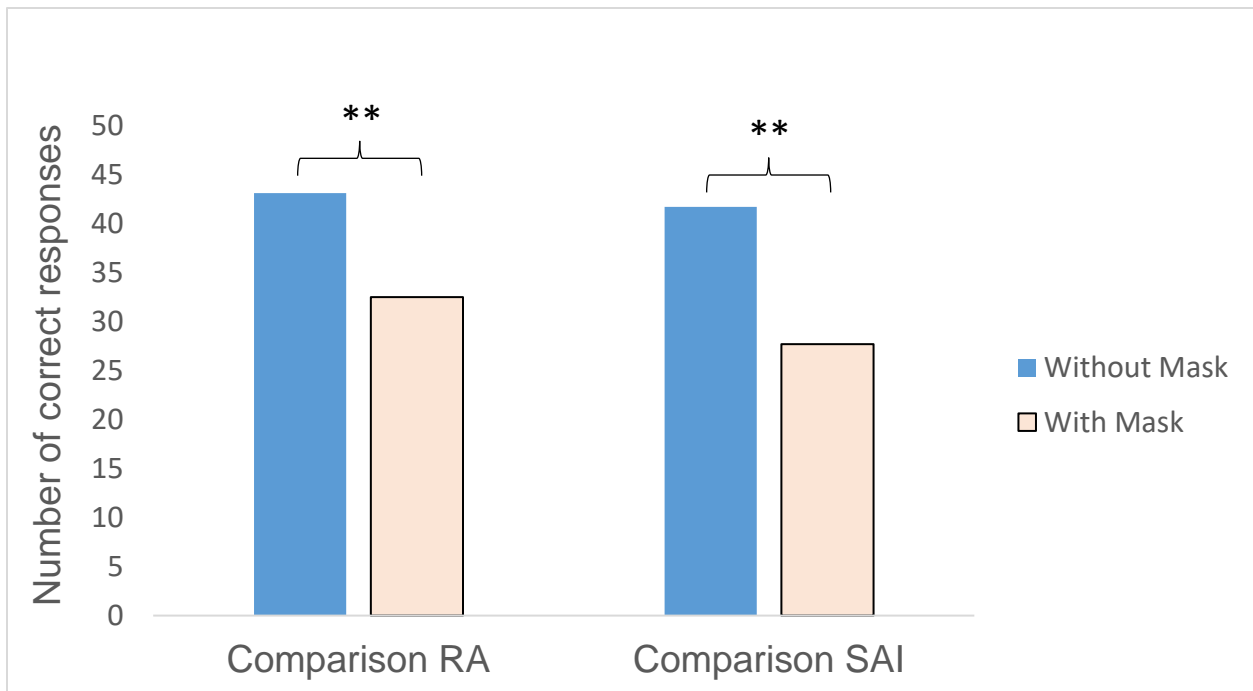


Figure 6. Comparison of non-masked and masked trials in Mask 2 condition

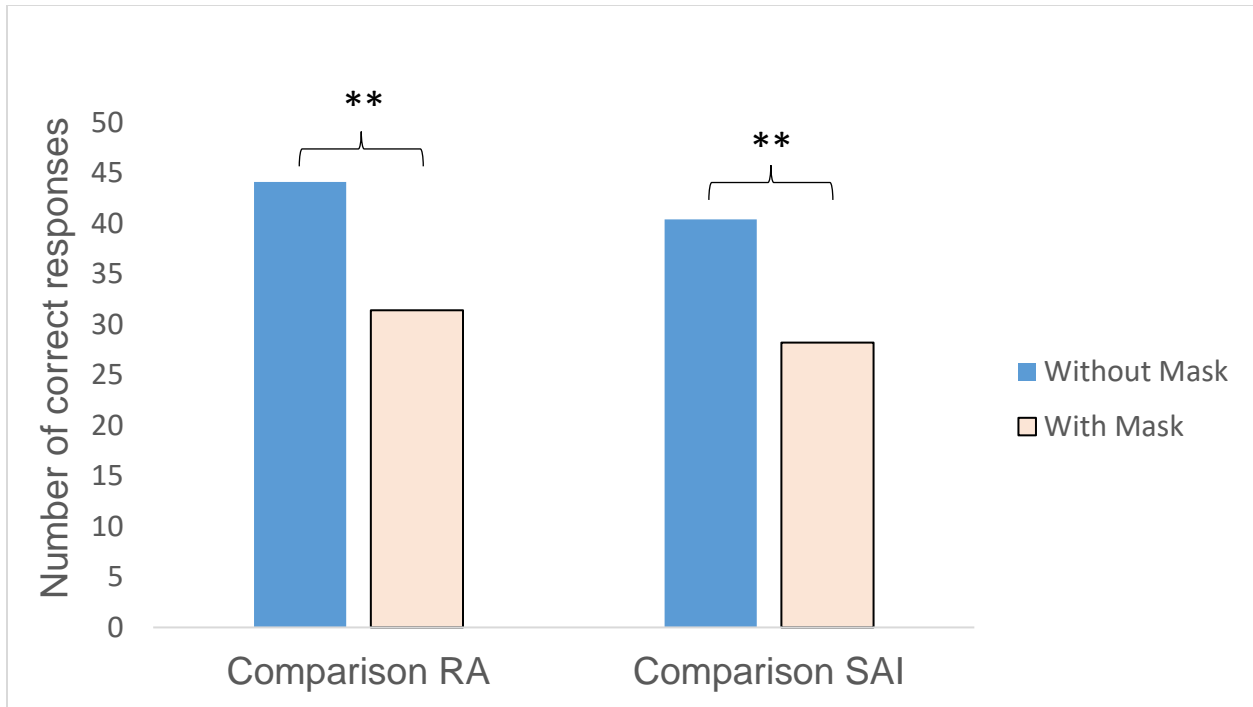


Figure 7. Comparison of non-masked and masked trials in Mask 3 condition

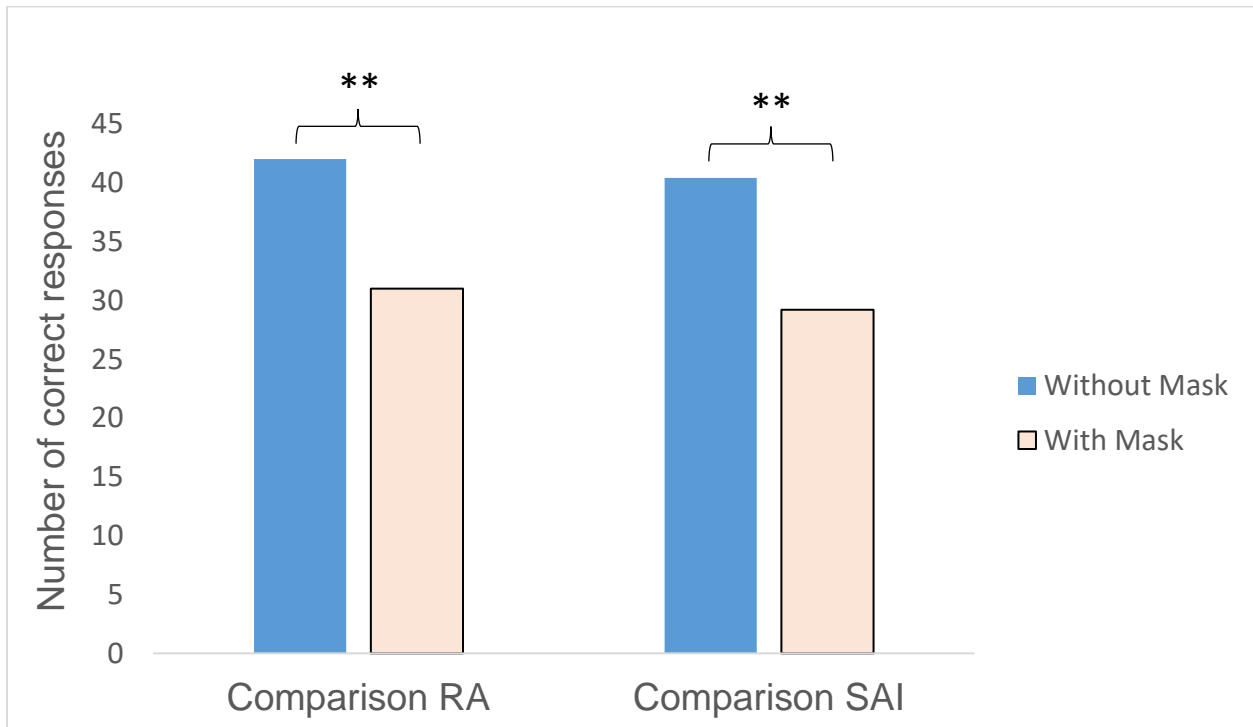
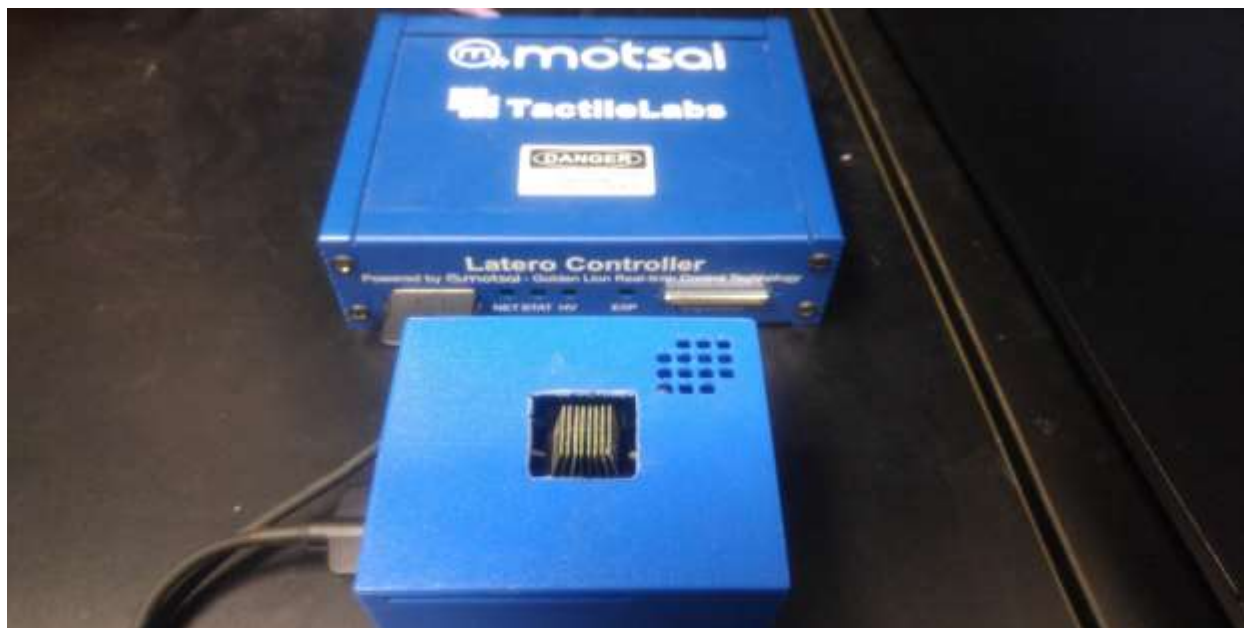


Figure 8. Comparison of non-masked and masked trials in Mask 4 condition

Appendix A



Appendix B

We used a high-speed camera, Panasonic DMC-FZ200, to capture the images used to calculate the pin's displacement caused by an increase in IV. The camera was able to capture 60 frames per second. To start, we set up a mock TAM trials with three IVs: 50, 100, and 150. The experimental parameters remained the same as experiment 1. These values were chosen because discerning the movements made by the pins in TAM stimuli with lower IVs was difficult. During each trial, we used the high-speed camera to capture the pin's displacement in each IVs. Next, a group of JPEG files containing a full range of movement made by a pin was examined (the pin that we examined was chosen arbitrarily, but the chosen pin was consistent throughout the process). We compared the pixel position of the pin at its starting point and at the extent of its full movement in each IVs in the JPEG files. The difference between the two resulted in the pin's displacement in each IVs. The result indicated a linear increase in pin's displacement with the increase of IV (see below). In addition, we also examined the pixel position between each pin at rest. Since we knew that there was a 1.2mm gap between each pin at rest, we obtained all the values to calculate the pin's displacement caused by an increase in IV.

IV	Difference in pixel positions (<i>pix</i>)
50	2,999
100	6,001
150	9,000
At rest between pins	57,003

Thus,

$$1 \text{ IV} \times \frac{9,000 \text{ pix}}{150 \text{ IV}} \times \frac{1.2 \text{ mm}}{57,003 \text{ pix}} \approx 0.00126 \text{ mm} = 1.26 \mu\text{m}$$

References

- Bensmaia, S. J., Leung, Y. Y., Hsiao, S. S., & Johnson, K. O. (2005). Vibratory adaptation of cutaneous mechanoreceptive afferents. *Journal of neurophysiology*, *94*, 3023-3036.
- Biswas, A., Manivannan, M., & Srinivasan, M. A. (2015). Vibrotactile sensitivity threshold: nonlinear stochastic mechanotransduction model of the Pacinian Corpuscle. *IEEE transactions on haptics*, *8*, 102-113.
- Bolanowski, S. J., Gescheider, G. A., Verillo, R. T., & Checkosky, C. M. (1988). Four channels mediate the mechanical aspects of touch. *Acoustical Society of America*. *84*, 1680-1694.
- Chambers, M. R., Andres, K., Duering, M. V., & Iggo, A. (1972). The structure and function of the slowly adapting type II mechanoreceptor in hairy skin. *Experimental Physiology*, *57*, 417-445.
- Darian-Smith, I., Davidson, I., & Johnson, K. O. (1980). Peripheral neural representation of spatial dimensions of a textured surface moving across the monkey's finger pad. *The Journal of physiology*, *309*, 135-146.
- Eid, M., Korres, G., & Jensen, C. B. F. (2015, May). SOA thresholds for the perception of discrete/continuous tactile stimulation. In *Quality of Multimedia Experience (QoMEX), 2015 Seventh International Workshop on* (pp. 1-6). IEEE.
- Friedman, R. M., Khalsa, P. S., Greenquist, K. W., & LaMotte, R. H. (2002). Neural coding of the location and direction of a moving object by a spatially distributed population of mechanoreceptors. *Journal of Neuroscience*, *22*, 9556-9566.
- Gardner, E. P., & Palmer, C. I. (1989). Simulation of motion on the skin. I. Receptive fields and temporal frequency coding by cutaneous mechanoreceptors of OPTACON pulses

- delivered to the hand. *Journal of Neurophysiology*, 62, 1410-1436.
- Gescheider, G. A., Bolanowski, S. J., & Verrillo, R. T. (1989). Vibrotactile masking: Effects of stimulus onset asynchrony and stimulus frequency. *Acoustical Society of America*, 85, 2059-2084.
- Gescheider, G. A., Bolanowski, S. J., & Hardick, K. R. (2001). The frequency selectivity of information-processing channels in the tactile sensory system. *Somatosensory & Motor Research*, 18, 191-201.
- Gescheider, G. A., Bolanowski, S. J., Pope, J. V., & Verrillo, R. T. (2002). A four-channel analysis of the tactile sensitivity of the fingertip: frequency selectivity, spatial summation, and temporal summation. *Somatosensory & Motor Research*, 19, 114-124.
- Gescheider, G. A., Bolanowski, S. J., & Verillo, R. T. (2004). Some characteristics of tactile channels. *Behavioural brain research*, 148, 35-40.
- Gescheider, G. A., Sklya, B. F., Van Doren, C. L., & Verrillo, R. T. (1985). Vibrotactile forward masking: psychophysical evidence for a triplex theory of cutaneous mechanoreception. *The Journal of the Acoustical Society of America*, 78, 534-543.
- Iggo, A., & Muir, A. R. (1969). The structure and function of a slowly adapting touch corpuscle in hairy skin. *The Journal of Physiology*, 200, 763-796.4.
- Iggo, A., & Ogawa, H. (1977). Correlative physiological and morphological studies of rapidly adapting mechanoreceptors in cat's glabrous skin. *The Journal of Physiology*, 266, 275-296.
- Johansson, R. S. (1976). Skin mechanoreceptors in the human hand: receptive field characteristics. In Y. Zotterman (Ed.), *Sensory functions of the skin in primates*. (pp. 159-170). Oxford: Pergamon Press.

- Johansson, R. S. (1978). Tactile sensibility in the human hand: receptive field characteristics of mechanoreceptive units in the glabrous skin area. *The Journal of Physiology*, *281*, 101–125.
- Johansson, R. S., & Vallbo, A. B. (1979). Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *The journal of physiology*, *286*, 283-300.
- Johansson, R. S. & Vallbo, A. B. (1983). Tactile sensory coding in the glabrous skin of the human hand. *Trends in Neuroscience*, *6*, 27-32.
- Johnson, K. O., & Hsiao, S. S. (1992). Neural mechanisms of tactual form and texture perception. *Annual Review of Neuroscience*, *15*, 227-250.
- Johnson, K. O., & Lamb, G. D. (1981). Neural mechanisms of spatial tactile discrimination: neural patterns evoked by braille-like dot patterns in the monkey. *The Journal of physiology*, *310*, 117-144.
- Kirman, J. H. (1974a). Tactile apparent movement: The effects of interstimulus onset interval and stimulus duration. *Perception & Psychophysics*, *15*, 1-6.
- Kirman, J. H. (1974b). Tactile apparent movement: The effects of number of stimulators. *Journal of Experimental Physiology*, *103*, 1175-1180.
- Kirman, J. H. (1983). Tactile apparent movement: The effects of shape and type of motion. *Perceptions & Psychophysics*, *34*, 96-102.
- Lakatos, S., & Shepard, R. N. (1997) Constraints common to apparent motion in visual, tactile, and auditory space. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1050-1060.

- Morioka, M., Whitehouse, D. J., & Griffin, M. J. (2008). Vibrotactile thresholds at the fingertip, volar forearm, large toe, and heel. *Somatosensory and Motor Research*, 25, 101-112.
- Mountcastle, V. B. (2005). *The sensory hand*. Cambridge, MA: Harvard University Press.
- Olausson, H., & Norrsell, U. (1993). Observation on human tactile directional sensibility. *The Journal of physiology*, 464, 545-559.
- Olausson, H., Wessberg, J., & Kakuda, N. (2000). Tactile directional sensibility: peripheral neural mechanisms in man. *Brain research*, 866(1-2), 178-187.
- Pei, Y. C., Hsiao, S. S., Craig, J. C., & Bensmaia, S. J. (2010). Shape invariant coding of motion direction in somatosensory cortex. *PLoS biology*, 8(2), e1000305.
- Roudaut, Y., Lonigro, A., Coste, B., Hao, J., Delmas, P., & Crest, M. (2012). Touch sense: organization and molecular determinants of mechanoreceptive receptors. *Channels*, 6, 234-245.
- Sherrick, C. E., & Rogers, R. (1966). Apparent haptic movement. *Perception & Psychophysics*, 1, 175-180. doi:<http://dx.doi.org/10.3758/BF03215780>
- Vallbo, A. B., & Johansson, R. S. (1978). The tactile sensory innervation of the glabrous skin of the human hand. *Active touch*, 2954, 29-54.
- Vallbo, A. B., & Johansson, R. S. (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Hum Neurobiol*, 3, 3-14.
- Zhao, Israr, & Klatzky. (2015). Intermanual Apparent Tactile Motion on Handheld Tablets. World Haptics Conference. Evanston, 2015. Illinois, IL.