UNDERSTANDING THE NEURAL CORRELATES OF VISUAL-TACTILE MULTISENSORY INTEGRATION

by

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ABSTRACT

Multisensory integration is known as the brain's ability to integrate separate streams of sensory input into a single percept and is a cognitive process we use every day to form our experiences. In order to better understand the behavioral and neural mechanisms of visuotactile integration we conducted a two-part experiment. To establish whether viewed touch influenced felt touch, we first ran a behavioral experiment in which subjects viewed touches at the same time they felt vibrotactile stimuli on their own hand. Touches either occurred on the same finger in both modalities (congruency trials) or were in different locations (incongruent trials). When asked to respond on which finger they felt the tactile stimulus, subjects were significantly more accurate at localizing touch when the touches were congruent, as predicted. A similar paradigm was conducted in the scanner, and analyzed using event-related fMRI and MVPA to examine what brain regions are active during visuotactile integration. No regions were significantly active during congruent versus incongruent trials, however incongruent trials resulted in significant activation in right DLPFC, right OFC, and ACC compared to congruent trials. Significant activation in these areas provides preliminary evidence of higher-order processing involved during incongruent touch. MVPA using a whole-brain searchlight did not result in a significant ability to decode between congruence and incongruence of touch.

Chapter 1

INTRODUCTION

Multisensory Integration

Imagine you are at your local party scene, looking to find your friend before you head home. The room is poorly lit so it's hard to spot them, and the music is blasting making it especially hard to hear their voice in a crowded room. How do you locate your friend using your limited sensory capabilities? In everyday life, we combine information from multiple sensory modalities to create a representation of what we perceive and experience. Although your information enters via many individual streams, you are able to integrate information across modalities to develop a multisensory representation and inform your decision. The brain can integrate separate streams of sensory input into a single percept, a process known as multisensory integration. We can manipulate how sensory inputs are presented in a localization task to further understand how multimodal stimuli are characterized by the brain.

Background Research

How are we able to perceive the world around us? The process by which we accurately gather meaningful information can be described using the causal inference model (Kording et al., 2007). Given a bimodal sensory event, the brain has the ability to determine whether the event occurred as a result of two sensory cues from one cause ($C = 1$) or two sensory cues from two different causes ($C = 1$). Figure 1 demonstrates how this might work in the ventriloquist effect. If the speech sounds from the human speaker are presented in close proximity to a puppet displaying talking movements, a viewer will perceive the speech sounds as coming from the puppet itself (Warren, Welch, & McCarthy, 1981). Additionally, Kording et al. (2007) devised the ideal-observer model which explains that the observer makes their final estimate in the most efficient way possible, weighing the information from both sensory cues.

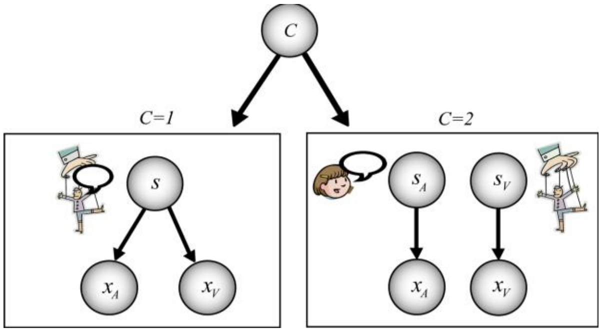

Figure 1 The causal inference model in the case of the ventriloquist effect, as depicted in Kording et al. (2007).

Framing the idea of multisensory perception within the causal inference model, when there are two separate causes (C = 2) we can integrate sensory information using the optimal weighting principle to identify a final estimate. Using this model, sensory information that is more reliable is given a larger weight relative to sensory information that is less reliable (Ernst & Banks, 2002; Helbig & Ernst, 2007; Helbig & Ernst, 2008). In this sense, multisensory integration is conducted in a statistically optimal way to minimize variance as much as possible to most accurately calculate the final estimate of a cause.

What is formally known as the crossmodal congruency effect informs us that information presented in one modality can serve as a distractor towards information presented in another modality. If information from two or more modalities are presented in the same spatial location, it is called congruent. On the other hand, if information from two or more modalities are presented in spatially different locations, it is called incongruent. It has been well-established in the literature that performance differs for congruent versus congruent and incongruent stimuli, such that individuals are much faster and more accurate at locating congruent stimuli than incongruent stimuli (Costantini, Migliorati, Donno, 2018; Zopf, Savage, Williams, 2010; Zopf, Savage, Williams, 2013). This discrepancy can be used to establish multisensory integration effects between different modalities.

Multisensory integration has been studied across various modalities including vision, touch, auditory and motor systems. One of the most prominent integration effects comes from an audiovisual illusion known as the sound-induced flash illusion. Violentyev, Shimojo, & Shams (2005) demonstrate a classic example of how one sensory stream can alter your perception during multimodal stimulus presentation. In the illusion, when a black circle flashed on a screen was paired with two auditory beeps participants perceived the circle as flashing twice on the screen. The same effect did not occur however, if the flash was paired with only a single beep. The sound-induced flash illusion is an example of an auditory cue changing your perception of the visual stimulus. The illusion specifically occurs when the modality cues are incongruent in terms of continuity. The auditory cue, which is presented in a discontinuous manner, effectively alters the perception of the visual cue, which is presented in a continuous manner. However, the opposite effect does not seem to occur where the continuous modality alters your perception of the discontinuous modality. The opposite effect can also occur, where visual information alters your perception of auditory stimuli. In the McGurk effect, viewing a video of a person speaking the syllable [ga] while simultaneously hearing the syllable [ba], viewers oftentimes hear the resulting syllable [da] (McGurk & MacDonald, 1976). This particular example relies on principles of speech perception using vision and audition. The syllable [ga] has similar features to [da] when presented visually, and the syllable [ba] has similar features to [da] when presented auditorily. Therefore, when individuals see [ga] but hear [ba], the final estimate is based on the averaging of information from both modalities to form a new fused percept of the syllable. In this way, visual information can strongly influence speech perception (MacDonald & McGurk, 1978).

Audiovisual integration effects have been more intensively studied via various illusions, however there are many other modalities in which multisensory integration can be observed. In this thesis, we will focus on understanding how vision and touch integrate. One example of this uses the mirror box illusion, in which subjects see a mirror reflection of their own hand in a different location as their own hand. For example, in Liu & Medina (2017), the hand behind the mirror was rotated to a spatially conflicting angle relative to the hand the subject saw in the mirror (i.e. mirror hand palm up, hidden hand palm down). Then, subjects were asked to make synchronous or asynchronous hand movements with both hands. During synchronous hand movements, subjects experienced multisensory integration such that they felt that their hand behind the mirror was in the same posture as what they saw, even though it actually in the opposite postural position. Conversely, asynchronous movements do not result in the same effect. The motoric incongruency decreases the likelihood that you perceive the hand in the mirror as your own hand. Ultimately, this is one example of evidence that multisensory integration can also occur relative to the body.

In sum, cognitive researchers have extensively studied the behavioral mechanisms of multisensory integration (Igarshi, Kimura, Spence, & Ichihara, 2008; Johnson, Burton, & Ro, 2006; Tipper et al., 1998). On the other hand, more work needs to be done to explain the underlying neural mechanisms for these processes. Several neuroimaging studies have used fMRI to examine where the brain localizes the effect of viewed touch on felt touch and found increased activation in somatosensory areas upon the visual experience of viewing touch (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Bufalari Aprile, Avenanti, Di Russo, & Aglioti, 2007; Ebisch et al., 2008; Keysers et al., 2004). However, to our knowledge, limited research has been done to localize the mechanistic properties of visuotactile integration, namely congruent versus incongruent touch. Using multiple methodological approaches and analytical techniques, we can hopefully be more accurate in describing the neural correlates of multisensory integration.

Beauchamp, Pasalar, & Ro (2010) conducted a behavioral and neuroimaging experiment to investigate visuotactile integration in a basic detection task. In both tasks, subjects received either multisensory or unisensory touches, by watching videos of a hand being touched and feeling a vibrotactile stimulus on their own hand. These stimuli also varied based on the reliability of each modality input. Behavioral results showed that when stimuli were less reliable, subjects were more accurate if presented with multisensory stimuli overall, and the reliable modality was more influential in predicting response. Thus, vision can actively influence our perception of touch to the hand. Beauchamp et al. (2010) followed up with a neuroimaging task using the same basic design to determine how multisensory touch was localized in the brain and how the neural representation changed as a function of reliability. First, they found significant activation in somatosensory cortex, visual cortex, and intraparietal sulcus (IPS). After comparing connection strengths between lower and higher order multisensory areas, they found that reliable visual stimuli presented with high connection weighting between visual cortex and IPS and unreliable visual stimuli presented with decreased connection weighting between these regions. The same pattern emerged for somatosensory stimuli. Beauchamp et al. (2010) ultimately demonstrate that altering the reliability of a modality may influence behavioral and neural weighting mechanisms. Instead of tactile detection, in the following study we will use tactile localization task to understand the neural correlates of visuotactile integration.

Noppeney (2012) laid out different case scenarios for how the brain processes multisensory integration. One possibility is that there are brain regions partially or solely responsible for multisensory integration such that the combined representation of various sensory modalities exists in this region. Second, it is possible that the brain regions associated with various sensory modalities (visual cortex, somatosensory cortex, motor cortex, etc.), are connected through some unknown pathway and are integrated in primary areas themselves. To examine this question, Rohe and Noppeney (2016) conducted a multi-stage experiment in which subjects were presented with audiovisual stimuli that varied across four different locations in each modality, and two different reliability levels in each modality. Given the crossmodal stimuli presented, subjects were asked to localize either the visual or auditory stimulus. From this behavioral task, subjects were found to more strongly weight visual information than auditory information when estimating the signal location, and especially when the visual reliability was high. The same task was performed in the MRI scanner and analyzed using MVPA to decode differences auditory and visual signals and their corresponding reliability weightings. Part of their findings demonstrated that the computational principles that guide multisensory signals translate neurally, such that higher level cortices like intraparietal sulcus (IPS) are involved in multisensory integration. MVPA has been shown to be incredibly powerful in characterizing cognitive processes.

There are many different methods of applying computational techniques to neuroscience, one of them being multi-voxel pattern analysis (MVPA). The MVPA approach can be used to decode specific patterns of activation from fMRI data (Norman, Polyn, Detre, & Haxby, 2016). MVPA allows researchers to gain substantially more statistical power by avoiding spatial averaging of individual voxels like typical fMRI analysis. Instead, the analysis uses a pattern classification algorithm to train the data and then see if it can correctly identify your chosen experimental conditions. This analysis technique has been used in the past to further our understanding of multisensory integration (Rohe & Noppeney, 2016; Rohe & Noppeney, 2015). The following study will use MVPA to decode the pattern of activity during different types of multimodal stimuli in a visuotactile localization task.

Current Experiment

The research presented seeks to address two main questions: (1) In a behavioral tactile localization task, what is the effect of viewed touch on felt touch, and (2) using fMRI and MVPA what are the neural correlates of visuotactile multisensory integration?

A two-part study was conducted to address the questions above, including both a behavioral and neuroimaging experiment. With regards to the first question, a behavioral experiment was conducted to establish a multisensory integration effect in a tactile localization task. Although researchers have studied this paradigm before, we wanted to confirm the presence of multisensory integration even when the spatial location of the viewed and felt hands differed. Eventually when we moved this experiment into the scanner, the location of the viewed hand is spatially much farther away from the felt hand. In our behavioral experimental set-up subjects' hands were placed directly in front of a monitor so the spatial location slightly differed. After a threshold detection procedure, subjects watched videos of a hand being touched on one of four fingers (index, middle, ring, pinky) while being touched simultaneously on one of their own fingers (excluding the thumb). Subjects had to respond where they perceived the physical touch on their own hand. Congruent trials were trials in which the finger touched in the video was the same as the finger stimulated on the subject's hand. Incongruent trials were trials in which the finger touched in the video was different than the finger stimulated on the subject's hand. If there is visuotactile multisensory integration in this task, then we would expect subjects to have more accurate localization of touch on congruent trials, less accurate localization of touch on incongruent trials. Additionally, during incongruent trials we expect the distribution of errors to be biased towards the visual stimulus.

Next, we asked what are the neural correlates of visuotactile multisensory integration? A similar experiment was conducted using fMRI and analyzed using standard event-related analyses and MVPA. The design of this neuroimaging experiment was similar to the first behavioral task, only with just two visual and tactile locations (index and middle) instead of four. As with the previous experiment, subjects first completed a short forced-choice detection task outside the scanner to determine a baseline tactile threshold. Then in the main imaging task, subjects reported which finger they felt the actual touch on using an MRI-compatible button box. Again, we were interested in where multimodal stimuli are localized in the brain. We predict that we will find significant activation in brain regions responsible for multisensory integration as opposed to unisensory processing or that we will see significant activation in regions already linked with various sensory modalities (i.e. somatosensory cortex, visual cortex). We may also find some combination of these two hypotheses to be true.

Lastly, to further understand differences between multimodal stimuli we analyzed our fMRI data using multi-variate pattern analysis (MVPA). If the brain processes congruent and incongruent trials differently then we should be able to use our collected data as classifiers to successfully predict whether the subject was experiencing a congruent versus incongruent multimodal stimulus. In other words, the pattern of activation across voxels should be significantly different for a congruent versus incongruent trial.

Chapter 2

BEHAVIORAL EXPERIMENT

Materials and Methods

Subjects

Eighteen subjects participated in the behavioral experiment (five male). All subjects were undergraduate students at the University of Delaware and were monetarily compensated for their time spent completing the experiment. These subjects were collected on a voluntary basis by the experimenter.

Stimuli

Both visual stimuli and tactile stimuli were used to create a basic detection and localization task. Visual stimuli involved a 1 s video of the dorsal side of a left hand being touched by another individual on the tips one of four fingers (index, middle, ring, or pinky). In other words, there was a touch presented in every video. The touching hand approached the other hand until t = 500 ms. In every video, the touching hand presented the viewed touch on the still hand from 500 ms after the video onset to 666 ms. The touching hand left the other hand from 667 ms until 1 s. All videos were edited to fit the accustomed timing using Adobe Premiere.

Tactile stimuli involved a vibration delivered to the subject's left hand on the tip of one of four fingers (index, middle, ring, or pinky). Tactile stimuli were created using Audacity software and presented through bone conductors which were attached to the dorsal tip of each finger on the subject. The timing parameters matched those of the visual stimuli. During congruent trials the felt touch on the subject's hand happened at the exact moment of the viewed touch, t = 500 ms after the video onset for a 166 ms touch. Throughout the entire stimulus 100Hz of background noise was played with an amplitude of -44db except during the tap when frequency increased to 120Hz. The amplitude of the tap varied between either -32db and -37db or -37db and -42db for stimuli during the staircase detection task. A 65% accuracy score was used to determine one amplitude level to be used for all trials during the main localization task.

Experimental Design

The behavioral experiment consisted of two short tasks, the staircase detection task and the localization task.

Staircase Detection Task

The first component of the behavioral experiment was an adjusted staircase detection task. Subjects had their left hand placed directly in front of a monitor and were presented with varying tactile stimuli on either their index, middle, ring, or pinky finger. The subjects' hands were covered so that they could not see their own hand. Subjects wore headphones that played brown noise to eliminate hearing any vibrations. The task was to verbally respond as to which of their own fingers the felt touch was presented on while the experimenter recorded the responses using the keyboard. This task was programmed using MATLAB. There were 11 sets of stimuli based on the 11 amplitude levels ranging from -32db (higher intensity) to -42db (lower intensity), however subjects only received half of the stimuli during the task. All subjects started with stimuli of amplitude level of -37db and then continued to receive either stronger (-36db to -32db) or weaker (-36db to -42db) stimuli based on their accuracy score (+/- 65%) during the first set of trials. Each trial type was presented 10 times on each finger in a 4 (finger: index, middle, ring, pinky) x 6 (amplitude level: either -36db to -32db or -36db to -42db) design for a total of 240 trials. Throughout all trials, subjects listened to brown noise playing from a separate speaker to cover any miniscule sounds from the bone conductors.

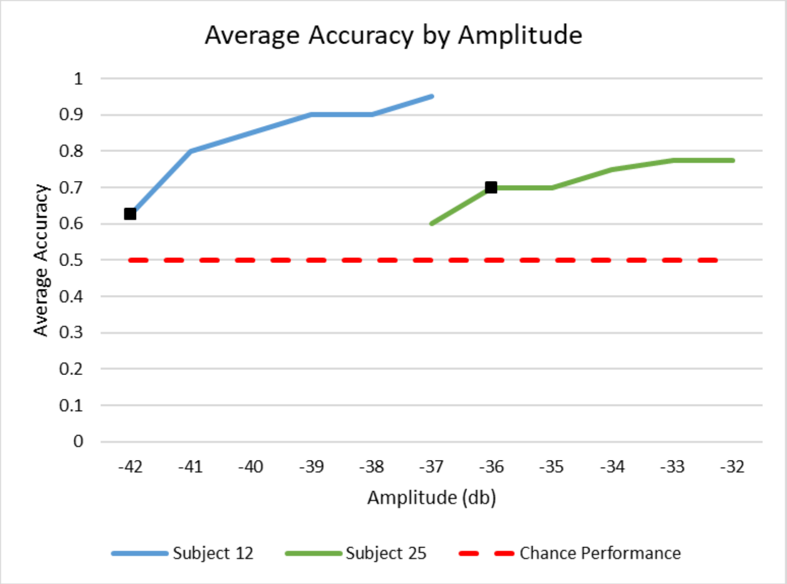

Figure 2 The detection curve for subjects 12 and 25, respectively, where the black square indicates the chosen amplitude level closest to 65%. Red dashed line at 0.5 depicts chance performance.

At the end of the task, accuracy scores were calculated for each amplitude level across finger type. One amplitude level was chosen for each subject in which the accuracy score was closest to 65%. Figure 2 shows an example detection curve for two subjects. 5 subjects had a threshold at -42, 1 at -40, 3 at -38, 3 at -37, 3 at -36, and 3 at -34. These stimuli were then used as the tactile stimuli during the next localization task.

Visual-Tactile Localization Task

The second component of the behavioral experiment was the main task in which subjects viewed a touch while feeling touch on their own hand. Hand placement and set up was the same as in the previous task, and subjects wore headphones that played brown noise to eliminate hearing any vibrations. Again, the task was to verbally respond on which finger a tactile stimulus was presented while seeing a hand being touched The experimenter manually entered subjects' responses using a keyboard. Unlike the staircase detection task, all stimuli were multimodal such that a touch was presented in both modalities, visual and tactile. The experiment was programmed using MATLAB. The trials were presented randomly across conditions in 5 separate blocks in a 4 (Visual Location: index, middle, ring, pinky) x 4 (Tactile Location: index, middle, ring, pinky) design for a total of 16 different trial types. Each trial type was presented 6 times per block, for a total of 30 trials per condition per subject. Congruent trials consisted of trials in which the visual location and tactile location were the same, whereas incongruent trials consisted or trials in which the visual location and tactile location differed. The intertrial interval was randomized between 1.0-1.5 s, and subjects had a maximum response time of 3 seconds.

Results

Our analyses aimed to target our broader question about visuotactile multisensory integration; Does viewed touch have a significant effect on the perception of felt touch in a tactile localization task? All behavioral data was analyzed in RStudio. 64 observations in which the subject had no response were removed from the dataset before analysis. In addition to our main question, we addressed other related points in the following analyses.

First, we were interested in the baseline effect of congruency on accuracy scores. In other words, will subjects be more accurate overall on congruent trials than incongruent trials? This question was answered with a binomial generalized linear mixed effect model (LMEM). Our model included a random slope and intercept for the congruency variable to account for random variation between subjects. There was a main effect of congruency on accuracy scores ($z = 4.885$, $p < .001$). On average, subjects were about 79.4% accurate on congruent trials, but only 60.9% accurate on incongruent trials (see Figure 3).

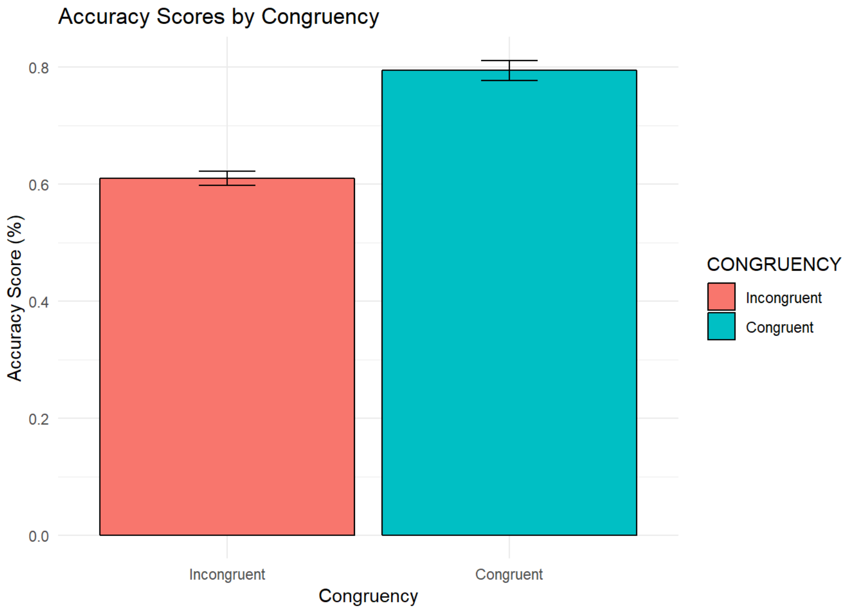

Figure 3 Bar graph showing significant effect of congruency on accuracy scores with confidence intervals plotted.

Given that the size of the fingertip representations in the brain likely differ as a function of usage, with the index finger represented as larger than the pinky, we were curious as to whether subjects differed in performance on each finger. Will subjects have significantly different accuracy scores for the different tactile locations (index, middle, ring, and pinky)? To answer this question, we ran a binomial generalized linear mixed effect model. The dependent variable was accuracy and the predictor variable was tactile location, modeled with a random slope and intercept. Unlike ANOVAs, LMEMs compare one condition to all the other conditions. In our model we compared middle finger accuracy scores to those for the other three location. This was because we expected the middle finger, which accuracy was highest on, to be significantly better than the other fingers. Using the linear mixed effect model people were most accurate on the middle finger, scoring an average of 73.8%. Subjects were significantly less accurate at localizing the touch on the ring, with 60.9%, and pinky fingers, with 59.5% (z = -2.115, p = 0.034; z = -2.843, p = 0.004). The finding for index finger was non-significant. Mean accuracy scores for each tactile location are visually depicted in Figure 4.

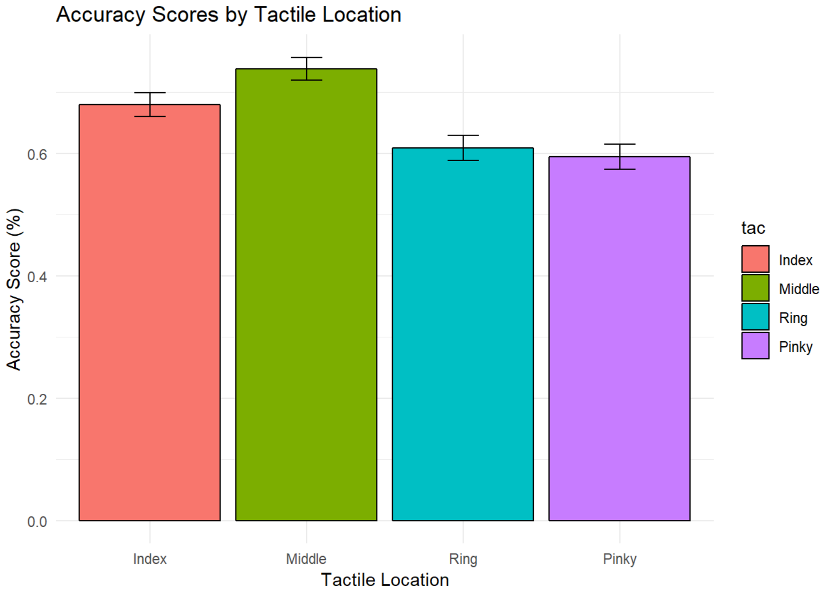

Figure 4 Bar graph showing mean accuracy scores by tactile location (index, middle, ring, pinky) with confidence intervals plotted.

After quantifying the base effect of tactile location, we were interested in understanding how the visual information could potentially bias accuracy scores. Basically, does the absolute distance (regardless of direction) between the tactile and visual locations modulate accuracy? Again, we modeled this with a generalized linear mixed effects model using binomial as the family distribution. The dependent variable was accuracy and the predictor variable was absolute visual distance, which was calculated as the absolute value of the distance in units between the given visual and tactile locations (0, 1, 2, or 3). The absolute visual distance was a significant predictor of accuracy scores, such that as distance increased accuracy decreased ($z = -4.063$, $p < 0.001$). Figure 5 plots the accuracy scores for each unit of absolute visual distance and their confidence intervals. Average accuracy dropped from 79.4% on congruent trials to 62.8% when visual distance was 1 unit, then 58.9% when visual distance was 2 units, and increased to 59.6% when visual distance was 3 units. A follow-up model was conducted in which all trials where the visual distance was 0 were removed from the analysis. This would determine if the effect of visual distance on accuracy scores was still significant when we only consider incongruent distance, e.g. 1, 2, and 3. The absolute visual distance, given only distances of 1, 2, and 3, was not a significant predictor of accuracy scores ($z = 1.202$, $p = 0.229$).

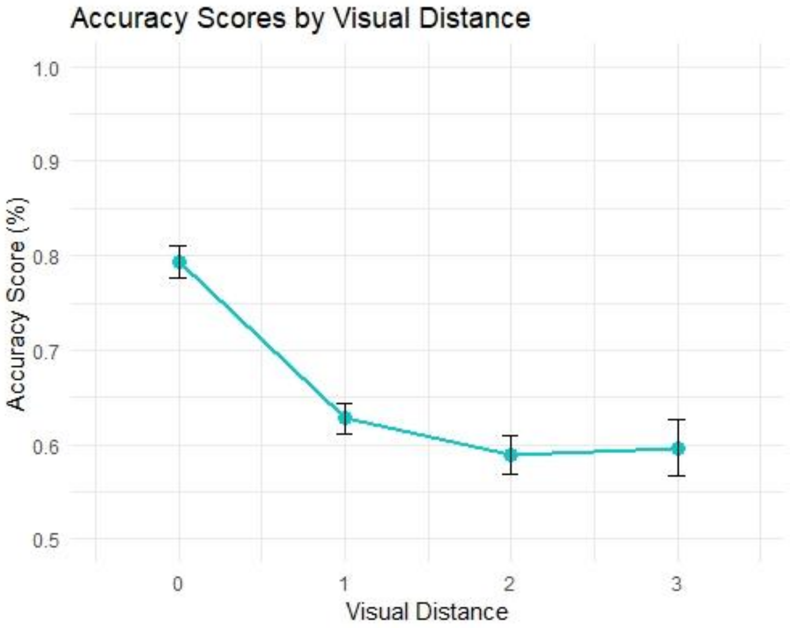

Figure 5 Line graph showing mean accuracy scores by the absolute distance between the tactile and visual locations with confidence intervals plotted.

Similarly, we examined whether the distance of the tactile location from the visual location (non-absolute) modulated accuracy. For this case, we were interested in seeing if there was a directional influence on differences in accuracy scores. In this case, directional visual distance was calculated as the directional shift of the visual location minus the tactile location. Using a generalized linear mixed effects model with a binomial distribution, we modeled accuracy scores against directional visual distance. Unlike the absolute visual distance, the directional visual distance was not a significant predictor of accuracy scores ($z = 1.528$, $p = 0.127$).

The final main question we were interested in was whether the visual location combined with tactile location would be a stronger predictor of responses for tactile localization than simply the tactile location. As a check before our question of interest in this analysis, we modeled the tactile location with response choice to ensure that tactile location was a significant predictor. As opposed to the previous questions, we used a linear mixed effect model with a normal distribution to model this effect. A random slope and intercept for our predictor was still included in the model. Results from the model show that tactile location is a significant predictor of response choice during the tactile localization task ($t = 10.648$, $p < 0.001$). Now we are interested in whether visual location is also a significant predictor of responses, along with the interaction between tactile and visual locations. A visual location main effect and interaction effect were added to the LMEM, accounting for additional random slopes and intercepts. There was still a main effect of tactile location ($t = 9.713$, $p < 0.001$) as well as a main effect of visual location ($t = 3.673$, $p = 0.002$). However, the interaction between the tactile and visual locations were not significant. Combining our results from the previous two models, we computed an analysis of deviance table to determine if the latter model was a significantly improved fit for our data set. The model including both main effects for visual and tactile locations as well as their interaction was a significantly better fit when compared to the model with only tactile location as a predictor ($\chi^2 = 693.56$, $p < 0.001$). To visualize the effect of viewed touch on felt touch we plotted histograms showing the percentage of responses across all visual and tactile locations (Figure 6).

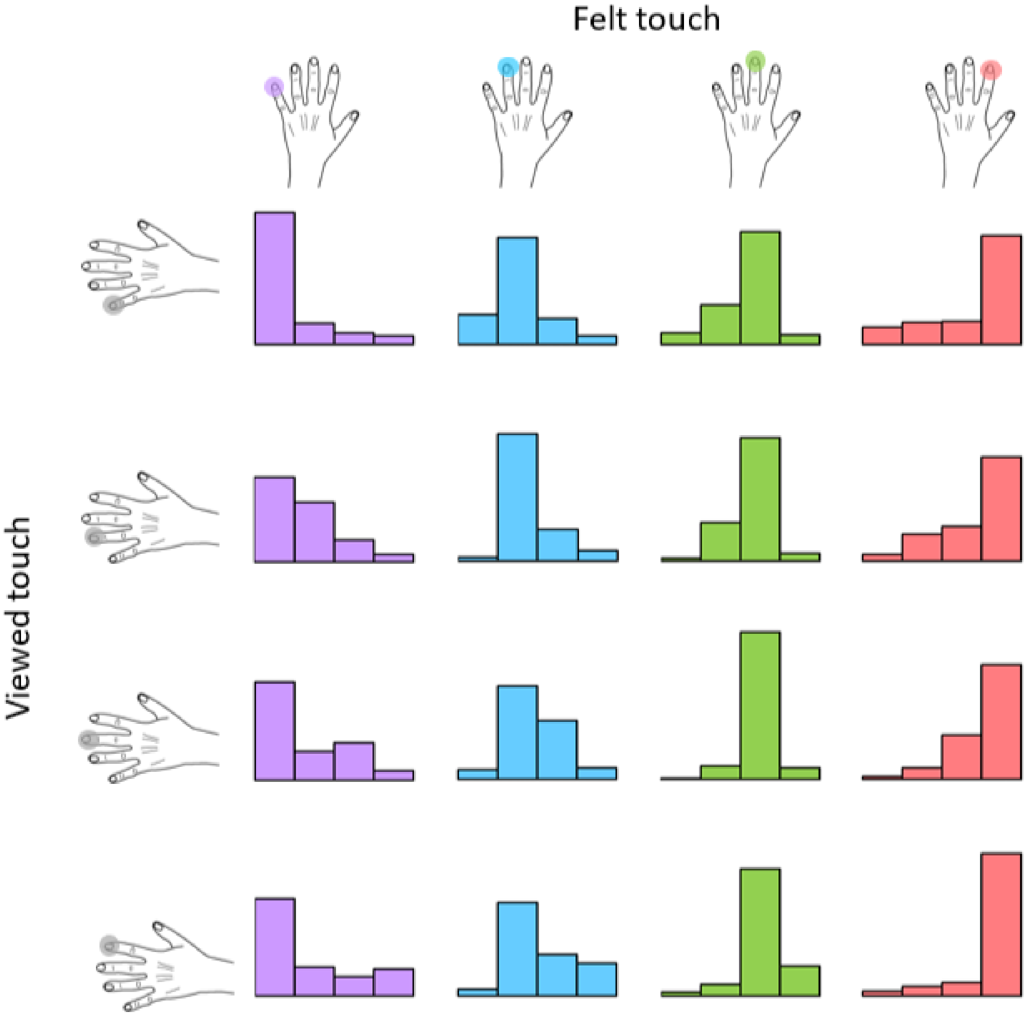

Figure 6 Histogram plot showing percentage of responses across all possible trial types (Tactile Location x Visual Location). Each plot contains four bars, one for each possible response type (pinky, ring, middle, index).

Discussion

The behavioral experiment was aimed at analyzing a congruency effect between different visuotactile stimuli to eventually examine in the scanner. While the main interest was in this congruency effect, we also explored a few additional questions. We predicted that subjects would be significantly more accurate at localization with congruent stimuli than incongruent stimuli, and that this would be modulated based on the distance between the visual and tactile stimulus. Our analyses produced four significant main findings that support our hypothesis.

First, we found a main effect of congruency on accuracy scores, such that subjects were significantly more accurate during congruent trials than incongruent trials. This result is directly and most obviously in line with our main prediction. We are much more likely to respond with greater accuracy when the location of the visual and tactile stimulus on the hand are aligned. This finding is consistent with the crossmodal congruency effect, and that individuals are better at localizing congruent stimuli than incongruent ones. When individuals experience multimodal congruent stimuli, they are quicker to respond compared to multimodal incongruent stimuli. When there is incongruence, however, visual stimuli can certainly influence the final estimate of the tactile sensation (Pavani, Spence, & Driver, 2000).

Second, we found that subjects were significantly less accurate on the ring and pinky fingers compared to the middle finger. Although this isn’t directly related to our prediction with regards to incongruent and congruent stimuli, it is interesting to note that different fingers may constitute differences in somatic representation (Duncan & Boynton, 2007; Ejaz, Hamada, Diedrichsen, 2015; Iwamura, Tanaka, & Hikosaka, 1980). This may explain why accuracy scores were lower on the ring and pinky fingers. Even though we accounted for differences in baseline tactile threshold, sensory information can vary greatly from individual to individual and within individuals, especially when it comes to touch (Murray, Ionta, & Wallace, 2019). In addition, it has been well established that our sense of touch can vastly differ across various body parts (i.e., tips of fingers, dorsal side of hand, limbs, back), so it makes sense that this concept could also apply to our individual fingertips.

Third, we found a main effect of the absolute visual distance on accuracy scores. Subjects were significantly less accurate at localizing a touch when the distance between the tactile and visual locations were farther apart. The results from this model produce similar conclusions to our finding of a main effect of congruency. In addition to the broader finding that subjects are more accurate on congruent than incongruent trials, the main effect of absolute visual distance tells us that the distance between stimulus locations also plays a factor in our localization. When the distance between the tactile and visual locations increased from 0 to 1, 2, or 3 accuracy drops significantly. Localization can likely vary as a result of the distance between two stimuli. It is possible that you are more likely to make an error when locations are slightly further apart. On the other hand, when locations for multimodal stimuli differ drastically, it may become more obvious where the stimuli are being presented.

Fourth, we found that a model fitting both the tactile and visual locations was significantly more predictive of responses than a model fitting just the tactile location. To begin with, this result demonstrates that individuals are using two sensory inputs (vision and touch) to make their decision about where they felt only a single sensory input (touch). Obviously, individuals should take into consideration where the tactile stimulus is presented when they are making their decision, and this is supported by our main effect of the tactile location on response choice. But, in everyday life we combine information from multiple sensory streams to obtain a given representation of our perceptual experience. This idea is further supported by the plotted histograms of all trial types, where we see that incongruent trial types have much more variation than congruent trial types. Additionally, we can see that the mean response slightly shifts towards the viewed touch during incongruent conditions.

The results presented above give us a clearer picture of how combined sensory input can influence our decision-making process in a localization task. If subjects show differences in sensory processing for congruent and incongruent stimuli, then we expect to also find differences in their neural representation with fMRI and MVPA.

Chapter 3

NEUROIMAGING EXPERIMENT

Materials and Methods

Subjects

Two subjects participated in the neuroimaging experiment (2 female). All subjects were undergraduate students at the University of Delaware and were monetarily compensated for their time spent completing the experiment. These subjects were collected on a voluntary basis by the experimenter. One out of two subjects were excluded due to signal dropout in all functional runs, leaving one subject for all analyses in this section.

Stimuli

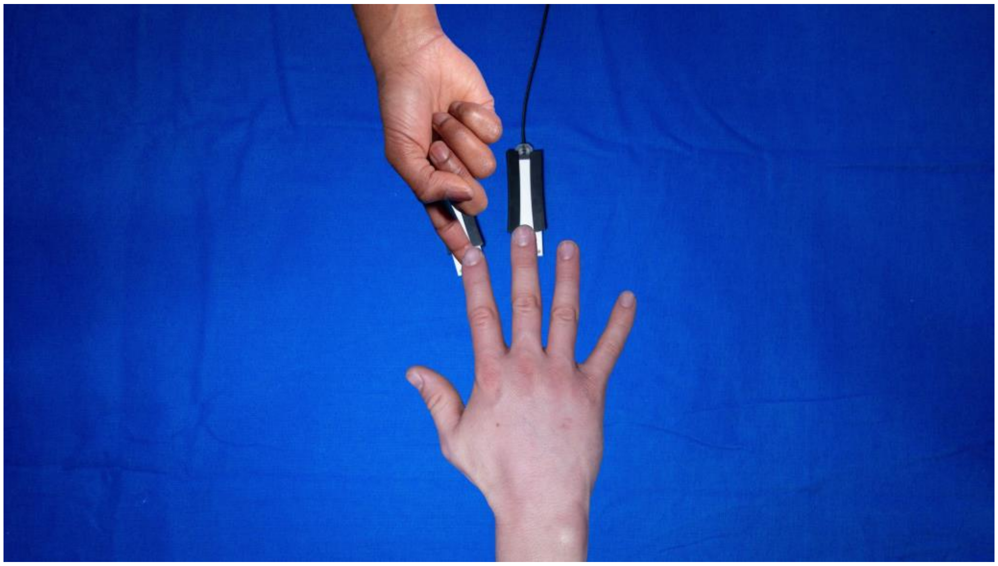

Figure 7 Example of visual stimuli in the condition where the index finger is being touched by another hand.

Both visual stimuli and tactile stimuli were modified to use in a basic detection and localization task. Participants viewed a 2.5 s video of the dorsal side of a right hand being touched by another individual on the index or middle finger (see Figure 7). The first and last 500 ms of the video included just a still view of the hand. The touching hand approached the still hand from 501-1167 ms, touched the still hand from 1168-1333 ms, and withdrew from the still hand at from 1334-2000 ms. Videos were edited using Adobe Premiere software. The touch was presented on the palmar side of the index finger in the video as well as on the palmar side of the subject's own finger such that both the viewed and felt touches were congruent. The palmar side of the finger was selected to elicit the most neural signal since, in general, individuals are more receptive to touch on the palmar side as opposed to the dorsal side of the hand.

Tactile stimuli, presented during the video, were vibrations delivered to the subject's right hand on the tip of either the index or middle finger. Tactile stimuli were created using Audacity software and presented through MRI-compatible tactile stimulators which were attached to the palmar tip of each finger on the subject (also see Figure 2). The timing parameters matched those of the visual stimuli, such that the touch on the subject's hand happened at the exact moment of the touch presented in the video, t = 1168 ms. Throughout the entire trial, there was no background oscillation noise until the touch was presented with a frequency of 120 Hz and variable amplitude. The amplitude of the touch varied between either -33db and -50db during the detection task. For reference, -33db produced a strong, suprathreshold touch, while -50db produced a weaker, but still suprathreshold, sensation. Two amplitude levels were chosen and used in the main localization task. Average accuracy scores were calculated across each amplitude level. The amplitude level for the reliable condition was chosen for each subject in which the accuracy score was closest to 75%. Similarly, the amplitude level for the unreliable condition was chosen for each subject in which the average accuracy score was closest to 55%.

Experimental Design

The neuroimaging experiment consisted of several tasks to target the questions of interest. First, subjects completed a forced-choice detection task in a short behavioral session. Neural data was collected during two separate scanning sessions in which subjects completed a total of 8 runs of a localization task, two different localizers, and two structural scans.

Detection Task

First, subjects completed a forced-choice detection task outside of the scanner. The detection task was designed to set up a base threshold level for the two types of reliability levels (low and high) which would be used in the main localization task. Subjects sat in front of a monitor and had their right hand placed directly in front of the monitor. The subjects' hands were covered so that they could not see their own hand. They were presented with tactile stimuli on either the palmar side of their index or middle finger. As with the behavioral experiment, the task was to verbally respond as to which of their own fingers the "touch" was presented on while the experimenter recorded the responses using the keyboard. The maximum response time per trial was 2.5 s. Each trial type was presented 15 times on each finger in a 2 (finger: index or middle) x 18 (amplitude level: -50db to -33db) design for a total of 540 trials. This was divided into 5 even blocks. Tactile stimuli were randomized within each block across finger and amplitude level. Throughout all trials, subjects listened to brown noise playing from a separate speaker to cover any miniscule sounds from the MRI-compatible stimulators.

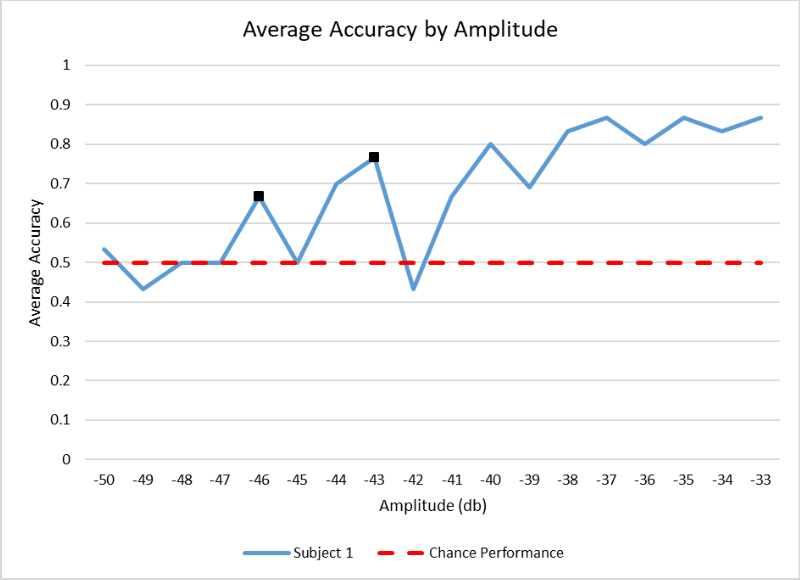

Figure 8 The detection curve for subject 5 where the black squares indicate the chosen amplitude level greater than and closest to 55% and 75% accuracy, respectively. Red dashed line at 0.5 depicts chance performance.

At the end of the task, accuracy scores were calculated for each amplitude level across both finger types. Figure 8 shows the detection curve for one subject during the task. Two levels were chosen and then used in the main localization task. A 75% accuracy score determined the final amplitude level used for the reliable condition, whereas a 55% score determined the final amplitude level used for the unreliable condition. Amplitude levels chosen were closest to and greater than these predetermined values of 75% and 55%. These stimuli were then used as the tactile stimuli during the main localization task.

Visual-Tactile Localization Task

The main task in the scanner consisted of a localization task, similar to the localization task in the behavioral experiment. Subjects viewed a touch on the palmar side of the index or middle finger tip of a right hand while feeling touch on their own right hand. The task was to respond as to which of their own fingers the touch was presented on using an MRI-compatible button press with their opposite (left) hand. Unlike the forced choice detection task, all stimuli were multimodal such that a touch was presented in both modalities, visual and tactile. The experiment was initially set to be a 2 (Visual Location: index or middle) x 2 (Tactile Location: index or middle) x 2 (Tactile Reliability: high or low) design for a total of 8 different trial types. However, due to a coding error, tactile reliability and visual location were confounded, such that every tactile stimulus on the index finger was low reliability, whereas every tactile stimulus on the middle finger was high reliability. This error made it so that we were unable to examine the influence of stimulus reliability and were unable to develop models of participant behavioral performance that could be utilized for neuroimaging experiments – the initial intent of the experiment. However, with these data, we could still examine the neural correlates of visuotactile congruency. The entire task included 8 runs total where each run was approximately 12 minutes. Each trial was presented 10 times per run, for a total of 80 trials per condition per subject. On congruent trials, the visual location and tactile location were the same, whereas incongruent trials consisted or trials in which the visual location and tactile location differed. The intertrial interval was consistently 5 s, and subjects had a response window of 1.5 s.

Region of Interest Localizers

Two localizers, including a tactile localizer and a visual hand localizer, were included to determine some regions of interest for MVPA. The tactile localizer and visual hand localizer were meant to localize areas of the brain used for processing felt touch and viewing hands, respectively. Knowing the precise regions involved in these conditions could inform potential pre-defined masks to perform MVPA and decode the different types of multimodal stimuli.

Tactile Localizer

The tactile localizer was intended to localize the area of the brain used for processing felt touch on the tips of the index and middle fingers. Stimuli used during this task were different than the tactile stimuli used during the localization task. Subjects felt a 30 Hz frequency paired with a -25db amplitude (relatively strong vibration pattern) for 2 s on and 0.5 s off, for a total of 12 seconds. One run of the localizer consisted of 12 trials of this sequence and took approximately 5 minutes. The stimuli were played through the same MRI-compatible stimulators used for the main localization task and detection task.

Visual Hand Localizer

Figure 9 Example stimuli used for visual hand localizer; hand, chair, body (from left to right).

The visual hand localizer was intended to localize the area(s) of the brain used for processing viewed hands, contrasted against chairs and headless bodies. Subjects viewed three categories of images, hands, chairs, and headless bodies, in three separate blocks. Images were 400 px x 400 px greyscale images of hands, chairs, or headless bodies, used in previous literature (see Figure 9) (Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010). The basic design of this localizer was a replication of an earlier experiment in which participants saw a 14 s fixation point at the start of the task, end of the task, and in between each block (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2011). In each trial, subjects viewed an image for 800 ms and a blank screen for 200 ms. Each block contained 84 images (36 unique), where 6 images were randomly chosen to be shown twice consecutively in the block. As a manipulation check, subjects had to press a button on an MRI-compatible button box with their left hand each time an image was presented twice in a row. Subjects only completed one run of this task which was about 5 minutes.

MRI Data Acquisition

The anatomical MRI scans were collected from each subject using a 3T MR Siemens Magnetom Prisma scanner at the University of Delaware. Images were T1-weighted rapid gradient-echo (MP-RAGE) sequencing with a repetition time (TR) of 2080 mm, voxel size of 0.70 x 0.70 x 0.70 mm, resulting in a slice thickness of 0.70 mm.

The functional scans were collected with a repetition time (TR) of 1000 ms and flip angle of 61 degrees. Voxel size was 2.0 x 2.0 x 2.0 mm, resulting in a slice thickness of 2.0 mm.

Data Preprocessing

After collection, all scans were converted to NIfTI format for further processing and analysis using FMRIB Software Library (FSL). The structural images were skull-stripped using the brain extraction tool (BET) which performed robust brain center estimation (Smith, 2002). A fractional intensity threshold of 0.20 was used to ensure the entire brain space was included in the extraction. All functional data were motion corrected using MCFLIRT 4-stage correction (Jenkinson, Bannister, Brady, & Smith, 2002).

Standard Event Related Analyses

Standard event related analyses for the tactile localizer, visual hand localizer, and visual-tactile localization task were performed using a general linear model in FEAT (Woolrich, Ripley, Brady, & Smith, 2001). All motion corrected functional images were used as the inputted 4-D data and spatially smoothed with a 2 mm kernel. No slice timing correction was applied to the data. For registration, the brain extracted image was used as the main structural scan and then mapped onto the same image using 6 or 12 DOF as the standard space. We modeled our experimental conditions using a double-gamma HRF form, added temporal derivative, and applied temporal filtering. We modeled all conditions against baseline to start. For the visuotactile localization task, the time when the participant was making the response was modeled as a covariate of no interest. Motion parameters from MCFLIRT were also factored into the model as covariates of no interest. Once the model was defined, the high pass filter cutoff was estimated automatically.

Multi-Voxel Pattern Analysis

The multi-voxel pattern analysis (MVPA) was performed on the fMRI data to decode potential patterns of activation for congruent versus incongruent trials. Our searchlight analysis was done within the whole-brain using the beta weights of each voxel for each functional map. The binary brain mask image was extracted using BET brain extraction. Each beta weight map was first registered to the standard space for the subject. All beta weights for the four conditions we had (tactile index-visual index, tactile index-visual middle, tactile middle-visual index, tactile middle-visual middle) were concatenated across the eight runs in time. Concatenation was performed in FSL. Since we wanted to decode the patterns of activation between congruent and incongruent trials, conditions were simply labeled as congruent or incongruent (e.g. tactile index-visual index was a congruent label). These data were analyzed using CoSMoMVPA package with a linear discriminant analysis and spherical searchlight size of 100 voxels.

Results

Standard Event Related Analyses

All results shown below are displayed at the corrected p-value using false discovery rate (FDR). Results shown are from the second subject.

Region of Interest Localizers

Tactile Localizer

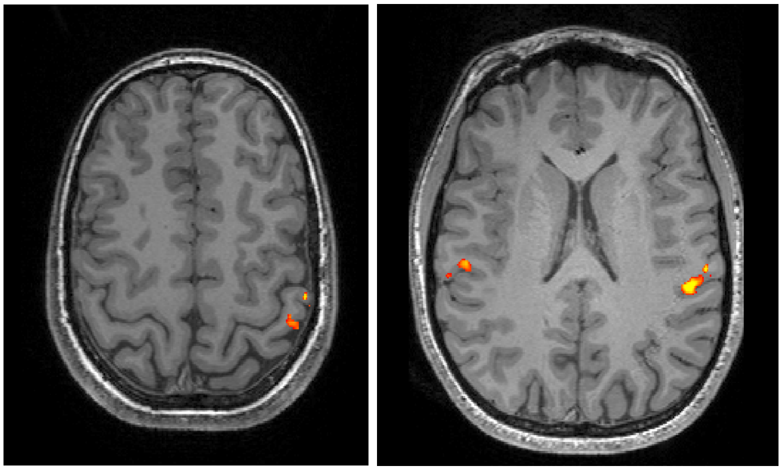

Figure 10 Somatosensory activations resulting from touch condition on S1 (left) and S2 (right) in tactile localizer task.

We observed significant activation in both left S1 and bilateral S2 during the time when the subject felt the vibrations on their finger (Figure 10). In this analysis we only modeled the touch condition, so our contrast was simply a function of touch.

Visual Hand Localizer

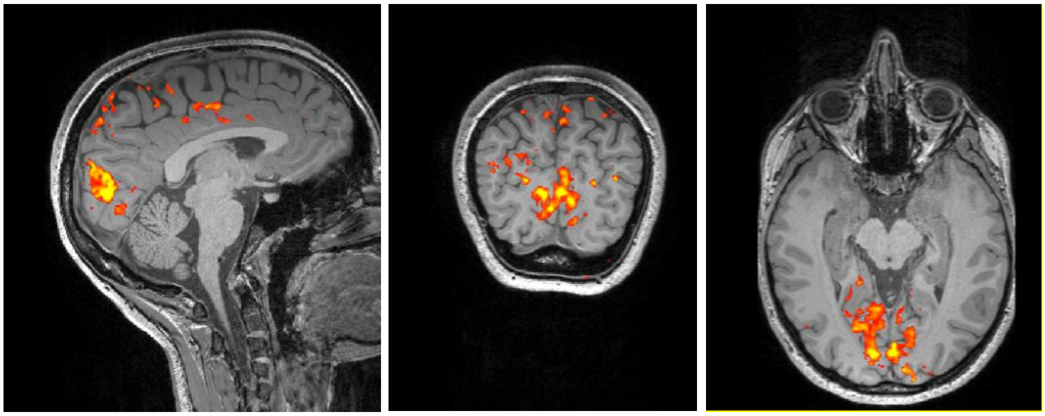

Figure 11 Visual cortex (V1) activation resulting from hand condition relative to body and chair conditions in visual hand localizer task, shown in sagittal (left), coronal (middle), and axial (right) views.

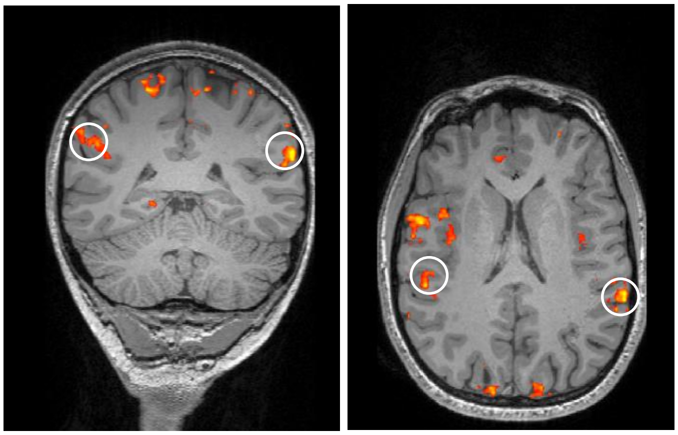

Figure 12 Bilateral S2 activation resulting from hand condition relative to body and chair conditions in visual hand localizer task, shown in coronal (left) and axial (right) views.

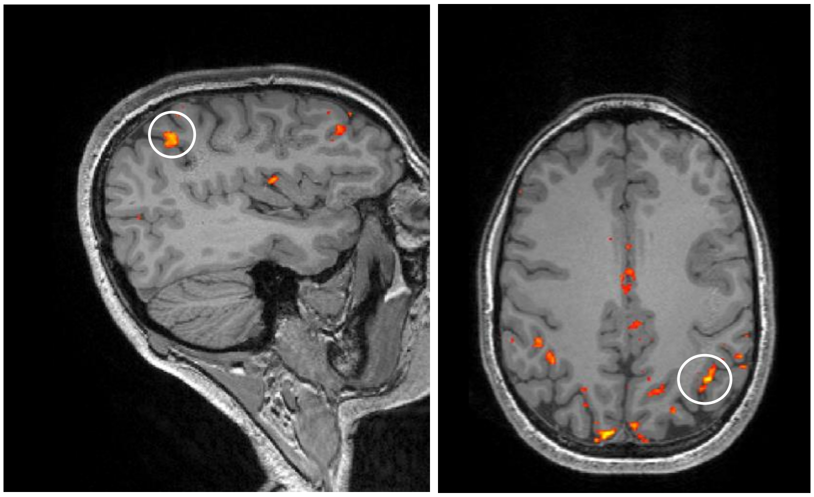

Figure 13 Hand knob activation resulting from hand condition relative to body and chair conditions in visual hand localizer task, shown in sagittal (left) and axial (right) views.

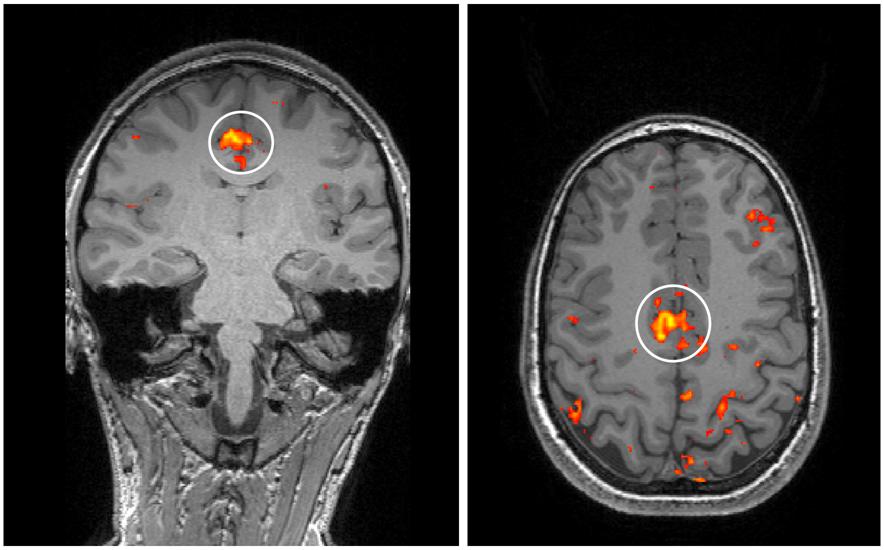

Figure 14 Middle cingulate cortex (MCC) activation resulting from hand condition relative to body and chair conditions in visual hand localizer task, shown in coronal (left) and axial (right) views.

The analysis for the visual hand localizer was a comparison of the hand picture condition relative to the body and chair picture condition. This was our main comparison of interest. We observed significant activation in several different areas. Most prominently, we observed strong activation in primary visual cortex (V1) (Figure 11). Additionally, the comparison resulted in significant activation in bilateral secondary somatosensory cortex (S2) (Figure 12), left hand knob (Figure 13), and middle cingulate cortex (MCC) (Figure 14).

Visual-Tactile Localization Task

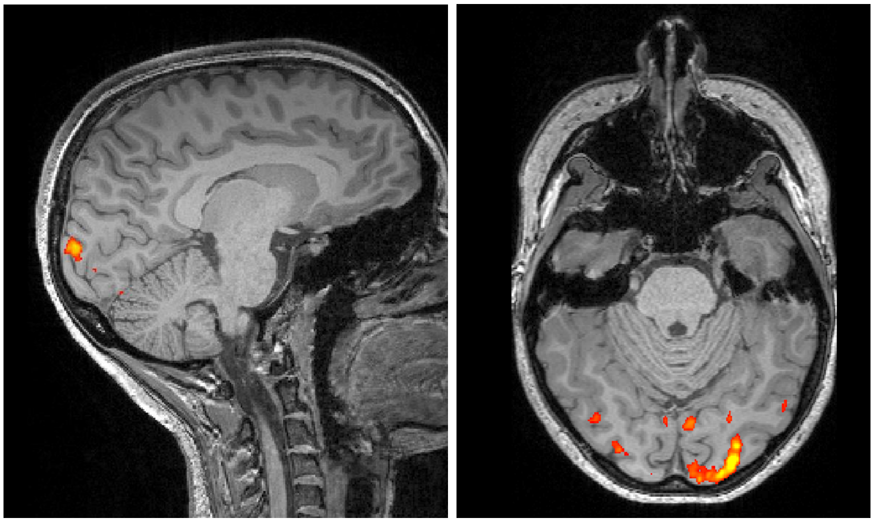

Figure 15 Visual cortex activation averaged from all multimodal stimuli relative to a baseline of rest.

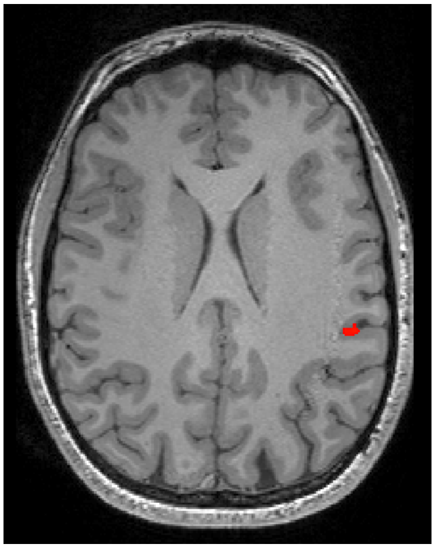

Figure 16 Secondary somatosensory cortex (S2) activation averaged from all multimodal stimuli relative to baseline of rest.

We performed several comparisons to analyze the fMRI data from this task. First, we wanted to establish where we saw activation for across all multimodal conditions, including tactile index-visual index (T_1V_1), tactile index-visual middle (T_1V_2), tactile middle-visual index (T_2V_1), tactile middle-visual middle (T_2V_2). To do this we averaged all four of these conditions together using an F-test. We found significant activation in a large network of areas including visual cortex (Figure 15), and secondary somatosensory cortex (S2) (Figure 16). F-tests averaging across congruent conditions (T_1V_1, T_2V_2) and incongruent conditions (T_1V_2, T_2V_1) separately did not result in any additional findings apart from what we found in the previous analysis.

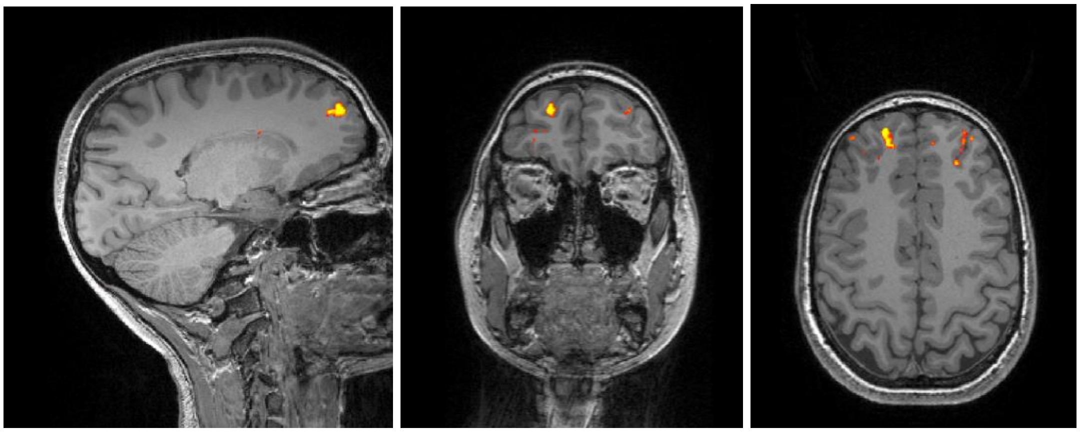

Figure 17 Right dorsolateral prefrontal cortex (DLPFC) activation resulting from the incongruent condition relative to congruent condition, shown in sagittal (left), coronal (middle), and axial (right) views.

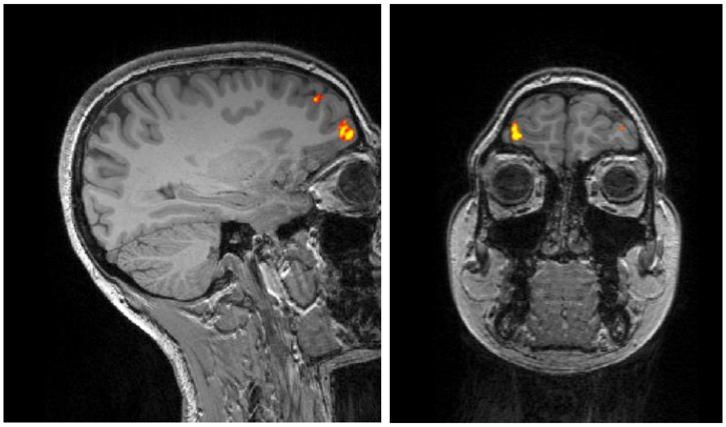

Figure 18 Right orbitofrontal cortex (OFC) activation resulting from the incongruent condition relative to congruent condition, shown in sagittal (left) and coronal (right) views.

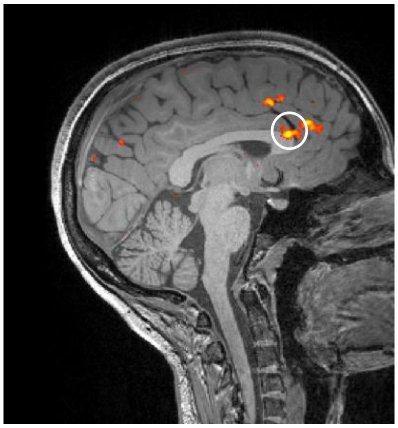

Figure 19 Anterior cingulate cortex (ACC) activation resulting from the incongruent condition relative to congruent condition, shown in coronal view.

The following analyses were conducted to localize the differences between congruence and incongruent visuotactile stimuli in the brain. Our main comparisons of interest were the congruent conditions relative to the incongruent conditions (T_1V_1, $T_2V_2 – T_1V_2$, T_2V_1) and vice versa, the incongruent conditions relative to the congruent conditions (T_1V_2, $T_2V_1 – T_1V_1$, T_2V_2). In the first comparison, congruent relative to incongruent, we found no significant activation. In the latter comparison, incongruent relative to congruent, we find significant activation in several different locations. First, we find significant activation in right dorsolateral prefrontal cortex (DLPFC) (Figure 17). We also find significant, but weaker activation bilaterally, in left DLPFC. This significant activation spreads towards the right orbitofrontal cortex (OFC) (Figure 18). Additionally, we find significant activation in anterior cingulate cortex (ACC) (Figure 19).

Multi-Voxel Pattern Analysis

Using MVPA, we did not find any significant clusters in the whole-brain searchlight that could successfully decode between congruent and incongruent trials. Therefore, we did not do permutations to determine if there were any areas ability to perform above chance level in decoding congruence.

The original intent of this analysis was to perform MVPA in pre-defined masks for S1, localized by the tactile localizer task, and areas significantly active while viewing hands, localized by the visual hand localizer task. Since we did not find any significant clusters during the whole-brain searchlight, we did not search within potential regions of interest as defined by the localizers.

Discussion

The neuroimaging experiment aimed to localize neural correlates of visuotactile integration when we contrast congruence and incongruence of touch, and vice versa. We predicted that we would find significant neural activation present in areas already linked with sensory modalities such as somatosensory cortex or visual cortex, or in areas used for higher-order processing for multisensory integration such as intra-parietal sulcus. We found a few significant areas of activation when we subtract congruent touch from incongruent touch including dorsolateral PFC, OFC, and ACC. However, we found no significant areas of activation when we subtract incongruent touch from congruent touch, the opposite activation. Additionally, MVPA did not show any significant clusters in the whole-brain searchlight that could successfully decode between congruent and incongruent trials.

Our main result shows significant areas of activation when we contrast incongruent touch relative to congruent touch in orbitofrontal cortex, prefrontal cortex, and anterior cingulate cortex. There is accumulating evidence that OFC and PFC are involved with learning and the dynamic decision-making process (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). However, this still poses the question about whether these frontal brain regions are simply involved with decision-making in general, or if they are necessary regions for processing specifically incongruent multimodal stimuli. Wilson, Takahashi, Schoenbaum, & Niv (2014) propose, among many claims, that OFC may be necessary for differentiating perceptual information from different modality cues. There is a possibility that, the neural activation we see in OFC is part of some conflict resolution resulting from the incongruence of stimuli. Another fMRI study also found significant activation in medial ACC and DLPFC during incongruence between auditory and visual cues (Mayer, Ryman, Hanlon, Dodd, & Ling, 2017). Given our findings in these brain regions as well, ACC and DLPFC might be involved in processing conflicting sensory stimuli. Additionally, there may be similar processing mechanisms for integration across different modality types, such as touch, vision, and audition. In sum, we may be seeing these higher-order brain areas active due to the complex decision-making process that participants need to use to select a final estimate of the tactile location when touch is incongruent, rather than congruent. Further research should investigate the mechanistic properties of modality incongruence in further detail to make the distinction between conflict resolution in general relative to specifically multisensory tasks.

Based on our findings, we do not see any sensory areas of the brain significantly active when we compare congruent touch relative to incongruent touch, or vice versa. We might have expected increased somatosensory or visual cortex activation during congruent touch, given that our behavioral data demonstrated a clear crossmodal congruency effect, where subjects were significantly more accurate in localizing congruent touch. Part of the reason we may not be seeing increased somatosensory activation during congruent touch could be due to overall weak activation of S1from the vibrotactile stimulus. In our tactile localizer, we found much stronger and larger activation of bilateral S2 than S1 with much stronger vibrotactile stimuli. Tactile stimuli presented in the visuotactile localization task were substantially weaker, since they were based on the subject's individual threshold defined by the forced-choice detection task. The weaker vibrotactile stimuli, combined with previous research that shows that vibrotactile stimuli result in much stronger S2 activation than S1, might explain some of our findings (Beauchamp, Yasar, Kishan, & Ro, 2007).

Another possible explanation for our neuroimaging results could be the lack of statistical power. Although formal statistical power analyses for neuroimaging studies are not typically done, we can safely say that given our $N = 1$, we have low statistical power to detect an effect. Furthermore, with just one subject we have even less of a chance to detect an effect if this effect is relatively small. This might be one possible explanation for the lack of significant clusters in predicted areas, and makes it difficult to generalize our results to a larger population. While our sample size is low, we are studying a relatively simple perceptual task so we have limited reason to believe performance on localization would be drastically different across subjects, after accounting for individual tactile thresholds. Within our single subject, there was strong statistical validity due to the large number of trials per condition across many runs. First, since part of the analysis plan included MVPA, we wanted to have many runs so the classifier was better able to generalize among many runs (Coutanche & Thompson-Schill, 2012). Second, the intended experimental design included 80 trials per condition across 8 runs in total. Considering the coding error, we are left with 160 trials per condition. Combining our large number of trials per condition and runs in total, this increases our power to detect effects in our data.

Chapter 4

GENERAL DISCUSSION

In the presented study we seek to address two main questions: (1) Can we establish the crossmodal congruency effect in a tactile localization task and find an effect of viewed touch on felt touch, and (2) how can we identify the neural correlates of visuotactile integration using fMRI and MVPA? We predicted that first we would find an effect of viewed touch on felt touch and that final estimates would drift towards the visual estimate, as in line with the optimal weighting principle. Neurally, we predicted that congruence and incongruence of touch would be localized in the brain either in regions already linked with sensory regions or higher-order areas for processing integration, and that these would have significantly different patterns of activation. To answer our questions, we conducted a behavioral and neuroimaging experiment in which subjects viewed touch in a spatially similar or different location than they felt touch on their own hand.

The results from our first experiment demonstrate a clear congruency effect, and replicate the basis for the crossmodal congruency effect, supporting our initial hypotheses. Subjects were significantly more accurate on congruent trials than incongruent trials. By comparing models that predict response from tactile location and both tactile and visual locations, we provide additional evidence that there is an effect of viewed touch on felt touch (Johnson et al., 2006; Pavani et al., 2000; Tipper et al., 1998).

The results from our standard event-related analyses of fMRI data provide preliminary evidence that congruent and incongruent bimodal touch is processed using higher-order brain regions, such as orbitofrontal cortex or prefrontal cortex. MVPA did not result in any conclusive findings. With one subject, our neuroimaging experiment likely has a low power to detect effects, even though we are studying a relatively basic perceptual task.

Given the coding error in the presented study, future studies might address the effect of reliability on integration in a neuroimaging study. In Beauchamp et al. (2010) altering the reliability of the tactile and visual stimuli significantly influenced neural patterns of activation in a detection task. However, altering reliability of visuotactile stimuli in a localization task has yet to be researched with neuroimaging techniques. Additionally, full models of participant behavioral performance of visuotactile integration using a localization task have yet to be created. Rohe & Noppeney (2016) developed an extensive model of audiovisual integration in a localization task. In general, auditory-visual integration has been more extensively researched with this type of localization task, relative to visual-tactile integration. Further research can provide additional insights towards the neural mechanisms of visuotactile integration.

Overall, we present two main findings. First, behavioral results demonstrate that viewed touch can alter our perception of felt touch in a tactile localization task. Second, neuroimaging results provide some evidence that when faced with incongruent touch relative to congruent touch, several frontal areas of the brain may be involved in discriminating the location of the tactile stimulus.

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