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An Investigation into Peripersonal Space Representations in Older Adults

By

Emily K. Bloesch

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

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ABSTRACT OF THE DISSERTATION

An Investigation into Peripersonal Space Representations in Older Adults
by

Emily K. Bloesch

Doctor of Philosophy in Psychology

Washington University in St. Louis, 2013

Richard A. Abrams, Chair

Peripersonal space is the space immediately surrounding one's body. This space is believed to have a unique representation in order to facilitate successful interaction with the surrounding environment. Supporting this theory, there are consistent findings of changes in cognition within as compared to beyond peripersonal space, including differences in visual attention and perception. However, research on peripersonal space in healthy populations has largely focused on young adults. Representations of peripersonal space take place in multimodal brain regions, areas that show structural and functional changes during senescence. Because of this, there is reason to suspect that older adults represent peripersonal space differently than young adults and that this will lead to measurable changes on tasks that rely on those representations. The present experiments used a behavioral approach to examine age differences on three distinct, but related phenomena that rely on peripersonal space representations. Experiment 1 assessed the rate and strength of the rubber hand illusion, a multimodal illusion that primarily occurs when a dummy hand is within the peripersonal space representation of a person's real hand. Experiment 2 measured the perceptual consequences of tool use and the ability to flexibly incorporate a tool into one's peripersonal space representation. Experiment 3 looked at the extent to which attention is automatically biased toward the space near an outstretched hand. Finally, the relationship among the tasks was examined to assess the extent to which the three paradigms are measuring the same construct.

All three experiments showed significant age-related effects. Young adults consistently exhibited changes in performance when performing the tasks within as compared to beyond peripersonal space. Older adults, however, had the same pattern of performance regardless of whether they performed the task within or beyond peripersonal space. Surprisingly, there were no correlations among the experimental measures, suggesting that the selected tasks may be measuring different aspects of peripersonal space. These results have implications for our understanding of mobility and goal-directed action declines in older adults.

Chapter 1: Introduction

Perception is important. We need it to be able to know what is in our environment. However, perception is not the end goal; this is because there is often not much use in perceiving what is around us if we can't act on it. Action is the end goal, and it has been proposed that the purpose of attention and perception is to support action (Hommel, 1998). However, humans are limited in the actions they can perform. One such limitation is spatial: for the most part, we can only act on objects that are within the space reachable by our limbs. This reachable space forms a bubble around our bodies that is commonly known as 'peripersonal space.' There is evidence that, because this is the space in which we act, peripersonal space is represented in the brain differently than extrapersonal space. These representations, and the possible changes in them across the lifespan, are the focus of the current dissertation.

In what follows, I will discuss peripersonal space and the neural mechanisms that support its representation, followed by how it has been studied behaviorally. Next, neural and behavioral changes in older adults will be presented, along with a discussion regarding how those changes relate to peripersonal space representations. Finally, I will report three experiments that examine peripersonal space representations in older adults.

Neural Mechanisms of Peripersonal Space Representation

Peripersonal space, while often discussed and defined as a behavioral construct (i.e.: *reachable* space), can also be defined in terms of the neural properties of the underlying representation. When approached in this way it is clear that there exist multiple representations of peripersonal space, with different parts of the body coded separately (Farnè, Demattè, & Làdavas, 2005). For example, there are independent representations for the arms/hands (Graziano, Yap, & Gross, 1994), neck, face, and mouth (Rizzolatti, Luppino, & Matelli, 1998;

Rizzolatti, Fogassi, & Gallese, 2002). All of these representations play a role in forming a complete peripersonal space representation; however, the focus of this dissertation will be on the representation of the arms and hands because of the role it plays in reaching and grasping movements.

Arm and hand representations rely heavily on the activity of bimodal and multimodal neurons. Bimodal neurons respond to two different sensory modalities, typically vision and touch, and multimodal neurons respond to vision, touch, and audition. These neurons are commonly found in both the premotor (PM) cortex and intraparietal sulcus (IPS), and to a lesser extent in the precuneus and putamen (Rizzolatti et al., 1998; Luppino, Murata, Govoni, & Matelli, 1999, Cavanna & Trimble, 2006). These neurons have very specific properties. First, their visual and tactile receptive fields (RFs) are in spatial register, meaning that the two RFs code the same area of space. Second, the visual RFs are limited in depth, only coding the area immediately around a body part. Third, visually-related activity shows a gradient, with activity decreasing with increasing distance from the body part. Finally, visual RFs are body-part centered, not retinally centered. This means that the RFs of these neurons are not anchored to gaze position, they are anchored to the physical location of the arm and hand. Therefore, bimodal and multimodal neurons are active when an object is near the arm regardless of where the arm is in space (Làdavas, 2002).

Graziano et al. (1994) demonstrated these bimodal neuron activity patterns in monkeys through an elegant single-cell recording experiment. In it, the visual RFs of bimodal neurons in the PM cortex were tested by positioning the monkey's arm in multiple different locations while the monkey maintained fixation, then stroking the arm to provide tactile stimulation. They found that when the tactile RFs were stimulated through stroking, the associated visual RFs followed

the arm regardless of eye position. This demonstrates both that the visual RFs are body-part-centered, as well as that the visual and tactile RFs are in spatial register. In a second experiment, the monkey's gaze was varied in addition to arm position while an object was advanced toward the monkey's arm. Although arm position varied and there was no consistent relationship between arm and gaze position, the visual RFs still followed the arm. What is interesting is that the authors also found that some cells followed the arm even when it was occluded, meaning that these responses must be mediated in part by proprioception.

Bimodal neurons also have the interesting property of having flexible-sized RFs. While there is a default size for both the visual and tactile RFs of these cells, the visual RFs appear to have the ability to expand in size to accommodate different needs. Iriki, Tanaka, and Iwamura (1996) recorded the activity of cells in the macaque anterior IPS during a reaching task. The size of the visual and tactile RFs was first measured by moving food pellets toward the monkey's hand in a method similar to that used by Graziano et al. (1994), wherein gaze was held constant and arm position manipulated. Afterward, the monkey was trained to retrieve out-of-reach food pellets using a small rake. After merely five minutes of practice with the rake, the visual RFs expanded to include not only the space around the hand originally coded, but also the entire length of the rake. However, this effect was short-lived: after three minutes of retrieving pellets without the rake, the RFs contracted back to their original size. This surprising result suggests that tools used to extend functional reach may become incorporated into the representations of our limbs, which in turn affects the boundaries of peripersonal space.

Receiving input from multiple modalities is necessary for a peripersonal space representation, but in order to form a cohesive picture of the world surrounding our bodies the information from these multiple sources must also be integrated. External visual and tactile

information must be combined with internal proprioceptive and vestibular feedback so we can know not only what is in our environment, but also how our bodies are positioned in relation to external objects and, oftentimes, how our movements change the spatial relationship between these objects and our bodies. One of the regions that has been studied for its role in this process is the posterior parietal cortex (PPC). While the PPC is a functionally heterogeneous area that is involved in many different tasks, one task in particular it is associated with is multimodal integration.

The PPC lies between the vision, auditory, and somatosensory cortices, and it integrates information from all these areas into one multimodal representation of space that is usable for various purposes, such as reaching or eye movements (Anderson, 1997). It is also able to integrate motor information with the sensory input; because of this, it is believed that the PPC's activity during attentional tasks represents its role in movement planning (Anderson & Buneo, 2002). Supporting this belief, it has also been found that the PPC is involved in picking action plans during conflict, such as when multiple actions can be used to accomplish a goal (Coulthard, Nachev, & Husain, 2008).

Dividing the PPC in two is the intraparietal sulcus (IPS), an area that is highly involved in peripersonal space in general and, more specifically, hand- and arm-centered peripersonal representations. The IPS not only has bimodal neurons, it is also strongly functionally connected to the PM cortex, an area that itself has a higher proportion of bimodal than unimodal neurons (Rizzolatti et al., 1998; Luppino et al., 1999). This 'frontoparietal circuit' has been extensively studied in monkeys and has been found to represent many facets of hand actions, such as complex object manipulation, precision grip, movement execution, mental rotation of the hand, and imagined movements (Rizzolatti et al., 1998; Rizzolatti et al., 2002). Interestingly, merely

observing hand actions by other monkeys also activates this circuit, and this activity is triggered only by viewing the hand (not other similar body parts, such as the foot). Thus, this circuit has both cognitive and motor functions: the motor function is primarily to transform visual information about objects into hand movements for interaction, while the cognitive functions include space perception and action imitation (Rizzolatti et al., 2002). These functions cannot yet be verified to be the same in humans, as single-cell recording is not possible. However, the parietal and motor cortices are organized in a similar manner in both humans and monkeys, so it is not unreasonable to conclude there is likely similar functioning in both species (Rizzolatti et al., 1998).

It is clear that there are two somewhat distinct neural streams involved in the processing of incoming visual information, dorsal and ventral, and it has been theorized that the two serve different roles. All visual information first goes through the lateral occipital cortex (LOC), proceeding then to either the inferotemporal/occipitotemporal cortex (ventral stream) or the PPC/occipitoparietal cortex (dorsal stream) (Goodale & Milner, 1992). The ventral stream processes information commonly used for object identification, such as form and color, whereas the dorsal stream, which contains the PPC, processes spatial information, such as motion and location relations amongst multiple objects (Haxby, Grady, Horowitz, Ungerleider, Mishkin, Carsons, et al., 1991; Ungerleider & Haxby, 1994). The distinction between these two streams is important because they play separate roles in representing space. The ventral stream is associated with vision for identification, while the dorsal stream is associated with vision for action (Shmuelof & Zohary, 2005). Because action takes place within reachable space, the dorsal stream is active in representing peripersonal space (Graziano & Cooke, 2006).

Support for a functional separation of the dorsal and ventral streams has been found in patient populations, in which double dissociations have been found. Dorsal stream lesions impair attentional deployment in peripersonal but not extrapersonal space, whereas ventral stream lesions produce impairment in extrapersonal but not peripersonal space (Butler, Eskes, & Vandorpe, 2004). Additionally, ventral stream lesions impair object recognition but do not interfere with the ability to grasp objects (James, Culham, Humphrey, Milner, & Goodale, 2003), and dorsal stream lesions impair grasping ability but not object recognition (Perenin & Vighetto, 1988). In healthy adults the dorsal stream has been found to be instrumental in grasping objects, since this task requires assessing the three-dimensional properties of an object in order to orient and form the hand in an appropriate way (Culham, Danckert, DeSouza, Grati, Menon, & Goodale, 2003). An interesting by-product of this functional separation is that perception and action are sometimes affected differently by visual illusions. While perception, controlled by the ventral stream, falls victim to illusions such as the Müller-Lyer or Ebbinghaus, actions performed on these stimuli are often correct and resist the illusion (Haffenden & Goodale, 2000; Milner & Dyde, 2003; Vishton, Stephens, Nelson, Morra, Brunick, & Stevens, 2007).

Research combining behavioral tasks and functional magnetic resonance imaging (fMRI) has also shed light on the role the IPS and its functionally connected areas play in guiding hand movements and representing peripersonal space. One such study examined the consequences of performing an action in near (peripersonal) space as compared to far (extrapersonal) space (Weiss, Marshall, Wunderlich, Tellmann, Halligan, Freund et al., 2000). In the experiment, participants performed two different tasks with a laser pointer while in the scanner: a dot location task and a line bisection task. All factors other than distance to the visual display were held constant, such as the action required and the visual angle of the stimuli. The authors found that

both tasks activated the same visuomotor areas when performed in peripersonal space, namely the PPC (including the IPS) and ventral PM. In far space, visuoperceptual areas were activated for both tasks, including bilateral ventral occipital cortex and right medial temporal cortex. These findings indicate peripersonal space will be represented as such, regardless of the demands of the task being employed.

In a similar study, Makin, Holmes, and Zohary (2007) investigated the roles of both vision and proprioception in hand-centered peripersonal space representations. Participants underwent fMRI while performing a simple judgment task in which they reported whether a moving ball was going to hit a cardboard target which was either near to or far from their hands. The authors varied the availability of both vision and proprioception, creating four conditions. In the first, vision and proprioception were both present, meaning participants could see their hand close to the near target and feel it resting in the same place. In the second, vision was present, but proprioception was not. In this case, participants rested their real hand on their chest and a dummy hand was placed close to the near target; they could see the dummy hand, but not their real hand. In the third, proprioception was present but vision was not, meaning their real hand rested close to the near target but was occluded. In the fourth condition, both vision and proprioception were absent. Here, their real hand rested on their chest and no hand, either real or dummy, was close to the near target. This design allowed the authors to determine which brain areas rely on visual or proprioceptive information (or a combination of the two) from the hand and to learn how these areas differentially respond when objects are within or beyond hand-centered peripersonal space representations.

Makin et al. (2007) found that the posterior IPS showed the most activity for the ball approaching the hand when there was visual information about hand presence, and that this was

the same regardless of whether the hand was real or a dummy hand. This is consistent with the idea that the pIPS codes visual information in hand-centered coordinates, with information about hand location itself being principally vision-based. On the other hand, the anterior IPS and the ventral PM cortex showed the most activity for the approaching ball when the real hand was present, regardless of whether it was visible or occluded. This indicates the aIPS relies primarily on proprioceptive information for coding hand-centered space. These results support the idea that the IPS and ventral PM code space in hand-centered coordinates, either visual or somatosensory depending on the feedback that is available.

The IPS is also functionally connected to a few cortical areas that make up what has been termed the human parietal reach region (PRR), including the PM cortex, precuneus, and the superior parieto-occipital sulcus (sPOS). Studies involving executed or even merely planned hand movements have consistently shown activity of these areas. For example, Filimon, Nelson, Huang, and Sereno (2009) had participants reach to targets while varying visual feedback by illuminating either just the target (leaving the hand invisible) or by illuminating the target and the reaching hand. Regardless of the visibility, reaching activated the fronto-parietal circuit of the PM and IPS, as well as the precuneus and sPOS. Visible reaching activated the sPOS significantly more; however, this suggests that the PRR is active for all types of reaching, with some areas weighted preferentially depending on the type of feedback that is available. Indeed, the activity in these areas seems quite robust, present even during reaching preparation (Astafiev, Shulman, Stanley, Snyder, Van Essen, & Corbetta, 2003) and during passive viewing of objects that are within reach (Gallivan, Cavina-Pratesi, & Culham, 2009).

The neural underpinnings of peripersonal space representations in healthy, well-functioning systems are important to study in order to understand how and why this system may

break down in older adults. There are known brain changes that accompany aging, and the knowledge of the functions of those changing areas allows one to predict possible behavioral consequences. The specific effects of aging on the cortical areas that represent peripersonal space will be discussed after a summary of how neural representations of peripersonal space are expressed behaviorally.

Behavioral Mechanisms of Peripersonal Space Representation

Peripersonal space can also be conceived of as the space immediately surrounding our bodies (Holmes & Spence, 2004). Objects that are within our peripersonal space can be easily acted upon, whereas objects outside of this space can only be acted upon with effort, such as by first moving our bodies closer. This distinction perhaps may seem minor, but having an object within peripersonal space causes it to be represented differently than if it were in extrapersonal space. With these different representations come different appropriate responses to and perceptions of those objects. This section will discuss the attentional and perceptual differences between peripersonal and extrapersonal space representations, as well as properties of some cognitive processes when responding to objects that are in peripersonal space.

Attentional changes in peripersonal space can best be described as changes in the deployment or behavior of selective attention. One example of this is the change of reference frame for coding spatial information in peripersonal space. Reference frames are used to identify the locations of objects, with a specific object being the point of reference. There are multiple types of reference frames, including egocentric or body-centered (“The notebook is on the table in front of me.”), allocentric or object-centered (“The notebook is next to the coffee cup.”), or even action-centered (“The notebook is within reach when I lean forward.”), and the one that is used is often dictated by the task at hand. The reference frame that is used affects how selective

attention is deployed, and thus affects how objects in the environment are attended to; in other words, depending on the reference frame, different objects are more likely to enter attention. For example, if one were using a body-centered reference frame, objects near the body are more likely to fall into the spotlight of selective attention than objects further away (Tipper, Lortie, & Baylis, 1992).

In a series of experiments, Tipper and colleagues examined the relationship between reaching ability and spatial reference frames (Tipper et al., 1992; Meegan & Tipper, 1998). Participants reached to a yellow LED target presented on a board in front of them while simultaneously ignoring a red LED distractor that appeared on some trials at a different location. The distractor could be in front of the target and thus in the action path of the hand to reach the target, adjacent to the target and thus near the endpoint of the action path, or behind the target and thus beyond any part of the action path. Additionally, participants started each trial either with their hand at the bottom of the display (near their bodies) or at the top of the display (far from their bodies).

Tipper et al. (1992; Meegan & Tipper, 1998) found that when participants started trials with their hands at the bottom of the display, distractors that were below and next to the target caused the greatest amount of interference, increasing reaction times and movement times, whereas distractors beyond the target did not affect performance. However, when participants started the trial with their hands at the top of the display, the opposite pattern of interference was observed. This is because with the hand at the top of the display, distractors that had previously been beyond the action path were now in it, and vice versa. The explanation for this is that participants were using an action-centered (Tipper et al., 1992) or hand-centered (Meegan & Tipper, 1998) reference frame. Because of this, it did not matter if the distractors were near the

target or near the participants' bodies; it mattered only if the distractor was near the hand or in the hand's action path when reaching to the target. These frames of reference allowed those specific distractors to enter attention because attention was deployed to the area surrounding the hand and in the hand's action path.

Delayed disengagement of attention has also been observed for objects near the hands. Abrams, Davoli, Du, Knapp, and Paull (2008) tested the effects of having the hands near a visual display while participants performed basic visual attentional tasks. The first experiment tested visual search, during which participants searched for a target letter amongst distractors while holding their hands either near to or far from the display. When their hands were near the display, participants exhibited steeper search slopes, indicating that they spent more time on each individual item as compared to when their hands were far from the display. Importantly, there was no main effect of hand posture. This rules out possible explanations such as increased difficulty in performing the task or decreased comfort with the hands near the display, because if that were the case it should affect overall performance, leading to a main effect.

The finding of a steeper search slope when the hands are near the display was also seen when participants performed the same task but with their hands occluded, as well as when the hands were near the display but participants responded with their feet. All can be explained by activity in bimodal, hand-centered neurons: when the hands are near an object, regardless of whether they are visible or whether an action is being performed with them, hand-centered neurons in the IPS and PM cortex become activated because an object of attention is now in the peripersonal space near the hands. This activity is thought to bring with it an enhancement in the processing of objects near the hands, leading to a more thorough evaluation of such objects (Abrams et al., 2008).

Further support for a delayed disengagement of attention for objects near the hands was given in Experiment 2, which tested inhibition of return (IOR). Abrams et al. (2008) compared a Posner cuing condition with a traditional IOR paradigm and found that with hands near the display there was no difference on the cuing task, but there was significantly less inhibition on the IOR task. Because attention disengaged more slowly with the hands near the display, participants were able to respond more quickly when the target appeared in the previously-cued location.

Attention appears to be prioritized in the area near the hands, particularly near the palms (Reed, Grubb, & Steele, 2006), and stimuli that enter into the peripersonal space of the hands are subjected to an increase in visual sensitivity that accompanies attentional prioritization (Dufour & Touzalin, 2008). This can emerge in a number of different ways, from an increase in the ability to detect low-luminance stimuli near the hands (Dufour & Touzalin, 2008) to a bias toward targets that appear near the hand in Posner cuing tasks, regardless of the validity of the cue (Reed et al., 2006). These effects are believed to occur because objects near the hands activate hand-centered, bimodal and multimodal neurons, recruiting additional brain areas than would be active if the task were a unimodal one performed far from the hands.

If bimodal neurons are indeed what account for the above results, then tasks using multiple modalities should produce similar patterns of behavior as those using only one modality. This has been tested using a paradigm known as ‘cross-modal cuing’ (Kennett, Spence, & Driver, 2002). Participants are given an uninformative visual or tactile cue near one hand, and then they must detect a target near one of their hands that is presented in the opposite modality. Kennett et al. (2002) found that responses were faster for valid (same hand) cues even when the cue was in a different modality than the target, leading to the conclusion that the two modalities are linked in some way. To further test this, participants then performed the same task but with

their arms crossed. The same results were found, with valid cues speeding responses for the opposite-modality targets located in the same area of external space. In other words, a valid tactile cue on a participant's right hand (but in the left half of hemispace) facilitated responses to a visual target located near the right hand. One interpretation as to why this occurs is that bimodal neurons respond to both the visual and tactile stimuli, and because their receptive fields are anchored to the hand it does not matter where in the external environment the hand is located. No matter the position or reference to the body, those neurons will respond to the visual and tactile cues and targets.

The perception of objects in peripersonal space is also different than when those objects are in extrapersonal space. One of the most extensively used tests to examine this is line bisection. Line bisection is an ideal task in many instances because it is easy to administer and produces fairly consistent within-participant results. In a typical line bisection task, participants are given lines of varying length and are simply asked to place a mark in what they perceive to be the center of the line. With this method, the line is always presented in peripersonal space because it must be reachable in order for the participant to make a manual response. However, variations in method have eliminated the need for line bisection to require the traditional manual response. This includes using a laser pointer to bisect lines that are out of reach (Garza, Eslinger, & Barrett, 2008), using keyboard controls to move a cursor to bisect lines (Dellatolas, Vanluchene, & Coutin, 1996), and presenting pre-transected lines and having participants judge whether the bisection is to the left or right of center (McCourt & Garlinghouse, 2000).

An interesting yet quite consistent effect seen with line bisection is that when neurologically normal, healthy young adults perform the task in peripersonal space they exhibit a slight leftward bias. This is known as pseudoneglect, and is considered by many to be the result

of an asymmetry in the deployment of spatial attention (Jewell & McCourt, 2000). According to this theory, spatial attention in peripersonal space is primarily controlled by the right hemisphere; because of this, left visual hemispace is over-emphasized, leading to an over-representation of the left half of a line presented across both hemifields (Fink, Marshall, Weiss, & Zilles, 2001; Bjoertomt, Cowey, & Walsh, 2002). This over-representation causes the left half to appear slightly longer, leading to bisection slightly to the left of center. Methods using fMRI and either manual line bisection or judgments of pre-transected lines have found activity in the IPS, PM cortex, and POS (Weiss et al., 2000; Weiss, Marshall, Zilles, & Fink, 2003), as well as a right-hemisphere dominance for these areas (Fink et al., 2001).

This explanation for pseudoneglect has been supported by research in patient populations. Patients with hemi-neglect, who exhibit a deficiency in attending to one half of their visual environment, also show a bias on line bisection tasks. However, the nature of their neglect and its impact on line bisection depends on the location of the lesion. Halligan and Marshall (1991) reported on a patient with a lesion in his right PPC and some surrounding areas, but with a wholly intact left hemisphere. This patient exhibited severe left hemi-neglect, leading to line bisection responses to the right of center, but only when the line was presented in peripersonal space. When lines were presented in extrapersonal space, the patient was able to bisect the lines very near to the true center. In a similar study involving a patient with a right parietal lesion, Berti and Frassinetti (2000) not only used a simple manual line bisection task in near and far space, but also incorporated tools. Their patient showed neglect in near but not far space, and so bisected lines correctly in far space but with a rightward bias in near space. However, when the patient was given a tool with which to bisect the lines in far space, she then exhibited the same rightward bias as she did in near space. Interestingly, one can even see this trend in studies using

healthy young adults and line bisection. Young adults bisect lines to the left of center in peripersonal space, but at veridical center in extrapersonal space (Jewell & McCourt, 2000). When asked to bisect lines in extrapersonal space using a tool, however, the leftward bias re-emerges (Longo & Lourenco, 2006). This presumably occurs in both patients and healthy adults because tool use extends the RFs of bimodal neurons (as illustrated by Iriki et al., 1996), effectively bringing far space into the peripersonal representation.

While patient studies are informative, it can be difficult to know the extent to which the conclusions can be generalized to a healthy population. This problem can be overcome by using techniques such as repetitive transcranial magnetic stimulation (rTMS), which uses magnetic pulses to reduce activity in targeted brain areas. It has been found that applying rTMS to the right PPC in healthy young adults causes participants to bisect lines significantly to the right of center in near space, performing similarly to patients with right PPC lesions (Bjoertomt et al., 2002). However, there was no change in performance when bisecting lines in far space. Taken with the patient and neuroimaging literature, this is strong evidence for the theory that not only does the right PPC code peripersonal space, but that peripersonal space is represented differently than extrapersonal space, both functionally and neurally.

Older Adults

It is well-established that there are a number of changes that accompany aging, including alterations in cognition, physical capability, and brain structure and function. While little has been done to directly examine how older adults represent peripersonal space, there is some evidence to suggest that there are measurable differences in these representations with age. Much is already known about brain areas that represent peripersonal space, and many of these areas are ones that consistently show changes during senescence. Given that, it should be possible to

predict peripersonal space representation changes with age, as well as the type of behavior that might be affected. This section will discuss first the neural changes associated with aging, and then studies involving older adults that use behavioral measures to detect changes in peripersonal space representations.

Neural Changes in Older Adults

Brain-based changes in older adults can be examined in two different ways. The first method is structural, which tracks physical changes in the brain with age, including white- and gray-matter reductions, volumetric declines, and white matter integrity. The second method is functional, employing imaging methods such as PET or fMRI, to compare patterns of activity across age groups. Structural and functional changes can be correlated. For example, in some older adults, volumetric declines in the frontal lobe can lead to compensatory activity, in which a task that activates one hemisphere in young adults will activate both in older adults (Cabeza, Anderson, Locantore, & McIntosh, 2002).

Structural studies consistently find volumetric declines with age in the parietal cortex. Because the parietal cortex plays such a large role in creating peripersonal space representations, tissue loss here could compromise the ability to create or maintain an up-to-date, spatially accurate representation. Gray matter declines have been reported in the superior and inferior parietal lobes (Good, Johnsrude, Ashburner, Henson, Friston, & Frackowiak, 2001, Lehmbeck, Brassens, Weber-Fahr, & Braus, 2006), the parieto-occipital lobe (Murphy, DeCarli, McIntosh, Daly, Mentis, Pietrini, et al. 1996), and for the parietal lobe as a whole (Xu, Kobayashi, Yamaguchi, Iijima, Okada, & Yamashita, 2000). White matter declines, evidence of a decrease in myelination, have also been reported in the parietal lobe and in the precuneus in particular (Lehmbeck et al., 2006). The putamen, the only subcortical structure to have bimodal properties,

experiences similar age-related structural changes (Hedden & Gabrieli, 2005). Declines here have been associated with older adults' performance on tasks involving balance (Rosano, Aizenstein, Studenski, & Newman, 2007) and the learning of simple motor skills (Raz, Williamson, Gunning-Dixon, Head, & Acker, 2000).

One study of particular interest compared the effects of aging on unimodal and multimodal sulci, with unimodal sulci residing in the temporal and occipital lobes and multimodal in the frontal and parietal lobes (Kochunov, Mangin, Coyle, Lancaster, Thompson, Rivière, et al. 2005). Sulcal widening, as well as a decrease in depth, is thought to result from decreases in white and gray matter, which decreases the gyri thickness. It was found that sulcal width increased with age for both uni- and multimodal sulci, but significantly more for multimodal sulci. Accompanying this was a greater decrease in multimodal sulci depth as compared to unimodal. However, two sulci in particular showed the greatest rate of change with age: The IPS and the POS. These two sulci are believed to be integral in creating peripersonal space representations and are also part of what is thought to be the human parietal reach region (Filimon et al., 2009). As a result, changes here would be expected to adversely affect the representation of peripersonal space.

There is no doubt that a loss of hand function accompanies aging. There are many changes that occur, including declines in muscle control, tactile sensitivity, dexterity, and strength (Carmeli, Patish, & Coleman, 2003; Ranganath, Siemionow, Sahgal, & Yue, 2001). However, some of these changes are not just musculoskeletal, but rather can be partially explained by changes in functional activity in the frontal and parietal lobes. Functional imaging during tests of grip strength have found that older adults over-activate both motor and frontal areas in order to maintain performance as compared to young adults, including showing bilateral

activity regardless of the hand used (Ward & Frackowiak, 2003). This over-activation is positively correlated with age, especially in areas such as the IPS and ventral PM.

An interesting pair of imaging experiments has also demonstrated how activation patterns change on simple motor tasks with age. Young and older adults performed isolated or coordinated wrist or ankle flexions, providing a gradient of simple to difficult movements (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005). For the simple isolated movements, older adults showed activity in the same network of areas as young adults, but with greater activation. However, for older adults performing the coordinated movements, activation was greater and extended outside the network used by young adults. Older adults activated frontal areas young adults either did not or activated minimally, including the PFC and ventral PM. A follow-up using the same method (Heuninckx, Wenderoth, & Swinnen, 2008) found that successful performance in older adults was positively correlated with frontal activity, suggesting older adults are maintaining performance through the use of cognitive strategies and external information, a process not necessary for young adults. Compensatory activity may be occurring because activity in the primary motor network for these tasks, including the PPC and PM areas, is no longer sufficient for optimal performance.

Older adults also have changes in the functional separation of the dorsal and ventral streams. In young adults, the ventral stream is active in tasks of object recognition, whereas the dorsal stream is involved in processing spatial information and is active during reaching and grasping (Haxby et al., 1991). However, in older adults the separation is not so distinct. Grady and colleagues (Grady, Haxby, Horowitz, Schapiro, Ungerleider, et al. 1992) showed in an fMRI experiment that young adults exhibited strong occipitotemporal activation in a face-matching task and occipitoparietal activation in a dot location-matching task, with little overlap. Older

adults, on the other hand, showed co-activation of both of these areas during both tasks. This suggests that these areas are less functionally specific in older than young adults. Behavioral tests of tasks typically thought to be attributed more strongly to either the dorsal or ventral stream have also shown a decline in separability of the streams with age (Chen, Myerson, & Hale, 2002). Because the dorsal stream is associated with peripersonal space representations (Butler et al., 2004), the loss of specialization of this stream in older adults may signal a decline in the ability to accurately form those representations.

Peripersonal space representations are known to rely on activity in the PPC, the IPS and sPOS specifically, as well as PM cortex. As discussed above, these are all areas that have been found to change with age, whether the changes are structural or functional. In other cortical areas such as the frontal lobe, volumetric declines and functional changes are known to correlate with cognitive performance (Cabeza et al., 2002). It is reasonable to predict, therefore, that changes in the areas supporting peripersonal space representations will lead to performance changes in older adults, be they motoric, attentional, or perceptual. Support for this prediction is presented in the following section.

Behavioral Changes in Older Adults

While there has not been much behavioral research done on peripersonal space representations in older adults, studies have for the most part been consistent in finding age differences across tasks. Much like work with young adults, line bisection is a common test that has produced reliable results in aging samples. With manual line bisection, young adults exhibit a tendency to bisect to the left of true center (Jewell & McCourt, 2000). Older adults, on the other hand, not only do not exhibit this leftward bias, they actually have a rightward bias (Fujii, Fukatsu, Yamadori, & Kimura, 1995; Jewell & McCourt, 2000). This occurs even when manual

abilities are eliminated (Chen, Goedert, Murray, Kelly, Ahmeti, & Barrett, 2011) and when implicit tasks are used to account for the possibility of strategy differences (Barrett & Craver-Lemley, 2008). While gender differences are not always found (Fujii et al., 1995), when they are present older women have performance more similar to young adults than older men do (Chen et al., 2011; Barrett & Craver-Lemley, 2008).

This age and gender difference is theorized to be the result of the declines in the parietal lobe discussed above. In young adults, the right hemisphere is thought to be more active in the control of spatial attention, leading to an asymmetry in attentional deployment (Fink et al., 2001). Because of parietal lobe changes, older adults do not have this hemispheric dominance for spatial tasks, requiring activation of the left hemisphere to compensate (Chen et al., 2011). This compensatory pattern has been found in the frontal lobe (Dolcos, Rice, & Cabeza, 2002), and while it has not yet been tested using neuroimaging methods for the parietal lobe, the behavioral evidence is consistent with a compensatory hypothesis.

Older adults have also been shown to perform differently than young adults on more direct tests of peripersonal space representations. For example, cross-modal attention has been found to change with age. For this task, participants are given an uninformative visual or tactile cue near one hand, and then they must detect a target near a hand that is presented in the opposite modality. Young adults show response facilitation when the cue and target locations are congruent, and this is true when their hands are uncrossed and crossed (Kennett et al., 2002). Older adults, on the other hand, show only part of this pattern. When the task is performed with uncrossed hands, older adults do show facilitation for congruent cross-modal cues, although not as strong as young adults; however, when the hands are crossed this facilitation disappears (Poliakoff, Ashworth, Lowe, & Spence, 2006). This could occur for a few reasons. First, older

adults may represent multisensory information differently in peripersonal space, perhaps due to alterations in the parietal lobe, where the sensory integration process takes place. Second, hand-centered representations may not be as flexible in older adults, leading to a decreased ability of the hands to be fully spatially represented regardless of their spatial location (Poliakoff et al., 2006).

Providing support for the latter of the two hypotheses given above is a study conducted by Bloesch, Davoli, and Abrams (in press). We tested both young and older adults on a selective reaching task (Tipper et al., 1992) to examine the effects of distractors in and beyond a reach's action path. We replicated Tipper et al.'s (1992) results in our young adult sample, with distractors in the action path causing the most interference regardless of the starting position of the hand. When their hands started at the bottom of the display, our older adult sample also showed this pattern, with distractors below the target (and in the action path) slowing reaction times and movement times. However, when they began with their hands at the top of the display, distractors below the target, but now no longer in the action path, still produced the most interference. Distractors above the target, in the action path, produced the least amount of interference.

This strange pattern can be explained through a degradation of hand-centered representations. It has been theorized that young adults show hand-centered (Meegan & Tipper, 1998) reference frames because bimodal neurons prioritize the space surrounding the hands, so distractors in that space are more salient than distractors not in that space. Older adults in our experiment were not using a hand-centered reference frame; their pattern of responses indicated the use of a body-centered reference frame. This might occur if hand-centered space is not being

represented as strongly or as accurately, resulting in the need to use a different reference for spatial coding.

Ghafouri and Lestienne (2000) used a sensorimotor approach to evaluating peripersonal space representations in older adults, having participants draw imaginary ellipses in different planes in the space in front of their bodies. The premise was that measuring goal-directed movements can reveal how 3-D space was represented. The authors compared the abilities of young and older adults to orient ellipses in three different planes, frontal, sagittal, and horizontal, by first showing participants a template and asking them to reproduce it. In comparing the plane of motion of each participant's finger, they found that older adults had smaller plane volumes than young adults, indicating a compression in the representation of peripersonal space. Furthermore, by comparing performance across the different planes, they were able to show that the motor component was not responsible for the errors; rather, older adults were representing the spatial coordinates incorrectly.

Although these behavioral tests are in line with peripersonal representations changing with age, not all studies find age differences. Barrett and Craver-Lemley (2008) used a drawing task in which they asked participants to draw a single picture (such as a tree or a house) on a blank sheet of paper and then measured how off-center the drawing was placed. The authors hypothesized that, similar to line bisection findings, young adults would displace their drawings to the left of center, while older adults would be at or to the right of center. Additionally, because of the implicit nature of the task, the results would be not be impacted by possible strategy differences between age groups. However, both young and older adults displaced their drawings equally to the left of center. Interestingly, a different implicit drawing task in the same series of

experiments did show age differences, and it is unclear what may be the cause of these divergent results.

A similarly-motivated study looking for directional errors in object placement failed to find age differences as well (Jue, Meador, Zamrini, Allen, Feldman, & Loring, 1992). In this experiment, young and older adults learned visuospatial arrays containing ten objects and were then asked to recreate them from memory. Again, both age groups showed overall leftward directional errors, and while older adults had greater absolute errors than young adults, this did not alter their significant leftward placement. It is not immediately apparent why these two studies, employing somewhat similar methods, did not find age differences. Other studies using seemingly implicit dependent measures, such as ellipse drawing, have shown these differences, suggesting that changes in performance with age are not just due to changing strategies. Perhaps the measures used in the previous two studies were simply not reliable enough, with too much variability to detect age differences. Regardless, understanding why peripersonal space representations seem to sometimes, but not always, show age-related changes will help us understand the changes that may be occurring with age and how they might affect motoric ability.

Chapter 2: Overview of Present Study

As outlined above, there is evidence to support the possibility that older adults represent peripersonal space differently than young adults, and that this will lead to measurable changes on tasks that rely on those representations. The behavioral studies discussed above provide some of this evidence, but given the paucity of research in this area the exact nature of age-related changes in peripersonal space representations is not clear. The following experiments used a behavioral approach to examine three distinct, but related phenomena that rely on peripersonal space representations. Experiment 1 assessed the rate and strength of the rubber hand illusion, a multimodal illusion that primarily occurs when a dummy hand is within the perihand representation of a person's real hand. Experiment 2 measured the perceptual consequences of tool use and the ability to flexibly incorporate a tool into one's perihand representation. Experiment 3 looked at the extent to which attention is automatically biased toward the space near an outstretched hand.

The goal of the experiments was to provide a systematic investigation into age-related changes in peripersonal space representations by examining, within a single sample, performance on these three attentional and perceptual tasks. After examining the three experiments separately for age-related changes in performance, the relationship among the tasks was evaluated. The purpose of this was to determine the extent to which these tasks, which are believed to be measuring the same construct, are indeed tapping into the same perihand mechanism. These experiments provide a foundation for beginning to understand when and how age-related changes in peripersonal space representations are expressed.

Chapter 3: Overall Session Method

Participants

Fifty older adults were recruited from the Washington University in St. Louis Psychology Department's older adult volunteer pool, and 53 young adults were recruited from Washington University's undergraduate population. Table 1 shows the mean age, vision, handedness, tactile sensitivity, and gender for both age groups. Participants were screened for handedness, physical ability, and health. Participants were excluded if they had any self-reported neurological disorders, were left-handed, did not have full use of their right hand, arm, and shoulder, had a diagnosed movement disorder, or had a diagnosed eye disease. The complete health questionnaire given to participants can be found in Appendix 1. Older adults were compensated \$10/hour of participation, and young adults received course credit. The overall session lasted approximately two and a half hours.

Procedure

All participants were given the same protocol-wide procedure. Upon entering the lab, participants had their visual acuity tested by the experimenter and then filled out a health questionnaire, the Edinburgh Handedness Inventory (Oldfield, 1971), and a demographics questionnaire (Appendix 3). After completing these forms, the experimenter then administered a two-point discrimination task to measure tactile sensitivity. All participants completed the tasks in the same order, which was the first half of the rubber hand illusion, tool use, attentional cuing, and finishing with the second half of the rubber hand illusion.

Table 1. Young and older adult sample characteristics

	Older Adults (n = 50)	Young Adults (n = 53)
Age	<i>M</i> = 70.88 (range: 65-85)	<i>M</i> = 19.17 (range: 17-21)
Gender	37 Female, 13 Male	35 Female, 18 Male
Vision	20/24.6	20/21.6
Handedness	76.48	73.73
2-Point Discrimination	2.43 cm	1.30 cm

Chapter 4: Experiment 1

The rubber hand illusion (RHI) occurs when synchronous tactile stimulation is applied simultaneously to both a person's occluded real hand and a visible fake hand, causing the person to erroneously feel ownership of the fake hand (Makin, Holmes, & Ehrsson, 2008). The RHI is associated with activity in the brain regions responsible for coding peripersonal space, namely the PPC, intraparietal cortex, and PM cortex (Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004). It is theorized that the illusion arises when multisensory integration of vision, touch, and proprioception allow hand-centered peripersonal representations to shift onto the rubber hand, allowing the sensation that the touch felt on one's occluded hand is being produced by the touch that is seen on the rubber hand (Kammers, Verhagen, Dijkerman, Hogendoorn, Vignemont, & Schutter, 2009). A common by-product of the illusion is proprioceptive drift, the feeling that one's real hand is moving toward the location of the rubber hand. In fact, the illusion can be strong enough to bias hand movements, producing reaching errors that would occur only if participants felt that their real hand was in the location of the rubber hand (Zopf, Truong, Finkbeiner, Friedman, & Williams, 2011).

The RHI is thought to reflect properties of bimodal, hand-centered neurons (Lloyd, 2007). That is, for the RHI to work, the dummy hand must be within the bounds of bimodal neuron visual receptive fields. If it is within such RFs, that allows the visual information of the dummy hand to be integrated with the tactile feedback from the real hand, allowing the hand-centered representation to shift. By systematically varying the distance between a participant's real hand and the dummy hand, Lloyd (2007) was able to show that at distances up to 27.5 cm the illusion can still be achieved, but beyond that the strength declines significantly. Lloyd (2007) proposed that the RHI may provide a useful test to examine the integrity and spatial range

of bimodal neuron RFs, and thus is a good candidate for detecting possible age-related changes in multimodal integration. The question has not yet been examined in older adults, but given the structural changes known to occur in multimodal brain areas with age, older adults may have either a reduced strength of the RHI or a smaller maximum distance at which the illusion can be achieved.

Method

Materials and Procedure

A picture of the experimental set-up is shown in Figure 1. Participants sat on one side of a 30 cm-wide table, with the experimenter sitting across from the participant on the opposite side of the table. A 28 cm x 45 cm wooden barrier was situated approximately 20 cm to the right of the participants' midline, and participants were instructed to sit with their trunks near the table and their right forearm resting on the right side of the board. A realistic plastic hand was placed on the table on the left side of the board. The distance of the plastic hand from the edge of the table matched the distance of the participant's real hand from the edge of the table. A black felt cloth was draped across the table and participant from the shoulders to the wrist, eliminating vision of the participant's right arm and of the empty table between the participant and the plastic hand. This produced a setup in which the participant's real hand and the plastic hand appeared to be sticking out from the far edge of the cloth in a similar manner; the participant could only see the plastic hand, as the board occluded the right hand. The experimenter could see both hands equally well. To the participant's left, approximately 60 cm from the wooden barrier, was a 27.94 cm-high support. A 91-cm ruler was placed on top of the support and the barrier, spanning the distance of the two.



Figure 1. Experimental set-up for the rubber hand illusion. The experimenter sat at a table across from the participant. The participant rested her right hand on the right side of an occluding board, and the plastic hand was visible on the table to the left of the board. The real and plastic hands were covered to the wrist by a black cloth. A ruler spanned the distance of the occluding board and the support.

Each trial began with the plastic hand being placed on the table at one five predetermined distances from the participant's real hand. After verifying that the participant was ready, the experimenter began simultaneously stroking the plastic hand and the real hand with two small paintbrushes. Participants were instructed to keep their right arm and hand as motionless as possible during the experiment and to watch the plastic hand during the trial. Synchrony and timing of the strokes were maintained with a metronome that rested on the table that was visible to the experimenter but was blocked from the participant's view by the wooden barrier. The metronome was silent but provided a visual cue that allowed the experimenter to maintain a frequency of 60 strokes per minute.

During a trial the participant received a maximum of 60 strokes on both their real hand and the plastic hand. After the 60th stroke, two perceptual judgments were made. First, a subjective rating of the illusion was obtained by asking participants to rate the extent to which they agreed or disagreed with the statement, “It seemed as though the touch I felt was caused by the experimenter touching the plastic hand” (Lloyd, 2007). They responded using a seven-point scale ranging from -3 to +3, with -3 being “strongly disagree” and +3 being “strongly agree.” A rating of +3 corresponded to a strong subjective feeling of the illusion, as it meant that the participant felt that the tactile stimulation on their real hand was coming from the plastic hand. After providing a rating, participants then were instructed to look at the ruler and to indicate the number on the ruler that corresponded to the felt location of their real hand. This measured proprioceptive drift. The point at which the ruler crossed the wooden barrier was varied by trial so as to ensure participants were giving a unique estimate each time.

If the experience of the illusion was never strong enough during the trial to receive a subjective rating of +3 (strongly agree), participants received the maximum 60 strokes. If at any point during the trial participants’ experienced the illusion strongly enough to give it a subjective rating of +3, they immediately reported the rating to the experimenter. At the moment the participant reported a rating of +3 the trial was terminated and participants were prompted to provide the felt location of their hand using the ruler. Values of both perceptual ratings and the number of strokes administered were recorded by the experimenter between trials, at which time participants were instructed to briefly move their right hand and arm before replacing it in the designated location for the next trial.

The plastic hand was placed to the left of the participant’s real hand so that the distance between the hands was 10, 20, 30, 40, or 50 cm. The participant’s real hand, once placed on the

right side of the occluding board, did not change locations. The plastic hand appeared at each of the five distances one time per block, with the order of the distances randomly determined for each participant. After the order was determined for the first block, that order was maintained for three more blocks. Therefore, participants completed four blocks of five trials, with the first two blocks occurring at the beginning of the experimental session and the last two blocks occurring at the end of the session, with Experiments 2 and 3 interposed.

Results

One older adult participant (72 years old) was excluded for failing to follow instructions. Two young adult participants (mean age: 19 years) were also excluded because they were unable to complete all four blocks of the experiment.

Median subjective ratings of the illusion were first analyzed for each age group using a Friedman's nonparametric test for repeated measures, with the five distances separating the real and plastic hands (10-50 cm) as a within-subject factor. As can be seen in Figure 2, both young and older adults showed a pattern wherein closer distances between the hands produced higher subjective ratings of agreement, with the rating decreasing as distance increased (Young Adults: $\chi^2(4) = 119.51, p < .001$; Older Adults: $\chi^2(4) = 74.92, p < .001$). In order to assess where the differences in ratings among the five distances occurred, a Wilcoxon matched-paired signed ranks test was performed for each age group comparing the rating given for each distance to the rating for the next-closest distance. For young adults, the rating at each distance was significantly different than the ratings for the distances immediately adjacent. The median rating at 10 cm was significantly higher than at 20 cm ($Z = -4.30, p < .001$); the rating at 20 cm was higher than at 30 cm ($Z = -4.13, p < .001$); the rating at 30 cm was higher than at 40 cm ($Z = -3.73, p < .001$); the rating at 40 cm was higher than the rating at 50 cm ($Z = -3.33, p = .001$) ($n = 51$ for all pairwise

analyses). Older adults, however, did not show this pattern. For older adults, the rating at 10 cm was higher than at 20 cm ($Z = -3.83, p < .001$), and the rating at 20 cm was higher than at 30 cm ($Z = -3.85, p < .001$) ($n = 49$ for all pairwise analyses). Beyond this, there were no other significant differences in subjective ratings, however it is likely that this is because older adults were at the extreme low end of the scale in their responses and could not have lower ratings.

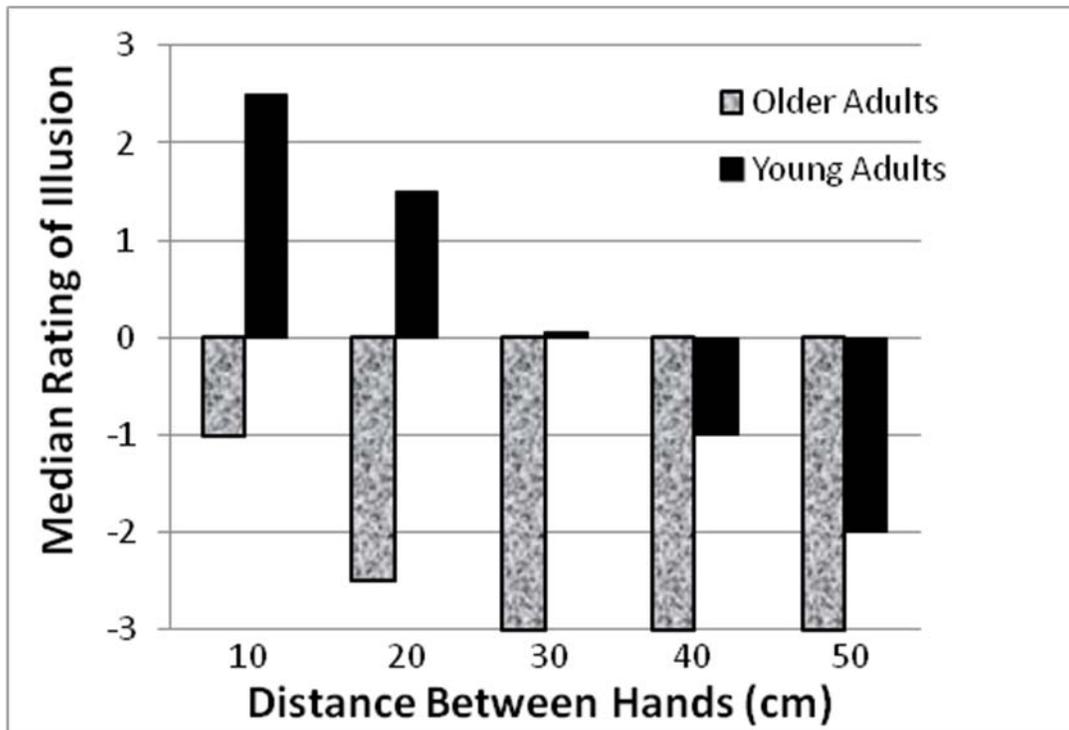


Figure 2. Median subjective ratings of the illusion for young and older adults. Ratings were based on a seven-point Likert scale (-3, strongly disagree, to +3, strongly agree), which participants used in response to the statement: “It seemed as though the touch I was feeling on my real hand was being caused by the experimenter touching the rubber hand.”

In addition to identifying performance patterns within each age group, it is also of interest to compare performance between age groups. To do this, subjective ratings at each distance were compared using Mann-Whitney U Test, with age group as a between-subjects factor. At every distance, young adults gave a higher subjective rating of the illusion than older adults (10 cm: $U = 902.00, p = .019$; 20 cm: $U = 803.50, p < .005$; 30 cm: $U = 645.00, p < .001$; 40 cm: $U =$

599.50, $p < .001$; 50 cm: $U = 748.50$, $p < .001$) (young adult $n = 51$, older adult $n = 49$). This indicates that the young adults experienced the illusion more strongly than older adults at every distance.

Proprioceptive drift was calculated by subtracting the number on the ruler that participants reported as matching the felt location of their hand from the number on the ruler that matched the actual location of their hand. This difference was then converted into a ratio by dividing it by the actual distance between the real and dummy hands. Therefore, at all distances a ratio of “1” means that participants reported their real hand felt as though it was in the location of the dummy hand, and a “0” means that participants reported their real hand felt as though it was

Table 2. Measures of proprioceptive drift for young and older adults as a function of distance between the participant’s real hand and the dummy hand. Drift represents the distance between the actual location of the participant’s hand and the felt location of the hand at the end of each trial. The top panel contains the mean drift for all trials in the session. The bottom panel contains the mean drift for only trials in which participants gave a subjective rating of +3. Also reported are the number of participants who reported a rating of +3 and the number of trials, in parentheses, contributing to the mean for each distance.

Distance (cm) All Trials	Young Adults		Older Adults	
	<i>M</i> Drift (SD)		<i>M</i> Drift (SD)	
10	9.64 (6.41)		7.69 (5.73)	
20	9.77 (8.92)		6.43 (6.65)	
30	8.21 (9.22)		5.03 (6.32)	
40	5.94 (6.39)		4.94 (7.65)	
50	5.91 (7.90)		4.24 (6.47)	
Distance (cm) Trials Rated +3	Young Adults		Older Adults	
	<i>M</i> Drift (SD)	N Participants (Trials)	<i>M</i> Drift (SD)	N Participants (Trials)
10	14.14 (5.16)	27 (91)	13.04 (5.68)	21 (73)
20	21.98 (7.67)	18 (45)	16.44 (9.66)	16 (34)
30	28.08 (11.52)	9 (21)	25.05 (13.36)	6 (10)
40	28.58 (24.75)	3 (5)	30.16 (21.26)	5 (8)
50	37.25 (27.98)	3 (3)	16.32 (13.81)	5 (10)

in its actual location (no drift). The ratios were analyzed with a 2 (Age Group: young, old) x 5 (Distance: 10-50 cm) mixed-factors ANOVA, with the means of the difference scores reported in Table 2 and a graph of the ratios shown in Figure 3. There was a main effect of Distance, with the ratio of drift being the largest at 10 cm and decreasing as distance increased ($F(4, 404) = 157.55, p < .001, \eta^2_p = .61$). There was also a main effect of Age Group ($F(1, 101) = 5.57, p < .05, \eta^2_p = .05$), with young adults have a higher ratio of drift overall than older adults. Finally, there was an Age Group x Distance interaction ($F(4, 404) = 3.56, p < .01, \eta^2_p = .03$), with young adults having a greater ratio of drift than older adults at the three closest distances, but similar ratios of drift at the two farthest distances.

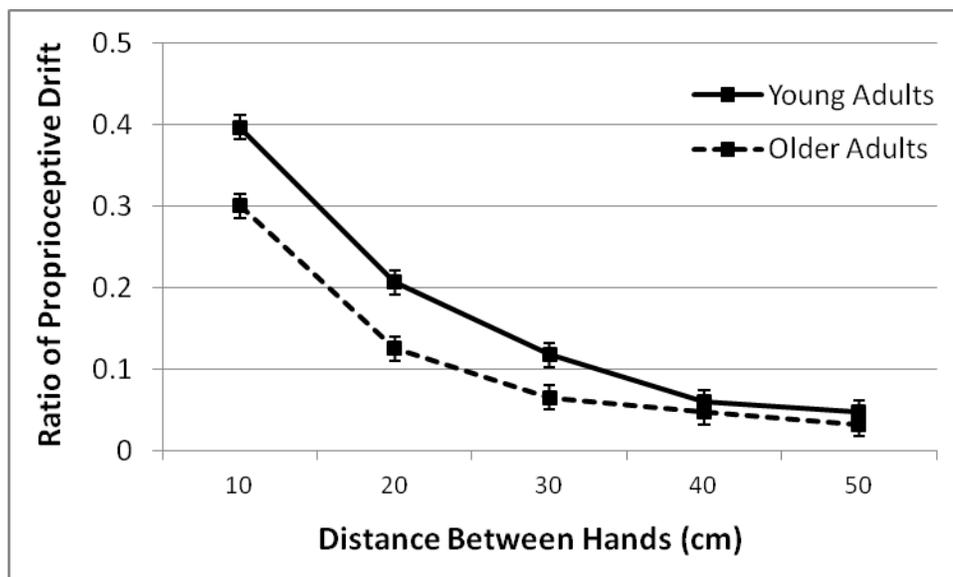


Figure 3. Ratio of proprioceptive drift as a function of distance and age group.

To examine the mean number of strokes participants received, we also considered only trials in which participants gave a subjective rating of +3. The data are shown in Table 3. As discussed previously, the mean number of strokes must then be analyzed by comparing the age groups separately at each distance, which was done for the three closest distances. There were no

differences in the mean number of strokes for young and older adults at any of the three distances (10 cm: $t(46) = 1.87, p > .10$; 20 cm: $t(32) = .04, p > .10$; 30 cm: $t(13) = 1.08, p > .10$).

Correlations among the three experimental measures, age, and the three sensory measures were also assessed and can be seen in Table 4. The experimental measures (subjective rating of

Table 3. Mean number of strokes participants received on trials in which they reported a subjective illusion rating of +3, with standard deviations in parentheses. Also reported are the number of participants who reported a rating of +3 and the number of trials, in parentheses, contributing to the mean for each distance.

Distance (cm)	Young Adults		Older Adults	
	<i>M</i> Strokes (SD)	N Participants (Trials)	<i>M</i> Strokes (SD)	N Participants (Trials)
10	30.28 (14.74)	27 (91)	22.17 (15.07)	21 (72)
20	30.78 (16.93)	18 (45)	31.03 (17.83)	16 (34)
30	38.06 (15.77)	9 (21)	28.83 (16.85)	6 (10)
40	34.67 (15.86)	3 (5)	29.00 (8.57)	5 (8)
50	49.00 (18.19)	3 (3)	39.12 (23.90)	5 (10)

the illusion, proprioceptive drift, and mean strokes) are the grand means based on performance when the plastic hand was at a distance of 10 cm. Because the rubber hand should be fully within the perihand representation at this distance, the responses given at 10 cm should provide the strongest measure of the rubber hand illusion. There were significant correlations among the three experimental measures. As the subjective rating of the illusion increased, proprioceptive drift rate increased ($r(98) = .689, p < .01$). As the subjective rating of the illusion increased, the number of strokes given per trial decreased ($r(98) = -.750, p < .01$). Finally, as proprioceptive drift increased, the number of strokes given per trial decreased ($r(98) = -.640, p < .01$). The only experimental measure that correlated with age was the subjective rating of the illusion, with the rating decreasing as age increased ($r(98) = -.277, p < .01$).

Age was correlated with two of the sensory measures, visual acuity and tactile sensitivity. As age increased, visual acuity worsened ($r(98) = .284, p < .01$) and tactile sensitivity decreased ($r(98) = .629, p < .01$). There was only one significant correlation between the sensory and experimental measures, and that was between visual acuity and proprioceptive drift. As visual acuity decreased, the proprioceptive drift increased ($r(98) = .211, p < .05$). However, it is unlikely that this is a meaningful correlation. This is because there were very few people with visual acuity worse than 20/25 (for example, only five participants had 20/40 vision). Thus, because a subset of this already quite small portion of the sample experienced the illusion strongly, it produced a significant correlation. Visual acuity does not appear to be responsible for the age differences in the illusion though, in particular because acuity does not correlate with either of the other experimental measures. Additionally, removing the five participants with 20/40 vision eliminates the correlation ($r(93) = .067, p > .05$).

Finally, reliability of the subjective ratings of the illusion for all five distances was tested. Split-half reliability was examined by comparing the Blocks 1 and 2 (which occurred at the beginning of the experimental session) to Blocks 3 and 4 (which occurred at the end of the experimental session). There was a strong positive correlation between the two halves for both age groups (Young Adult: $r = .92$; Older Adult: $r = .92$), suggesting that the subjective rating of the illusion is highly reliable.

Table 4. Correlations among dependent measures, age, and measures of sensory function. The rubber hand illusion variables (subjective rating, proprioceptive drift, and mean strokes) are the grand means based on performance when the plastic hand was at a distance of 10 cm.

	Age	Vision	Handedness	Tactile Sensitivity	Subjective Rating	Proprioceptive Drift	Mean Strokes
Age	1.00	.284**	.049	.629**	-.277**	-.170	-.014
Vision		1.00	.081	.160	.116	.211*	-.187
Handedness			1.00	.032	-.076	-.087	.074
Tactile Sensitivity				1.00	-.113	-.019	.020
Subjective Rating					1.00	.689**	-.750**
Proprioceptive Drift						1.00	-.640**
Mean Strokes							1.00

* = Correlation is significant at the .05 level.

** = Correlation is significant at the .01 level.

Discussion

The rubber hand illusion relies on the multimodal integration of vision, touch, and proprioception. Because older adults exhibit changes in multimodal brain areas, it was hypothesized that this would adversely affect older adults' experience of the illusion as compared to young adults. Indeed, when assessing young and older adults' subjective experience of the illusion, there are large differences. Young adults experience the illusion more strongly than older adults regardless of the distance between the real and dummy hands. What is most striking is that the age differences in the experience of the illusion were observed even at the two closest distances, 10 cm and 20 cm. At these distances the illusion is most likely to occur for both age groups. However, older adults as a group subjectively rate the illusion as being weak or even virtually non-existent at these distances.

Correspondingly, there was also an age difference in the experience of proprioceptive drift. Young adults reported greater drift at all distances, but again, at the two closest distances the difference between the age groups was most apparent. The reports of proprioceptive drift aligned well with the subjective ratings of the illusion – at the closest distance, both drift and the subjective ratings were the highest for both groups, decreasing systematically as the dummy hand moved further away from the real hand. However, older adults experienced less drift even at the closest distance, and it declined more quickly than for young adults. This is further support that young adults experience all aspects of the rubber hand illusion more strongly than older adults.

Surprisingly, there was not an age difference in the number of strokes given on trials in which the illusion was strongly achieved. This lack of difference can be viewed as a byproduct of the methodology. The only situation in which there would be variability in the number of strokes given on a particular trial was when the participant reported, mid-trial, that he or she was experiencing the illusion maximally. That is, when the illusion experience would be rated a +3. Because of this, only trials given a rating of +3 were analyzed for each group. The lack of difference suggests that when the two age groups do strongly experience the illusion, the experience appears to be similar. A difference does emerge in comparing the number of participants and trials during which a subjective rating of +3 was given: more young adults report subjective ratings of +3 more often than older adults. In spite of this, the large age differences in the subjective rating of the illusion and proprioceptive drift were in line with our prediction and are what would occur if older adults had an altered or degraded perihand representation.

Chapter 5: Experiment 2

There is ample evidence showing that tools can be used to extend peripersonal space. This has been demonstrated in patients with neglect in extra- but not peripersonal space: These patients can substantially remediate their symptoms on simple, behavioral tests of neglect by using a tool to act in extrapersonal space (Halligan & Marshall, 1991). In healthy humans, tool use can also change perception. When judging the distance to an object just beyond reach, distance perception is fairly veridical. However, when a person is given a tool to extend reachable space and asked to make the same judgments, the objects are then perceived to be closer than they actually are (Bloesch, Davoli, Roth, Brockmole, & Abrams, 2012; Witt & Proffitt, 2008). Furthermore, just giving someone a tool is not enough, it must be a tool that will aid in extending reachable space (Berti & Frassinetti, 2000) and that a person intends to use (Witt, Proffitt, & Epstein, 2005).

The observed spatial compression may be occurring because tools allow one to bring objects into peripersonal space, and once there they appear closer than without the tool because there now exists ability to interact with them. However, if the tool is difficult to use, interaction with distant objects may not be possible and peripersonal space may not be extended (Linkenauger, Witt, Stephanucci, Bakdash, & Proffitt, 2009).

Currently, no studies have been done examining the effects of tool use on perception using an older adult sample. However, older adults may not show the same pattern of spatial compression that young adults do. If older adults have different or compromised representations of peripersonal space, their representations might not be as flexible as young adults'. This means that older adults may not have the ability to extend their peripersonal space representations during tool use, which would lead to no effect or a reduced effect of tool use on distance

estimates. In Experiment 2, this was directly tested in young and older adults by comparing distance judgments to objects after reaching to the object with the hand or with a tool. Young adults showed the expected pattern of spatial compression following tool use, judging targets to be closer after reaching with the tool than after reaching with their hand. Older adults, however, did not show any modulation of their distance judgments after reaching with a tool as compared to their hand. This supports the hypothesis that older adults have altered or compromised peripersonal space representations and thus are not able to flexibly incorporate the tool into those representations.

Method

Participants

In addition to the participants that completed the entire experimental session, 25 additional young adults (mean = 19.41 years) completed only the current experiment. These participants were recruited from Washington University's undergraduate population and received course credit in exchange for their participation, which lasted approximately 30 minutes.

Stimuli, Apparatus, and Procedure

Participants provided distance estimates to a target circle presented at varying locations on a table by adjusting the distance between two reference circles until both distances perceptually matched. The experimental set-up is shown in Figure 4. Participants sat at a 152.4 cm x 152.4 cm table that was covered with white fabric, which eliminated any possible landmarks. A yellow circle (2.54 cm x 2.54 cm) was fixed to the table centered at the midline of the participant's body, 20 cm from the edge of the table. A projector that was mounted from the ceiling projected the yellow target and white reference circles, all 2.54 cm diameter. The yellow target circle could appear at one of ten different locations, 44, 49, 54, 59, 64, 69, 74, 79, 84, or 89

cm away from the fixed yellow circle. The two reference circles had an initial separation of 6.35 cm and were always 35.88 cm away from the fixed yellow circle closest to the participant.

Participants were told that at the beginning of each trial they would see a yellow circle projected onto the table that would be a variable distance away, but always centered at their midline. When they saw this circle, they were to reach out and point to its location on the table, maintaining the gesture until the white reference circles appeared on the table five second later. When the reference circles appeared, participants brought their hands back to their bodies and then increased the distance between the reference circles until it matched the distance between the yellow circles. The reference circles could be moved by pressing one of two large buttons that were fixed to a board that was held on the participants' laps. The left button increased the

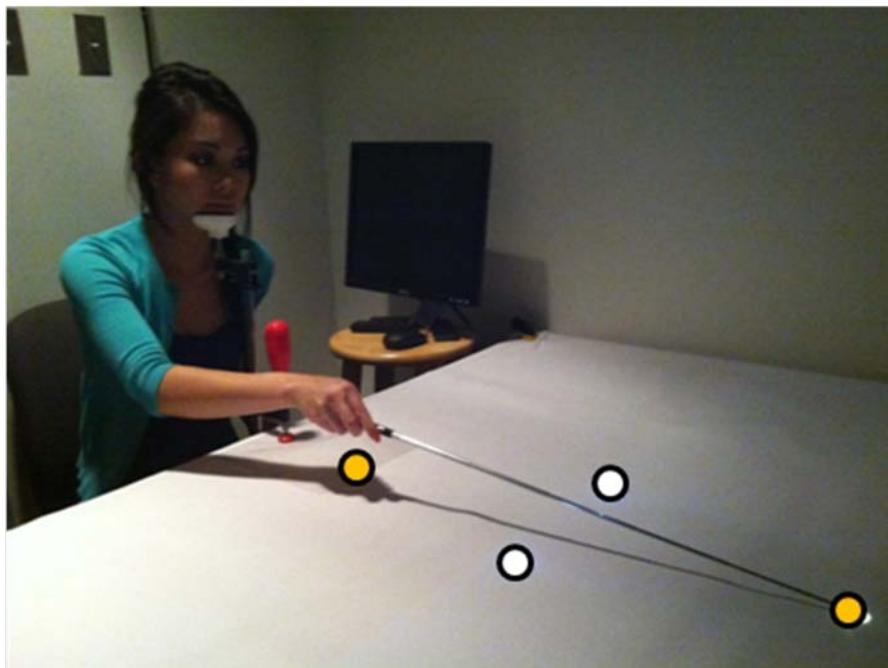


Figure 4. Experimental set-up. A yellow circle was affixed to the table near the participant's body, and a second yellow target circle was projected onto the table at a variable distance. Participants were to reach out with either their hand and point to the yellow target circle or reach out with a tool and touch the yellow target circle (simulated in this figure for clarity). Two white reference circles were then projected onto the table, and participants used response buttons to adjust the distance between the two white dots until it perceptually matched the distance between the two yellow dots.

distance between the reference circles and the right button decreased the distance. Participants were instructed to be as accurate as possible and were given an unlimited amount of time to make each estimate. After the estimate was made, any key on the computer keyboard was pressed, which recorded the response and began the next trial.

There were two conditions, hand pointing and tool pointing, which were manipulated within-subject. In the hand pointing condition, participants reached out with their right hands and pointed to the location of the projected yellow circle. In the tool pointing condition, participants reached out with a 64.77 cm-long baton-like tool, held in their right hands, and touched the location of the projected yellow circle. The distances of the projected yellow circles were such that the circles were beyond reach of the hand but within reach of the tool for all participants. Each distance was presented once per block. Participants completed eight blocks of ten trials, with the order of distances independently randomized within each block. Participants used one pointing condition for the first four blocks and the other condition for the final four blocks, with condition order counterbalanced across participants. Participants received four practice trials at the beginning of each half of the experiment. Distances of the projected yellow circle were randomly chosen for these trials, and the experimenter was present to ensure that participants understood the task. During the experiment no feedback was given. The first 25 young adult participants and all the older adult participants were alone in the experimental room during the session following the practice trials. The subsequent 60 young adult participants completed the session with the experimenter in the room with them recording their responses.

Results

Three older adults (mean: 72.33 years) and one young adult (19 years) were excluded for failing to follow instructions. Additionally, after the first 25 young adult participants it was

determined that the experimental protocol was not being implemented correctly. Because of this, these 25 young adult participants (mean: 19.44 years) are excluded from analysis.

Participants' estimates of the distance to the yellow projected circle were found by calculating the distance between the two reference circles at the end of each trial. These estimates were analyzed using a 2 (Group: young, old) x 2 (Reach: hand, tool) x 10 (Distance: 44-89 cm) mixed-factors ANOVA. As expected, there was a main effect of distance, such that as the distance between the projected yellow circle and the fixed yellow circle increased, participants' distance estimates increased also ($F(9, 88) = 241.87, p < .001, \eta^2_p = .96$). Overall, young and older adults had equal distance estimates ($F(1, 96) = 3.15, p > .05$). However, there was a significant Group x Reach x Distance interaction ($F(9, 88) = 2.32, p = .02, \eta^2_p = .19$). As has been found previously, young adults showed a compression of perceived distance when reaching with the tool: distance estimates were smaller after a tool reach than after a hand reach, with the difference between the two reach types getting slightly larger as distance increased (Figure 5). Older adults did not show this pattern. Instead, older adults' distance estimates were not affected by the type of reach they performed (Figure 6).

Young adult data were also analyzed separately from older adult data in order to ensure that young adults showed the predicted pattern of performance. Young adults continued to show a significant Reach x Distance interaction ($F(9, 42) = 2.41, p < .05, \eta^2_p = .34$, with distance estimates being smaller after reaching with the tool than with the hand and this difference getting larger as distance increased. Older adults, however, showed neither a main effect of Reach ($F(1, 46) = 1.07, p > .10, \eta^2_p = .023$) nor a Reach x Distance interaction ($F(9, 38) = 1.32, p > .10, \eta^2_p = .238$).

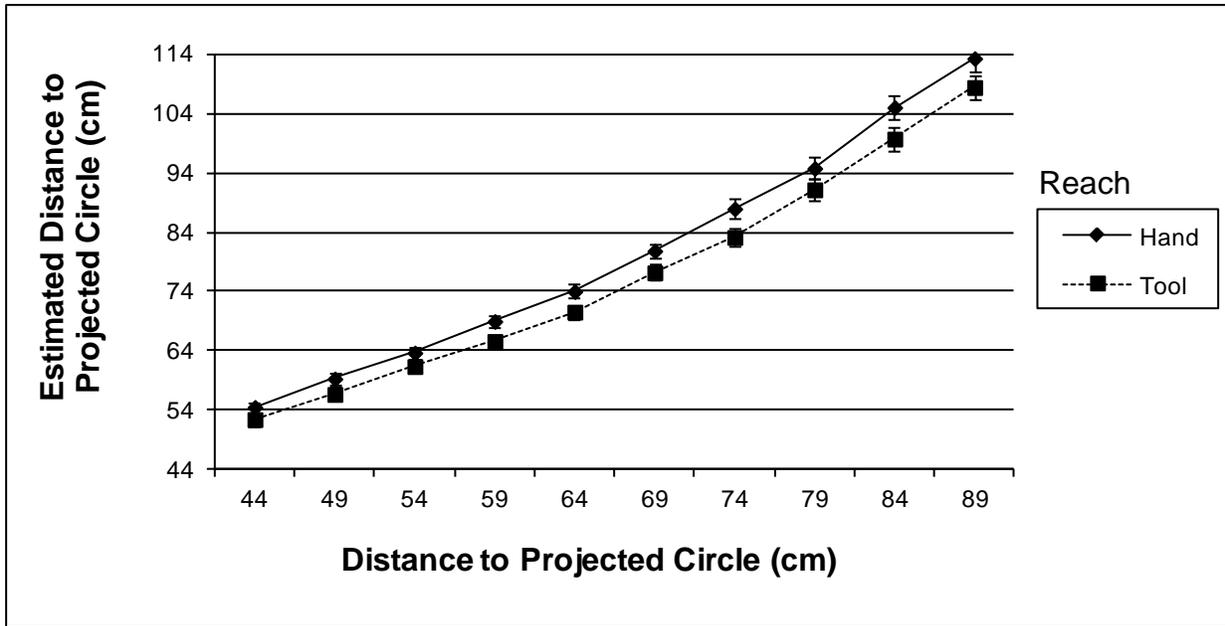


Figure 5. Young adults' distance estimates to the projected circle as a function of distance of the object and reach type.

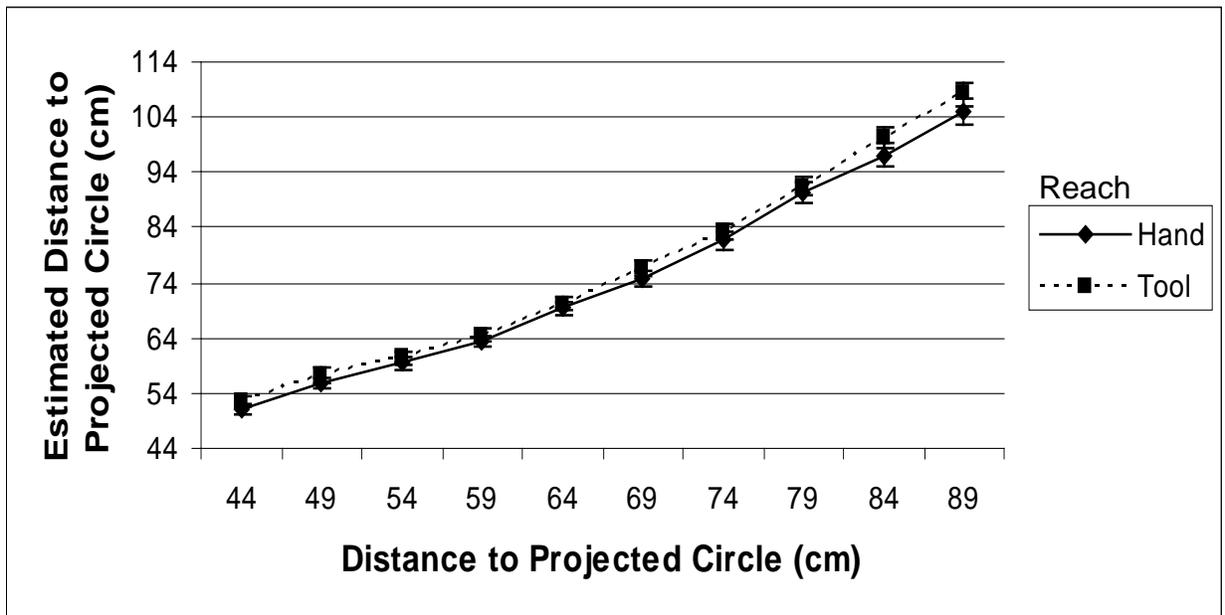


Figure 6. Older adults' distance estimates to the projected object as a function of distance of the object and reach type.

Finally, split-half reliability for each age group was examined by comparing distance estimates given during even-numbered blocks to distance estimates given during odd-numbered

blocks. There was a strong correlation between these blocks for young adults ($r = .98$) and older adults ($r = .97$), indicating excellent reliability.

Discussion

It has been repeatedly found that using a tool to reach out and interact with a distant object causes the object to be judged as closer than when that same object cannot be interacted with (Bloesch et al., 2012; Witt & Proffitt, 2008). In the present experiment, we found the same results. As predicted, young adults showed a pattern of spatial compression after reaching to a projected object with a reach-extending tool: they judged these objects to be closer than when they reached with their hands, and thus could not interact with the object. Older adults, however, did not show this pattern. Older adults had similar distance estimates for objects regardless of whether they reached to the object with their hands or with a tool – the ability to interact did not affect distance perception. In fact, the distance judgments for older adults were numerically smaller after reaching with their hands. This pattern is inconsistent with what would be expected if older adults were using the tool to functionally extend their peripersonal space.

It has been shown that young adults are able to incorporate a tool into their peripersonal space representations, allowing those representations to extend outward to include the length of the tool (Holmes & Spence, 2004; Witt et al., 2005; Witt & Proffitt, 2008). It is presumed that this ability relies on an accurate and flexible representation of the body and, in particular, the hands. Given that the neural regions that code and update perihand space decline with age, older adults may not have a representation that is as accurate or, at the very least, as flexible as that of young adults. Because of this, older adults may not have the ability to accommodate a tool in their perihand representations.

Chapter 6: Experiment 3

Attention appears to be prioritized in the areas surrounding the hands (Abrams et al., 2008; Dufour & Touzalin, 2008; Reed et al., 2006). One manner in which this can be seen is as a bias toward detecting objects near an outstretched hand. Reed et al. (2006) found that, in a cuing task, young adult participants were faster to detect targets that appeared on the same side of the display as the participant's extended hand, regardless of the validity of the cue. The effect is believed to occur because stimuli near the hands activate hand-centered, bimodal neurons, recruiting additional brain areas than would be active for stimuli not near the hands.

The effect of extending a hand during a basic visual attention task has never been examined in older adults and is the purpose of this experiment. A traditional cuing paradigm was used, wherein participants responded to a target that was preceded by a cue. On a given trial the cue was either valid, accurately predicting the target location, or invalid, inaccurately predicting the target location. In cuing paradigms such as this, older adults show patterns of behavior similar to young adults, with facilitation at validly-cued locations and slowed response times for invalidly-cued locations (Nissen & Corkin, 1985). However, the pattern may be different between young and older adults when a hand is near the display. If older adults do in fact have declines in multimodal brain areas, they should exhibit a reduced prioritization of space near their hands, and the presence of a hand near the stimuli should have a smaller effect on target detection compared to young adults.

Method

Materials and Procedure

In this task, participants assumed a series of body postures while completing a cuing paradigm. The display initially consisted of three items on a white background: a central fixation

cross flanked on each side by two unfilled squares with black borders. Each square was 2.15 degrees on a side, centered 6.1 degrees from the central fixation. Participants were instructed to maintain fixation on the central cross through the experiment. The series of events for each trial can be seen in Figure 7. Each trial began by presenting the fixation cross and two flanking squares simultaneously on the screen. After 1000 ms one of the squares was cued by darkening the border for 200 ms. Immediately following this, the target was presented by filling in with black one of the squares. Participants were instructed to respond as quickly and accurately as possible whether the target appeared on the left or right side of fixation. To do this, participants

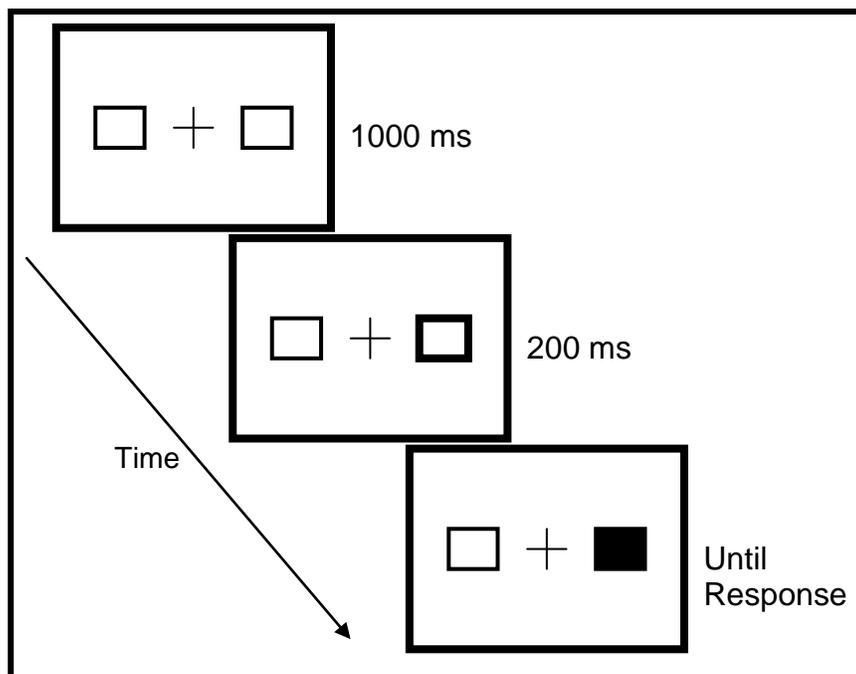


Figure 7. Events of an individual trial. Two squares flanked a central fixation cross. Next, the border of one of the squares became bold, acting as a cue. Finally, one of the squares became filled in black, indicating the target. The target was validly-cued on 70% of the trials.

held their index and middle fingers of one hand on the “b” and “n” keys on a standard keyboard; the “b” key was used for a left-side target, and the “n” key for a right-side target. Viewing distance was 40 cm and was maintained with a chinrest.

There were four blocks of 160 trials; in each block, 112 trials (70%) were validly-cued, in which the target appeared on the same side as the cue, consistent with Reed et al. (2006). The remaining 48 trials (30%) were invalidly-cued, in which the target appeared on the opposite side of the cue. Participants were not informed of the probability of a valid cue; they were instructed to ignore the cue location.

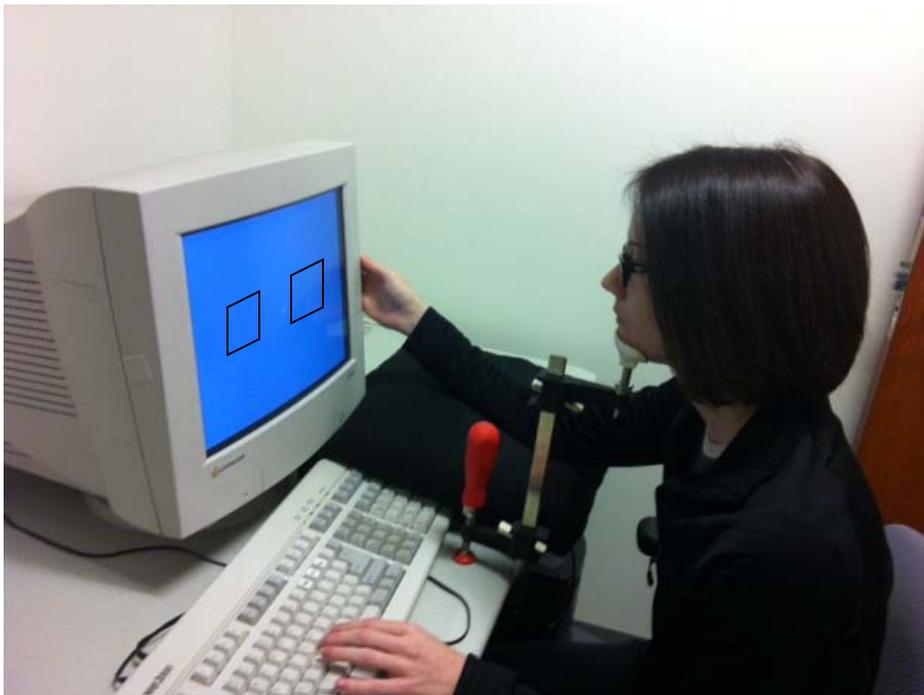


Figure 8. Experimental set-up. A participant sat with her chin in a chinrest at a computer. One hand rested on the keyboard, and the non-responding hand was either held on the lap or was outstretched so that the palm was on the side of the monitor.

The postures were specified by a fully-crossed combination of hand proximity and response hand: Participants could respond with either their left or right hand, and the non-responding hand could be either near to or far from the display. An example of the experimental set-up is shown in Figure 8. When the hand was near to the display, participants rested their elbows on a pillow on the desktop and placed their hands so the middle finger was resting on a

2.54 cm square piece of Velcro attached to the side of the monitor. When the hand was far from the display, participants were instructed to place their hands on their lap. Posture was blocked within-subject, and block order was counterbalanced across participants.

Results

Two older adults ($M_{\text{age}} = 71.00$) and seven young adults ($M_{\text{age}} = 19.43$) were removed due to excessive error rates ($>8\%$). Reaction times were first converted to z-scores (for each participant) in order to control for general slowing. A 2 (Response Hand: left, right) x 2 (Hand Proximity: far, near) x 2 (Target Side: left, right) x 2 (Cue Validity: valid, invalid) x 2 (Group: young, older adult) mixed-factors ANOVA was performed on the z-scored RTs of correct trials. There was a main effect of Cue Validity, with validly-cued trials producing faster RTs than invalidly-cued trials ($F(1, 89) = 1023.82, p < .001, \eta^2_p = .920$), shown in Figure 11. There was also a main effect of Response Hand, in which participants were faster when responding with their right as compared to left hands ($F(1, 89) = 7.69, p < .01, \eta^2_p = .080$). Finally, there was a main effect of Proximity. When the non-responding hand was near the display participants had faster RTs than when the non-responding hand was far from the display ($F(1, 89) = 5.36, p < .05, \eta^2_p = .057$).

Before discussing the highest-order interaction, which involves all five factors, it is useful to examine the key findings. Figure 9 shows these data, which are the z-scores for young and older adults as a function of only hand proximity and target side. In looking at young adults, it is clear that when the non-responding hand is far from the monitor, target side has no impact on performance. However, when the non-responding hand is near the monitor, young adults are faster to respond to a target that is near the non-responding hand. This replicates the finding of Reed et al. (2006). Older adults, however, do not show this pattern. For older adults, RTs are

comparable for targets appearing both near to and far from the hand, regardless of whether the hand is near to or far from the monitor. Of course, this result can only be understood within the context of the significant five-way interaction (Response Hand x Hand Proximity x Target Side x Cue Validity x Group, $F(1, 89) = 6.72, p < .05, \eta^2_p = .070$), shown in Figure 10. When young adults performed the task with their non-responding hand far from the display, reaction times were unaffected by the location of the target. Additionally, the effects of valid and invalid

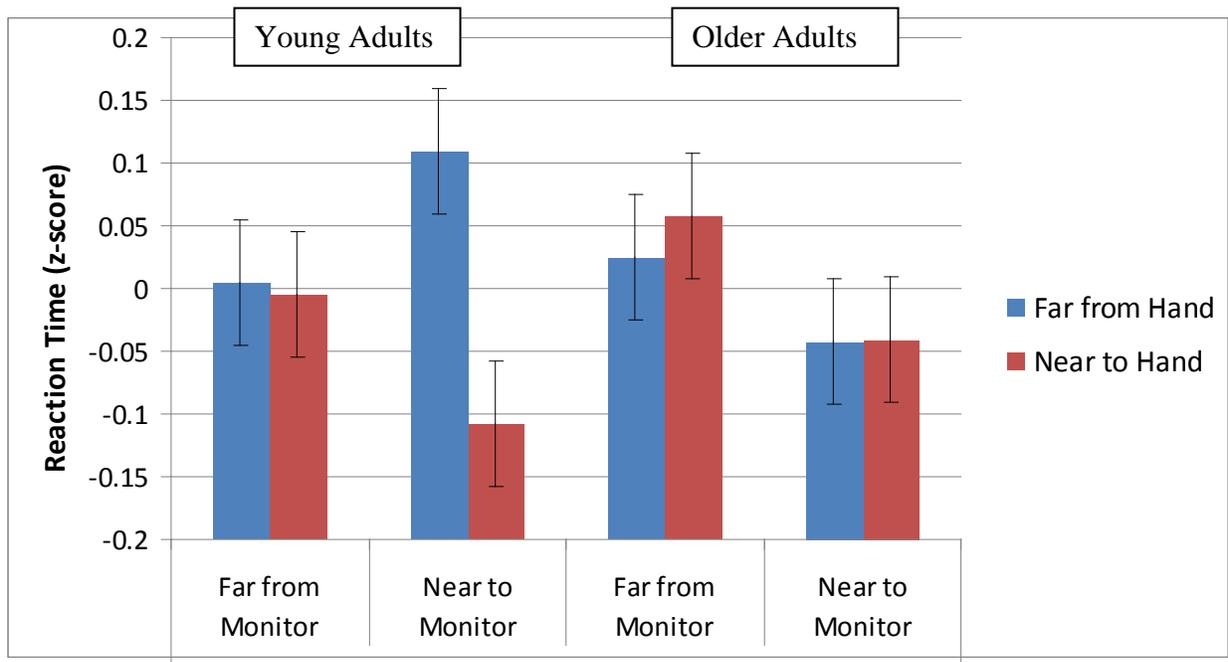
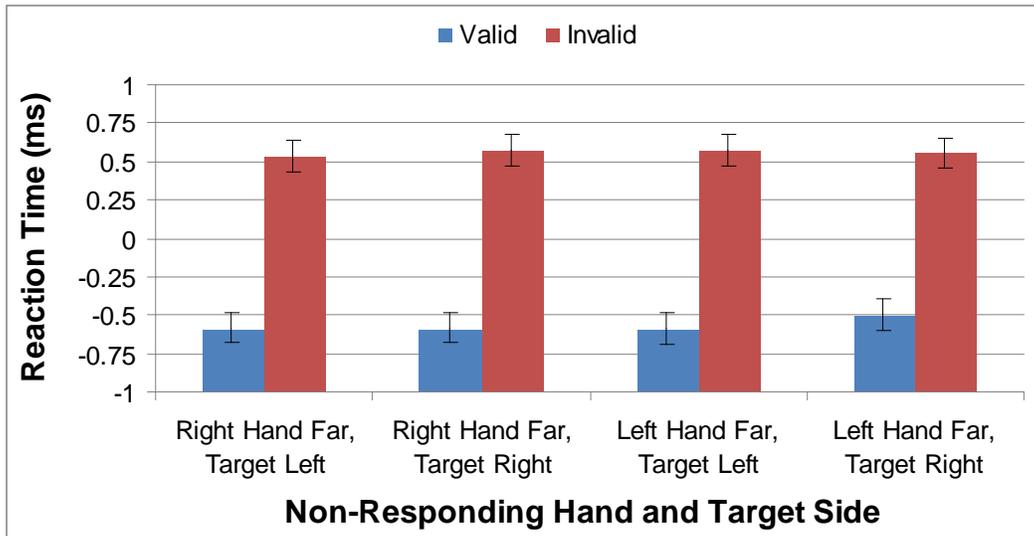


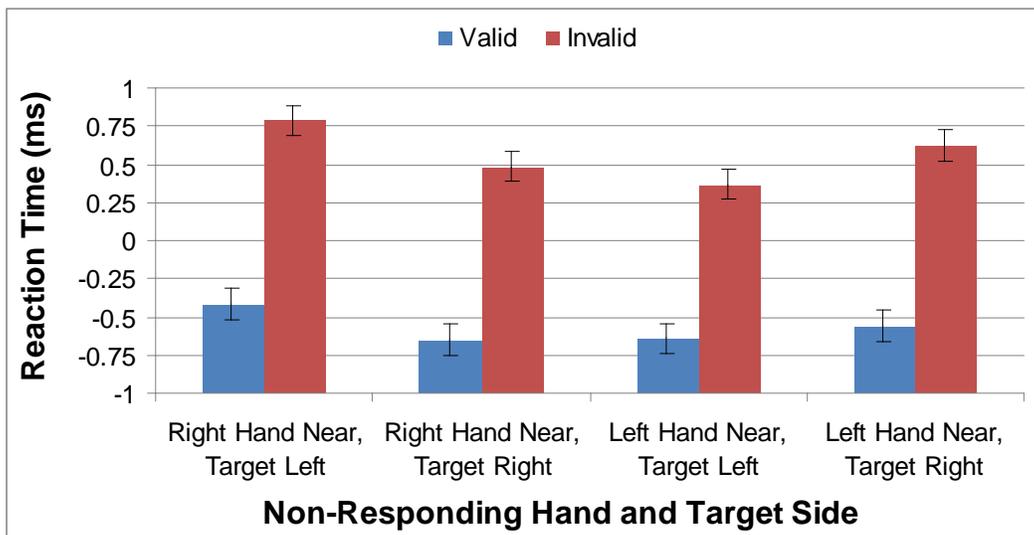
Figure 9. Mean z-scores for young and older adults as a function of hand proximity and target side. Error bars are the standard error of the mean.

cues were similar for both target locations. However, when their non-responding hand was near the display, reaction times were dependent on both target side and validity. Targets appearing on the same side as the nearby hand were responded to more quickly than targets appearing on the opposite side. This benefit was different for valid and invalid cues: the cost of an invalid cue was smaller if the target was presented near the hand. In other words, when young adult participants were cued to the side of the screen away from their hands, they were faster to shift attention

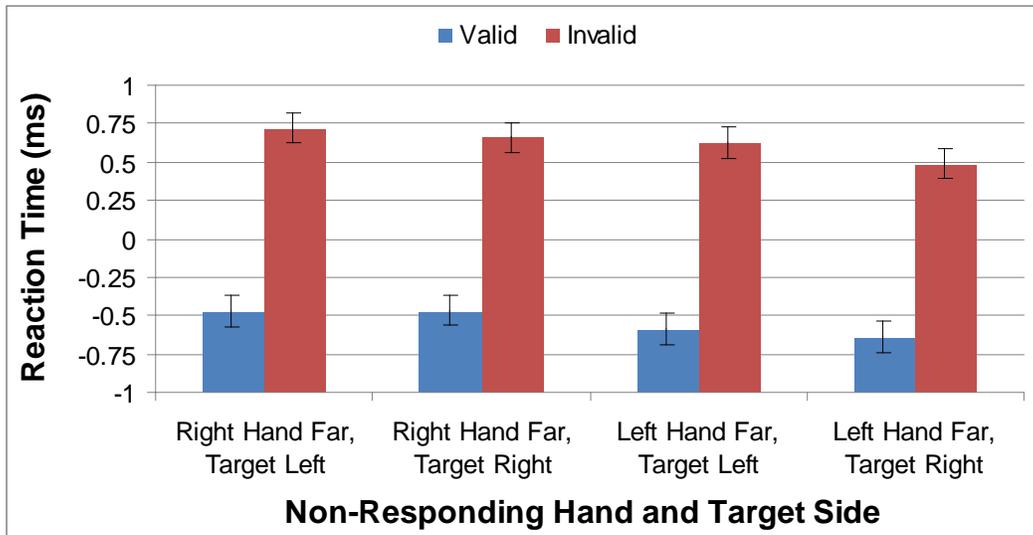
toward the target appearing near their hand than when the cue was near their hands and they had to then shift their attention to a target appearing far from their hands. Older adults, however, did not show any modulation of performance based on hand proximity.



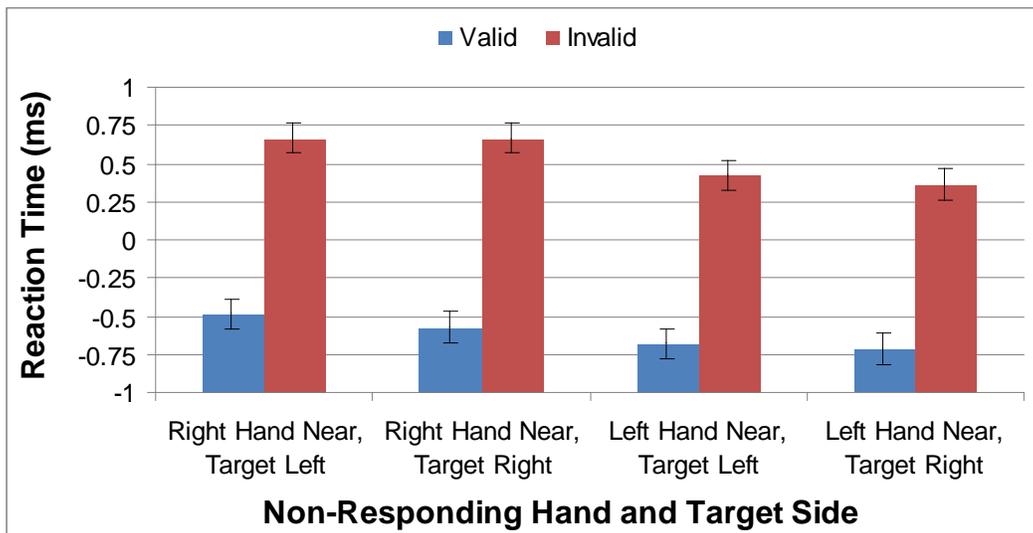
Panel A: Young Adults, Non-Responding Hand Far from Display



Panel B: Young Adults, Non-Responding Hand Near to Display



Panel C: Older Adults, Non-Responding Hand Far from Display



Panel D: Older Adults, Non-Responding Hand Near to Display

Figure 10. Z-scores for young and older adults as a function of hand proximity, target side, and cue validity. Error bars represent the standard error. Panel A shows z-scores for young adults when the non-responding hand was far from the display. Panel B shows z-scores for young adults when the non-responding hand was near to the display. Panel C shows z-scores for older adults when the non-responding hand was far from the display. Panel D shows z-scores for older adults when the non-responding hand was near to the display.

Young and older adult data were also analyzed separately in order to ensure that young adults showed the expected pattern of performance. Indeed, young adults had a Response Hand x

Hand Proximity x Target Side x Validity interaction ($F(1, 42) = 10.00, p < .005, \eta^2_p = .192$), showing that performance was altered by hand proximity to the display. Older adults, on the other hand, did not show any interactions involving Hand Proximity.

Previous studies have shown that older adults show effects of cue validity that are similar to young adults when the task is performed in the traditional manner, with hands far from the display. To test if this was true for the current experiment also, z-scores for correct trials when hand proximity was far were analyzed using a 2 (Response Hand) x 2 (Target Side) x 2 (Cue Validity) x 2 (Group) mixed-factors repeated-measures ANOVA. As shown in Figure 11, there was still a main effect of Validity ($F(1, 89) = 919.79, p < .001, \eta^2_p = .912$), but Validity did not interact with Group ($F < 1$). Both age groups had comparably slower z-scored RTs on invalid as compared to valid trials. This is consistent with prior findings showing that both young and older adults are able to use top-down information to guide performance, such as they would get from a cue (Hartley, Kieley, & Slabach, 1990).

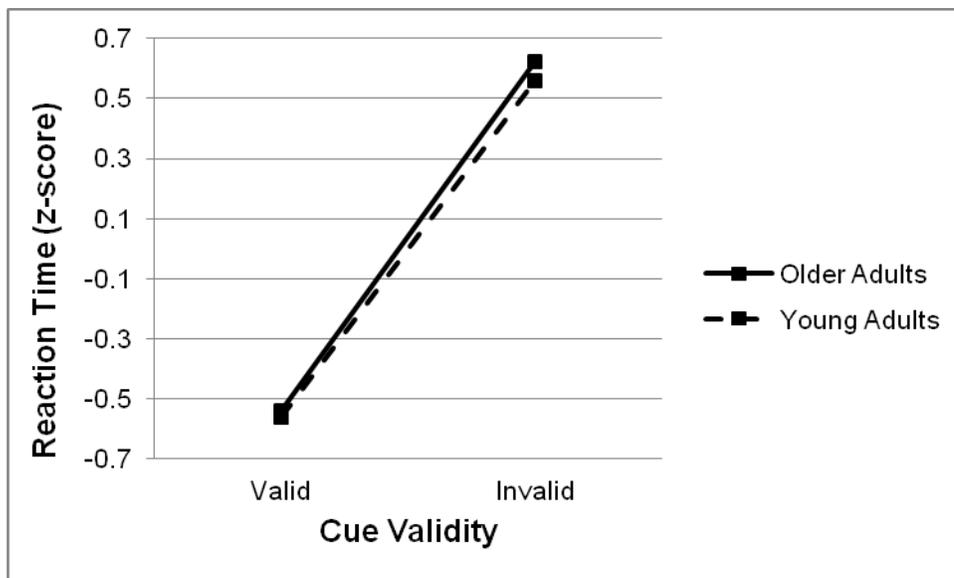


Figure 11. Reaction time as a function of cue validity and age group. Only the means from trials in which the hands were held far from the display are shown.

Error rates were analyzed with the same 2 (Response Hand) x 2 (Hand Proximity) x 2 (Target Side) x 2 (Cue Validity) x 2 (Group) mixed-factors repeated-measures ANOVA. There was a Response Hand x Target Side x Validity x Group interaction ($F(1, 89) = 5.00, p < .05, \eta^2_p = .053$), shown in Table 5. Young adults had a higher error rate on invalid as compared to valid trials, but this pattern was similar across response hand and target side. For older adults, error rates were higher for right-side targets regardless of response hand, but only on valid trials. For invalid trials, error rates were similar across response hand and target side. Given the similarity of error rates across conditions for young adults, it is unlikely that the reaction time results are the product of a speed/accuracy tradeoff. This is less clear for older adults. Older adults do exhibit an advantage in reaction time for right-side targets, conditions in which they also have the highest error rates. The right-side RT advantage might then be due to a speed/accuracy tradeoff. Importantly though, there were no interactions involving proximity. Because of this, there is no reason to believe that differential error rates between the age groups are causing the differential changes in RTs associated with proximity.

		Older Adults		Young Adults	
Response Hand	Target Side	Valid	Invalid	Valid	Invalid
Left	Left	.05	.28	.06	1.30
	Right	.27	.31	.15	1.08
Right	Left	.07	.42	.07	1.14
	Right	.29	.37	.14	1.23

Table 5. Error rates in percent for young and older adults as a function of response hand, target side, and cue validity.

Split-half reliability for each age group was assessed by comparing the RTs on even-numbered trials to odd-numbered trials. For both young and older adults there was a strong

correlation between these trials (Young Adults: $r = .981$; Older adults: $r = .968$), indicating high reliability.

Discussion

In the present study young and older adults were tested on an attentional cuing task, both with and without their hands near the visual display. When performed in the typical fashion, with hands far from the display, young and older adults show similar patterns of performance (Nissen & Corkin, 1985). The present study also found that when the hands were far from the display, both age groups used the cue to guide performance, resulting in faster reaction times on validly-cued as compared to invalidly-cued trials. For young adults, however, performance can be altered by simply placing one's hands near the visual display (Reed et al., 2006). The current experiment found that young adults were faster to detect a target when it appeared near the hand, and that this advantage was even greater for invalidly-cued targets. This indicated that young adults could more easily shift attention toward their hand than away from it. Older adults, however, showed no such attentional bias to near-hand space. For older adults, having a hand near the display did not produce reaction time patterns that were different than when a hand was far from the display.

It has been hypothesized that young adults show changes in performance when a hand is near the display because the items in the display fall into perihand representations. When this occurs, those items engage not only traditional visual areas in the occipital cortex, but also benefit from additional activity in multimodal neural areas. Perihand representations are supported by multimodal activity in the IPS, PM, and precuneus – areas that all show changes during senescence. Because of these neural changes, older adults might not represent perihand space the same way young adults do, and objects falling in this space might not be subjected to

the same specialized processing. The result of this would be that, unlike young adults, older adults do not show a bias to deploy attention to perihand space, consistent with the current findings.

Chapter 7: Inter-Experiment Analysis

Peripersonal space is still a fairly new topic of investigation, even when considering only the work done to date with young adults. Because the strongest evidence for the existence of specialized perihand representations has come from research with clinical populations and single-cell recording in monkeys, the paradigms used in this research are often also used to examine perihand representations in healthy humans. Popular paradigms that have been modified for healthy human studies include tool use (Witt et al., 2005), cross-modal cuing (Kennett et al., 2002), and comparing the effects of an object being inside as compared to outside of hand-space (Abrams et al., 2008; Reed et al., 2006). The strong relationship between tasks used with healthy humans and those used with clinical populations and monkeys has led to high face validity – it is rarely questioned whether studies purporting to test a property of perihand space in healthy adults are in fact doing so. Because of this, the extent to which these tasks reported in the literature do measure the same construct is unknown. The goal of the present analysis is to examine the relationship among the three experiments reported in the current study in order to assess the extent to which they are indeed measuring similar aspects of perihand space.

The effects that have been found in the three current experiments – the rubber hand illusion, attentional cuing near the hands, and tool use - are believed to rely on intact perihand representations. In the rubber hand illusion, the rubber hand must be within the bounds of one's perihand representation in order for the illusion to arise. With attentional cuing, when the target falls within the bounds of one's perihand representation, the target is more quickly detected. Finally, when using a tool to extend reach outward to an object, the perihand representation is able to extend outward as well to encompass the length of the tool, resulting in the object appearing closer than when reaching without a tool. It is likely that there are individual

differences in the extent to which one's perihand representation will impact performance on the three tasks; however, it is reasonable to predict that within a given individual, perihand representations will exert an influence to a similar extent across tasks. Thus, if the effects seen in all three of the current experiments are due to perihand representations, then there should be a positive correlation among the three tasks in young adults. Older adults may also show a positive correlation if perihand representations are intact in a portion of the sample. However, an attenuated correlation could be expected. The selected tasks show variability based on the manipulation of hand proximity or interaction – if performance is not based on this factor, individual variability might decline and produce a restricted range of performance, reducing the ability to detect a correlation.

Method

First, index variables for each experiment were created. For the attentional cuing experiment, the index represented the benefit of having the target appear on the same side of the screen as the hand when the hand was held near the screen. To calculate this, only the blocks in which the hand was near the screen were considered. Reaction times of trials in which the target appeared near the hand, regardless of cue validity, were subtracted from RTs of trials in which the target appeared far from the hand. Thus, positive values indicate how much faster, in milliseconds, participants were to respond to the target when it appeared near to as compared to far from the hand, showing a bias for near-hand targets. Negative values indicate how much slower participants were to respond to a target near as compared to far from the hand.

For the tool use experiment, the index variable was created by first calculating the mean estimated distance for trials in which participants performed a reach with their hand and, separately, the mean estimated distance for trials in which participants performed a reach with

the tool. Next, the mean estimated distance for tool-use trials was subtracted from the mean estimated distance for hand-reach trials. Positive values indicate how much closer, in centimeters, participants estimated the projected circle to be after reaching with the tool than with their hand. Negative values indicated how much farther participants estimated the projected circle to be after reaching with the tool than with their hand.

For the rubber hand illusion, index variables were created for the subjective rating of the illusion, proprioceptive drift, and the number of strokes given on each trial. These consist of the median subjective rating for all trials, the mean felt displacement of the hand for all trials, and the mean number of strokes given on trials in which the participant gave a subjective rating of +3, respectively.

Results

Participants from Experiments 1-3 who were excluded for either not completing the protocol or failing to follow instructions were excluded from the present analyses as well. The means and standard deviations for each of the index variables for each age group are show in Table 6. Pearson correlations were calculated for young and older adults separately among the five index variables. In order to control for multiple comparisons, a Bonferroni correction was applied, leading to an alpha level set at .005.

Table 6. Mean, standard deviations, and number of participants for age group for each of the index variables used to represent the present study’s experiments.

Age Group	Attentional Cuing (ms)	Tool Use (cm)	RHI Subjective Rating	RHI Mean Strokes	RHI Proprioceptive Drift (in)
Young Adults	<i>M</i> = 9.01 <i>SD</i> = 11.70 n = 50	<i>M</i> = 17.99 <i>SD</i> = 10.79 n = 24	<i>M</i> = 1.21 <i>SD</i> = 2.21 n = 50	<i>M</i> = 45.11 <i>SD</i> = 18.17 n = 50	<i>M</i> = 3.80 <i>SD</i> = 2.53 n = 50
Older Adults	<i>M</i> = -.52 <i>SD</i> = 18.55 n = 49	<i>M</i> = -6.96 <i>SD</i> = 46.09 n = 47	<i>M</i> = -.20 <i>SD</i> = 2.64 n = 50	<i>M</i> = 44.84 <i>SD</i> = 21.03 n = 50	<i>M</i> = 3.01 <i>SD</i> = 2.23 n = 50

In the young adult group, although 51 participants completed the entire experimental protocol, the first 25 participants were removed from the tool use data analysis because of a failure in implementation. Thus, the data for all 51 participants was used to calculate the correlations among the attentional cuing and rubber hand illusion index variables. The 25 participants that completed the entire protocol, including the tool use experiment after the procedure was changed, were used to calculate the correlations involving the tool use experiment.

Table 7. Correlations among the index variables for the three experiments, attentional cuing, tool use, and the rubber hand illusion, for young adults. The ‘n’ is the number of participants used to calculate each correlation.

	Attentional Cuing	Tool Use	RHI Subjective Rating	RHI Mean Strokes	RHI Proprioceptive Drift
Attentional Cuing	$r = 1.00$ n = 50	$r = .129$ n = 24	$r = .180$ n = 50	$r = -.071$ n = 50	$r = .071$ n = 50
Tool Use		$r = 1.00$ n = 24	$r = .029$ n = 24	$r = .049$ n = 24	$r = -.198$ n = 24
RHI Subjective Rating			$r = 1.00$ n = 50	$r = -.665^{**}$ n = 50	$r = .698^{**}$ n = 50
RHI Mean Strokes				$r = 1.00$ n = 50	$r = -.774^{**}$ n = 50
RHI Proprioceptive Drift					$r = 1.00$ n = 50

* correlation significant at the .05 level

** correlation significant at the .01 level

As can be seen in Table 7, young adults did not have any significant inter-experiment correlations; the only significant correlations were among the variables in the rubber hand illusion, a finding consistent with the results reported in Experiment 1. There was a positive correlation between the subjective rating of the rubber hand illusion and the rating of

proprioceptive drift ($r(48) = .698, p < .001$), a negative correlation between the subjective rating and the number of strokes given on trials rated +3 ($r(48) = -.665, p < .001$), and a negative correlation between the rating of proprioceptive drift and the number of strokes given on trials rated +3 ($r(48) = -.774, p < .001$). There were no correlations between the index variables for attentional cuing and tool use, nor between these two index variables and the index variables for the rubber hand illusion.

As can be seen in Table 8, older adults showed the same pattern of correlations as young adults. There were not any significant inter-experiment correlations; the only significant correlations were among the variables in the rubber hand illusion, again, a finding consistent with the results reported in Experiment 1. There was a positive correlation between the

* correlation significant at the .05 level

** correlation significant at the .01 level

	Attentional Cuing	Tool Use	RHI Subjective Rating	RHI Mean Strokes	RHI Proprioceptive Drift
Attentional Cuing	$r = 1.00$ n = 49	$r = .007$ n = 46	$r = -.169$ n = 49	$r = .133$ n = 49	$r = .201$ n = 49
Tool Use		$r = 1.00$ n = 47	$r = -.093$ n = 47	$r = .085$ n = 47	$r = .040$ n = 47
RHI Subjective Rating			$r = 1.00$ n = 50	$r = -.675^{**}$ n = 50	$r = .871^{**}$ n = 50
RHI Mean Strokes				$r = 1.00$ n = 50	$r = -.544^{**}$ n = 50
RHI Proprioceptive Drift					$r = 1.00$ n = 50

Table 8. Correlations among the index variables for the three experiments, attentional cuing, tool use, and the rubber hand illusion, for older adults. The ‘n’ is the number of participants used to calculate each correlation.

subjective rating of the rubber hand illusion and the rating of proprioceptive drift ($r(48) = .675, p < .001$), a negative correlation between the subjective rating and the number of strokes given on trials rated +3 ($r(48) = -.871, p < .001$), and a negative correlation between the rating of proprioceptive drift and the number of strokes given on trials rated +3 ($r(48) = -.554, p < .001$). Similar to young adults, there were no correlations between the index variables for attentional cuing and tool use, nor between these two index variables and the index variables for the rubber hand illusion.

Scatterplots showing the relationship among the rubber hand illusion subjective rating, tool use, and attentional cuing experiments are shown in Figure 12. This figure illustrates one reason for the lack of significant correlations – for both age groups there is a fairly restricted range of performance, especially for the tool use index variable. In spite of the restricted range, a visual inspection of Figure 9 does show that young adults have a weak yet positive relationship among all the index variables, while older adults have a non-existent or negative relationship among the index variables.

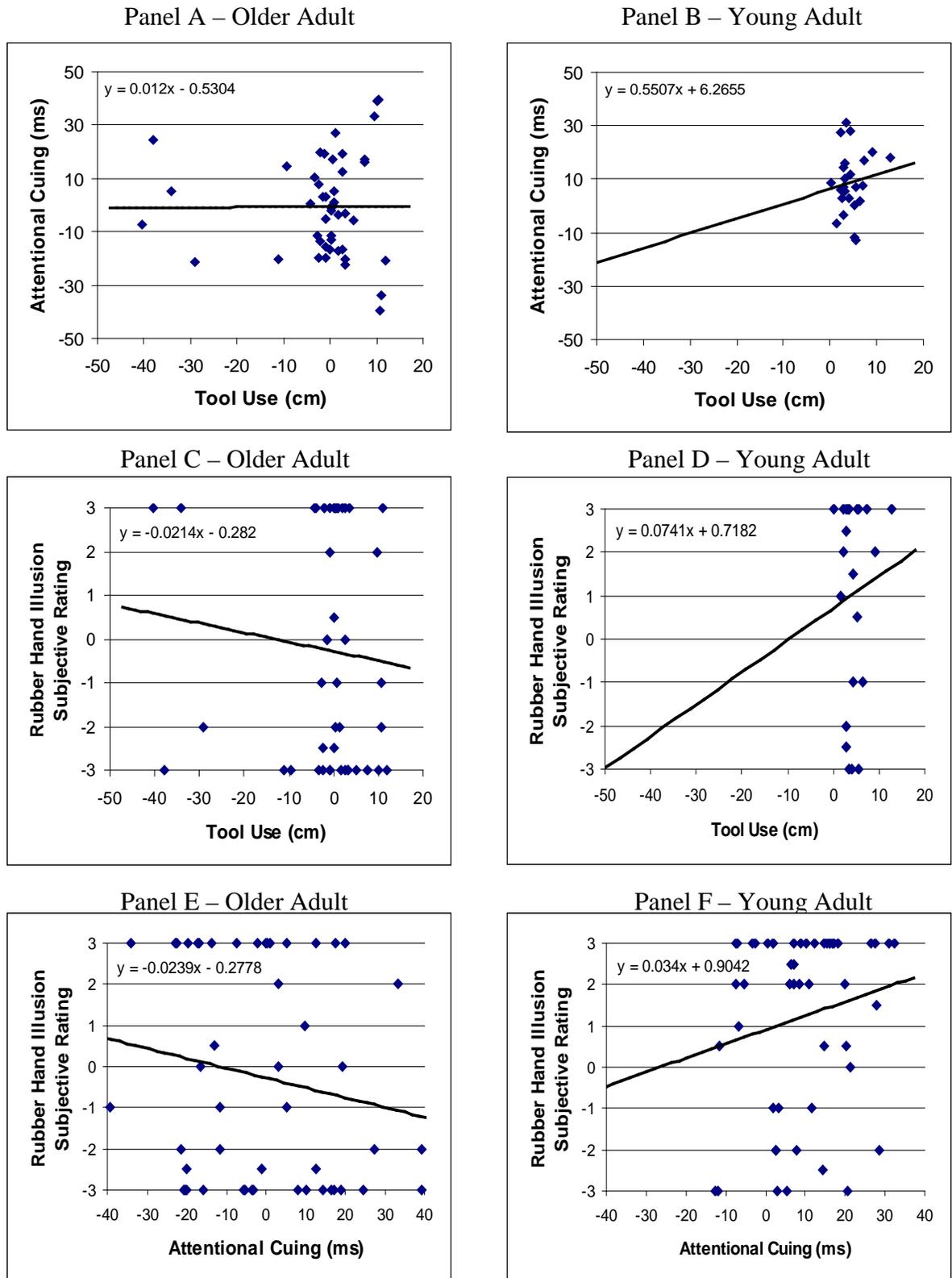


Figure 12. Scatterplots showing the relationship among the index variables representing each experiment for older and young adults. Line represents the line of best fit.

Discussion

The effects of the three experiments that were conducted as part of the present study, the rubber hand illusion, tool use, and attentional cuing, are all hypothesized to occur as a result of the changes in attention and perception in perihand space representations. Because of this common foundation, it would be expected that there would be a correlation among performance on the three experiments for young adults. However, since older adults are thought to have altered or degraded perihand representations, it was not expected that there would be a strong correlation among the experiments for elderly participants. Surprisingly, neither age group had correlations among the experiments. There are at least two possible reasons why these correlations might not have been found.

The first possibility is that there is a relationship among the experiments, but the correlations are weak and there is not enough power to detect them with the current sample size. The correlations do support this possibility: the correlations for young adults are small but in the expected direction, whereas the correlations for older adults are virtually non-existent and, in some cases, in the opposite direction. It could be that by increasing the sample size these relationships would more clearly emerge for young adults. Adding to the difficulty in detecting correlations is that the range of individual differences on each experiment is not large, producing a somewhat restricted range. A larger sample of young and older adults may also increase the variability of the index measures, making a correlation more apparent.

The second possibility is that there is in fact no relationship among the tasks. In this view, although we believe these tasks are all based on perihand representations, they are not. A less severe position would be that all the tasks are based on perihand representations, but are based on different mechanisms underlying perihand representations. There are a number of attentional

and perceptual changes associated with performing a task in as opposed to outside of perihand space, but currently it is unknown if the same mechanism gives rise to both types of changes. If the mechanism that leads to alterations in attention in perihand space is slightly different than the one that leads to perceptual changes, the relationship among tasks that measure these two aspects of cognition differentially could be attenuated. For example, as discussed in Chapter 4 on the rubber hand illusion, it appears that different mechanisms underlie one's subjective rating of the illusion and the feeling of proprioceptive drift. The former relies on visual-tactile integration, while the latter relies on visual-proprioceptive integration. Because of this, the relationship among these variables, even within the same experiment, is often weak. Given the differences between the current experimental tasks and their physical and cognitive demands, it is possible that the three phenomena tested in the current study are also relying on slightly different underlying mechanisms. Because of this, even though the tasks do rely on perihand space in general, they are tapping into different specific aspects of those representations.

General Discussion

Peripersonal space is the space immediately surrounding one's body, and while this may seem like an arbitrary construct it has been found that there are significant changes in cognition within as compared to beyond peripersonal space (Abrams et al., 2008; Jewell & McCourt, 2000; Reed et al., 2006). Importantly, the changes in cognition are also linked to changes in how one interacts with the surrounding environment (Berti & Frassinetti, 2000; Butler et al., 2004; Longo & Lourenco, 2006). This supports the popular theory that peripersonal space representations facilitate successful interaction with the environment. Perihand space, peripersonal space representations that are anchored to the hands, are constructed through activity in multimodal brain regions such as the premotor cortex, intraparietal sulcus, precuneus, and putamen (Cavanna & Trimble, 2006; Luppino et al., 1999; Rizzolatti et al., 1998). These areas are ones that show changes during aging. For example, there are structural and functional changes in the IPS (Kochunov et al., 2005), precuneus (Lehmbeck et al., 2006), putamen (Hedden & Gabrieli, 2005), and PM (Ward & Frackowiak, 2003) in normal aging. Even though the changes just noted are commonly reported, very little work has examined whether neural changes in multimodal regions in older adults result in changes in perihand representations. The goal of the present studies was to determine the nature and extent of possible age-related changes in perihand representations.

In young adults, perihand representations can be probed by comparing performance on attentional and perceptual tasks completed both within and outside of perihand space. Modeling that, the current experiments used three paradigms that show differential effects depending on where in space (in perihand or extrahand space) the paradigm is performed: the rubber hand

illusion, tool use, and attentional cuing. Age differences on these tasks were assessed in three experiments.

Experiment 1 tested the rubber hand illusion. In this illusion, synchronous visual and tactile stimulation on a dummy hand and a participant's real hand result in feelings of ownership over the dummy hand and proprioceptive drift, a mis-localization of the real hand as closer to the dummy hand. The RHI occurs as a result of the multisensory integration of vision, touch, and proprioception, and because of this it primarily occurs when the dummy hand is within the perihand representation of the participant's real hand. Thus, by varying the distance between the participant's real hand and the dummy hand, the RHI can provide a measure of the spatial extent of perihand representations in young and older adults. Young adults had stronger subjective ratings of the illusion, and this was true regardless of the distance between the real and dummy hands. In fact, older adults as a group consistently experienced the illusion either weakly or not at all. In spite of this striking age difference in subjective ratings, the magnitude of proprioceptive drift was similar for young and older adults, suggesting that when older adults did experience the RHI, their experience was similar to young adults'. Importantly, experience of the RHI was not correlated with visual acuity or tactile sensitivity. If the decrease in older adults' experience of the illusion was not due to declines in individual senses, it is likely that the decrease is instead due to an inability to effectively integrate these individual senses. Given that multisensory integration is a hallmark of perihand space, the changes found in the RHI in older adults are evidence that perihand representations change with age.

Experiment 2 examined the effects of tool use on distance perception. In young adults, tools that extend one's reach can be flexibly incorporated into perihand representations (Bloesch et al., 2012; Witt et al., 2005). Young and older adults' ability to incorporate a tool into perihand

representations was examined here by having participants judge the distance to a target after reaching out to it with either their hand or with a tool. Importantly, when reaching with their hand the target was always far enough that it could not be physically touched, but when reaching with the tool the participant could always touch the target. Young adults showed a pattern of performance in which distance perception depended on their reach type: targets were judged to be closer after reaching with the tool than after reaching with their hand. This is the pattern that would be expected if young adults were able to extend their perihand representations to include the length of the tool, which would then also bring the target into perihand space. Older adults, however, did not show this pattern. Older adults had equivalent distance estimates after both hand and tool reaches. Thus, older adults were not able to incorporate the tool into their perihand representations, showing a lack of flexibility that is present in young adults.

Finally, Experiment 3 examined how attentional cuing interacted with hand space. Attention is prioritized to the space near the hands, and because of this when young adults hold a hand near a display they are faster to detect targets appearing near that hand (Reed et al., 2006). The effect is believed to occur because stimuli near the hands activate hand-centered, bimodal neurons, recruiting additional brain areas than would be active for stimuli not near the hands. Experiment 3 showed that young adults do indeed show a significant advantage in responding to targets appearing near the hands. This advantage was even greater for invalidly-cued targets, indicating that participants were faster to shift attention toward as opposed to away from their hand. Older adults, however, did not show this attentional prioritization of hand space. Older adult performance was not altered by having a hand near the monitor – they were just as fast to respond to targets appearing far from the hand as targets appearing near the hand. This result is

consistent with older adults having altered perihand representations – a degraded representation would not bias attention toward the hand on the present cuing task.

As just described, the effects observed in all three experiments showed consistent and predicted age-related changes. Older adults exhibit both structural and functional changes in multisensory brain regions that support perihand space representations, but until the present experiments there has been very little evidence that these neural changes lead to behavioral changes. While older adults do have declines in sensory ability, including losses in visual acuity and tactile sensitivity, these declines were not predictive of the changes in performance on the experimental tasks. Additionally, all the stimuli in the three experiments were presented far above threshold. These two factors combine to suggest that older adults' altered performance was not due to a lack of access to the unimodal information; rather, the problem may have been in integrating the unimodal information into a multisensory representation. Perihand representations are, primarily, multisensory – they arise out of the integration of visual and tactile information, with contributions from proprioception as well. Therefore, a decline in multisensory integration would result in altered perihand representations in older adults and might be the mechanisms that caused the changes in performance observed in the present study.

Relationships Among Tasks

If an individual's performance on the three experiments described above does depend on the influence of perihand representations, then it is reasonable to predict that there should be a positive relationship among the tasks. In other words, an individual that shows a large effect of hand proximity on one task, there should be a corollary large effect on the other tasks. However, as shown in the inter-experiment analysis, there were no significant correlations among any of the experiments for either young or older adults. While this is unexpected, there are a number of

possible reasons for the failure to find a correlation. The first set of reasons is statistical. There may simply not be enough power to pick up on a significant correlation if it is small, and if so a solution could be to increase the sample size. Also problematic is that it appears that within each age group there is a somewhat restricted range of performance across tasks, which is known to attenuate correlations. The scatterplots in Chapter 7 illustrate not only the range restriction, but also show that young adults do have non-significant correlations among tasks in the expected (positive) direction.

Another reason for the lack of correlation across tasks, which has theoretical implications for the study of perihand space, is that the three tasks may be tapping into different aspects of perihand space. There is evidence that paradigms that are ostensibly measuring similar processes have different brain activity patterns corresponding to different sensory integration demands. For example, in the rubber hand illusion there are different patterns of activation for the subjective feeling of ownership over the rubber hand and proprioceptive drift: the premotor cortex is correlated with feelings of ownership, whereas the PPC is correlated with proprioceptive drift (Brozzoli, Gentile, & Ehrsson, 2012). Rohde et al. (2011) found that these two measures were associated with different sensory integration demands. The subjective feeling of ownership arose from visual-tactile integration, whereas proprioceptive drift arose from visual-proprioceptive integration. Additionally, even though the two measures are two aspects of the same paradigm, they can be orthogonal (Rohde et al., 2011).

Makin et al. (2007) also found differences in brain activity for coding perihand space depending on sensory input. They reported preferential activity in the posterior IPS when there was visual information about the hand, regardless of whether it was the participant's real hand or a dummy hand, suggesting that the pIPS codes information about hand location in principally

visual terms. The anterior IPS and ventral PM, however, showed preferential activity for objects in hand-space when there was both visual and proprioceptive information, suggesting that the aIPS and PMv code information about hand location using multiple sources.

The studies just discussed support the possibility that perihand space is not a unidimensional construct. When tasks that rely on perihand representations use different types of sensory integration (visual-tactile, visual-proprioceptive, or a combination of all three sources of information), different mechanisms, and in fact even different brain regions, are used. The three experiments used in this dissertation vary widely in both cognitive and motoric demands. The rubber hand illusion relies on visual, tactile, and proprioceptive integration; tool use relies on visual and proprioceptive integration; attentional cuing relies on visual and tactile integration. The differences in integration among tasks might be enough to engage different perihand mechanisms, leading to a weak relationship among the tasks even for young adults.

A final factor that has not been explored is the relationship between static and dynamic perihand representations. Many prior studies manipulated perihand space by having participants perform the task with their hand(s) resting far from or near to the display (Abrams et al., 2008; Reed et al., 2006). When one or both of the hands is near the display the presented items are in perihand space, but passively so: the participant is not interacting with the display or items contained in it. This is quite different from studies using more dynamic measures. For example, in studies looking at selective reaching (Bloesch et al., in press; Tipper et al., 1992), participants move their hand to the stimulus on each trial, actively bringing items into perihand space. It seems clear that both static and dynamic manipulations show perihand space effects, but the relationship between the two manipulations is unknown. The present experiments rely on both static manipulations in the rubber hand illusion and attentional cuing, as well as a dynamic

manipulation in tool use. If there are differences in the mechanisms used in static compared to dynamic perihand representations, that could also attenuate the correlation between tool use and the other two paradigms.

Implications for Physical Ability and Mobility

Balance, mobility, and hand actions are physical abilities that decline with age (Carmeli et al., 2003; Rosano et al., 2007). While this is driven in part by musculoskeletal declines, it is worth considering the role that changes in peripersonal space representations may play. Balance and movement both require multisensory integration. In this dynamic process, sensory information is first integrated and then differentially weighted to take into account the most relevant piece of information at any given point in time and adjust the body accordingly (Jeka, Oie, & Kiemel, 2008). In other words, at any moment visual, proprioceptive, tactile, or vestibular information may be most useful for maintaining a stable posture or moving through the environment, and the dynamic reweighting of information based on utility allows that information to be used most effectively. Thus, it can be presumed that a decline in multisensory integration will adversely affect balance and mobility. There is evidence that this is true for older adults: the process of reweighting sensory information is altered in older adults, but even more so in fall-prone older adults (Jeka, Allison, & Kiemel, 2010). Older adults are simply not as good as young adults at successfully integrating and weighting sensory information to avoid postural instability. Additionally, when training balance control in older adults, it appears that the gains that are made are due to an increase in multisensory integration (Hu & Woollacott, 1994).

In a direct study linking multisensory integration and fall risk, Setti et al. (Setti, Burke, Kenny, & Newell, 2011) found that fall-prone older adults incorrectly integrate visual and auditory information to a greater extent than non-fall-prone older adults. These authors,

mirroring Hu & Woollacott (1994), found that balance training not only improved balance, but also led to more efficient multisensory integration, indicating that there is a relationship between these two factors (Merriman, Whyatt, Setti, Gillian, Young, Ferguson et al., 2012). These studies examined multisensory integration on a larger scale than what occurs within hand space, but the mechanism for integration is the same among these studies and those in the present dissertation. Therefore, it is likely that the declines in multisensory integration found in the three experiments here would also have a relationship with declines in balance and mobility in older adults.

Additionally, the present findings have implications for goal-directed hand movements. Declines in representations of perihand space should have the most direct impact on hand movements such as reaching and grasping, as these actions rely on perihand representations (Filimon et al., 2009). Bloesch et al. (in press) found that older adults relied on an attentional reference frame centered on the trunk instead of on the hand (unlike young adults), and that this altered their pattern of goal-directed reaching. If older adults prioritize objects in the environment based on a reference frame other than the location relative to their hands, that has the potential to profoundly impact interaction. Many daily actions are based on what should be relatively simple hand movements, from cooking to bathing to taking medication. These are the types of hand actions that may be compromised because of changing perihand representations in the elderly.

Finally, the present study can impact our understanding of the use of mobility aides in the elderly. Older adults may rely on canes and walkers to traverse the environment, but there is not much research concerning older adults' ability to incorporate these aides into their body representations. When young adults use a tool, multisensory integration shifts from the hands to the distal end of the tool as the perihand representation expands to include the tool length

(Holmes, Spence, Hansen, Mackay, Calvert, 2008). This expansion of the space in which multisensory integration can occur allows for a more precise use of the tool. Experiment 2 in the current dissertation found that older adults do not extend perihand space to include the length of a tool, meaning that multisensory integration cannot occur at the end of the tool. If integration is not occurring along the tool length, or even just at the end of the tool, older adults are getting less accurate information about where in space their mobility aide is located. If this is the case, this would present a further challenge in the use of a walker or cane in addition to the physical limitation that initially prompted its use. Further research will need to be done to evaluate the interaction of perihand space and mobility devices for older adults.

Conclusions

The results of the present dissertation provide further evidence that older adults have altered or degraded perihand representations relative to young adults. This impacts basic cognitive functioning such as attention and perception across a variety of tasks. Surprisingly, the three paradigms tested did not exhibit a performance relationship, suggesting that it may be the case that tasks purporting to test perihand space are in fact tapping different aspects of this construct. Further research should elucidate these differences, as well as their contributions to mobility and physical functioning during aging.

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Appendix 1.

HEALTH QUESTIONNAIRE

ID _____ (For Researcher Use Only)

Age _____ Gender _____ Race _____ Height _____ Weight _____

Education years completed _____ Highest degree earned _____

Item #	Bold = Screen Out if “Yes”	Yes	No
1	Do you have high blood pressure? 1a. If yes, do you take medication to control it? Name of medication(s) _____ 1b. Number of years you have been taking medication for high blood pressure _____ 1c. Has anyone in your immediate family been diagnosed with hypertension? If so, whom? _____		
2	a) Have you ever been told of a heart problem? b) If yes, what specific problem? _____		
3	Have you ever had open heart surgery?		
4	Do you have a family history of heart problems?		
5	Have you had a head injury with loss of consciousness for more than 5 minutes?		
6	6a. Do you get regular exercise? 6b. If yes, how many days each week? _____		
7	7a. Do you have arthritis (rheumatism)? If yes, indicate how severe your arthritis is Severe Moderate to Severe Moderate Mild 7b. Do you have full use of your shoulders and arms? 7c. Are you right-handed?		
8	Do you have glaucoma?		
9	Do you have cataracts?		
10	Do you have macular degeneration?		
11	16a. Do you use a hearing aid? 16b. If so, do you still have trouble hearing with the aid? Yes _____ No _____		
12	Have you ever suffered a stroke?		
13	Have you ever suffered a TIA (transient ischemic attack)?		

		Yes	No
14	Have you ever had convulsions (seizure)? If yes, were you given any medication? Yes_____ No_____		
15	Do you have Parkinson's disease?		
16	Do you suffer from Huntington's disease?		
17	Do you suffer from multiple sclerosis?		
18	Have you ever had encephalitis or meningitis?		
19	Have you ever had brain surgery?		
20	Have you ever undergone surgery to clear arteries to the brain?		
21	Have you ever been diagnosed with brain tumor?		
22	34a. Do you have diabetes (sugar disease)? 34b. If so, do you have to take insulin? Yes_____ No_____ 34c. Do you have diabetic retinopathy? Yes_____ No_____		
23	Have you ever had cancer (other than skin)? If yes, what kind? _____		
24	Have you ever had problems with your thyroid?		
25	Are you receiving kidney dialysis?		
26	Do you suffer from liver disease?		
27	Have you ever been treated for alcohol or other drug abuse?		
28	Do you usually take three or more alcoholic drinks a day?		
29	Have you ever been diagnosed with peripheral neuropathy?		
30	Have you ever been unconscious for more than 1 hour during surgery?		
31	Have you ever been diagnosed with a mental or emotional illness?		
32	Have you ever been hospitalized with mental or emotional problems?		
33	Have you ever received electroshock therapy?		

Appendix 2.

Demographics Questionnaire

What is your age? _____

Gender (circle one): Female Male

Ethnicity/Race:

1. African/ African American
2. Asian/ Asian American
3. Caucasian/ European American
4. Hispanic/ Hispanic American
5. Native American
6. Other _____

Education (in years) _____