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Age differences in hemispheric asymmetry: An investigation using dichotic listening, tactile, and visual hemifield memory tests.

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AGE DIFFERENCES IN HEMISPHERIC ASYMMETRY: AN INVESTIGATION USING DICHOTIC LISTENING, TACTILE, AND VISUAL HEMIFIELD MEMORY TESTS

by

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ABSTRACT

Age differences in hemispheric asymmetry were investigated by using lateralization memory tasks in different sensory modalities in order to examine current theories of aging and hemispheric asymmetry. Participants included 45 young and 16 older right-handed adults. In the auditory domain, participants were dichotically presented with two different word lists simultaneously and asked to pay attention to and memorize only the list presented to one ear. Then, an immediate and a delayed recognition test were given. The test was repeated with the other ear using new word lists. In the visual domain, participants were asked to memorize the visual stimuli that were presented either to their left or right visual field. Then, an immediate and a delayed recognition test were given. In the tactile domain, participants were instructed to feel and memorize textures that were presented to one hand only. Following the presentation, an immediate and a delayed recognition test were given. The test was repeated using the other hand and a new set of stimuli. Results showed a greater right ear advantage in the older group compared to the younger group on the dichotic listening memory task but age-related changes in asymmetry were not found on the other tasks. In addition, an age-related decline in recognition memory was found on the dichotic listening and tactile tasks. The findings of the study did not consistently support the current theories of aging and hemispheric asymmetry.

DEDICATION

This dissertation is dedicated to my grandmother, Im Hi Choi, whose two wishes were to see me accomplish two things while she was still with us: walk down the aisle and obtain my Ph.D. degree. She passed away on November 12, 2005, a few months before my wedding day, and less than a year before the completion of my Ph.D. studies.

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Finally, I extend a very special thanks to my mother, whose unconditional love, faith, and support have made the completion of graduate studies possible and enjoyable, and to my life partner, Michael Kim, who makes my life much brighter.

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CAT	computerized axial tomography
cm	centimetre
dB	decibel
EEG	electroencephalogram
ERP	event related potentials
DLMT	Dichotic Listening Memory Test
fMRI	functional magnetic resonance imaging
HAROLD	hemispheric asymmetry reduction in old adults
Hz	hertz
LEA	left ear advantage
LGN	lateral geniculate nucleus
LH	left hemisphere
M	mean
mm	millimetre
ms	millisecond
MMSE	Mini Mental State Exam
MRI	magnetic resonance imaging
PET	positron emission tomography
REA	right ear advantage
RH	right hemisphere
TRMT	Tactile Recognition Memory Test
VHMT	Visual Hemifield Memory Test

WMS-III	Wechsler Memory Scale – Third Edition
WRAT-3	Wide Range Achievement Test – Third Edition

1.0 Introduction

1.1 General

It is well known that the two cerebral hemispheres are anatomically and functionally different. This is supported by abundant converging evidence from in vivo and post-mortem research in neuroanatomy, neurochemistry, neuropsychology, and neuroimaging. There is also evidence that these asymmetries are affected by conditions that alter the anatomical and functional integrity of the brain, such as brain damage and aging. The present study examines theories of hemispheric asymmetry and aging using novel memory tasks developed to assess cognitive asymmetry in three different sensory modalities, namely, auditory, tactile, and visual domains.

1.2 History

In 1836, Marc Dax presented a short paper at a medical society meeting in France (Finger & Roe, 1996). He had worked as a physician for many years and had seen many patients suffering from aphasia. Although this observation was not new, Dax was the first one to discover an association between loss of speech and the side of the brain where the damage had occurred: In more than 40 patients with aphasia, the damage was always on the left. He concluded that each hemisphere of the brain controls different functions and that speech is controlled by the left hemisphere (LH). However, this paper aroused little interest at the meeting and it was soon forgotten (Finger & Roe, 1996). It was not until Broca's demonstration in 1861 that the concept of cerebral dominance (i.e., one side of the brain is more important for certain functions than the other side) began to gain acceptance.

In 1861, Paul Broca met a patient named Leborgne (also known as Tan) in a hospital at Bîcetre (Benjamin, 1997). Broca found that the man lost his ability to speak at the age of 30 and about a decade later the right side of his body started to become paralyzed. When the patient died, Broca studied his brain and its lesions. He concluded that there were two periods, one in which the third frontal convolution was damaged, and another period in which the disease gradually spread toward other regions of the brain. These periods corresponded to the progression of the symptoms: The first period lasted ten years, during which only speech was abolished. In the second period of eleven years, right side paralysis occurred. Broca concluded that language ability is located in the LH and suggested that the two hemispheres had different functions.

Since the work of Dax and Broca, it had been recognized that damage to the LH produces disturbances of language function, whereas damage to the right hemisphere (RH) usually does not grossly affect language functions. In 1868, John Hughlings Jackson proposed his idea of the "leading" hemisphere, arguing that in most people the left side of the brain was the leading side (Springer & Deutsch, 1993). From then on, the LH was believed to be dominant not only for language but for other higher cognitive functions as well. The RH was often referred to as the "nondominant" hemisphere. Interestingly, it was also Jackson who argued that this one-sided view of the way brain functions were organized was wrong after observing a patient with visuospatial difficulty following a RH tumour. Although other similar reports began to appear, researchers were more interested in localizing various functions within the LH. Until the 1960s, the view that the RH might have its own special capabilities was not given wide support, but as evidence accumulated, the concept of cerebral dominance was replaced by the concept of hemispheric specialization or hemispheric asymmetry of functions, which emphasized that each hemisphere has its own distinct functions (Bogen, 1969; Davidson & Hugdahl, 1995; Hellige, 1993).

1.3 Methods of Measurement

Hemispheric asymmetry research has benefited from a variety of techniques that can be used to make inferences about the role of each cerebral hemisphere. Some techniques, such as dichotic-listening tests for auditory functions, tactile tests for somatosensory functions, and visual hemifield presentations for visual functions are inexpensive and easy to manufacture and apply, and therefore, available to any interested researcher (Bryden, 1982). Neuropsychological tests used to test verbal and "nonverbal" functions are also easily accessible in both research and clinical settings. In contrast, other techniques such as event-related potentials (ERPs), computerized axial tomography (CAT), positron emission tomography (PET), and magnetic resonance imaging (MRI) are not as accessible because of their high cost (Hellige, 1993). In this section, various techniques used in hemispheric asymmetry research are reviewed.

1.3.1 Auditory Tasks

The auditory system may be divided into five separate relay stations (Bryden, 1982). An auditory stimulus activates neurons in the cochlear nucleus. Among the subdivisions of the cochlear nucleus, the ventral acoustic stria enters the second level, the superior olivary complex. From there, both inhibitory and excitatory impulses are projected to the dorsal and ventral nuclei of the lateral lemniscus, which make up the third-level relay station. Up to the level of the nuclei of the lateral lemniscus, the auditory system projects bilaterally. However, from the nuclei of the lateral lemniscus, projections are mainly contralateral, projecting to the fourth relay station, the inferior colliculus in the tectum. The contralateral fibres then innervate the medial geniculate body in the pulvinar of the thalamus, which is the fifth relay station, sending its axons to neurons in the auditory cortex in the posterior superior temporal gyrus (Blumenfeld, 2002; Bryden, 1982). Therefore, although auditory signals from one ear reach both auditory cortices in the temporal lobes, the contralateral projections are stronger and predominant. This ultimately favours representation of the contralateral ear in the auditory cortex.

The primary test used to study functional hemispheric asymmetry in the auditory system in both brain-damaged and normal individuals is the dichotic-listening task (Jäncke & Shah, 2002; Kimura, 1961a, b). Initially, it was Broadbent (1954) who developed the dichotic-listening technique to simulate the attentional load experienced by air traffic controllers when receiving information from multiple flights simultaneously. However, it was Kimura who adapted this task for the study of hemisphere function and popularized it in the field of hemispheric asymmetry. The method is variable but generally involves the simultaneous presentation of two different and competing auditory signals to the ears. In 1961, Kimura published two papers that demonstrated a clear relation between speech lateralization and performance on a dichotic-listening task. In her studies, the procedure involved the presentation of short lists of numbers, arranged so some numbers came to the left ear while others came to the right ear simultaneously (Kimura, 1961 a, b).

Generally, in dichotic-listening tasks, a right ear advantage (REA), which means superior accuracy reports from the right compared to the left ear, is observed for linguistic processing, reflecting LH specialization, and a left ear advantage (LEA) is observed for some forms of nonlinguistic processing, reflecting RH specialization (Bryden, 1982). The direction of the ear advantage depends on the task, and not on the nature of the stimulus itself. For example, when messages are presented in different emotional tones of voice, a REA is observed when attending to linguistic content, but a LEA is observed when attending to the tone of voice or emotional prosody (Bryden & MacRae, 1988; Ley & Bryden, 1982).

Kimura (1967) argued that the REA for verbal stimuli or linguistic content is caused by several interacting factors. First, the auditory input to the contralateral hemisphere is more strongly represented in the cortex. Second, auditory information that is sent along the ipsilateral pathways is suppressed by the contralateral information. Third, the LH is specialized for language processing, so information that reaches the ipsilateral RH has to be transferred across the corpus callosum to the LH language-processing areas.

Until a few years ago, the brain structures involved in the dichotic-listening task were thought to be the temporal lobes following Kimura's (1961b) finding that temporal lobe excision resulted in a decrease in performance on the ear contralateral to the removal. However, using functional MRI (fMRI), Jäncke and Shah (2002) recently demonstrated that additional brain regions are involved during the task. When 10 right-handed, normal participants listened to consonant-vowel syllable pairs to detect a target syllable, they were asked to either concentrate on the stimuli presented in both ears, only in the left ear, or only in the right. They found general activations in fronto-temporal networks during all conditions of the dichotic-listening task. When participants were asked to attend to stimuli presented to both ears, strong bilateral activity was observed in the inferior frontal gyrus, Broca's area, the left middle frontal, and in the left superior temporal gyrus. When participants were asked to concentrate on stimuli presented to the left ear, additional activity in the right inferior frontal gyrus was observed and when participants attended to the right ear, stronger activations in Broca's area and the left superior temporal gyrus were observed. This study showed that the frontal lobes, as well as the temporal lobes, play a crucial role during the dichotic-listening task.

In sum, Kimura's findings offered the field of neuropsychology an exciting opportunity to assess hemispheric specialization for speech in neurologically healthy individuals as well as in brain-damaged individuals. Researchers are now including other techniques such as fMRI to discover other neural structures that are involved during the task.

1.3.2 Tactile Tasks

Although many studies have used dichotic-listening procedures, relatively few have used somatosensory or tactile procedures to study hemispheric specialization. In the somatosensory system, the ascending sensory fibres from the skin and joints cross the midline and project to the postcentral gyrus of the opposite hemisphere. There is also sensory representation in the precentral gyrus (the primary motor cortex).

In addition, both ipsilateral and contralateral sides of the body are represented in each hemisphere in the secondary sensory area along the superior border of the Sylvian fissure in the parietal cortex. There is also evidence for bilateral representation of the lower part of the face area in the postcentral region. Therefore, despite the general assumption that the somatosensory system is completely crossed, evidence indicates that some information is projected via ipsilateral pathways (Bryden, 1982; Penfield & Rasmussen, 1950).

Nevertheless, the predominantly crossed representation of the somatosensory system would lead one to expect right-side (i.e., LH) advantages for verbal tasks and left-side (i.e., RH) advantages for nonverbal tasks. Although the anatomical situation is relatively simple, tactile stimuli are difficult to construct and control, and this seems to be one of the reasons that there are so few studies in this modality (Bryden, 1982). Once the researcher determines which stimuli to use, the task can be designed in two ways. One procedure is to stimulate one hand at a time (i.e., unimanual) and the other is to stimulate both hands simultaneously (i.e., bimanual). Some researchers reported differences between the two tasks. For example, Minami, Hay, Bryden, and Free (1994) studied laterality effects in the discrimination of tactile patterns presented to the fingertips of right-handed participants. A small right-hand advantage was observed for a sequential task and a small left-hand advantage was noticed for a spatial task when both hands were stimulated at the same time. On unimanual tasks, no laterality effects were observed with sequential tasks, but a right-hand advantage was found for a spatial task. The researchers concluded that there were differences between bimanual and unimanual presentations and that the effects related to hemispheric specialization were more evident with simultaneous presentation of stimuli to both hands.

However, many studies have found greater sensitivity in the left hand regardless of type of task (Benton, Levin, & Varney, 1973; Dodds, 1978; Koenig, 1987). Using a unimanual task, Benton et al. (1973) examined tactile perception of the direction of linear punctate stimulation of brief duration on the palms of the right and left hands of right-handed normal participants and found a left-hand advantage. Dodds (1978) also found a left-hand advantage using a tactual recognition task using six random forms presented in various orientations. Harris (1980) reviewed evidence for left-hand superiority in recognizing Braille characters in normal participants unfamiliar with these shapes. Using a bimanual method, Koenig (1987) had right-handed, male participants palpate two different artificially created textures consisting of 0.5 mm high components simultaneously with the index and middle finger of each hand. Then the participant was asked to respond orally by giving the two texture numbers from the visual board that corresponded to the two stimuli just palpated. The results indicated a left-hand advantage. Although these studies found a left-hand advantage, it is unclear whether this was due to the stimuli characteristics that are predominantly processed by the RH such as shape and orientation, or the possible RH specialization in processing tactile stimuli. Therefore, further research is necessary to determine each hemisphere's contribution to tactile perception and processing.

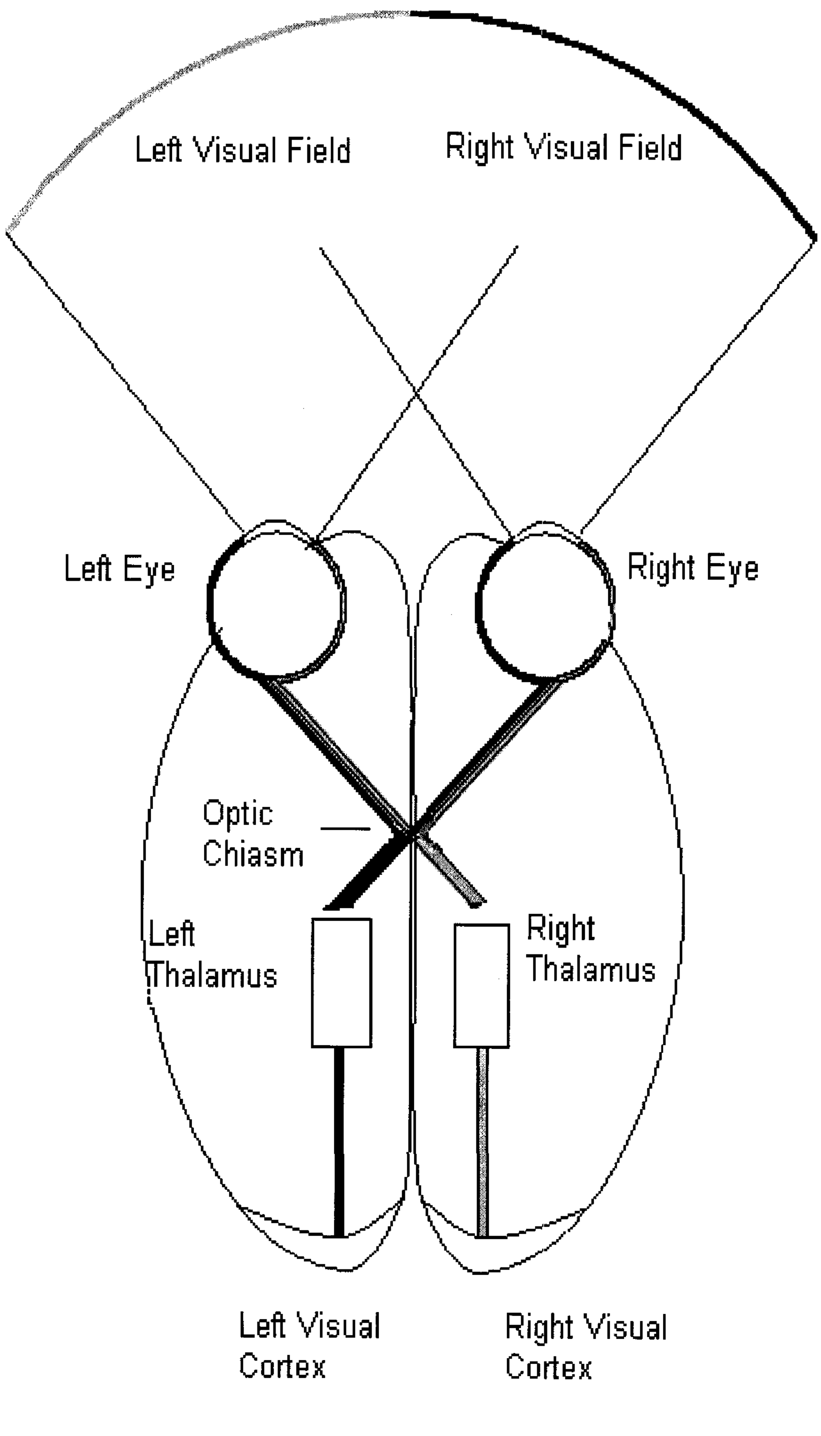
1.3.3 Visual Tasks

Kimura's (1961a, b) work with a verbal dichotic-listening task prompted others to extend her logic to visual paradigms (Cherry, Hellige, & McDowd, 1995; Elias & Kinsbourne, 1974; Nebes, Madden, & Berg, 1983; Obler, Woodward, & Albert, 1984). However, the anatomy and functioning of the visual system are sufficiently different from those of the auditory system to make a completely analogous procedure difficult to achieve. In the visual modality, the left half of each retina sends its ascending fibers to the left visual cortex, and the right half of each retina sends its fibers to the right visual cortex (see Figure 1). This means that the image of objects lying to the right of the line of sight for either eye is transmitted to the left cortex, while that lying on the left of the line of sight pass to the right visual cortex (Kolb & Whishaw, 1996).

In order to ensure that the task is adequately analogous to the dichotic-listening task, one must present material lateralized to one visual field or the other, not to one eye or the other (Bryden, 1982). In addition, when one designs lateralizing stimuli, it is not simply a matter of presenting stimuli to one side or the other of the line of sight. The eyes are constantly in motion, shifting from one location to another; therefore, some control must be applied over this. One method that was often used in the past was to fix the image of the target on the retina so that when the eyes moved, the target moved with them. This was accomplished either through the use of a contact lens system (Pritchard, Heron, & Hebb, 1960) or through the use of a prolonged after-image (MacKinnon, Forde, & Piggins, 1969). However, these techniques are now rarely used to study perceptual asymmetries because of the associated technical problems (Bryden, 1982). The more contemporary approach is to present the stimuli briefly so that the eyes do not have the time to move from one location to another during the exposure. It takes approximately 180 ms to initiate a saccadic eye movement to move the eyes to a new fixation point (Hugdahl, 1996; Woodworth, 1938). However, when the participant does not know which of two locations will be stimulated, it may take up to 300 ms to initiate an eye movement (Bryden, 1982).

The major finding with the visual half-field technique is a right visual field (i.e., LH) preference for word recognition, when words and nonwords are briefly flashed on the screen (Boles, 1994; Cherry et al., 1995; Kimura, 1966). Better performance for left

Figure 1. A diagrammatic representation of the visual system pathway (Adapted from: Bednar, 1997)



field presentations is seen for visuospatial tasks, like shape and form identification, and face processing (Boles, 1994; Cherry et al., 1995; Kimura, 1966; McKeever, 1986). For example, Kimura reported that normal individuals identified letters presented to the right visual field more accurately than the ones presented to the left visual field but that non-alphabetic stimuli (forms and dots) were better recognized in the left visual field. These results were consistent with the view that the RH plays a dominant role in processing visual stimuli compared to the LH.

1.3.4 Localized Brain Activity Measures

Currently, new methods allow the *in vivo* comparison of the hemispheres in both healthy individuals and patients, at both anatomical and functional levels. A variety of electrophysiological measures are the oldest and still commonly used techniques to study brain activity. Electroencephalograms (EEGs) and measures of ERPs are the two most popular techniques. The EEG is a continuous recording of electrical activity from which the ongoing activity is broken down into several frequency ranges. The frequency of greatest interest is usually 8 to 12 Hz (the alpha frequency); suppression of activity in the alpha range is thought to reflect ongoing processing. EEG studies have shown greater suppression in alpha activity over the LH than the RH during a variety of verbal tasks and the opposite has been found for certain nonverbal tasks (e.g., spatial or musical tasks; Davidson & Schwartz, 1977; Galin & Ornstein, 1972; Morgan, McDonald, & McDonald, 1971). The ERP is a recording, time-locked to a particular stimulus event. The electrical responses to several repetitions of the stimulus event are averaged and the resulting average ERP is examined for the magnitude and latency of various positive and negative shifts in electrical potential.

With both of these techniques, electrodes are placed at various sites on the scalp and the results from different recording sites are compared. When the goal is to study hemispheric asymmetry, differences between the electrical activity are measured at homologous sites on the two sides of the scalp.

Auditory evoked potentials are a subclass of ERPs. As the name suggests, the "event" is an auditory stimulus in this method. Researchers have conducted a number of experiments recording auditory evoked potentials from the LH and RH of participants (Molfese, Freeman, & Palermo, 1975; Molfese, 1978; Molfese, 1984). They consistently found that the LH auditory evoked potentials to speech stimuli were larger in amplitude compared to the RH potentials, whereas non-speech stimuli produced an opposite pattern.

An advantage of these electrical measures is that they have excellent temporal resolution (e.g. ERPs resolve the dynamic pattern of events in the human brain down to the millisecond range; Brandeis & Lehman, 1986), but they have poor spatial resolution (they might localize activity with a resolution of a few inches). Other techniques such as CAT scans, MRI, and angiograms offer better spatial resolution (1-2 mm) but much lower temporal resolution (ranging from approximately 30 seconds to over 30 minutes). Such techniques are useful for studying morphological asymmetries in the brain but are not able to provide a dynamic picture of how activation changes during task performance (Brandeis & Lehman, 1986).

However, methods such as PET and fMRI, can provide dynamic pictures by measuring regional cerebral blood flow (Beason-Held, Golski, Draut, Esposito, & Resnick, 2005; Jäncke & Shah, 2002). When a particular area of the brain has been metabolically active, localized increases in carbon dioxide lead to a dilation of blood vessels serving that area. As a consequence, blood flow is increased to that area. Now that there are techniques to measure the relative amounts of blood flow to localized brain areas, it is possible to determine how the regions of greater activation change with differences in task demand. As noted earlier, depending on the specific technology employed, a participant must engage in the same task for anywhere from 30 seconds to several minutes in order for the measures to be taken, and this requirement places limits on the types of tasks that can be used and the inferences that can be drawn (Wood, Flowers, & Naylor, 1991). In general, during verbal tasks, regional cerebral blood flow has been found to be greater for specific areas of the LH than for homologous areas of the RH (Kelley et al., 1998; Posner, Petersen, Fox, & Raichle, 1988).

Additional techniques are sometimes used to study hemispheric asymmetry. One example is the Wada or sodium amytal test (Wada & Rasmussen, 1960). In the Wada procedure, sodium amytal is injected unilaterally into the carotid artery. The carotid artery on each side provides the blood supply to the ipsilateral hemisphere. This technique is used prior to certain types of neurosurgery to identify which hemisphere in a particular patient is dominant for language and/or to assess memory functioning in each hemisphere (Loring et al., 1990). Research using this technique suggests that the LH is dominant for speech in 90-95 percent of right-handed adults (Rasmussen & Milner, 1975).

Various research strategies and techniques enable researchers to examine hemispheric asymmetry. From this brief review of research methods, it is apparent that no single approach can provide a complete picture of hemispheric asymmetry and function. With this in mind, the strongest findings will emerge when a number of different techniques are used in combination to examine the same issues and converging evidence is found.

1.4 Participant Populations

1.4.1 Patients with Unilateral Lesions

Some of the strongest evidence of cerebral lateralization comes from studies of individuals with brain damage (Bohbot et al., 1998; Boll, 1974; Fontenot & Benton, 1971; Hough, 1990; Rubino, 1970). Studies of unilateral brain damage can be useful because if damage to the LH produces a different effect than damage to the RH, then one can relate the behaviour to functional cerebral asymmetry.

Before the unilateral lesion studies are reviewed, several methodological issues must be considered: 1) it is extremely unlikely that a brain lesion will destroy a single functional system without intruding on other functionally separate systems or disrupting the connections between them; 2) one must recognize that the brain-injured patient may use quite a different strategy for carrying out a task than does a normal individual; 3) it is often not possible to obtain premorbid measures of performance, so one cannot be certain about the effects of a particular surgery; and 4) it is difficult to draw inferences regarding structure-function relations in healthy individuals given that most patients with unilateral lesions used in many studies had long-standing epilepsy that might have altered hemispheric organization (Hellige, 1993; Springer & Deutsch, 1993).

Researchers have discovered hemispheric specialization for processing various stimuli from studying individuals with unilateral lesions. Fontenot and Benton (1971) compared right-handed patients with lesions of the RH or LH to a control group of patients without cerebral lesions on a task involving the perception of the direction of tactile stimulation applied to the palms of the hands. Whereas patients with lesions of the LH showed significant impairment only on the right hand, bilateral impairment in patients with lesions of the RH was observed. In the control group, there was no difference apparent in the accuracy of tactile perception of direction between the left and right hands. As a result of this investigation, the researchers concluded that the RH played an important role in mediating spatial perception in the tactile domain. However, Fontenot and Benton also noted that the results should be interpreted with caution because they used a tactile-visual matching procedure to assess the tactile perception of direction, and therefore, the cross-modal nature of the task may have played a part in the finding of bilateral impairment in patients with RH lesions. Indeed, cross-modal performance has been found to be poorer than intra-modal performance (Garbin, 1988; Picard, 2006). That is, more errors likely occur when the information acquired in one modality is tested in another modality (e.g. touch to vision).

Similar results were found in Boll's study (1974). Three tests of tactile-perceptual ability commonly used in neuropsychological practice (Tactile Finger Localization, Finger-tip Number Writing Perception, and Tactile Form Recognition) were administered to 30 participants with RH lesions and 30 participants with LH lesions. The results showed that patients with RH damage were more impaired on the contralateral and ipsilateral sides of the body than were patients with lesions of the LH. Total errors were also greater in the RH group than in the LH group. This study suggests that the RH plays a greater role than the LH in producing tactile-perceptual deficits in patients with brain lesions.

The study of patients with specified lesions in the LH or RH may yield valuable insights into the functional basis of side advantages in various tasks. For example, unilateral medial temporal lobe damage yields material-specific impairments. Extensive damage to the right medial temporal region, including the hippocampus, impairs spatial memory whereas similar damage in the LH impairs verbal memory (Milner, 1965; Smith & Milner, 1989). Smith and Milner found that patients with left or right temporal lobe excisions performed as well as control participants when asked to recall the location of 16 objects immediately after presentation. However, the patients with right temporal excisions including extensive resections of the hippocampal region were impaired after a 4-minute delay. These results suggest that patients with right hippocampal region lesions were able to encode the spatial location of the objects, but they could not retain the information compared to patients with left temporal lesions, patients with smaller right hippocampal region lesions, and normal controls.

Rubino (1970) selected two types of material (nonsense words and nonsense figures) to present to three groups of participants: patients with left temporal lobe lesions; patients with right temporal lobe lesions; and normal participants. The participants with left temporal lesion displayed a deficit in the identification of the words and the participants with right temporal lesion showed a deficit in the identification of the figures. Both groups performed worse on both tasks compared to the normal group.

The effects of selective damage to medial temporal lobe structures can also be examined. Bohbot et al. (1998) investigated patients with unilateral lesions of various medial temporal lobe structures on spatial tasks (invisible sensor task, eight-arm radial maze task) and non-spatial working memory tasks. In addition, the patients were assessed with a complex visuo-spatial memory task (Rey-Osterrieth Figure) and a word-list learning task (Rey Auditory Verbal Learning Test). The patients had undergone thermo-coagulation with a single electrode along the amygdalo-hippocampal axis to alleviate their epilepsy. With this surgical technique, lesions to single medial temporal lobe structures can be carried out and the precise location of the lesion can be confirmed with MRI. The patients were classified into two groups: those with lesions involving the hippocampus without damage to the parahippocampal cortex, and those with damage to the parahippocampal cortex. One of the main cortical inputs to the hippocampus comes via the parahippocampal cortex. Thus, if lesions outside the hippocampus block inputs to the hippocampus, this could result in a functional hippocampal lesion (Van Hoesen, 1982). The results indicated that the right hippocampus was important for visual-spatial memory tasks (object location, Rey-Osterrieth Figure immediate and delayed recall) and the left hippocampus was important for verbal episodic memory tasks (Rey Auditory Verbal Learning Test delayed recall). Patients with lesions either to the right or to the left hippocampus were unimpaired on several memory tasks, including the invisible sensor task. However, patients with lesions to the right parahippocampal cortex were impaired on this task, suggesting that the parahippocampal cortex plays a crucial role in spatial memory.

The effects of unilateral frontal lobe lesions have been investigated as well. Hugdahl, Bodner, Weiss, and Benke (2003) examined perception of consonant-vowel syllables in patients with left or right frontal lobe lesions and in normal controls. Consonant-vowel syllables were dichotically presented and the participants were asked to respond by verbally indicating or pointing to the syllables on a response sheet. The patients with right frontal lesions as well as the controls showed a REA of the same magnitude although the overall performance was lower in the right frontal lesion group compared to the controls. Patients with left frontal lesions showed no ear advantage at all, and their right ear scores were impaired compared to both the control group and the right frontal lesion patient group. The researchers concluded that dichotic-listening tasks tap into a neuronal circuitry that involves the frontal lobes and that the frontal lobes serve an important function in speech perception. As such, they added that dichotic-listening tests may not test temporal lobe functions exclusively. Their results are consistent with the findings from Jäncke and Shah's (2002) fMRI study using normal participants.

1.4.2 Split-brain Patients

The split-brain patient provides a unique opportunity for exploring the function of each hemisphere. The term split-brain denotes complete sectioning of the corpus callosum, including anterior commissure, dorsal and ventral hippocampal commissures, and in some cases, the massa intermedia (Gazzaniga, 1970). Commissurotomies are performed on patients for the relief of severe, intractable epilepsy to prevent the spread of seizures across the brain. The inclusion of these patients in hemispheric lateralization research is based on the fact that each hemisphere is most strongly associated with the opposite half of the body (Bouma, 1990). If the isolated LH can perform a certain task but the isolated RH cannot, then there is good evidence that the LH is important for performance on the specified task (Gazzaniga, 1970).

However, similar to research involving individuals with unilateral lesions, there are problems of interpretation associated with the findings of split-brain research (Bouma, 1990). First, the nature of the patient sample must be kept in mind. They are usually few in number and they vary greatly in age at the time of original brain damage, age at operation, and the etiology, severity, and location of lesion. Also, most had severe and longstanding epilepsy, and are unlikely to have had normal brain functioning prior to surgery. Furthermore, early brain damage may also lead to abnormal functioning, development, and/or reorganization of functions. Second, commissurotomy itself may lead to certain cognitive disturbances. Often, the operation is followed by a general impairment of memory. Not surprisingly, patients show greater difficulty learning to associate names with faces after surgery and they are severely impaired in performing new movements that require interdependent regulation of speed and timing between the left and the right hand. Finally, functioning of the hemispheres may be different from that in normal individuals. In the normal brain, the hemispheres communicate with each other and it is possible that activity in one hemisphere inhibits activity in the corresponding region in the other hemisphere. For example, it has been suggested that in normal individuals, the language capacities of the RH are inhibited by those in the LH (Bouma, 1990; Moscovitch, 1976). Therefore, these factors must be kept in mind when interpreting hemispheric specialization for various tasks in this patient sample.

Researchers have found that specific classes of verbal stimuli (i.e., consonant-vowel syllables versus digits) elicit various degrees of asymmetry in split-brain patients. Springer, Sidtis, Wilson, and Gazzaniga (1978) studied the contribution of left ear stimuli to dichotic-listening performance in five right-handed, male patients following commissurotomy. Patients were asked to identify in writing both members of a pair of competing stimuli, either digits or consonant-vowel syllables. Dichotically presented consonant-vowel syllables showed a substantial REA for each patient, whereas the ear asymmetry with digits as stimuli was considerably reduced. That is, in four out of five cases, the report of digits presented to the left ear was over 80 percent correct. The results suggest that there are differences in types of speech stimuli and their respective degree of ipsilateral inhibition. Indeed, a more recent study using normal individuals indicated low correlations among verbal stimuli (Jäncke, Steinmetz, & Volkman, 1992).

Researchers have also explored hemispheric specialization by administering nonverbal tasks to individuals with commissurotomy. Milner and Taylor (1972) tested 7 commissurotomized patients and 10 neurological patients with intact commissures as controls on a delayed matching of tactile pattern task. The patients were required to feel an irregular wire shape carefully with one hand and then, after a short delay, to select that shape again by touch only from a set of four similar ones. The results showed that left-hand performance was superior to right in commissurotomized patients, thus demonstrating RH specialization for the perception and recognition of nonsense wire shapes. There was no difference in performance between the two hands in the control group. These results suggest that both cerebral hemispheres normally participate in such tasks, but the RH plays a predominant role.

Some patients undergo a partial commissurotomy, in which a portion of the corpus callosum is spared. Kumar (1977) studied short-term memory for a tactual task in patients with complete and partial commissurotomy. Four of the patients had complete cerebral commissurotomy for treatment of epilepsy and two patients had the same procedure except that the posterior portion (splenium) of the corpus callosum was spared. They used a test in which the participant felt designs and then reproduced them by drawing with the same hand immediately following the stimulus presentation. In the patients with complete commissurotomy, the left hand produced fewer errors compared to the right hand. In the patients with partial commissurotomy, there was no difference between the right and left-hand performance suggesting that the splenium of the corpus callosum plays an important role in coordinating interaction between the two hemispheres.

In general, research with split-brain patients has increased our understanding of functional lateralization. Research shows that although complex linguistic functions are mainly served by the LH (Dean & Hua, 1982; Kimura, 1961a; Sperry, 1968), the type of verbal stimuli affects the degree of involvement in each hemisphere (Springer et al., 1978). In addition, although nonverbal functions are predominantly linked to the RH, evidence from comparison studies of patients with commissurotomy versus non-commissurotomized individuals shows that both cerebral hemispheres normally participate in nonverbal tasks (Kumar, 1977; Milner & Taylor, 1972).

1.4.3 Neurologically Normal Individuals

Initially, hemispheric specialization research mainly examined brain-damaged patients and/or postmortem brains, raising questions about extending these findings to healthy individuals. Starting in the 1980s, hemispheric asymmetry research using "normal" individuals began to flourish (Bryden, 1982; Cherry et al., 1995; Hellige, 1993). The methods used to assess hemispheric asymmetry in neurologically intact individuals are generally the same as the ones used to assess the function of the LH and RH in individuals with brain damage. Perceptual asymmetries observed between the left and right side and verbal and nonverbal performance discrepancies are assumed to reflect functional differences between the hemispheres for a particular task. However, one should be cautious when interpreting data obtained from lateralization tasks. Evidence from studies of brain damage and sodium amytal procedures indicate that 96 percent of right-handers have speech represented in the LH (Rasmussen & Milner, 1977; Segalowitz & Bryden, 1983) but only about 75 -85 percent of normal right-handed participants show a REA in verbal dichotic-listening tasks (Bryden, 1982). This shows that the results obtained from brain-damaged versus normal individuals using different procedures are not perfectly correlated. Therefore, it is important to consider the possibility that side advantages or performance asymmetries are influenced by other factors which are unrelated to hemispheric asymmetry (Bryden, 1982).

1.5 Biological Asymmetries

1.5.1 Neuroanatomical Asymmetries

Investigations of anatomical asymmetries began in the 19th century (Finger & Roe, 1996). However, the field did not gain widespread attention from researchers until the 1960s (Geschwind & Levitsky, 1968; McRae, Branch, & Milner, 1968). In most human brains, the frontal region of the RH is wider and protrudes further forward than the LH but the occipital region of the LH is wider and protrudes further backward compared to the RH (Bradshaw & Nettleton, 1983). In addition, there seems to be a difference in the grey matter to white matter ratio between the two hemispheres. Gur et al. (1980) found more grey matter relative to white matter in the LH than in the RH, particularly in the frontal (including precentral regions) and suggested that the organization of the LH emphasized processing or transfer within regions rather than transfer across regions compared to the RH.

However, the most evident and studied anatomical asymmetry of the brain is the planum temporale, which is a small triangularly shaped area located immediately posterior to Heschl's gyrus and the primary auditory cortex (in the LH, it is an extension of Wernicke's area; Hughdahl, 1996). Geschwind and Levitsky (1968) studied 100 right-handed adult brains and confirmed the presence of asymmetries in the planum temporale. It was larger on the left sides in 65 percent of the brains, approximately equal in 24 percent, and larger on the right in 11 percent. Geschwind and Levitsky suggested that this asymmetry is an anatomical marker of the specialization of the LH for language. Subsequent review of this same sample of brains using more precise measurements found 63 percent larger on the left, 21 percent on the right, and 16 percent equal (Galaburda, Corsiglia, Rosen, & Sherman, 1987). It is interesting to note that these numbers are closer to the REA observed in dichotic-listening performance in normal right-handed individuals (i.e. 75-85 percent, Bryden, 1982) than evidence of 96 percent LH speech representation in right-handed, brain-damaged individuals from Wada testing (Rasmussen & Milner, 1975).

Asymmetries of planum temporale are associated with asymmetries of the lateral or Sylvian fissure, which is longer on the left than on the right in most brains (Cunningham, 1892). Rubens, Mahowald, and Hutton (1976) reported that the lateral run of the fissure is shorter on the right side, before it turns upward. It turns upward earlier and ends at a higher level on the right than the left side.

Sylvian fissure morphology is associated with an asymmetry of the angles formed by the posterior branches of the middle cerebral arteries as they loop over the fissure, wider on the right than the left in most people (Annett, 2002). This may reflect physiological differences in the perfusion of brain tissue in left and right temporal areas (Galaburda, 1995). Ratcliff, Dila, Taylor, and Milner (1980) examined the asymmetry of the posterior Sylvian branches of the middle cerebral artery by using the carotid angiograms of 59 patients in whom the lateralization of speech representation was known from sodium amytal tests (39 with LH speech, 11 with bilateral speech, and 9 with RH speech). The branches of the middle cerebral artery that leave the posterior part of the Sylvian fissure typically slope more sharply downward on the left side than right, forming a narrower arch. They found asymmetry of these vessels in the group of patients with LH speech representation but a reduced asymmetry in patients with atypical (bilateral or RH speech representation) cerebral dominance for speech.

The use of recent imaging techniques has made the examination of structural-functional relations possible in laterality research. Strauss, LaPointe, Wada, Gaddes, and Kosaka (1985) attempted to link a cognitive measure of language dominance to neuroanatomical asymmetry evidence. These researchers administered a dichotic-listening task to patients with medically refractory seizures. The results of these tests were considered in light of the width of the posterior Sylvian region as revealed through carotid angiograms. The results revealed that neurological patients who show a REA (suggesting LH language dominance) are more likely to have a wider left posterior Sylvian region and patients who show a LEA are more likely to have a wider right posterior Sylvian region. This study shows that it is possible to associate cognitive results with neuroanatomical asymmetry.

Recently, Chiarello, Kacinik, Manowitz, Otto, and Leonard (2004) measured asymmetrical neural structures involved in language functioning (Heschl's gyrus, planum temporale, and planum parietale) using MRI and correlated these findings with visual field lexical task asymmetries in 20 male right-handers. They found task asymmetries to be positively correlated with asymmetry of the planum temporale. They also found a relation between the anatomical and behavioural asymmetries in that the participants with the greatest modal cortical asymmetry across regions were also likely to show the greatest variability in asymmetry across tasks. The authors concluded that individual differences in language laterality tasks may be associated with variation in asymmetry of posterior language structures and the absence of these asymmetries may be coincident with a less strictly localized distribution of function across hemispheres.

1.5.2 Neurochemical Asymmetries

Given that the two hemispheres are anatomically asymmetric, the presence of neurochemical asymmetries would not be surprising. Indeed, some neurotransmitters appear to be more abundant and more utilized in one hemisphere than the other. Oke, Keller, Mefford, and Adams (1978) showed an asymmetry in content of norepinephrine in the thalamus of 5 post-mortem, normal human brains. Specifically, the left pulvinar and the right ventrobasal complex (the area of the thalamus which receives most of the somatosensory input) were richer in norepinephrine than their contralateral counterparts.

Similarly, Amaducci, Sorbi, Albanese, and Gainotti (1981) showed hemispheric differences in choline acetyltransferase activity (an index of acetylcholine activity) in the Brodmann area 22 (Wernicke's area in the LH) in four post-mortem brains of patients who died with non-neurological disorders. The results showed that the left Brodmann area 22 contained greater choline acetyltransferase activity than the same region on the right.

In contrast, Rossor, Garret, and Iversen (1980) had found no asymmetric distribution of neurotransmitters in the human brain. However, Glick, Ross, and Hough (1982) reassessed the data of Rossor et al. and found asymmetric concentration of neurotransmitters. They found higher levels of dopamine and choline acetyltransferase in the left globus pallidus than in the right.

In a review of the evidence on the neurotransmitter substrates of neural systems, Tucker and Williamson (1984) argued that neurotransmitter pathways are lateralized in the human brain. They concluded that dopamine is more abundant in the LH and norepinephrine is more abundant in the RH. Associated with this lateralization, processes dependent on dopamine (e.g. complex motor operation) are more dominant in the LH than in the RH and processes dependent on norepinephrine (e.g. integration of bilateral perceptual input) are more dominant in the RH compared to the LH.

In sum, there are various anatomical and chemical asymmetries present in the human brain and these asymmetries are linked to functional differences in some cases. However, this is more true for anatomical than for neurochemical asymmetries because of a relative paucity of studies examining neurochemistry and function in tandem. Despite this scarcity of research, the available research suggests that generally, dopamine and choline acetyltransferase activity are more abundant in the LH and norepinephrine is more abundant in the RH. However, one should be cautious when summarizing the research findings because handedness information on the individuals from whom the brains were obtained was missing in most of the reviewed studies.

1.6 Individual Differences

Most of the research reviewed is based on studies in which participation was restricted to right-handed individuals because it is generally acknowledged that the pattern of hemispheric asymmetry is related to handedness (i.e., reduced laterality effect in left-handers contrasted with right-handers; Segalowitz & Bryden, 1983). Some have also suggested that there are gender differences regarding hemispheric asymmetry, that is, more lateralization in men than in women (Lake & Bryden, 1976; Wada, Clark, & Hamm, 1975), but there is no consensus on this issue (Bryden, 1982; Jäncke, Schlaug, Huang, & Steinmetz, 1994; Raz et al., 2004). Many researchers have examined the relation between participant attributes, such as gender and handedness, and hemispheric asymmetries (Jäncke et al., 1994; Lake & Bryden, 1976; Rasmussen & Milner, 1975; Wada et al., 1975).

Wada et al., (1975) pioneered investigations of gender-related differences in brain anatomy by measuring the surface of the right and left planum temporale in 100 postmortem adult brains (aged 17 to 96 years) of people who had died from non-neurological conditions and were free of central nervous system abnormality. Generally, they observed that the left planum temporale was larger than the right planum temporale in both genders, but the reverse pattern was observed more often in women. However, their result must be interpreted with caution because handedness information was not reported in this study.

Handedness information is easier to obtain through *in vivo* studies. Kulynych, Vladar, Jones, and Weinberger (1994) investigated the relation between gender and the anatomy of the planum temporale in 24 right-handed participants. They measured the surface of the planum temporale using MRI and replicated the results obtained by Wada et al. (1975). They observed a larger right planum temporale than left more often in women compared to men. That is, in women, 5 out of 12 had larger left than right, 6 had larger right than left, and 1 had equal surface area. In men, 10 out of 12 had larger left than right, 1 had larger right than left, and 1 had equal surface area.

However, not all researchers have found these gender-related differences in planum temporale anatomy, and there is considerable controversy. Jäncke et al. (1994) measured planum temporale surface area using MRI in a sample of healthy adults and did not find any sex differences in size or asymmetry. Recently, Barta and Dazzan (2003) investigated sex differences by measuring the surface area of the cortex using a straightforward extension of stereologic methods to MRIs and also failed to find evidence for sex differences in size or asymmetry.

In addition to possible gender differences in lateralization, a difference in handedness also has been investigated. Lake and Bryden (1976) used a dichotic-listening task to study the effects of gender and handedness. They presented pairs of consonant-vowel syllables dichotically to female and male left- and right-handers and asked them to report the items they had heard. They found a significant sex difference, in that males were more lateralized than females. Specifically, in right-handed men, 94 percent showed a REA, whereas only 67 percent of the right-handed women did. No conclusion was drawn regarding handedness because the authors indicated that the social bias toward right-hand use makes drawing any relation between skill and preference difficult for left-handed people.

Rasmussen and Milner (1975) studied lateralization of speech in a group of 140 right-handed and a group of 122 left-handed and ambidextrous patients with epilepsy using sodium amytal testing. Of the right-handed patients, 96 percent had speech in the LH, 4 percent had speech in the RH, and none had evidence of bilateral control of speech. Of the left- or mixed-handed patients examined, 70 percent had speech in the LH, 15 percent had speech in the RH, and 15 percent had bilateral speech representation.

In a meta-analytic study, Kim (1994) reviewed 28 perceptual asymmetry experiments conducted from 1965 to 1992 to investigate whether left-handers have a greater variance in perceptual asymmetry than right-handers. Meta-analyses were run separately for verbal divided visual-field studies, verbal dichotic-listening studies, and free-vision face studies. The results revealed that in verbal divided visual-field studies, right-handers had a greater mean right visual-field asymmetry than left-handers but a greater variance in visual field asymmetry was found in left-handers than right-handers. In verbal dichotic-listening studies, right-handers had a greater mean REA than left-handers, whereas left-handers had a greater variance compared to right-handers. In the free-vision laterality studies, researchers used tasks that involve judging which of the two mirror-imaged chimeric faces, one with a smile to the viewer's left or one with a smile to the viewer's right, looks happier. The results showed that right-handers have a greater mean leftward bias than left-handers, and correspondingly left-handers have a greater variance than right-handers. Overall, the results suggest that right-handers have greater mean hemispheric asymmetry than left-handers, whereas left-handers have greater variance in hemispheric asymmetry than right-handers.

Recently, Dos Santos Sequeira et al. (2006) used structural MRI scans to examine planum temporal asymmetry and found an overall leftward (left greater than right) asymmetry, in which handedness, gender, or dichotic-listening ear advantage prevailed. The mean magnitude of the leftward asymmetry varied depending on the specific combination of the factors. A clear correspondence between structural and functional asymmetry was observed only among right-handed males (that is, more pronounced structural asymmetry was associated with an enlarged planum temporal on the left side, whereas the enhanced leftward asymmetry of left-handed females resulted from smaller volumes of their right planum temporale).

In sum, research findings concerning individual differences generally indicate that greater hemispheric asymmetries are found in right-handers compared to left-handers, and in men compared to women.

1.7 Cognitive and Behavioural Asymmetries

1.7.1 Dichotomies

Throughout the history of hemispheric asymmetry research, several dichotomies have been proposed by various researchers in order to integrate the functions of each hemisphere into a single fundamental dichotomy (Bouma, 1990; Bradshaw & Nettleton, 1981; Goldberg & Costa, 1981; Hellige, 1993; Semmes, 1968). In this section, some of the well-known dichotomies are reviewed.

1.7.1.1 Verbal/nonverbal

Earlier work on hemispheric asymmetry stressed the role of the nature of the stimulus. For example, in dichotic-listening tasks, a REA is found for verbal materials, and a LEA was found for nonverbal acoustic stimuli such as music (Doehring & Ling, 1971; Goodglass & Calderon, 1977; King & Kimura, 1972). However, later investigations found that ear and visual-field superiorities could be reversed for the same participants and stimuli as a function of an imposed set of strategies (e.g., during a dichotic-listening task using verbal stimuli, the experimenter could either ask the participant to identify the tone of the voice or repeat the words; Bryden, 1982). This suggested that it was not the stimulus material *per se* but rather the task requirements and the cognitive strategies induced by those requirements that determined the predominance of one or the other hemisphere. Therefore, this verbal and nonverbal stimuli dichotomy was reformulated to a verbal versus nonverbal processing dichotomy. However, one of the problems facing this verbal/nonverbal dichotomy is that the LH is not always dominant for verbal or language processing and the RH is not always dominant for nonverbal processing. For example, when judgments involving temporal order, duration, simultaneity, rhythm, or categorical perception are required while listening to music, there is no LEA (Bradshaw & Nettleton, 1981). Also, the RH has considerable speech comprehension capacity as will be described later (Beeman & Chiarello, 1998).

1.7.1.2 Focal/diffuse

In 1968, Semmes proposed that both simple and complex abilities are represented focally in the LH but diffusely in the RH. She found evidence of this organization from studying the sensory and motor abilities of both hands in brain-damaged patients. In patients with LH injury, sensorimotor deficits were found for both hands only after injury to the primary sensorimotor projection area. However, in patients with RH injury, sensorimotor deficits were found even when injury was outside of the primary projection areas. In addition, she found that injury to a specific area of the LH usually led to disruption of a specific function whereas equivalent injury to the RH typically disrupted more than one specific function. Semmes further argued that a focal representation of elementary functions in the LH would favour the integration of similar units and lead to specialization for behaviours that demand fine sensorimotor skills such as manual dexterity and speech. In contrast, a diffuse representation of elementary functions in the RH would favour the integration of dissimilar units and lead to specialization for behaviours that demand multimodal coordination and integration of information across wide areas of space such as visuospatial ability. Although this theory has received attention, her specific results have not been replicated (Hellige, 1993). However, in the field of hemispheric contributions to the processing of language, the LH is known to have a local bias in language processing (i.e., more involved in the processing of speech sounds and syntax), whereas the RH has a global bias (i.e., more involved in prosody, processing emotional content, and gist information; for an overview, see Beeman & Chiarello, 1998).

1.7.1.3 Analytic/holistic

Bradshaw and Nettleton (1981, 1983) suggested that an important difference between the two hemispheres was the extent to which a task demanded analytic versus holistic processing. They came to this conclusion by examining the data collected by other researchers and looking for similarities among tasks that reliably produced a LH advantage and contrasting them with similarities among tasks that reliably produced a RH advantage. Clinical observations of patients' drawings indicated that LH lesions are associated with problems in sequential organization, in which objects are sorted by conceptual or abstract categories, and with oversimplification or lack of detail in drawings. On the other hand, lesions of the RH showed over-attention to details, a lack of awareness of overall organization or form, and problems in dealing with maps, appreciating spatial wholes, perspective, and closure (Levy, 1974). Although this dichotomy helped to organize a vast literature in the area, it has been criticized because it has never been operationalized with sufficient precision to make empirical tests possible (Hellige, 1993). Regardless, the analytic/holistic dichotomy is still widely used to capture the fundamental difference between the two hemispheres.

1.7.1.4 Novel/routinized

Goldberg and Costa (1981) proposed that the RH is best equipped to process novel information and the LH is best equipped to assimilate and deal with familiar information. Based on neuroanatomical studies (Galaburda et al., 1978; Geschwind & Levitsky, 1968; Gur et al., 1980), Goldberg and Costa summarized that there is relatively greater emphasis on interregional integration inherent in the neuronal organization of the RH and on intraregional integration in the LH. In addition, areas of sensory and motor representations are proportionally larger in the LH, whereas the RH shows proportionally larger areas of associative cortex. As a result, the RH has a greater ability to perform intermodal integration and to process novel stimuli and the LH is more capable of unimodal and motor processing as well as the storage of well-learned information. When acquisition of novel information is needed, the RH plays a critical role in initial stages of acquisition whereas the LH is superior at utilizing well-routinized information. In sum, this process leads to a right-to-left shift of hemisphere superiority as a function of increased competence with respect to a particular type of processing. The RH is important for initial orientation and processing of novel information. Once an appropriate processing system for the novel information has been established, the LH takes over in its utilization. Their theory has been supported by research examining nonmusicians versus musicians (Bever & Chiarello, 1974; Gaede, Parsons, & Bertera, 1978), verbal naming of unfamiliar visual symbols (Gordon & Carmon, 1976), and face recognition (Reynolds & Jeeves, 1978).

In sum, instead of searching for a global dichotomy, all of these theories of dichotomy can be combined to conceptualize how each hemisphere operates.

1.7.2 Language

The view that the LH is dominant for all aspects of language has been replaced by the idea that there is hemispheric asymmetry for different components of language processing. Researchers have shown that the LH is dominant for producing overt speech, phonetic decoding, using syntax, and certain semantic processes (Kraemer & Zenhausen, 1993; Zaidel & Peters, 1981). In contrast, the RH is dominant for processing the pragmatic aspects of language, integrating information across sentences, and using context (understanding stories, jokes, and utterances in context; Foldi, 1987; Hough, 1990; Kaplan, Brownell, Jacobs, & Gardner, 1990; Weylman, Brownell, Roman, & Gardner, 1989).

For example, Hough (1990) examined the effects of delayed presentation of a central theme on the comprehension and interpretation of narratives in adults with either RH damage or LH damage and in normal individuals. The performance of subgroups of the brain-damaged participants was also examined (anterior versus posterior). Hough was interested in finding out whether individuals with brain damage were able to retain information without the aid of a central theme and subsequently to organize and comprehend this information when the theme was presented at the end of the narrative. The results showed that RH brain-damaged groups with anterior and posterior lesions were significantly less accurate and identified significantly fewer central themes when the theme was delayed until the end of a narrative than when the theme was presented at the beginning. The performance of normal controls and participants with LH damage was unaffected by the organization of the central theme in the narratives. Hough added that in participants with LH damage, although their poor linguistic skills may adversely affect theme identification, they retain an organizing principle in the comprehension of narratives.

Brownell, Simpson, Bihrle, Potter, and Gardner (1990) investigated appreciation of metaphoric and non-metaphoric alternative word meanings in 19 aphasic (LH damaged) and 15 non-aphasic (RH damaged) stroke patients. They used metaphoric and non-metaphoric polysemous words (words associated with at least two different meanings). On each trial, a participant saw a triad of words consisting of a target polysemous concept (e.g. "warm"), a synonym (e.g. "loving") of its secondary meaning, and a foil (e.g. "blanket") that was closely associated but not synonymous with the primary meaning of the target. An example of a non-metaphoric noun-based triad includes the target "account", the synonym "explanation", and the foil "withdrawal". The task was to pick the two words that were the most similar in meaning; thus the correct answer would be selection of the target and its synonym. The results showed that both patient groups performed worse overall than a group of non-brain-damaged control participants. Relative to the RH damaged patient group, the LH damaged patient group showed an appreciation of metaphoric alternative meanings. In addition, patients with

LH damage performed better on metaphoric adjective trials when there was high similarity between a word's dominant and metaphoric meanings compared to patients with RH damage. They concluded that patients with RH damage show a pervasive insensitivity to alternative interpretations of linguistic units, and that there is a special role for the intact RH in lexical-semantic processes related to metaphor comprehension. Language- processing research findings indicate that the RH is important in comprehending and organizing narratives and understanding metaphoric meanings.

1.7.3 Visuospatial Processes

The notion that the RH is dominant for all aspects of visuospatial processing has also been replaced by the idea that hemispheric asymmetry exists for different aspects of visuospatial processing. That is, each hemisphere specializes in processing different types of visuospatial information. For example, the RH is dominant for processing global aspects of visual stimuli whereas the LH is dominant for processing local aspects of stimuli. When individuals with unilateral brain damage are asked to draw an object, the nature of the drawings depends on which hemisphere has been injured (Bouma, 1990). When the RH is damaged, the drawing lacks spatial unity although individual components may be present. In contrast, when the LH is damaged, the drawings are usually lacking in detail, but an overall spatial organization is present. Similarly, when processing faces, patients with RH damage often recognize faces by focusing on distinctive features, such as a beard, whereas patients with LH damage often use more holistic or configural properties (Bradshaw, 1989).

In addition, evidence exists that the LH and RH are biased toward efficient use of higher and lower visual-spatial frequencies, respectively. Here, one must keep in mind that the absolute range of spatial frequencies contained in a stimulus is relevant and that the range of spatial frequencies that is most relevant for the task being performed is also considered. Moreover, the task-relevant frequencies are judged high or low relative to other frequencies contained in a stimulus. Using visual half-field experiments, researchers (Hellige, 1980; Hellige & Webster, 1979) found a RH advantage for the identification of perceptually degraded visual material (preserving lower visual-spatial frequencies). This makes sense when the predominant role of the RH in processing of visual information is considered. When the visual stimuli are more difficult to see (i.e., degraded), the RH plays a predominant role in processing.

Regarding localizing visual stimuli in space, it has been hypothesized that the LH makes more effective use of a categorization subsystem (i.e., provides efficient information about the relative location of an object such as "above and "inside of") and the RH makes use of a coordinate subsystem (i.e., provides efficient information about distance and absolute location; Kosslyn, 1987). For example, Michimata (1997) used a visual half-field experiment using "clock" stimuli to investigate hemispheric processing of categorical and coordinate spatial relations. For the categorical task, participants indicated whether the long and short hands of a clock were above or below the horizontal midline of the dial. For the coordinate task, they indicated whether the long and short hands of a clock formed an angle that was more or less than 60°. For both tasks, clock stimuli were either analog clocks (Visual version) or digital clocks from which participants generated images of analog clocks (Imagery version). The results showed that for both versions, there was a trend toward a LH advantage in the categorical task and a significant RH advantage in the coordinate task.

According to Hellige (1993), the above three dichotomies are interrelated. For instance, information about global versus local aspects of a stimulus is carried by relatively low versus relatively high ranges of spatial frequencies. In addition, computer simulation models imply that categorical aspects of spatial locations are computed better by networks with relatively small, non-overlapping receptive fields (similar to relatively high spatial frequencies), whereas coordinate aspects of spatial locations are computed better by networks with relatively large, overlapping receptive fields (similar to relatively low spatial frequencies).

1.7.4 Emotional Processes

There is some controversy in the literature concerning whether the RH is primarily involved in emotion, or whether the two hemispheres play complementary roles. Clinical observations have shown that damage to the LH is more often associated with catastrophic reactions, which include bursts of tears, swearing, anxiety, expression of irritation and aggressive behaviour, and depression, whereas RH injury leads to more indifferent reactions (e.g., a cheerful acceptance of disability and indifference toward failure; Gainotti, 1987). These findings suggest that the LH is more critically involved in processing positive emotions and the RH in processing negative emotions.

Other studies involving patients with unilateral brain lesions have shown that the RH plays a special role in all aspects of affective behaviours (Heilman, Bowers, Speedie, & Coslett, 1984; Heilman, Bowers, & Valenstein, 1993). For example, RH injury is more likely to lead to disruptions of prosody and intonation in speech, and this is true whether the emotion being expressed is positive or negative. Prosody is the part of speech that conveys shades of meaning by variations in stress and pitch, irrespective of the words used or the grammatical constructions. There are two types of speech prosody: emotional and propositional. Emotional prosody conveys one's emotions while speaking by changes in rhythm, pitch, distribution of stress, and melodic contour. Propositional prosody can alter the propositional message. That is, the rise in pitch at the end of a sentence can indicate a question in a sentence without an interrogative word or without reversed order (e.g., "Why") or without reversed order of noun and verb (e.g., "is he"). Generally, patients with RH damage have more difficulty in appreciating the emotional tone of spoken language, but not in understanding the linguistic content of sentences (Tucker, Watson, & Heilman, 1977). Heilman et al. (1984) studied patients with damage of either the RH or LH and control participants to determine whether patients with RH damage had a global (emotional and non-emotional) or limited (only emotional) prosodic defect. The results showed that patients with RH damage had decreased comprehension of emotional prosody (happy, sad, or angry) compared to either the LH group or normal controls whereas both patient groups had more impaired comprehension of propositional prosody than controls. The two patient groups did not differ. Therefore, the results suggest that the RH is dominant for comprehending emotional prosody but not propositional prosody.

Furthermore, several studies have shown that patients with RH damage have more difficulty than do those with LH damage in the recognition of emotional faces and the judgment of emotional situations (e.g. Cicone, Wapner, & Gardner, 1980). Similarly, the patient's ability to express affective states through emotional prosody in speech, facial expression and gesture is more impaired after RH lesions than after LH lesions (Ross, 1985). These findings suggest that the RH may be more important than the LH in the perception as well as expression of emotional behaviour.

Overall, research findings from cognitive and behavioural domains indicate hemispheric specialization for different functions. These differences exist when the brain processes information such as language, visuospatial information, and emotion.

1.8 Hemispheric Asymmetry and Aging

1.8.1 Research Methods in Aging Studies

There are different ways to investigate age differences. The two most popular methods are cross-sectional and longitudinal designs. The third type of method, which is seen to be the most favourable type by at least some researchers (Schaie, 1994; Finkel, Pedersen, Plomin, & McClearn, 1998), is the cross-sequential method. The cross-sectional method measures differences by comparing different age groups at a point in time, the longitudinal method measures changes within participants over a period of time, and the cross-sequential method involves longitudinal follow-up of an originally cross-sectional sample.

There are advantages and disadvantages associated with each method of study. Cross-sectional studies are generally easier, quicker, and less expensive to conduct but confound cohort differences with true aging or maturation differences. For example, age differences have been shown in cross-sectional studies (Horn & Cattell, 1967; Horn & Hofer, 1992; Verhaeghen & Salthouse, 1997), but there is the possibility that older individuals reached lower peak level performance than younger individuals because of environmental conditions (e.g., poorer nutrition or less formal education). In this case, part of the age differences observed at a single point in time might reflect cohort factors rather than aging (Ronnlund & Nilsson, 2006).

With longitudinal studies, aging effects versus cohort effects may be separated. However, even with longitudinal studies, one cannot necessarily generalize from one cohort to another and they are time-consuming and expensive to conduct. In addition, longitudinal designs cannot distinguish the effects of the measurement occasion from the effects of age (Botwinick, 1977). That is, both selective attrition and practice effects may attenuate estimated cognitive decline in longitudinal studies. Selective attrition occurs when individuals most likely to exhibit greater cognitive decline drop out from the study at higher rates; this indeed has been found in longitudinal studies (Ronnlund &Nilsson, 2006; Schaie, 1994). Consequently, cognitive decline is underestimated because studies tend to include only the subset of individuals most likely to return for follow-up testing. As well, practice effects of repeated cognitive testing can mask cognitive change (Hertzog & Nesselroade, 2003; Salthouse, 1999; Schaie, 1996). In addition to selective attrition and practice effects, the length of the follow-up interval influences the likelihood of detecting significant changes (Ronnlund & Nilsson, 2006). The inclusion of a cohort-matched sample at the time of retest is used by some researchers who want to estimate and adjust for potential practice effects (Schaie, 1988; Ronnlund & Nilsson, 2006).

The cross-sequential design allows for investigation of the confounds inherent in cross-sectional and longitudinal designs when used independently (Schaie & Baltes, 1975). These designs are presumed to be more precise and the results are seen to be more generalizable across time and cohorts. However, they are also expensive and time-consuming to conduct. Finkel et al. (1998) used cross-sequential methods of analysis to interpret data from the Swedish Adoption/Twin Study of Aging. They found that cross-cohort differences were much greater than within-cohort differences but partly attributed this trend to the shorter longitudinal period for the within-cohort (6 years) than the cross-cohort age range (30 years).

Although cross-sectional methods have been criticized, when potential confounds such as cohort differences in education attainment are controlled, the findings between the cross-sectional and longitudinal methods sometimes converge. Ronnlund, Nyberg, and Backman (2005) examined five-year changes in episodic and semantic memory in a sample of 829 participants ranging from age 35 to 80 years. They used a cohort-matched sample to control for practice effects. Their cross-sectional analyses indicated gradual age-related decrements in episodic memory. However, the longitudinal data revealed no decrements before age 60, even with a practice-effects adjustment. Semantic memory showed minor increments until age 55 longitudinally, with smaller decrements after 60. Interestingly, cross-sectional and longitudinal estimates of change for groups 60-85 years old were similar. In addition, when the researchers adjusted for differences in education, improvements up to approximately age 55 in semantic memory were shown in the cross-sectional estimate. This study showed that when potential threats to internal validity such as differences in education and practice effects are controlled, the cross-sectional and longitudinal aging patterns converged in both episodic and semantic memory.

In another study, Ronnlund and Nilsson (2006) examined aging patterns cross-sectionally and longitudinally using the Block Design Test from the Wechsler Adult Intelligence Scale-Revised (Wechsler, 1981). The cross-sectional analyses showed a gradual age-related deterioration from 35 to 85 years. In contrast, the longitudinal data indicated stable performance from ages 35-55 even with practice-effect and attrition adjustments. When cross-sectional differences were education-adjusted, a similar aging pattern emerged.

In sum, the results of cross-sectional and longitudinal studies need to be interpreted with caution unless proper adjustments are incorporated into the analyses. Research shows that when confounds are controlled, the results from cross-sectional and longitudinal studies show a similar aging pattern. In addition, the cohort effect seems to be more of an issue with younger cohorts (younger than 60) in most studies (Backman, Small, & Wahlin, 2001; Ronnlund et al., 2005).

1.8.2 Theories of Hemispheric Asymmetry and Aging

There is evidence that hemispheric asymmetries are affected by conditions such as aging that alter the anatomical and functional integrity of the brain. Recently, Dolcos, Rice, and Cabeza (2002) reviewed two models of hemispheric aging: the older, RH aging model (Albert & Moss, 1988; Brown & Jaffe, 1975; Goldstein & Shelly, 1981), which suggests that the RH shows greater age-related decline than the LH; and the more recent, hemispheric asymmetry reduction in old adults (HAROLD) model, which suggests that the activity in the prefrontal cortex during cognitive performances have a tendency to be less lateralized in older than in younger adults (Cabeza, 2002). In this section, evidence for these two different models of hemispheric asymmetry and aging are examined.

1.8.2.1 The RH Aging Model

The first suggestion of the RH aging hypothesis came from the observation that psychometrically measured nonverbal, visuospatial functions tend to decline more rapidly than verbal functions as people age (Goldstein & Shelly, 1981; Reitan, 1955a; Wechsler, 1958). The hypothesis is based on the assumption that the RH is dominant for psychometrically measured nonverbal, visuospatial functions whereas the LH is dominant for verbal functions. The age-related differential decline on the verbal and visuospatial subtests of the Wechsler Adult Intelligence Scale begins around age 40 with visuospatial measures declining to a much greater extent than verbal measures (Wechsler, 1958). Another theory of aging that indirectly supports the RH aging model is the "fluid" and "crystallized" intelligence theory (Horn & Cattell, 1967). This theory also suggests that over-learned verbal skills are more resistant to aging, while the novel, unfamiliar performance or "nonverbal" tasks appear to be most sensitive to age-related decline. The proper interpretation of this pattern of decline has long been a matter of dispute because a direct comparison may be confounded by the speeded nature and greater novelty of the more visuospatial tasks and the non-speeded nature and greater reliance on previously learned information of the more verbal tasks (Hellige, 1993; Mittenberg, Seidenberg, O'Leary, & DiGiulio, 1989). Nonetheless, many studies have found evidence supporting this hypothesis.

Goldstein and Shelly (1975, 1981) conducted two studies on age differences in hemispheric asymmetry. They used a variety of tests known to be sensitive to localized and diffuse brain injuries. Results were collected both from older participants and from patients with verified unilateral or bilateral cerebral lesions. In the first study (Goldstein & Shelly, 1975), it was hypothesized that if the effects of aging were similar to those of diffuse brain injury, then the performance patterns of aging participants should resemble those of patients with bilateral or diffuse cerebral dysfunction. That is, there would be less difference between the older brain-damaged and non-brain-damaged participants than there would be between the corresponding younger groups. They tested groups of younger brain-damaged, younger non-brain-damaged, older brain-damaged and older non-brain-damaged male participants with a battery of tests (Wechsler Adult Intelligence Scale and Halstead Battery of Neuropsychological Tests). The results did not show less difference between the older brain-damaged and non-brain-damaged individuals than between the corresponding younger groups. In the second study, Goldstein and Shelly (1981) tested the RH aging hypothesis by comparing older participants to patients with known lesions confined to either the RH or the LH. Again, they used tests from the Halstead-Reitan Neuropsychological battery, which included a number of sensorimotor tasks that were designed to index the presence and location of brain injury. The test results were scored in a way that produced "points" associated with RH versus LH function, such that a greater number of points was associated with poorer performance. The results indicated that, although both cerebral hemispheres deteriorate with age, RH functions age more rapidly than LH functions.

A series of experiments conducted by Myerson and colleagues (Lawrence, Myerson, & Hale, 1998; Myerson, Hale, Rhee, & Jenkins, 1999; Jenkins, Myerson, Joerding, & Hale, 2000) found evidence indicating that visuospatial skills are affected more than verbal skills by aging. Lawrence et al. (1998) examined the effect of aging on both verbal and visuospatial processing speed by using a cross-sectional design. They tested the same participants on four verbal tasks (single lexical decision, double lexical decision, category judgment, and synonym-antonym judgment) and four visuospatial tasks (line-length discrimination, shape classification, visual search, and abstract matching) in order to compare the rate of change. When the mean verbal and visuospatial response times of older groups were compared to the corresponding response times of the young adult groups, the slope of the visuospatial regression was greater than that for the verbal regression at all ages. Specifically, verbal processing time increased linearly by approximately 50 percent while visuospatial processing time increased exponentially by approximately 500 percent from 18 to 90 years of age. They concluded that aging affects visuospatial processing to a much greater extent than verbal processing.

Subsequently, Myerson et al. (1999) investigated verbal and spatial working memory using digit and location memory-span tasks with and without verbal and spatial secondary tasks in 20 young (M = 20.4 years) and 20 older individuals (M age = 67.0 years). They found a greater age-related decline in spatial working memory compared to verbal working memory. Both groups showed domain-specific interference, that is, naming colours selectively interfered with memory for digits, leaving memory for locations unaffected, and pointing to matching colours selectively interfered with memory for locations, leaving memory for digits unimpaired. The results of this study also support the hypothesis that visuospatial skills decline more than verbal skills in aging.

Recently, Jenkins et al. (2000) replicated the above experiments and designed another experiment to measure age-related changes in verbal and visuospatial abilities in 16 young (M = 19.9 years) and 16 older (M = 70.9 years) adults. The tasks were the verbal and visuospatial processing-speed tasks and verbal and visuospatial working-memory tasks mentioned above, and verbal and visuospatial paired-associates learning tasks. In the first two experiments, the results were consistent with the previous studies. In the third experiment, older adults had greater difficulty learning novel information than young adults overall, but older adults displayed greater deficits learning visuospatial information than verbal information. The researchers concluded that in sum, the differential deficits observed on both speeded and non-speeded tasks suggested that visuospatial cognition is generally more affected by aging than verbal cognition.

In addition to the studies that used verbal and visuospatial tests, studies that used various lateralization tests also support the RH aging hypothesis. For example, Clark and Knowles (1973) investigated the effect of aging on the dichotic-listening task using vocal and written recall conditions. One hundred twelve right-handed participants were divided into the age groups of 15 to 29, 30 to 44, 45 to 59, and 60 to 74 years. The participants within each age group were randomly assigned to one of two experimental groups. The groups differed in that the participants were instructed either to vocalize the dichotically presented digits at the time of recall or to write them down on a sheet. They found a decline in recall performance with age for both vocal and written recall conditions but the age-related decrement was predominantly for the left-ear material.

The RH aging hypothesis is also supported by various studies that used tactile stimuli. Despite an almost exclusive use of the right hand in tasks of manual dexterity, normal individuals were more proficient with the left hand in tactual perception of direction in space (Benton et al., 1973) or shape of random forms (Dodds, 1978; Riege, Metter, & Williams, 1980). For example, Riege et al. (1980) used non-meaningful wire shapes to investigate tactual recognition memory in young (aged 20-29), middle (30-39), old (60 to 69), and old-old (over 70) groups. The wire figures were presented twice for palpating for 15 seconds each (2 different figures per hand). Then, a recognition test was given immediately following the presentation phase in which the four target figures recurred three times each intermingled in random order with 12 other distractor figures. The wire figures were presented one after the other to the hand that felt them during the presentation phase. The young group showed RH superiority but this was reduced in the two older groups. Overall, they found a decline in recognition scores across age groups for both hands. However, the left hand demonstrated a greater decline with age, in particular, from young to middle-aged, and from old to very old groups.

The Tactual Performance Test (Halstead, 1947) has been used in a number of studies with aging individuals. In this test, the participant is blindfolded and is asked to fit blocks of various shapes and sizes into the spaces on the board that is set upright, first with his or her dominant hand, then with the nondominant hand, and finally with both hands as quickly as possible (Spreen & Strauss, 1998). As expected, the completion time decreases as the trials proceed in normal younger individuals. Many older individuals, however, show an atypical pattern of performance on this test. That is, after completing the task with the right hand, they fail to improve their performance when using the left hand in an immediately following trial (Price, Fein, & Feinberg, 1980). This difficulty is often associated with RH dysfunction, thus supporting the RH aging hypothesis.

Elias and Kinsbourne (1974) studied male and female younger and older participants using a visual hemifield paradigm with verbal and nonverbal stimuli. Participants were told to respond "same" or "different" using microswitches. Both older groups (male and female) had slower performance than the younger groups, but the age difference did not affect verbal and nonverbal processing in the same way for men and women. Men were equally proficient at verbal and nonverbal matching but young women were less proficient nonverbally than verbally and elderly women showed the same pattern of performance in amplified form. In other words, the RH aging hypothesis was supported by their female sample only.

Although many studies support the RH aging hypothesis, there is contradictory evidence (Mittenberg et al., 1989; Raz et al., 2004; Schear & Nebes, 1980). Schear and Nebes studied verbal and spatial memory in younger (M = 18.8 years) and older (M = 69.5 years) participants under identical task conditions. The participants recalled either the identities or spatial locations of seven letters arranged randomly within a 5 x 5 grid. In order to examine whether the participants encoded the verbal and spatial characteristics of the array differently, verbal and spatial interference tasks were administered during the retention interval. The results indicated that the memory decrement in the elderly was not greater for the spatial aspects of the stimulus array than for its verbal aspects. Therefore, they found no evidence for a greater decline with age in spatial memory than in verbal memory.

Shelton, Parsons, and Leber (1982) examined the RH aging hypothesis in 24 middle-aged (M = 37.6 years) and 24 older (M = 71.2 years) male participants. Participants performed structurally similar verbal and visuospatial paired-associate learning tasks that have been found sensitive to left- and right-hemispheric dysfunction, respectively. They found no evidence to support the RH aging hypothesis as performance decreased for both verbal and visuospatial learning tasks equally in the older group.

One study used an interesting method to investigate verbal and nonverbal memory in younger and older individuals. Janowsky, Carper, and Kaye (1996) had two groups of younger participants (M = 31.3 and 32.5 years) and one group (M = 71.4 years) of healthy elderly participants. Participants incidentally learned the identity and location of a group of objects and later verbally recalled the objects as well as recalling their previous spatial location. Younger participants were tested after retention intervals that equated their performance with that of the older participants. That is, the older participants were tested after a 1-day retention interval whereas one group of younger participants was tested after a 2-3 day retention interval so that their spatial recall performance would match the spatial recall performance of the older participants. The second group of younger participants was tested after a 1-week retention interval so that their verbal recall performance matched the verbal recall performance of the older participants. These retention intervals were derived through pilot testing. The measures of interest then were whether spatial memory was comparable in older and younger participants when verbal memory was the same and whether verbal memory was similar in older and younger participants when spatial memory was the same. When the performance of older and young participants on verbal recall was equated, older participants outperformed younger participants on spatial recall and when spatial recall was equated between groups, older participants performed worse than younger participants on verbal recall. The researchers concluded that memory did not change uniformly with age: verbal recall was more affected than nonverbal recall in aging. This is a result opposite to that which would have been predicted by the RH aging model.

Recently, Park, Lautenschlager, Hedden, Davidson, and Smith (2002) examined the distinctiveness and interrelations among visuospatial and verbal memory processes in short-term, working, and long-term memories in participants ranging in age from their 20s through to their 80s. The researchers found a continuous age-related decline across the life span for processing-intense tasks such as speed of processing, working memory, and long-term memory and relatively little differentiation between declines in visuospatial and verbal memory processes across the life span.

Ellis and Oscar-Berman (1989) reviewed cerebral hemispheric asymmetry in aging and in alcoholism. The researchers investigated alcoholism as well as aging because earlier studies had shown that alcoholism affects visuospatial skills more than verbal skills, similar to the effects purportedly found in aging. After an extensive review of empirical research findings based on laterality techniques, the researchers concluded that the pattern of functional laterality, both in alcoholics and in aging individuals, is similar to those of normal controls. They added that the results that show preservation of ability in some areas and impairments in other areas should be analyzed in terms of the complexity of the task involved and the overall contributions of cerebral information-processing mechanisms to intact performance.

Some researchers used various lateralization techniques and also failed to support the RH hypothesis. Nebes et al. (1983) examined the speed with which young and old participants identified stimuli in their right and left visual fields and performance on a dichotic-listening test using syllables. In the first experiment, they measured participants' response times for naming verbal and pictorial stimuli in their right and left visual fields. The verbal stimuli were the printed names of numbers between "one" and "twelve", and the pictorial stimuli were clocks with their hands set at the various hours. Thus, for each number between 1 and 12, there were two representations, one verbal and one spatial. The researchers argued that, although the clock faces had a readily available verbal label, actual identification of the time required a visuospatial discrimination.

Words were identified faster in the right visual field (i.e., LH) and pictorial stimuli in the left (i.e., RH) in both young and old groups. There was a main effect of age but not an age by stimulus type or by visual field interaction. That is, there was no evidence that aging produced a greater decrement in the RH than in the LH. In the second experiment, a dichotic-listening test was used with consonant-vowel syllables. Participants were given two different syllables simultaneously, one in each ear, and they had to report the two items. The results showed the typical REA, but there was no age by ear interaction.

Obler et al. (1984) administered two visual hemifield tasks to 96 right-handed participants divided into 3 age groups (young adults, 25-39 years; middle-aged adults, 50-64 years; older adults, 65-79 years). One task required a linguistic judgment in which the participant compared two, two-letter syllables written in upper and lower case presented one over the other, and the other required a judgment about human faces in which the participant saw the upper and lower sections of photographs of people. For both the verbal and the nonverbal tasks, participants were required to make a same/different judgment on stimuli presented in either the left or right visual field. The results showed that although older participants required longer exposures to achieve 80 percent correct and took longer to respond, there was no evidence of systematic change in direction or degree of lateralization related to age.

In summary, the RH aging hypothesis has been supported by some research findings but not others. Although the theory itself is interesting, a theory indicating a faster aging process of one hemisphere compared to the other mainly supported with visuospatial versus verbal ability studies (Goldstein & Shelly, 1981; Lawrence et al.,

1998) and single lateralization studies (Clark & Knowles, 1973; Elias & Kinsbourne, 1974) appears to be too simplistic.

1.8.2.2 The HAROLD Model

As various neuroimaging techniques became available, many researchers began to use these techniques to study hemispheric functioning. In PET and fMRI studies, higher-order cognitive functions, such as memory, have been associated with major activations in the prefrontal cortex (Fletcher & Henson, 2001). Upon investigating the effects of aging, researchers found that prefrontal activity during episodic memory retrieval was right-lateralized in younger adults but bilateral in older adults (Backman et al., 1997; Cabeza et al.,1997; Grady, Bernstein, Beig, & Siegenthaler, 2002; Madden et al. 1999). Evidence from such studies enabled Cabeza (2002) to propose the HAROLD model, which suggests that prefrontal activity during cognitive performances tends to be less lateralized in older adults than in younger adults. Cabeza further suggested that this change may help counteract age-related neuro-cognitive decline (compensation hypothesis) or reflect an age-related difficulty in recruiting specialized neural mechanisms (dedifferentiation hypothesis). In order to investigate this, Cabeza, Anderson, Locantore, and McIntosh (2002) measured prefrontal activity in young, low-performing old, and high-performing old people during verbal recall and recognition memory (selected using a composite memory score based on the results of four memory measures). They found that prefrontal activity during recognition memory was right-lateralized in young and low-performing old participants but bilateral in high-performing old participants. Cabeza et al. (2002) interpreted this as low-performing older adults recruiting a similar network as young adults but using it inefficiently, whereas high-performing older adults counteracted age-related decline through a reorganization of neuro-cognitive networks, supporting the compensation hypothesis.

Because the HAROLD model was mainly derived from functional neuroimaging research, it would be important to find converging evidence from other domains using various techniques. Because the model is relatively new, not much evidence is found in other domains. However, some studies indicate changes in frontal lobe structure and functioning with aging. For example, Raz et al. (2004) used MRI to examine structural changes in the brain. Specifically, they investigated age-, sex-, and hemisphere-associated differences in the cerebral cortex by measuring volumes of the cerebral hemispheres and of 13 specific regions of 200 healthy adults. They found that the cortical volume declined steadily during the whole adult life-span, with different cortical regions varying in the rate of decline. Interestingly, they found that the lateral prefrontal cortex exhibited the greatest age-related differences. Also, accelerated hippocampal shrinkage was noticed past 45 years of age. Men showed larger volumes in most areas when sexual dimorphism and body size were statistically controlled, and some regions (hippocampus and fusiform gyrus) showed steeper negative age-associated trends in men. The direction and magnitude of hemispheric asymmetry was inconsistent.

Mittenberg et al. (1989) studied right-handed young (20-35 years old) and old (55-75 years old) healthy participants using neuropsychological measures of lateralized and focal function that had been selected to eliminate systematic procedural differences among tests (e.g. timed vs. un-timed, over-learned vs. unfamiliar). The tests selected had demonstrated sensitivity to localized hemispheric function. The tests included Verbal Fluency (left-frontal), Recency for Words (left-frontal), Design Fluency (right-frontal), Recency for Pictures (right-frontal), Cross-Modal matching (left-parietal), Right-Left Orientation (left-parietal), Line Orientation (right-parietal), Facial Recognition (right-parietal), Memory for Nonsense Syllables (left-temporal), Hebb's recurring digits (left-temporal), Memory for Spatial Position (right-temporal), and Corsi's Blocks (right-temporal). They found that the functioning of both hemispheres showed equal vulnerability to the effects of aging, but more pronounced declines were evident in frontal abilities.

In summary, the RH aging model is supported by some behavioural studies in various domains but the evidence has been mixed. Available evidence for the HAROLD model, primarily functional neuroimaging evidence, is supportive of the model. The two models are not incompatible and may actually be complementary. That is, the HAROLD model may apply to prefrontal regions while the RH aging model may apply to other brain regions.

1.9 Objective of the Present Study

Since Dax and Broca, many researchers have attempted to find anatomical or functional differences between the two hemispheres of the brain. Accumulated evidence from these attempts shows that the two hemispheres are indeed anatomically, chemically, and functionally asymmetric (Doehring & Ling, 1971; Galaburda, 1995; Oke et al., 1978). In addition to these differences, some evidence indicates that the two hemispheres age at different rates. For example, many researchers (e.g., Goldstein & Shelly, 1975, 1981; Jenkins et al., 2000; Myerson et al., 1999) noticed that RH functions (e.g., visuospatial ability) declined more rapidly than those of the LH. Other evidence shows a decrease in the degree of asymmetry in performing cognitive tasks with aging (Cabeza, 2002).

In the past, many researchers have used dissimilar measures of verbal and visuospatial tasks, which can have differing psychometric properties, to study hemispheric asymmetry. Clearly, one cannot be certain whether these instruments tap skills exclusively mediated by homologous areas in the two hemispheres. In order to solve this problem, various lateralization tasks have been used to investigate hemispheric asymmetry but most of the tasks examined only the perception of the stimuli and not memory for the stimuli. The study of memory is important especially in older individuals because age-related declines have been reported, especially in episodic memory (Backman et al., 2001; Park & Gutchess, 2005).

This study is the first to examine age differences in auditory, visual, and tactile performances using the same participants. The present study systematically investigates age differences in hemispheric asymmetry using memory tasks in three different modalities. A modified dichotic-listening memory test, a novel tactile recognition memory test, and a visual hemifield memory test were used. All tests compared the left side and right side performance independently: The dichotic-listening memory test (DLMT) compared the performance of each ear on the same task, the tactile recognition memory test (TRMT) compared the performance of each hand on the same task, and the visual hemifield memory test (VHMT) compared the performance of each visual field. Additional departures from the typical approach to the questions of interest are that the tactile stimuli used in this task are purely textural and thereby are expected to elicit responses from both hemispheres given that somatosensory information is processed by both hemispheres. Potential correlations between measures from all three tasks were investigated in order to examine whether the relations (if any) among different asymmetry measures changed as a function of age.

The present study evaluates theories of hemispheric asymmetry and aging. Results from a pilot study involving younger individuals showed a REA on the DLMT and no side preference on the other two tasks. The RH hypothesis would be supported by a larger REA on the DLMT, a right-sided advantage on the TRMT, and a right visual field advantage on the VHMT in the older group compared to the younger group. The HAROLD model has mostly been examined and supported using neuroimaging evidence. Therefore, the present study investigates whether this model could be supported with behavioural measures. The HAROLD model would be supported by a decreased asymmetry on the DLMT in the older individuals. The other tasks are less likely to show a decline in hemispheric asymmetry with age given that they do not show asymmetry or side preference in younger individuals.

2.0 Method

2.1 Participants

The participants were right-handed (confirmed using the Edinburgh Handedness Inventory shown in Appendix A; Oldfield, 1971), native English-speakers with normal or corrected-to-normal visual acuity, and normal hearing, and no complaints of cognitive impairment. The younger group consisted of 45 undergraduate student volunteers from the University of Windsor. The ages of these 22 women and 23 men ranged from 18 to 27. The older group consisted of 10 women and 6 men (ages ranged from 63 to 84) who were recruited through advertisements placed in various senior centres in the community. One additional participant from the younger group and seven from the older group were excluded based on information gleaned from a health- status interview to determine eligibility for participation in the study (see Appendix B). The exclusion criteria included a history of a learning disability, neurological illness (e.g. stroke, tumour, epilepsy, Alzheimer's disease), carpal tunnel syndrome, Paget's disease, and any sensory impairment. The excluded participant from the younger group had a unilateral hearing loss, and the six older participants were excluded because of history of stroke, sensory impairment or in one case because English was a second language. Participant characteristics are displayed in Table 1. Members of the younger group received a course credit and members of the older group received $20 for their participation.

2.1.1 Participant Demographics

T-tests revealed no difference between the two groups in years of education, $t(59) = .11, p > .05$.

2.2 Procedures

2.2.1 General Procedures

The participants attended a single 70- to 90-minute testing session. The first procedure in this session was the brief health-status interview to determine eligibility. Eligible participants were then screened for deficits in tactile and visual perception and/or neglect using the Tactile Form Recognition Test (Reitan & Wolfson, 1993) and Bells Cancellation Test (Gauthier, DeHaut, & Joanette, 1989), respectively. The Tactile Form Recognition Test ruled out the presence of sensory deficits that would impair discrimination of the experimental tactile stimuli by palpation. The test requires participants to blindly identify a plastic shape (triangle, circle, square or cross) that is placed in their hand by pointing with the opposite hand to one of the four plastic shapes

Table 1. Participant Demographic Variables

	Group	
	Younger (n=45)	Older (n=16)
Age		
M	21.11	73.25
SD	2.08	6.40
Education		
M	13.92	15.13
SD	.93	2.80

mounted on a board. The participants completed this task twice for both hands; a cut-off of more than one error per side was used. In the Bells Cancellation Test, the participants were asked to circle all the bells on a sheet of paper printed with 35 bells and 245 other distractor figures (e.g. guitar, tree, key, saw, and car). The total number of missed bells on each side was measured and a cut-off of six in total or more than three omissions per side was used as recommended by Azovi et al. (2002).

The Mini Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975) was administered only to the older participants as a screening measure for cognitive impairment. The MMSE assesses orientation to time and place, attention, calculation, naming, repetition, comprehension, reading, writing, copying, and immediate and delayed recall. The total number of correct answers was recorded (maximum is 30). The abnormal error cut-off criterion from a possible 30 has been established for separate age and education groups by Crum, Anthony, Bassett, & Folstein (1993) and these cut-offs were used in the present study. All participants performed above the cut-off scores on the screening tests.

After successful completion of the screening procedures the experimental tasks (the DLMT, TRMT, and VHMT) were administered as was a series of common neuropsychological tests that acted as distractor tests (Wechsler Memory Scale-Third Edition [WMS-III], Digit Span and Spatial Span subtests [Wechsler, 1997]; Wide Range Achievement Test- Third Edition [WRAT-3], Reading subtest [Wilkinson, 1993]; Trail Making Test A and B [Reitan, 1955b]; and the Grooved Pegboard Test [Matthews & Klove, 1964]). Each test is described in Appendix C and descriptive statistics are shown in Appendix D. For the order of presentation see Appendix E.

2.2.2 Description of Experimental Tasks

2.2.2.1 DLMT

The DLMT test is a modified version of the Dichotic Word Listening Test (Auditec of St. Louis, 1991). This test uses an audio tape to present words in a male voice using a set of headphones (Koss UR-15C). The test first presents practice trials of single words presented randomly to the left or right side and test trials of word pairs being presented simultaneously. In the Dichotic Word Listening Test, the words "now repeat" were presented prior to each word pair but in the DLMT, those instructions were removed. In addition, the original test had two versions with each version containing 30 word pairs. Only the first ten word pairs of each version were used in the DLMT. The intensity of the word presentation was set at approximately 70 dB measured by a digital sound-level meter but adjusted accordingly when participants indicated that they could not hear the practice stimuli clearly.

The 10 practice trials served as a hearing screening test as well as a means of familiarizing the participant with the test. Following the presentation of each word, the participant was instructed to repeat the word and raise his or her right or left hand depending on the side of word presentation. All participants were able to repeat the words and indicate the sides without difficulty.

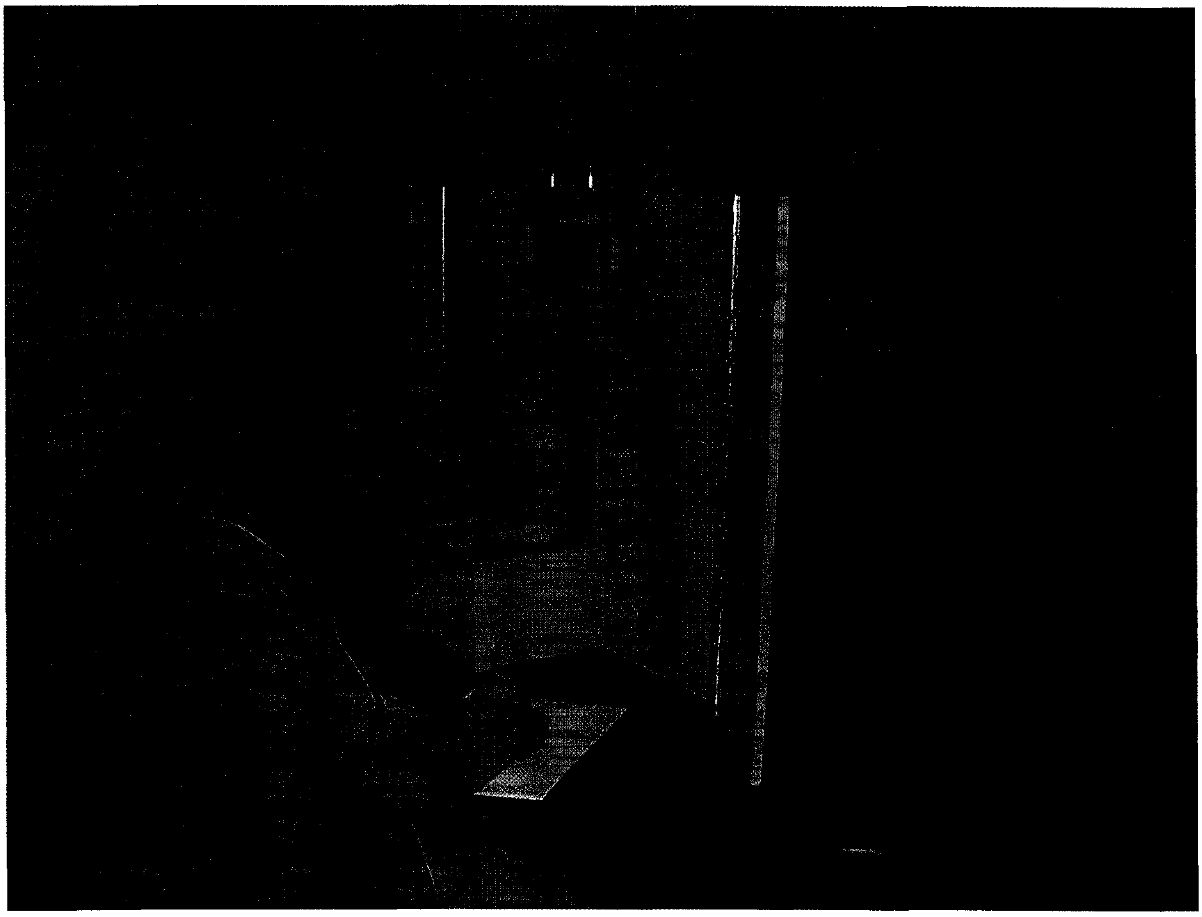
Following the practice trials, the testing began. The test stimuli consisted of ten pairs of words with each pair of words (one word per ear) being presented simultaneously at the rate of 4 seconds per pair. Participants were asked to remember the list of words that was presented to the specified ear (right or left first, counterbalanced among participants) while simultaneously being presented with a different word list to the other ear. Immediately following the presentation, the experimenter gave a recognition memory test that included the words presented to the specified ear and ten distractor words, in which the participants were instructed to say "yes" to the words that were presented to the specified ear or "no" to other words. A delayed-recognition test was given after a 15-20 minute delay with a new set of distractor words. Subsequently, the practice trials with ten new words were given and the test was repeated with the other ear with a new set of ten word pairs and new distractor words.

2.2.2.2 TRMT

The TRMT examines tactile memory by presenting tactile stimuli to either the right or left hand. This was done using a specially constructed apparatus with an opening for the hand and a mounting area inside that holds the experimental tactile stimulus. The stimuli were hidden from view and the participants wore ear muffs to eliminate auditory cues that may arise through texture palpation. The participant was asked to put one hand (right or left first, counterbalanced) through the opening and place the hand on the stimulus (Figure 2).

The stimuli consisted of pieces of 19 cm x 19 cm x 1 cm plywood covered with various textures (for a sample list of textures, see Appendix F). Each stimulus (five stimuli in total) was presented and the participant was asked to feel it for three seconds with the whole hand and remember it for later testing. Immediately following the presentation of the test stimuli, a recognition memory test was given by presenting the test stimuli and a set of five distractor stimuli in random order. The examiner asked the participant to say "yes" if it was a stimulus that was presented before, and say "no" if it was not. After a 15-20 minute delay, another recognition test was given using the test

Figure 2. Tactile Recognition Memory Test apparatus is shown in this figure. Each presentation lasted for three seconds and the participants were asked to feel the stimulus with their whole hand and to try and remember it for later testing.



stimuli and a different set of distractor stimuli. The test was repeated using the other hand and a new set of test and distractor stimuli.

2.2.2.3 VHMT

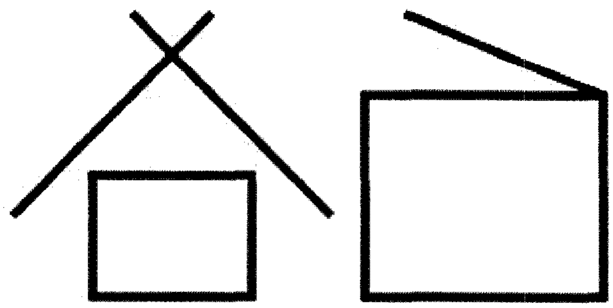
Participants used both a chin rest and a forehead bar to limit head movement while maintaining a distance of approximately 30 cm from the computer screen (see Figure 3). Stimuli for this experiment consisted of eight easy-to-verbalize figural designs for the practice trials and ten difficult-to-verbalize figural designs for the experimental trials, examples of which appear in Figure 4 (Silverberg & Buchanan, 2005). Each trial started with the presentation of a white fixation cross that remained at the centre of the black background for 2000 ms. Upon termination of the cross, a white rectangle containing a black figural design was presented to either the right or left visual field for 200 ms. The edge of the rectangle nearest the centre was approximately 5° of visual angle from centre. For all trials, participants were asked to keep their eyes focused on the centre of the screen (cross) and to avoid eye movements. A practice session consisting of eight presentation trials with each practice figural design appearing randomly to either the right or left visual field familiarized participants with the task. This practice session was followed by 40 experimental trials.

The experimental trials consisted of each of the ten figures (five figures per side) appearing pseudo-randomly with a constraint of not more than three consecutive presentations to the same visual field and that each visual field had 20 presentations (Five figures, each figure appearing four times in one visual field). Immediately following the completion of the presentation phase, a recognition memory test was given using the presented stimuli and ten other difficult-to-verbalize figural designs as distractors. The

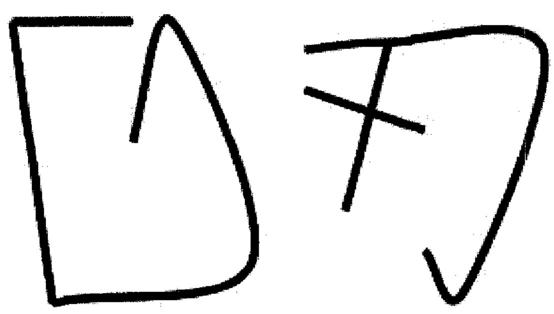
Figure 3. For the Visual Hemifield Memory Test, the participant puts her chin on the chin rest with a forehead bar to prevent movement of the head.

Figure 4. A sample of Visual Hemifield Test stimuli is shown. Easy-to-verbalize drawings used for practice trials are shown in a) and difficult-to-verbalize drawings for the test trials are shown in b).

a)



b)



items were presented centrally on the screen. Participants indicated whether they saw each design before by pressing one of two computer keys with their right hand. A delayed recognition test using ten different distractors was given after a 15-20 minute delay.

2.3 Experimental analysis

A mixed ANOVA with Delay type (immediate and delayed), and Side of Presentation (right or left) as within-subject variables and Age (younger and older) as a between-subject variable was used to analyze performance on each task. The dependent variable was the percentage of correct responses on each side, calculated by adding hits and true negatives out of total responses on the DLMT and TRMT tasks. For example, if a participant achieved 7 hits and no false positives (i.e., 10 true negatives) on a DLMT condition, then the calculation would be (7 + 10)/20 x 100, yielding 75%. Because the VHMT tested memory in a central display it was impossible to attribute false positives to a specific side and in this task only the number of hits was analysed.

In addition to the main analyses, because the same individuals completed all three tasks, it was possible to examine the extent to which the cognitive asymmetries measured by the different tasks were related to one another. By comparing the pattern of relations for younger and older participants, it was possible to determine whether there were age differences in the pattern of relations. In order to examine the relations among the tasks, a laterality index was calculated. This laterality index reflects the direction and magnitude of performance asymmetries. For each participant this index was calculated for each task using the formula:

$$\text{Lateralization index} = (R-L)/(R+L),$$

in which R represents the right-side hits and L represents the left-side hits. This formula is commonly used in lateralization or hemispheric asymmetry studies (Hiscock & Stewart, 1984; Strauss et al., 1985).

Finally, in order to examine the difference in the difficulty level of each task, the percentage of total correct responses for the immediate condition of each task (both sides combined) were analysed in a mixed ANOVA with Task as a within-subject variable and Age as a between-subject variable.

3.0. Results

Possible sex differences in performance were explored but there was no difference between the sexes so data from the two sexes were combined. Descriptive statistics for the younger and older groups are presented in Table 2.

3.1 Lateralization Tasks

3.1.1 DLMT

A main effect of Age was found with younger participants achieving a higher percentage of correct responses overall than older participants (90.22 % vs. 81.17%), $F(1, 59) = 18.19$, $p < .01$. A main effect of Side of Presentation was also found, $F(1, 59) = 30.38$, $p < .01$, such that the percentage of correct responses was higher for words presented to the right ear ($M = 89.64\%$) than the left ($M = 81.76\%$).

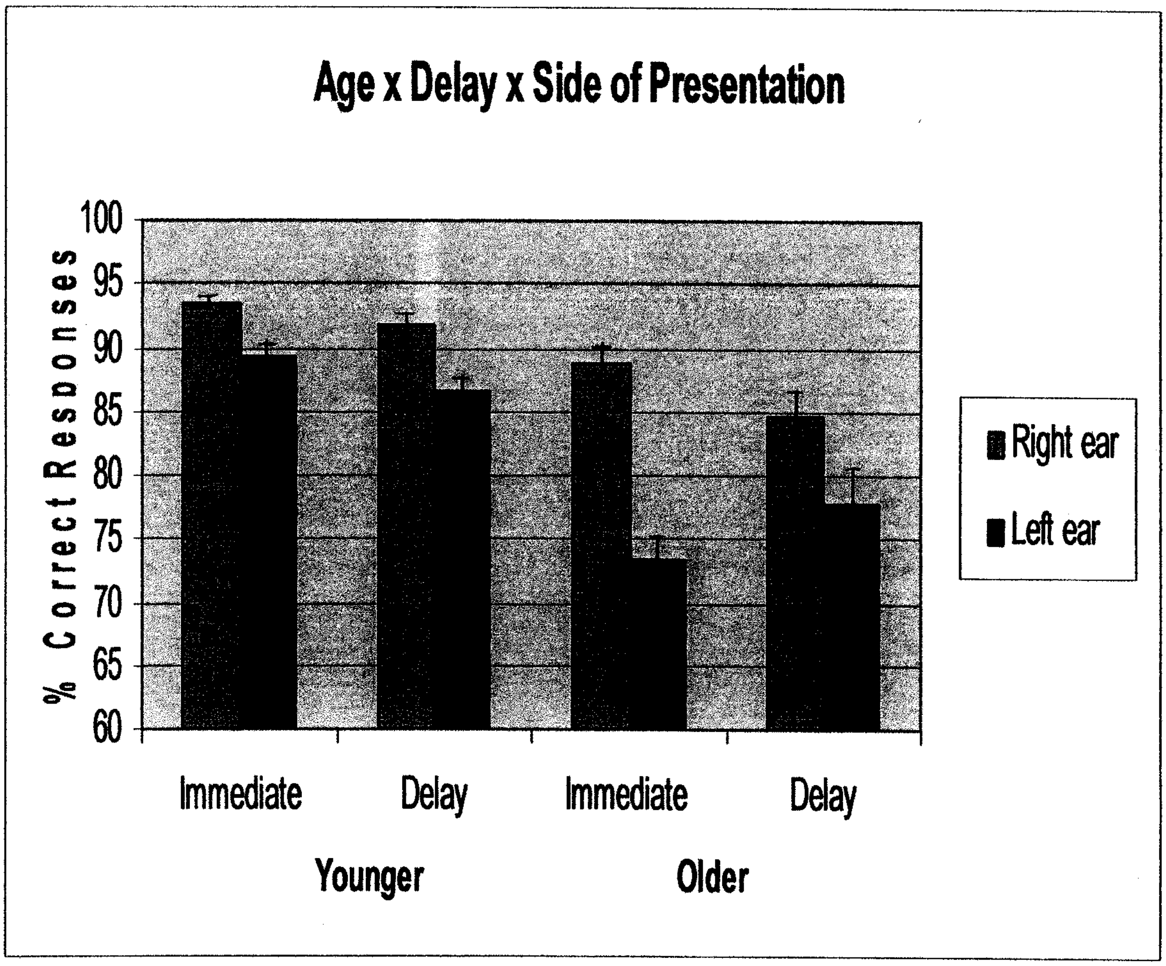
A three-way interaction of Delay, Side of Presentation, and Age was found, $F(1, 59) = 10.98$, $p < .01$ (see Figure 5). For the younger group, the difference in percentage of correct responses between the right and left sides did not change across the delay conditions but in the older group, the difference in percentage of correct responses

Table 2. Descriptive Statistics on Lateralization Task Measures by Age Group

	Younger				Older			
Measure	Min.	Max.	Mean	S.D.	Min.	Max.	Mean	S.D.
DLMT Immediate R H	5	10	8.76	1.15	5	10	7.81	1.94
DLMT Immediate R FP	0	2	.09	.36	0	1	.06	.25
DLMT Immediate L H	5	10	8.11	1.50	0	10	5.56	2.78
DLMT Immediate L FP	0	1	.24	.44	0	3	.88	1.15
DLMT Delay R H	4	10	8.42	1.34	3	10	7.31	2.33
DLMT Delay R FP	0	1	.07	.25	0	2	.38	.72
DLMT Delay L H	3	10	7.56	1.89	1	10	6.31	2.68
DLMT Delay L FP	0	2	.27	.54	0	3	.75	1.24
TRMT Immediate R H	3	5	4.67	.56	3	5	4.56	.73
TRMT Immediate R FP	0	3	.82	.78	0	4	1.63	1.09
TRMT Immediate L H	4	5	4.80	.41	4	5	4.63	.50
TRMT Immediate L FP	0	3	.78	.80	0	3	1.69	.79
TRMT Delay R H	2	5	4.71	.63	2	5	4.25	.93
TRMT Delay R FP	0	3	.56	.76	0	4	1.81	1.33
TRMT Delay L H	3	5	4.44	.66	3	5	4.56	.73
TRMT Delay L FP	0	3	2.06	.85	0	3	.95	.99
VHMT Immediate R H	1	5	3.93	.99	2	5	3.88	1.03
VHMT Immediate L H	1	5	3.76	1.09	3	5	4.00	.82
VHMT Delay R H	1	5	3.69	1.08	3	5	4.06	.68
VHMT Delay L H	1	5	3.91	1.13	3	5	4.19	.83

DLMT = Dichotic-listening Memory Test
TRMT = Tactile Recognition Memory Test
VHMT = Visual Hemifield Memory Test
R = right (ear or hand or visual field)
L = left (ear or hand or visual field)
H = hits
FP = false positives

Figure 5. Mean percentage of correct responses in the younger and older groups on the Dichotic-Listening Memory Test



between the right and left sides changed across the delay conditions. That is, there was a larger REA in the immediate condition than the delayed condition.

The interaction of theoretical interest involving Age and Side of Presentation was obtained, $F(1, 59) = 5.05$, $p < .05$, with a larger REA in the older group than the younger group (See Figure 6). A two-way interaction of Delay and Side of Presentation was also found, $F(1, 59) = 5.80$, $p < .02$, with a larger REA in the immediate condition than the delayed condition (see Figure 7). However, this result was likely influenced by the larger REA in the older group in the immediate condition.

3.1.2 TRMT

The Age and Side of Presentation interaction of theoretical interest was not obtained. However, a main effect of Age was found, $F(1, 59) = 58.76$, $p < .01$, with the younger participants obtaining a higher percentage of correct responses ($M = 89.78$ %) than the older participants ($M = 77.03\%$). In addition, an interaction of Age and Delay was found, $F(1, 59) = 4.43$, $p < .05$, with no difference in performance across the delay conditions in the younger group but a decrease in correct responses from immediate to delayed conditions in the older group (see Figure 8).

3.1.3 VHMT

There was no main effect of Age, Delay, or Side of Presentation and there were no interactions including Age and Side of Presentation.

3.2 Correlations of Lateralization Index Scores

Table 3 shows Pearson correlation coefficients of the laterality index scores across tasks and conditions for younger participants, for older participants, and for all participants

Figure 6. Mean percentage of correct responses for Right and Left sides (immediate and delayed conditions combined) in the younger and older groups on the Dichotic-Listening Memory Test.

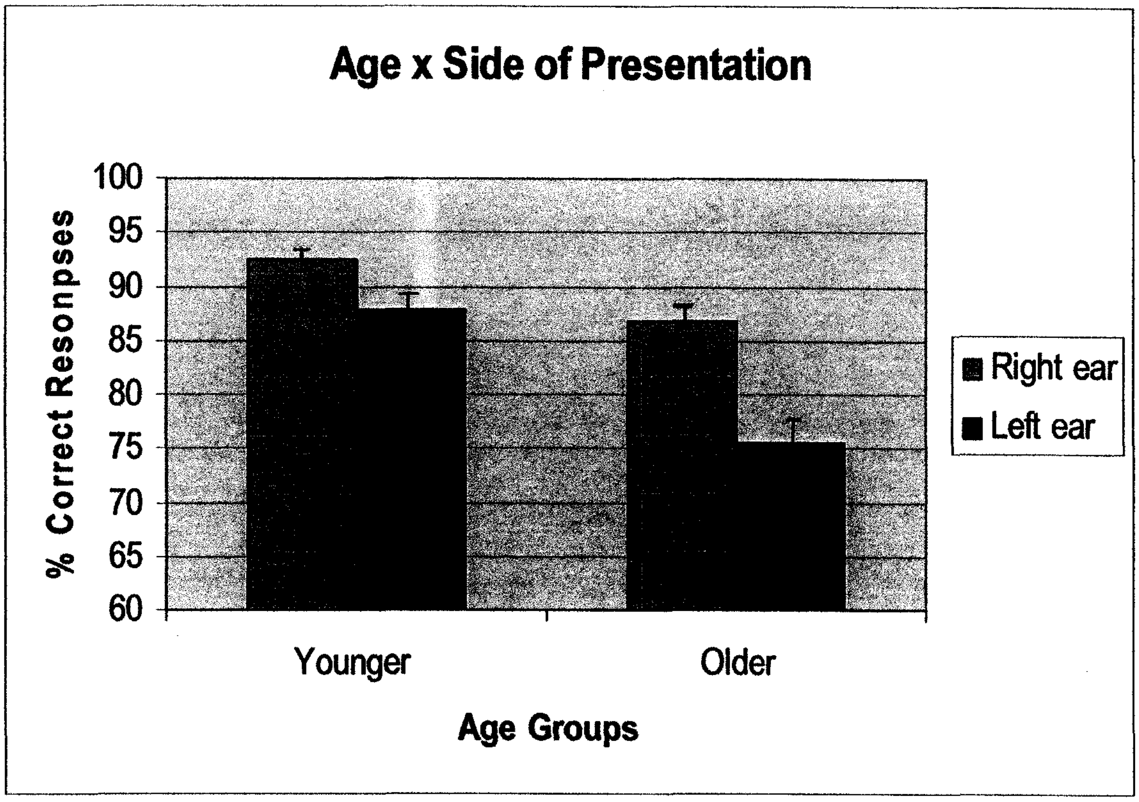


Figure 7. Mean percentage of correct responses for right and left sides in the immediate and delayed conditions (the groups combined) on the Dichotic-Listening Memory Test

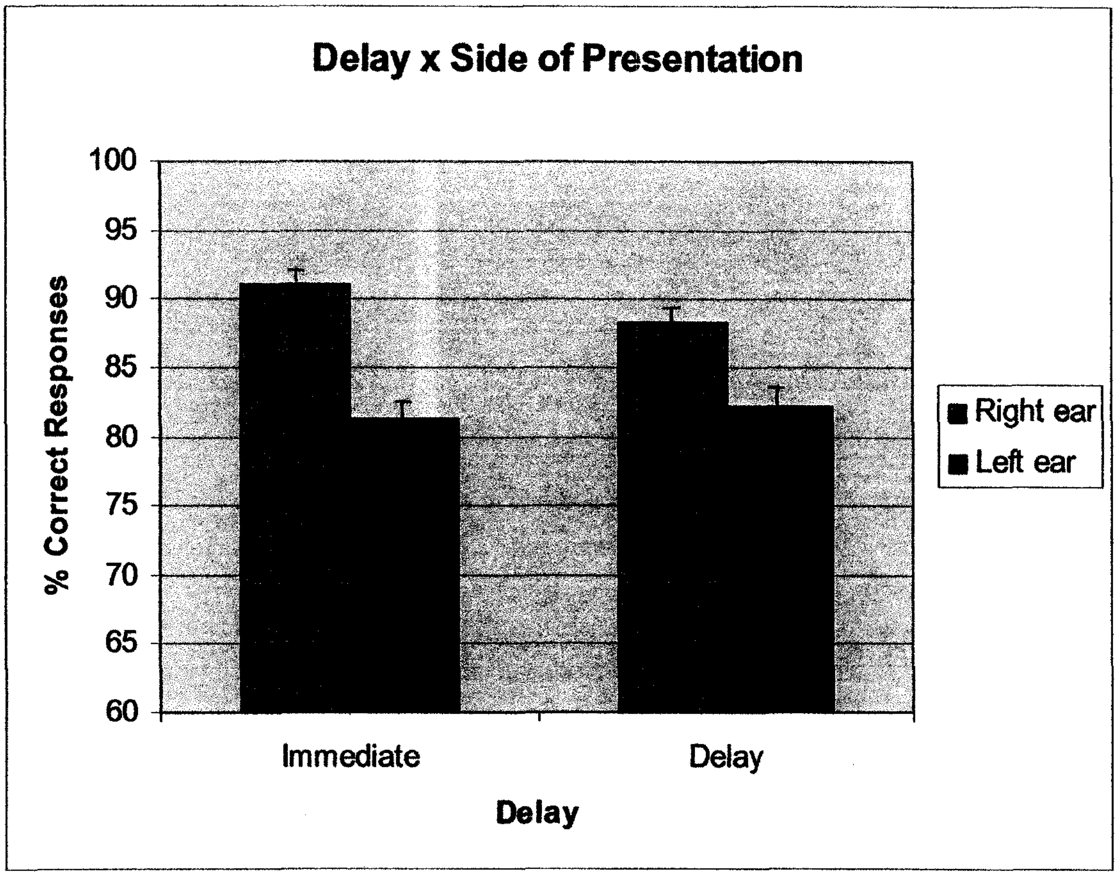


Figure 8. Mean percentage of correct responses on the immediate and delayed conditions (right and left sides combined) in the younger and older groups on the Tactile Recognition Memory Test

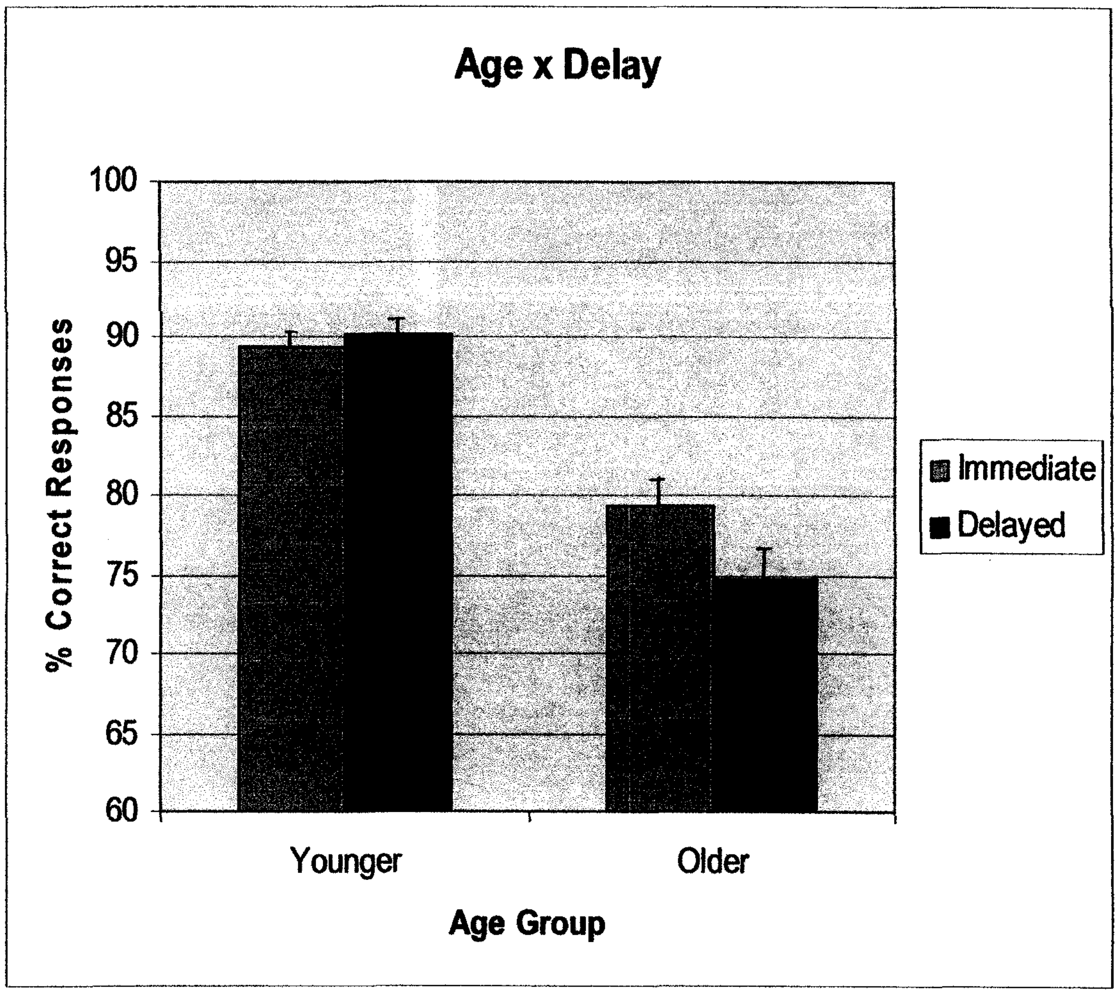


Table 3. Correlations of Laterality Index scores for Younger, Older, and Two Groups Combined

Index and Group	1	2	3	4	5	6
1. DLMT Immediate						
Younger	--	.54**	-.06	-.10	.04	-.10
Older	--	.73**	-.27	-.01	.11	.19
All	--	.61**	-.12	-.14	.01	.11
2. DLMT Delay						
Younger			-.24	-.34*	-.13	.08
Older			.08	-.04	.06	-.18
All			-.12	-.24	-.08	.02
3. TRMT Immediate						
Younger				.31*	-.19	-.26
Older				-.20	.14	-.04
All				.16	-.12	-.22
4. TRMT Delay						
Younger					-.06	-.20
Older					-.14	-.33
All					-.05	-.22
5. VHMT Immediate						
Younger						.65**
Older						.32
All						.59**
6. VHMT Delay						
Younger						
Older						
All						

Note. * p<.05 (2-tailed), ** p <.01 level (2-tailed).

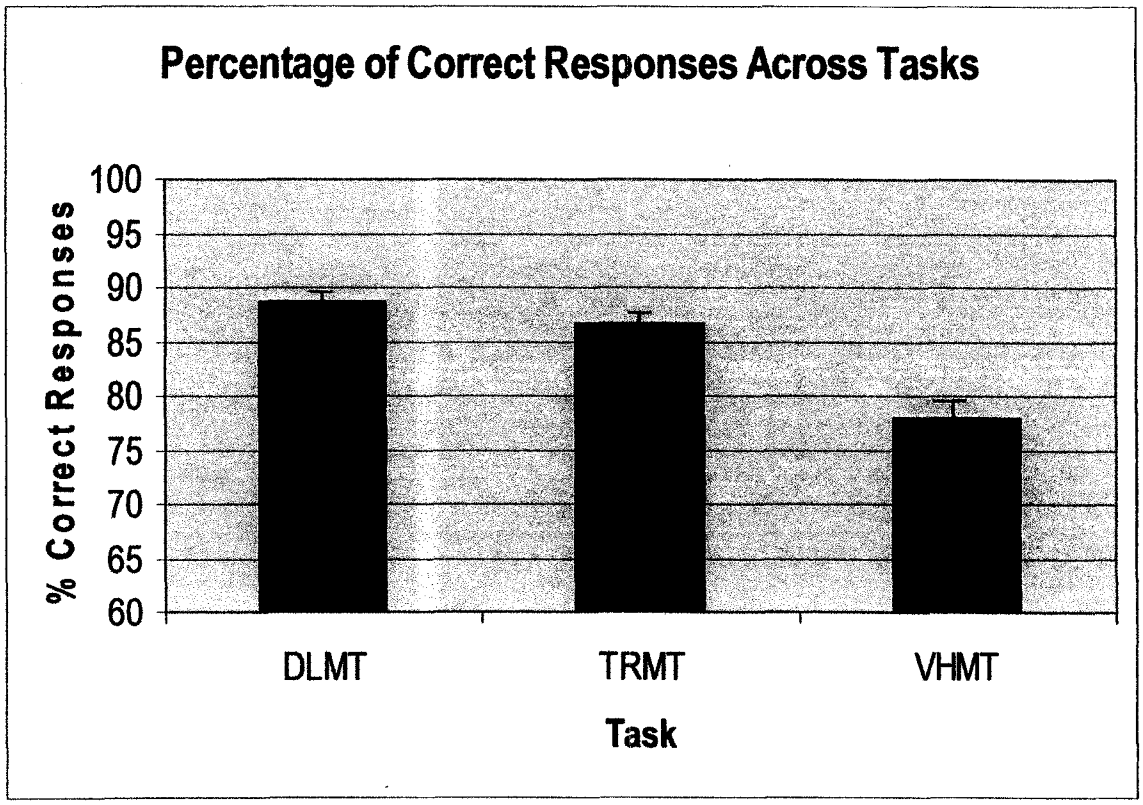
combined. There were no correlations among the three laterality tasks. That is, one's cognitive asymmetry on one task did not predict asymmetry on other tasks.

Within each task, when the two groups were combined, there were positive correlations between the immediate and delayed conditions of the DLMT and between the immediate and delayed condition of the VHMT ($p < .01$). For the TRMT, there was no correlation between the immediate and delayed conditions. When the groups were examined separately, there were correlations between the immediate and delayed conditions on all three tasks in the younger group and a negative correlation between the delayed condition of the DLMT and the delayed condition of the TRMT but the only correlation in the older group was between the immediate and delayed conditions of the DLMT.

3.3 Difficulty Level of Tasks

There was a main effect of Task, $F(2, 58) = 15.64$, $p < .01$ and Age, $F(1, 59) = 37.15$, $p <.01$, but no Task by Age interaction (F=2, 58) =. 41, $p = .67$. Pairwise comparisons showed that the overall performance on the VHMT was lower than on the other two tasks. There was no difference between the DLMT and the TRMT (Figure 9).

Figure 9. The graph showing the percentage of correct responses for the immediate condition of each task (both sides combined).



Note: DLMT = Dichotic Listening Memory Test
TRMT = Tactile Recognition Memory Test
VHMT = Visual Hemifield Memory Test

4.0 Discussion

4.1 Summary of Findings

The aim of the present study was to investigate age differences in hemispheric asymmetry using novel lateralized recognition memory tasks. This is the first study to date in which three different modalities in the same participants using a memory paradigm have been investigated. Using these tasks, the current theories in hemispheric asymmetry and aging research (i.e., the RH aging and the HAROLD hypotheses) were considered. The results of the present study did not fully support either hypothesis: age-related differences in hemispheric asymmetry from the DLMT supported the RH aging hypothesis but not the HAROLD hypothesis. In addition, when laterality-index scores were correlated among the three tasks, performance on one laterality task did not predict performance on the other tasks; however, the results indicated age differences in recognition memory performance on the DLMT and TRMT.

4.2 DLMT

The younger group performed better than the older group on the DLMT, consistent with earlier dichotic-listening studies (Alden, Harrison, Snyder, & Everhart, 1997; Gootjes, Strien, & Bouma, 2004; Hallgren, Larsby, Lyxell, & Arlinger, 2001). Also consistent with previous findings was the REA in both older and younger groups (Alden et al., 1997; Gootjes et al., 2004; Hallgren et al., 2001; Kimura, 1967) and an age-related decrease of left-ear performance (Alden et al., 1997; Bellis & Wilber, 2001; Clark & Knowles, 1973; but see Nebes et al., 1983's report of no age by ear interaction). The HAROLD model suggests a reduction in hemispheric asymmetry in older individuals but this was not the finding obtained here .

Several theories have been proposed to explain this increased ear asymmetry in the older individuals. The RH aging theory (Goldstein & Shelly, 1981) proposes that the functions of the RH decline faster with age than the functions of the LH. Therefore, the left ear would be more susceptible to an age-related decrease in dichotic-listening performance. Although the RH aging theory generated much interest in the past two decades, accumulated findings do not consistently support the global RH aging hypothesis (Cherry et al., 1995; Mittenberg et al., 1989; Schear & Nebes, 1980; Janowsky et al., 1996). Another theory that may explain the decline in left-ear performance is the corpus callosum deficit theory (Goldstein & Braun, 1974), which suggests that an age-related decrease in corpus callosum size causes less efficient transmission of the information from the left ear to the LH and therefore results in decreased left ear performance in older individuals. The corpus callosum serves a critical function in transmitting verbal information from the left ear via the RH to the language areas on the left (Kimura, 1967). Certainly, there is evidence that the size of the corpus callosum decreases with age (Sullivan et al., 2001; Weis, Jellinger, & Wenger, 1991) and that the size correlates with performance on dichotic-listening tasks in healthy individuals (Clarke, Lufkin, & Zaidel, 1993; Yazgan, Wexler, Kinsbourne, Peterson, & Leckman, 1995) and in patients with neurological diseases affecting white matter (Gadea et al., 2002; Reinvang, Bakke, Hugdahl, Karlsen, & Sundet, 1994).

The present study was the first to investigate immediate and delayed memory performance using a dichotic-listening procedure. The results of the DLMT showed that the encoded information was retained over a delay in the younger group for both sides but in the older group some information encoded by the right ear was lost whereas the information encoded by the left ear was retained. Research in memory and aging has shown evidence of age-related changes in both encoding and retention of episodic memory (Backman et al., 2001; Park & Gutchess, 2005). Both the frontal and medial temporal lobes have been shown to be critical to episodic memory (Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003). Raz et al. (2004) reported age-related changes in the prefrontal cortex and hippocampal regions without coincidental changes in hemispheric asymmetry. Because the present study is the first to investigate immediate and delayed memory of dichotically presented information, it is currently unclear why the difference in retention between the two hemispheres exists in older individuals. Therefore, further research is necessary to replicate the present findings.

4.3 TRMT

The younger group performed better on the TRMT task overall consistent with previous studies (Price et al., 1980; Riege et al., 1980). This finding (e.g. Price et al., 1980) has been partially explained by an age-related decrement in tactile sensitivity emerging from changes in mechanical properties of the skin with advanced age (Ivy, MacLeod, Petit, & Markus, 1992; Kenshalo, 1986). However, the change in tactile performance appears to be due to more than just peripheral changes associated with aging. Woodward (1993) reported an age-related decline in tactile discrimination thresholds even after controlling for skin sensitivity, and Resnick et al. (2000) found age differences in the area of the brain that is associated with tactual processing, the parietal cortex.

There was no side advantage in performance overall, which is in agreement with some of the previous tactile research findings that found no side advantage in normal individuals (Fontenot & Benton, 1971; Milner & Taylor, 1972) but is inconsistent with other findings that have found a left-hand advantage (Benton et al., 1973; Dodds, 1978; Koenig, 1987). However, most previous studies utilized different types of tactile stimuli that usually contained visuospatial characteristics (i.e., shapes and forms) except Koenig (1987). Koenig used six artificial textures consisting of a number of 0.5 mm high components in a bimanual recognition task but still found a left-hand advantage. However, Koenig used a cross-modal recognition method, in which a visual board that consisted of two-dimensional representations of the textures drawn in ink was shown and the participant was required to verbally indicate the correct choices. Therefore, it is difficult to determine whether the effect that was found was associated with the RH advantage of processing visuospatial information or processing textures. The present study was the first to examine tactile memory using textures obtained from the environment (i.e., non-artificial) as stimuli using an intramodal recognition method. Therefore, it is possible that the results obtained in the present study were a result of the equal capability of the hemispheres in processing these textures.

Another explanation for the failure to find a side advantage in the present study could be the use of a unimanual method rather than a bimanual method. Minami et al. (1994) indicated that there were differences between bimanual and unimanual presentations and that the effects related to hemispheric specialization were more evident with simultaneous presentation of stimuli to both hands. However, previous studies have found a left-hand advantage using unimanual methods in tactile research (Benton et al., 1973; Dodds, 1978; Harris, 1980).

More recent studies have used both unilateral and bilateral methods and found that both hemispheres are equally capable of processing tactile information (Brown &

Sainsbury, 2000; Clark & Geffen, 1990). Clark and Geffen examined judgments of simultaneity for somatosensory stimuli using both unilateral and bilateral conditions. Both index fingers were stimulated in the bilateral condition, whereas the index and middle fingers were stimulated in each unilateral condition (i.e., within left hand, within right hand). Participants had to report whether the two stimulus events occurred simultaneously. Clark and Geffen reported no difference in simultaneity thresholds for the bilateral condition (i.e., left hand stimulation preceding right hand; right hand stimulation preceding left hand). They also reported no difference in threshold values when the two unilateral conditions were examined suggesting that both hemispheres are equally capable of processing temporal tactile information.

Similarly, Brown and Sainsbury (2000) examined hemispheric asymmetry, interhemispheric transfer time, and age-related differences in judgments of simultaneity to tactile stimulation. Participants judged whether pairs of tactile stimulation to index and middle fingers were delivered simultaneously. Results of both bimanual and unimanual conditions supported a model of hemispheric equivalence in that both hemispheres were equally capable of making judgments of simultaneity to fine tactile stimuli. However, the older adults had significantly higher simultaneity thresholds than younger adults.

Therefore, the present findings along with previous findings (Brown & Sainsbury, 2000; Clark & Geffen, 1990; Fontenot & Benton, 1971; Milner & Taylor, 1972) suggest that when the visuospatial aspects of tactile information are minimized, the two hemispheres are equally capable of processing tactile information.

The results of the TRMT on the immediate and delay memory conditions reflect the participants' abilities to encode and retain tactile information. Encoding and retention of the tactile information were different between the two age groups. Age-related declines in encoding and retention of tactile information mimics that for verbal or visuospatial information (Backman et al., 2001; Park & Gutchess, 2005).

4.4 VHMT

Age-related changes in hemispheric asymmetry were not found on the VHMT task, and this is consistent with most previous studies (Cherry et al., 1995; Ellis & Oscar-Berman, 1989; Nebes, 1990; Obler et al., 1984 but see Elias & Kinsbourne,1974, who showed an age-related hemispheric asymmetry in females only). In contrast to previous findings, the present results did not show an age effect (Cherry et al., 1995; Nebes et al., 1983; Obler et al., 1984) or a side advantage (Kimura, 1966; McKeever, 1986). There are two possible explanations for the absence of age differences. One is that there are no age-related differences in cognitive abilities or processes involved in performing the VHMT. The VHMT is different from previous tasks in that only recognition memory rather than processing speed was measured. Processing speed has been shown to decrease with aging and previous visual hemifield studies have supported this notion (Cherry et al., 1995; Craik & McDowd, 1987; Jenkins et al., 2000; Kimura 1966; Nebes et al., 1983). However, the absence of decline because of not using a speeded task is unlikely given previous findings that indicate age-related differences in visuospatial memory (Shelton et al., 1982; Schear & Nebes, 1980). The absence of side advantage was also surprising given that visuospatial memory is associated with functioning of the right temporal lobe, including the hippocampus (Kimura, 1963; Miner, 1971) and that difficult-to-verbalize stimuli used in the present study likely limited verbal encoding of the stimuli. Another, more plausible explanation for the absence of age difference is the nature of the VHMT that prevented the measurement of false positive responses for each side.

4.5 Intercorrelations among tasks

The results of the present study showed that there were no systematic age-related changes in hemispheric asymmetry. That is, there were no consistent correlations among the three tasks. The independence of asymmetries measured by the three tasks is consistent with previous studies that have correlated various laterality tasks and failed to find any relations (Andresen & Marsolek, 2005; Cherry et al., 1995; Hellige et al., 1994; Jäncke et al., 1992; Teng, 1981; Wexler & King, 1990). For example, Jäncke et al. used seven different dichotic-listening tests (free recall of digit lists, free recall of consonant-vowel syllables, four different consonant-vowel syllable monitoring paradigms, and free recall of Morse codes) and found variable reliability scores and generally low intertest correlations. Cherry et al. (1995) used three different visual hemifield tasks (consonant-vowel-consonant nonsense trigrams, chair identification, and face processing) and also found no asymmetry correlations. This suggests that different laterality tasks measure and reflect very different aspects of hemispheric asymmetry. That is, even when participants are tested entirely within a single modality, performance asymmetries are often a combination of factors such as the direction and degree of hemispheric specialization for specific parts of information processing, complementarity of asymmetry, and interhemispheric communication (Hellige, 1993).

4.6 A comment on models of neurocognitive aging

The findings of the present study along with previous research findings in hemispheric asymmetry and aging suggest that it is difficult or perhaps impossible to find a common factor that explains age-related changes in neurocognitive functioning. However, researchers nonetheless continue to search for a common factor that could explain the neurocognitive aging processes. With the emergence of neuroimaging techniques, researchers have begun to explore in vivo neuroanatomical age-related changes and neuroanatomical correlates of cognitive processes. Neuroimaging studies have found age-related changes in the brain, more so in the frontal and temporal regions than in parietal and occipital lobes but the findings have been mixed (Raz et al., 2004; Raz, 2005; Resnick et al., 2000).

A hypothesis that currently seems to be dominating the field of psychology of aging is the frontal lobe hypothesis of neurocognitive aging, which states that cognitive functions supported by these areas are more susceptible to age effects than functions that depend on posterior and subcortical areas (West, 1996). Indeed, there is evidence for relative age-related changes in the frontal cortex, in terms of general decreased volume, decreased frontal myelin, development of neurofibrillary tangles, neurotransmitter responsivity, decreased metabolic activity, and decreased number of synapses and dendrites (Albert, 1993; Fulop & Seres, 1994; Gibson, 1983; Raz et al., 2004; Salmon et al., 1991; Uylings et al., 2000). However, the past tells us that one hypothesis is never enough to explain the complexities involved with the neurocognitive aging process. For example, just as it is the case that the entire RH does not age faster than the LH, not all frontal areas are implicated in cognitive aging, and not all cognitive aging depends on neuronal loss in the frontal cortex. Relevant age-related changes occur in other areas such as the temporal and parietal cortices as well as in the subcortical systems (Greenwood, 2000; Raz et al., 2004; Raz, 2005; Resnick et al., 2000).

Similarly, another emerging hypothesis of aging is the dopamine hypothesis, which states that the loss of dopamine receptors in the basal ganglia, the anterior cingulate, and the prefrontal cortex can explain a variety of age-related changes (Backmann et al., 2000; Braver et al., 2001; Li, Lindenberger, & Sikstrom, 2001). For example, Li et al. showed how loss of dopaminergic support can explain age effects on working memory, selective attention, and inhibition. Although the support for the new hypotheses may appear promising, a similar caution against extending the findings more broadly than warranted should be applied when interpreting results.

5.0 Conclusions

5.1 General Conclusions

The results of the present study do not fully support the RH aging hypothesis, which predicts a decrease with age in RH functioning, or the HAROLD hypothesis, which predicts a decrease in asymmetry in the frontal lobe functioning. Age-related cognitive effects appear to be heterogeneous depending on the task and the associated cognitive processes involved. Although many researchers have identified and continue to aim to identify a common factor that could capture the plethora of age-related changes, there seems to be no unitary factor that is broad enough to explain neurocognitive changes that occur with aging.

5.3 Directions for Future Research

Given the findings of the present study, it would be interesting to conduct further studies using the DLMT and the TRMT given the dearth of research in memory and lateralized tasks. The first step would be to establish reliability of the tests by replicating the findings and conducting reliability studies (e.g. test-retest, split-half). Once the reliability of the test instruments has been established, other studies could ensue. Regarding the DLMT, it would be interesting to examine recall versus recognition performance of each side given that aging affects recall more than recognition (Craik & McDowd, 1987; Kemps & Newson, 2006). Regarding the TRMT, it would be interesting to examine the TRMT using both bimanual and unimanual methods to see if there is a difference in hemispheric asymmetry given previous research findings showing that bimanual tasks are more sensitive in detecting hemispheric differences than unimanual tasks (Minami et al., 1994). In addition, for both tasks, distractor stimuli could be given more than once (in contrast to the present experiment in which each stimulus was only used once) in order to increase the difficulty of the task and also to investigate the performance difference between the present method and this method.

Another important step would be to examine the construct validity of these measures. One method would be to utilize functional neuroimaging techniques to examine the neuroanatomical correlates of these tasks. Another method would be to study individuals with right or left-sided brain dysfunction, such as patients with epilepsy, in order to determine whether the dysfunctional side is associated with poorer performance. It would be important to study individuals before and after temporal lobe excisions to determine whether the performance changes with surgery.

5.3 Practical Implications

The results from the DLMT suggest that older individuals would likely to remember information that is presented to the right ear more than to the left. This finding can be applied to people's daily functioning in a sense that when an older person is speaking on the telephone, he or she should put the phone to his or her right ear. In addition, this finding can be applied in a public setting. For example, when one wishes to present in front of older individuals in an enclosed setting, one may wish to set up the podium on the right side of people or set up the speaker in such a way that information could be detected well by people's right ear. This will likely facilitate the older individual's ability to absorb and retain information.

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Appendix A

Edinburgh Handedness Inventory

Participant Code: ________Date of Birth____________Age_____ Sex_______

Please indicate your preferences in the use of hands in the following activities by putting + in the appropriate column. Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, put ++. If in any case you are really indifferent put + in both columns.
Some of the Activities require both hands. In these cases that part of the task, or object, for which hand preference is wanted is indicated in brackets.
Please try to answer all the questions, and only leave a blank if you have no experience at all of the object or task.

		Left	Right
1	Writing		
2	Drawing		
3	Throwing		
4	Scissors		
5	Toothbrush		
6	Knife (without fork)		
7	Spoon		
8	Broom (upper hand)		
9	Striking Match (match)		
10	Opening box (lid)		
i	Which foot do you prefer to kick with?		
ii	Which eye do you use when using only one?		

Appendix B

Health Questionnaire

Background Information

Participant Code:

General Information

Do B/Age
Sex
Language (native, age, most frequent)
Handedness (writing, always?)

Education and Work History

Highest education
Learning problems?
Occupation
Other

Medical History

Previous hospitalizations
Stroke/TIA
Brain surgery/tumour
Head trauma (LoC, hospitalized overnight)
Seizures or epilepsy
Other neurological disorders (MS, PD, HD, CP, AD)
Cancer (time of dx, treatment)
Diabetes/Thyroid/HBP
Heart attack (cognitive change 24 hours later)
Carpal tunnel syndrome
Paget's disease
Birth history & developmental milestones
Numbness
Mental or emotional problems requiring treatment
Alcohol use (# per day)
Tobacco use
Colour blindness
Medication

Other

Memory

Complaints?
Examples
Type of memory affected (immediate, recent, remote)
Duration
Family History

Other Cognitive Skills

Concentration (focus, distraction)
Word-finding
Understanding conversation
Understanding reading material
Problem Solving
Driving

Mood

Sad/depressed?
Anxious/worried?

Other

Appendix C

Description of Distractor Tasks

WMS-III Digit Span

The first part of this two part test is the forward span in which the experimenter says a series of digits at one digit per second and the participant repeats the digits in the same order. The second part of the test is the backward span in which the participant is asked to repeat the digits backward. There are two trials per block, with the number of digits per trial ranging from two to nine in both forward and backward parts. The test is discontinued either when the participant misses both trials of a particular level or when all the trials are given, whichever comes first. The total number of correct trials and the longest forward and backward spans are measured.

WMS-III Spatial Span

This task is analogous to the Digit Span task except the experimenter taps a series of raised blocks on a board at a rate of one block per second and the participant repeats this pattern. The second part of the test is the backward span in which the participant taps the blocks in a pattern that is the reverse of the pattern presented by the experimenter. In the forward span the number of blocks increases after every second trial going from two to nine and in the backward span the umber increases from two to eight. The test is discontinued either when the participant misses both trials of a particular level or when all the trials are given, whichever comes first. The total number of correct trials and the longest forward and backward spans are measured.

WRAT-3 Reading

The participant reads aloud a series of words printed on a card and the number of correct responses is recorded. The test is discontinued when ten consecutive failed responses are observed or when all the words are read.

Trail Making Test Part A and Part B

In Part A, participants are asked to connect 25 randomly arranged numbers in numeric order as quickly as possible. In Part B, the participants connect 25 numbers and letters in alternating order with increasing number and alphabetical order as quickly as possible. The completion time of each part is measured.

Grooved Pegboard

The Grooved Pegboard consists of a metal board with a matrix of 25 randomly positioned holes. The participant fits the pegs into peg holes as quickly as possible in sequence, first with the right hand and then with the left hand. The completion time for each hand is measured.

Appendix D

Descriptive Statistics on Distractor Task Measures by Age Group (raw scores)

	Younger				Older			
Measure	Min.	Max.	Mean.	S.D.	Min.	Max.	Mean.	S.D.
WRAT-III Reading	38	55	47.16	3.93	43	57	52	4.38
Digit Span Forward Total	7	15	10.89	2.06	7	14	9.94	2.27
Digit Span Backward Total	4	12	6.87	1.77	4	11	6.44	1.83
Digit Span Total	11	25	17.76	2.98	11	25	16.50	3.69
Longest Digit Span Forward	5	9	6.91	1.14	5	8	6.50	1.03
Longest Digit Span Backward	3	7	5.00	1.13	3	7	4.75	1.18
Spatial Span Forward Total	6	13	8.93	1.62	4	10	6.69	1.62
Spatial Span Backward Total	5	11	8.02	1.32	6	8	6.44	0.81
Spatial Span Total	13	22	17.00	2.33	10	17	13.13	2.03
Longest Spatial Span Forward	4	8	6.16	0.82	3	6	4.75	1.07
Longest Spatial Span Backward	4	8	5.49	0.87	4	6	4.56	0.73
Trail Making Test A	12	45	19.62	6.26	19	44	31.63	7.78
Trail Making Test B	24	78	48.84	13.63	49	136	88.13	27.11
Grooved Pegboard Right	48	74	59.71	6.40	64	155	91.15	25.60
Grooved Pegboard Left	43	74	63.82	6.48	67	126	93.92	18.42

WRAT-III = Wide Range Achievement Test – Third Edition

Appendix E

Order of Task Presentation

Interview

Edinburgh Handedness Questionnaire

Mini-Mental State Examination (Older group only)

Bells Cancellation Test

Tactile Form Recognition Test

Visual Hemifield Memory Test-presentation of stimuli and immediate recognition

Dichotic-listening Memory Test-side 1-presentation and immediate recognition

Tactile Recognition Memory Test-side 1-presentation and immediate recognition

Visual Hemifield Memory Test -delayed recognition

Dichotic-listening Memory Test -side 1-delayed recognition

Tactile Recognition Memory Test -side 1-delayed recognition

Dichotic-listening Memory Test-side 2-presentation and immediate recognition

Tactile Recognition Memory Test -side 2-presentation and immediate recognition

Trail Making Test A &B

Spatial Span

Dichotic-listening Memory Test -side 2-delayed recognition

Tactile Recognition Memory Test -side 2-delayed recognition

Digit Span

WRAT-3 Reading

Grooved Pegboard Test

Appendix F

A Sample List of Textures Used

- Bubble pad
- Corduroy
- Corrugated fiberglass roofing
- Different grits of sand paper
- Expanded aluminum
- Flannel
- Foam carpet under-pad
- Foam packing material
- Half-round moulding
- Metallic coarse weave
- Nylon
- Plastic light diffuser
- Plush carpet
- Quilted mattress cover
- Rough side of tempered masonite
- Scotch-brite scouring pad
- Silk
- Wire mesh

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