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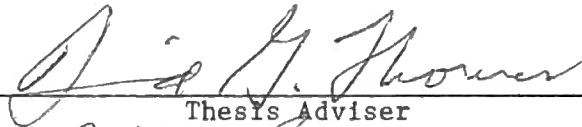
IN DEXTRALS AND SINISTRALS

By

CARY R. SAVAGE

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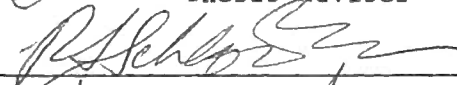Greeley, Colorado
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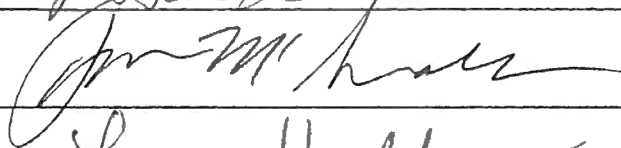Oklahoma State University
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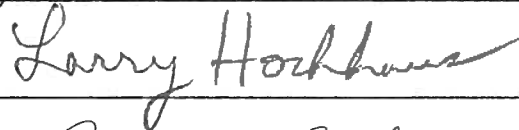the requirements for
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INFORMATION PROCESSING DIFFERENCES

IN DEXTRALS AND SINISTRALS

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Abstract

Visual evoked potentials (VEP) were collected from 40 males (20 left-handed and 20 right handed) during a simple reaction time (SRT) task to lateralized visual stimuli. Analysis of the SRT data indicated significant handedness by response hand and handedness by visual field interactions, with right-handers exhibiting the greatest effects. VEP N160 data showed only very robust hemisphere by visual field interactions, reflecting non-confounded effects of direct vs indirect stimulation, or interhemispheric transfer time (IHTT). Left- and right-handers did not differ in IHTT estimates from SRT (dextrals = 2.48 msec, sinistrals = 3.52 msec) or VEP N160 (dextrals = 6.37 msec, sinistrals = 6.71 msec) estimates. Finally, no significant correlations were found between SRT and VEP estimates of IHTT, nor between any of the SRT and VEP measures. It is concluded that left-handers and right-handers do not differ in IHTT at the splenium of the corpus callosum, nor do they differ in basic input mechanisms and initial processing in the visual cortex. It is proposed that differences between dextrals and sinistrals likely occur during complex tertiary cortical processing, and left-handers are less lateralized for this activity. Furthermore, these processes do not appear to be reflected in VEPs from occipital sites.

Information Processing Differences

in Dextrals and Sinistrals

The fact that individuals vary in their patterns of cerebral dominance has attracted much attention in the past, and continues to be the focus of considerable research. These differences in hemispheric control are believed to be reflected in the choice of dominant hand (Hardyck & Petrinovich, 1977; Kertesz, Black, Polk, & Howell, 1986; Witelson, 1985). For instance, right-handers (dextrals) are generally left hemisphere dominant for motor and language skills, while right hemisphere dominant for spatial tasks. Left-handers (sinistrals), by comparison, exhibit less consistent patterns of lateralization (Bryden, 1965; Carter, Hohenegger, & Satz, 1980; Combs, 1983; Fennell, 1986; Hardyck & Petrinovich, 1977; Hecaen & Sauguet, 1971; McKeever, 1986; McKeever & VanDeventer, 1977; Poston & Savage, 1985; Savage, Holloway, Thomas, & Poston, 1988; Shimizu & Endo, 1983). The focus of the current paper will be on these differences in cerebral organization between left- and right-handers. For the purposes of the current study, and convention, the terms "left-handed" and "right-handed" will refer to individuals who are primarily left- or right-dominant for a variety of motor functions.

Cerebral Determinants of Handedness

Before the following review can focus on cerebral differences, it must first be established that it is, in fact, cerebral processes which determine handedness, and not simply some peripheral process. If peripheral asymmetries are determinants of handedness then one would expect, for example, that the peripheral nerves in the right

arms of right-handers would conduct sensory information more quickly than the same nerves in the left arm. This asymmetry would presumably be reversed for left-handers. Tan (1985) tested this possibility by comparing speed of sensory conduction of the median and ulnar nerves between the right and left arms of dextrals and sinistrals. Tan did not find significant differences in nerve conduction velocities for any of the subjects tested, and concluded that speed of nerve conduction did not contribute to handedness.

Support for the importance of central nervous system (CNS) variation in right- and left-handers comes from findings of measurable differences between the brains of the two groups. Kertesz et al. (1986), for instance, found differences in left-right hemisphere asymmetries between the brains of dextrals and sinistrals. Using Magnetic Resonance Imaging (MRI), they discovered that the sulcular demarcation of the posterior operculum in the parietal cortex was greater in the right hemisphere of most right-handers than in their left hemisphere. They did not find this lateral asymmetry in the brains of left-handers. In a post-mortem anatomical study, Witelson (1985) found significant differences in the thickness of the corpus callosi of dextrals and sinistrals. She found that the corpus callosum was larger in left-handers by about 11%. Finally, in a review of the literature, Hardyck and Petrinovich (1977) concluded that behavioral studies and clinical lesion studies also indicated differences in the cerebral organization of dextrals and sinistrals.

In summary, it appears that differences between dextrals and sinistrals cannot be accounted for by peripheral processes alone,

such as nerve conductivity (Tan, 1985). Furthermore, there are

studies identifying anatomical differences (Kertesz et al., 1986;

Witelson, 1985), as well as functional differences (Hardych and

Petrinovich, 1977) between the brains of right- and left-handers.

The current author, therefore, concludes that differences in cerebral

organization are major determinants of handedness, and that these

differences constitute the most productive direction for future

research. Specifically, left- and right-handers may differ in their

ability to process information within each cerebral hemisphere. The

study of these differences in cerebral lateralization is believed to

be important in defining the etiology of handedness, as well as

providing normative functional descriptions of the two groups for

purposes such as clinical neuropsychology.

Handwriting Posture

One way to approach the study of cerebral organization is to

focus on differences in handwriting posture among left-handers.

Specifically, the differences involve whether or not a sinistral

curves his/her wrist over the paper when writing (an inverter), or

writes with more standard posture (a non-inverter). Levy and Reid

(1976; 1978) proposed that a relationship exists between handwriting

posture and underlying cerebral organization, particularly

organization for speech and spatial skills. They hypothesized that

left-handed inverters actually have the same underlying cerebral

organization for speech as right-handers, that is, with speech

located in the left hemisphere and spatial skills in the right.

Furthermore, these left-handed inverters were proposed to have

ipsilateral motor control of their hands. Thus, the motor commands would be initiated ipsilaterally, and the signals sent to the contralateral hemisphere for execution. Conversely, sinistrals who do not invert when they write were hypothesized to possess right hemisphere control of language and left hemisphere control of spatial functions.

While this focus on handwriting posture has generated a great deal of research, there is little conclusive evidence supporting the link between handwriting posture and underlying cerebral organization. For example, in a choice reaction time test, left-handed inverters were found to display motor and visuo-motor organization similar to left-handed non-inverters and right handers (Bradshaw, Nettleton, & Spehr, 1982). Results such as this indicate no relationship between handwriting posture and underlying cerebral organization. In two recent reviews of the literature (Fennell, 1986; Weber & Bradshaw, 1981), the authors conclude that Levy's hypotheses are not supported by empirical data from a variety of tasks, in visual, auditory, and verbal modes. Thus, this does not appear to be a productive approach to take, since it has not been reliably demonstrated that posture differences actually relate to underlying CNS organization.

Diffuse Cerebral Organization of Sinistrals

An alternative approach to the study of cerebral differences is to focus on the more diffuse CNS organization of sinistrals. Several investigators have proposed that left-handers are less highly lateralized than right-handers (e.g., Fennell, 1986; Poston & Savage,

1985; Savage et al., 1988). In other words, right-handers are more completely right-dominant, while left-handers are more mixed in their dominance. For instance, while dextrals normally have strong left hemisphere control of language (e.g., Geschwind, 1984), sinistrals are more bilateral in their processing of language (Fennell, 1986; McKeever, 1986; Miller, 1983; Tankle & Heilman, 1982). In a review of the literature, Carter et al. (1980) reported on previous studies which indicated that 95% of right-handers, but only approximately 24% of left-handers, had unilateral left hemisphere control of language. Thus, according to these figures, approximately 76% of the sinistral group had some degree of bilateral representation of language. These figures are also consistent with more recent research (Fennell, 1986; McKeever, 1986; Miller, 1983; Tankle & Heilman, 1982).

Bryden (1965), McKeever and VanDeventer (1977), and Piazza (1980) have demonstrated that left-handers show less evidence of lateral asymmetry in their performance on dichotic listening tasks. Dextrals are more consistently right ear dominant for these tasks, while sinistrals are less consistent in their superiorities. In the earliest of the three studies (Bryden, 1965), dextrals and sinistrals were compared on dichotic listening and tachistoscopic verbal recognition tasks. Dextral subjects were consistently more accurate with right side data presentations. Sinistrals, however, failed to show these consistent accuracy differences between right and left side tachistoscopic presentations, and were also much more variable in their laterality scores on dichotic listening.

Left-handers are less consistently lateralized on other measures

of laterality as well. For instance, Combs (1983) found greater congruence in right preferences on four performance measures of laterality (hand dominance, eye dominance, upper thumb and upper hand when hands are clasped). The most frequently observed pattern of laterality was that of total right dominance among both males and females. Individuals who were left dominant for any one measure, however, were much more diverse in their preferences on the other measures. In an unpublished study of 99 left- and right-handed individuals, Poston and Savage (1985) found that dextrals were more highly lateralized than sinistrals on a manual performance test, and on the Dean Laterality Preference Schedule (Dean, 1978). Savage, et al. (1988) also found fewer left and right hand speed differences on simple reaction time and finger oscillation tests among left-handers, when compared to right-handers.

Further support for the proposed diffuse lateralization of sinistrals comes from clinical studies of brain-damaged individuals. Among right-handers, for example, left hemisphere damage frequently results in disruption of oral language, reading, or writing; these symptoms are rarely the result of right hemisphere lesions (Hecaen & Sauguet, 1971; Reitan & Wolfson, 1985a). Hecaen and Sauguet (1971), however, found comparatively fewer differences between left-handed patients with right hemisphere brain damage and those with left hemisphere brain damage. In other words, the pattern of impairment among brain damaged sinistrals was less dependent on which particular hemisphere was lesioned. To illustrate this, they looked at differences between the two hemispheres on 50 types of symptoms in

brain damaged right- and left-handers. They found 47 significant between-hemisphere symptom differences among right-handers, and only 4 for left-handers. The researchers also found that damage to one side of the brain in left-handers often resulted in a pattern of deficits more commonly associated with damage to the opposite cerebral hemisphere. Finally, they noted that sinistral patients generally recovered behavioral functions more rapidly than dextrals following head injury. Hecaen and Sauguet interpreted the above observations as supporting the hypothesis of more diffuse lateralization among left-handers. It is important to add, however, that even left-handers showed some functional hemispheric asymmetries. Thus, although sinistrals were generally less highly and less consistently lateralized than dextrals, they were by no means completely ambilateralized.

Hardych and Petrinovich (1977) reviewed a series of studies and found, as did Hecaen and Sauguet (1971), that sinistral patients consistently showed greater recovery of functions following unilateral brain damage than right-handers. They concluded that left-handers are, as a group, less highly lateralized than their right-handed counterparts. Finally, as previously noted, Kertesz et al. (1986) found differences in anatomical asymmetries, as measured by MRI, between dextrals and sinistrals. They found that the right hemisphere of dextrals showed greater sulcular demarcation in one location of the parietal lobe, than in the corresponding site of the left-hemisphere. Sinistrals, however, did not demonstrate any such lateral asymmetries between the two hemispheres, as measure by MRI.

In summary, the research literature suggests that those individuals labeled "left-handed" are actually more ambilateralized than exclusively left-dominant. Indeed, the existence of highly lateralized left-handers appears to be a somewhat infrequent phenomenon. Furthermore, it is concluded that the study of lateralization differences is a productive approach to the overall question of cerebral organization of left- and right-handers. The more diffuse lateralization of sinistrals has been consistently demonstrated in the literature, as has its association with underlying CNS organization.

The Question of Cognitive Deficits Among Sinistrals

In taking this approach to dextral-sinistral differences, however, another issue is presented. The issue is as follows: Is the diffuse lateralization observed among left-handers the result of a pathological process and, therefore, indicative of underlying cognitive deficit (Bakan, 1974; Barry & James, 1978; Briggs & Nebes, 1976; Geshwind, 1984; Levy, 1969; Soper & Satz, 1984; Yeo & Cohen, 1983); or is it simply a reflection of naturally occurring differences in cerebral organization? In order to help the reader keep the two views separate in the discussion to follow, the former view will be referred to as the "cognitive deficit" perspective, and the latter the "natural variant" perspective.

The Cognitive Deficit Perspective

Researchers who take a cognitive deficit perspective (e.g., Bakan, 1974; Barry & James, 1978; Briggs & Nebes, 1976; Geshwind, 1984; Levy, 1969; Soper & Satz, 1984; Yeo & Cohen, 1983) have

proposed that left-handedness is the behavioral manifestation of compensation for problems in the left cerebral cortex. According to this view, sinistrals suffer from some kind of abnormality in the left hemisphere which forces them to become more diffuse in their lateralization, or even right hemisphere dominant for many functions that would normally be processed in the left hemisphere. A good example of this approach is Bakan (1974), who suggested that sinistrality might be the result of damage to the motor areas of the left hemisphere following perinatal hypoxia.

The cognitive deficit researchers also believe that the functional ambilateralization of sinistrals is a disadvantageous cognitive organizational style. They propose that the ability to isolate a hemisphere is necessary in order to efficiently perform certain cognitive functions, such as those requiring spatial or language skills. Levy (1969), for example, proposed that the bilateralization of language would result in deficits in spatial abilities among left-handers. In a later study (Yeo & Cohen, 1983), it was indeed demonstrated that females with a history of familial sinistrality showed decrements in spatial ability when compared to other groups. These results suggest that it might be some type of complex interaction between sex and lateral dominance which results in deficits in spatial skills, as females have sometimes been noted to have slightly lower spatial abilities (e.g., Yeo & Cohen, 1983).

As further support for the cognitive deficit hypothesis, Soper and Satz (1984) noted a higher incidence of non-right-handedness among the epileptic and autistic. Barry and James (1978) also found

lower levels of lateralization of language among autistic groups. In fact, Barry and James proposed that this lack of clear hemispheric specialization might be one factor which delays or obstructs the development of linguistic abilities among autistics. There is also at least one study suggesting lower intelligence scores among sinistrals. Briggs and Nebes (1976) administered the Wechsler Adult Intelligence Scale (WAIS) to adults of varying lateral dominance. They found that mixed- and left-handers had significantly lower scores than right-handers.

Finally, in a recent review of the literature, Geschwind (1984) proposed a straightforward dichotomy of cerebral dominance, which is consistent with a deficit perspective. What Geschwind labels "standard" dominance includes the majority of the population, who have left hemisphere control of language and handedness, and right hemisphere control of certain other functions. The second, "anomalous" dominance group includes anyone (including left-handers) who does not display this "standard" pattern. In the same review, Geschwind cited support for an association of sinistrality with immune disease and learning disorders, further implicating pathological origins of sinistrality.

The Natural Variant Perspective

Despite the evidence presented for the cognitive deficit perspective, there is an even larger body of research which supports a natural variant approach. For example, many researchers have failed to find a consistent relationship between birth stress, birth weight, prenatal stress, and epilepsy and left-handedness (Tan &

Nettleton, 1980; Dusek & Hicks, 1980; McManus, 1980). They conclude
that these factors are not related to the development of left-
handedness. Annett and Ockwell (1980) examined 217 sinistrals and
254 dextrals for evidence of stressful birth among left-handers.
They found no support for this hypothesis, nor did they find any
evidence of pathology of the left hemisphere among left-handed
individuals. Annett and Ockwell concluded that left-handedness was a
"natural phenomenon" in the majority of cases. Hicks, Dusek, Larsen,
Williams, and Pellegrini (1980) found that, although birth
complications might be associated with a decrease in right-
handedness, the numbers were not strong enough to account for left-
handedness. Simply stated, they believe that birth stress does not
actually "cause" sinistrality. Finally, in two different reviews of
the handedness literature (Hardyck & Petrinovich, 1977; Sunseri,
1982), it was concluded that there is no conclusive empirical support
for the proposed cognitive deficits among left-handers.

The cognitive deficit perspective is based partially on the
assumption that hemispheric specialization is advantageous for many
tasks, such as visual-spatial skills (e.g., Levy, 1969).
Interestingly, however, there is evidence that the decreased
lateralization of sinistrals might actually be advantageous for many
tasks, including those requiring spatial skills. Burnett and Lane
(1982), for instance, found that ambidextrous individuals
demonstrated increased spatial abilities on the Spatial Visualization
section of the Guilford-Zimmerman Aptitude Survey (Guilford &
Zimmerman, 1953). The lowest performance was found among subjects

who were either extremely right- or extremely left-handed. Furthermore, in a same-different choice reaction time task, non right-handers were found to be superior to right-handers (Beaumont & Dimond, 1975).

On a dichotic listening task, Lombardi (1982) concluded that the ambilateralization associated with sinistrality was an advantageous organizational style. Sinistrals processed dichotic material (in the form of consonant-vowel combinations) as accurately as dextrals in the left hemisphere, and better than dextrals in the right hemisphere. Not only was there no indication of left hemisphere handicap among left-handers, but there was also evidence for right hemisphere superiority. In a longitudinal study of dextrals and sinistrals, Kilshaw and Annett (1983) found that left-handers and ambi-handers were better at a peg moving task than right-handers. They hypothesized that dextrals were inferior in visuo-motor skills because of a right hemisphere motor deficit. Finally, in a recent study by Savage et al. (1988), left handers were found to be faster, although not always significantly, on all conditions of reaction time and finger tapping tests. It appears, therefore, that left-handers are at least as efficient as right-handers on visual-motor and motor tasks, despite their decreased lateralization for those skills.

In summary, the majority of evidence does not support a cognitive deficit approach, and instead suggests that there may be some advantage to bilateral organization. Thus, the high degree of lateralization found among most right-handers may actually be disadvantageous for some tasks. For instance, Kilshaw and Annett

(1983) did not find a left hemisphere advantage among right-handers
(left-handers and ambi-handers were superior on all conditions), but
did find a strong right hemisphere handicap in the same group (the
left hand of dextrals was dramatically slower than their right hand).
They argued that left-handedness has persisted as a natural variant
in humans because there are some advantages associated with this
cognitive organizational style. There is evidence suggesting that
sinistrality has been present in humans throughout their history.
For example, Spennemann (1984) found evidence of left-handedness
among our prehistoric ancestors by analyzing the grinding striations
of neolithic bone and antler implements.

The natural variant perspective would also be strengthened if a
genetic influence on sinistrality were established. Several
different types of genetic models have been postulated by Levy and
Nagyhaki (1972), Annett (1978), and more recently again by Annett and
Kilshaw (1983). Cioni and Pellegrinetti (1982) found motor and
sensory hemispheric specialization differences in two groups of full-
term newborns. The first group was offspring of right-handed parents
and siblings, while the second group had at least one parent or
sibling who was left-handed or ambidextrous. Lateral differences
were found in stepping, tactile responses, asymmetrical tonic neck
reactions, and time spent in head position. The presence of these
patterns of lateral dominance in the newborn provide support for the
importance of genetics, as there is little time for environmental
pressures to overwhelm genetic predispositions.

Further support for a genetic influence on lateralization comes

from a longitudinal study of dextral and sinistral children by
Fennel, Satz, and Morris (1983). They measured laterality of a group
of five year-olds and found that children who were right- or left-
handed at age five maintained their pattern of hand preference at age
11. This was not the case, however, for children who were initially
ambidextrous. It seems that, at least for children who are
demonstrably right- or left-handed, patterns of handedness are
established very early in life. The existence of a genetic influence
on handedness provides further support for the belief that
sinistrality is a naturally occurring variant in the human
population.

In summary, there seems to be conflicting evidence of increased
learning disorders, epilepsy, and autism among sinistrals (Bakan,
1974; Barry & James, 1984; Briggs et al., 1976; Geschwind, 1984;
Hicks & Dusek, 1980; Soper & Satz, 1984; Sunseri, 1982). There is
also disagreement concerning decreased spatial skills and increased
birth stress among left-handers (Annett & Ockwell, 1980; Burnett et
al., 1982; Dusek & Hicks, 1980; Geschwind, 1984; Hicks, et al., 1980;
Levy, 1969; McManus, 1980; Tan & Nettleton, 1980; Yeo & Cohen, 1983).
Although the most recent and convincing data fail to support a
deficit hypothesis, there is, nonetheless, some evidence of increased
brain pathology among the non-right-handed population. For instance,
Hicks and Dusek (1980) discovered an unexpected relationship between
handedness and giftedness in a group of 969 children: Although they
found that giftedness was associated with a decrease in dextrality,
they also noted an increase in brain pathology among the less

lateralized group. They, nonetheless, interpreted the results as disproving the cognitive deficit hypothesis. Hicks and Dusek instead proposed that the relationship between intelligence and degree of dextrality might be best represented by an inverted-U shaped curve. That is, with both the retarded and the gifted showing a decreased incidence of right-handedness.

Pathological Left-Handedness

This presents the reader with an interesting discrepancy: On the one hand, the vast majority of left-handers do not show any deficits, and may even show superiority on some tasks; on the other hand, there in an undeniable increase in brain pathology among sinistrals. Left-handers seem to be over-represented at both extremes of the functional continuum. This discrepancy may be explained by taking into consideration what Satz (Satz, 1972; Satz, 1973; Silva & Satz, 1979; Soper and Satz, 1984) calls "pathological" left-handedness. This model was specifically developed to account for the higher incidence of sinistrality among the brain-injured. The so-called "pathological" individuals would have, under normal environmental circumstances, developed to be right-handed. Due to some early injury to the left hemisphere, however, they manifest a left-handed preference. "Natural" left-handers, by comparison, are left-handed because of natural environmental and/or genetic factors. The "pathological" left-handers may be largely responsible for the higher incidence of learning disorders, epilepsy, autism, and birth stress observed among left-handers by many of the researchers. This minority of impaired sinistrals may also be deflating the overall

scores of left-handers on spatial skills tests.

To support their model, Silva and Satz (1979) analyzed EEG recordings of dextrals and sinistrals for evidence of asymmetric abnormalities. They found that, while left-handed individuals did have a higher rate of left brain dysfunction than right-handers, abnormal EEG was actually a better predictor of retardation than left-handedness itself.

Further support for the pathological left-handedness model comes from Savage et al. (1988). As stated previously, left-handers were somewhat faster on all conditions of a simple reaction time test. Paradoxically, however, the slowest reaction times came from three of the left-handed subjects. The responses of these three subjects were considerably slower than the group averages from left- or right-handers. The presence of these extreme scores among only a minority (10%) of sinistrals provides support for the concept of "pathological" left-handedness (Satz, 1972; Satz, 1973; Silva & Satz, 1979; Soper and Satz, 1984). It, therefore, appears that this model can account for the increased brain pathology periodically observed among sinistrals.

To sum up the conclusions thus far, most of the studies reviewed are consistent with Annett and Ockwell (1980), who determined that left-handedness is a natural variant in the majority of the population. Support is also found for Lombardi (1982) and Kilshaw and Annett (1983), who proposed that ambilateralization, frequently observed among so-called left-handers, may be a more advantageous style of organization on certain tasks (particularly visual-motor).

Finally, it is concluded that the pathological left handedness model
of Satz (Satz, 1972; Satz, 1973; Silva & Satz, 1979; Soper and Satz,
1984) can account for the increased brain dysfunction among
sinistrals.

CNS Determinants of Diffuse Lateralization

From this point on, the review will concern itself primarily
with naturally occurring left-handedness, which appears to be the
case for the vast majority of left-handers. It has now been
established that sinistrality, and the associated diffusion of
lateralization, reflect a natural variation in the population. Left-
handedness and ambilateralization are, therefore, not normally
associated with cognitive deficits. This brings us back to the
original question: If it is not a pathological process of some kind,
then what pattern of CNS organization is responsible for the
decreased lateralization observed among left-handers?

Anatomical Studies

Some researchers have hypothesized that decreased lateralization
is the direct result of better interhemispheric communication (e.g.
Witelson, 1985). Specifically, the hypothesis states that left-
handers are less lateralized than right-handers because their corpus
callosi transfer information more efficiently. One way to test this
hypothesis is to directly examine the brains of dextrals and
sinistrals. This is the approach taken by Witelson (1985), who found
that the corpus callosum was larger (by about 11%) in left-handed and
ambi-handed individuals than in consistent right-handers. She
proposed that this difference in anatomical connectivity between the

hemispheres is responsible for the differences in degree of lateralization between sinistrals and dextrals.

DeLacoste-Utamsing and Holloway (1982) had previously performed the same type of anatomical comparison between males and females, who also show differences in degree of lateralization. They discovered differences in shape and surface area between the corpus callosi of males and females. The splenium (posterior fifth) was significantly larger in females as compared to males. They also hypothesized that females might have better interhemispheric communication than males. It should be noted that the rational for both studies are based on the assumption of a relationship between size of the callosal commisures and speed of conductivity.

A related, although considerably less invasive, approach is to measure callosal thickness with MRI. In a recent study, Kertesz, Polk, Howell, and Black (1988) measured the area of the corpus callosi of left- and right-handers using this procedure. They did not find significant handedness or sex differences in callosal size, nor did they find a significant correlation between callosal size and measures of lateralization. There is, therefore, some disagreement between various anatomical findings. While two studies suggest a relationship between callosal thickness and decreased lateralization, a more recent study refutes it. Regardless of these results, however, the question of faster communication remains unanswered by anatomical studies. Although some of these studies point to anatomical differences, they do not establish whether or not the corpus callosi of left-handers actually transfer information more

efficiently, which is of course the real question of interest in the present study. In other words, a thicker corpus callosum is not necessarily a faster one.

SRT estimates of IHTT

One paradigm which has been proposed to actually measure the speed of interhemispheric communication, or interhemispheric transfer time (IHTT), was originally developed by Poffenberger (1912). He proposed that IHTT could be estimated by examining the differences in simple reaction times (SRT, tasks that do not require a discrimination to be made before the response) of each hand to stimuli presented in either visual field. Reaction times of the hand ipsilateral to the field of presentation (e.g., right hand, right visual field) were faster than reaction times of the hand contralateral to the field of presentation (e.g., right hand, left visual field). Poffenberger proposed that the difference between the mean reaction times of these contralateral and ipsilateral responses provided accurate estimates of IHTT. His reasoning was based on the knowledge that fibers from the nasal hemiretinae cross at the optic chiasm, while fibers from the temporal hemiretinae do not. Any stimulus presented to a particular visual field will, therefore, be initially represented in the contralateral hemisphere. Knowing that motor movements are controlled contralaterally, he proposed that responses of the ipsilateral hand were faster because all processing could occur intrahemispherically, while contralateral hand responses required interhemispheric communication in order to initiate a response. Due to the simplicity of the SRT task, Poffenberger

assumed that there were no intrahemispheric processing differences between the hemispheres. Thus, any differences between ipsilateral and contralateral responses provided pure estimates of transmission time between the hemispheres. His estimates of IHTT on two different subjects were "6 and 5 to 6" msec.

Subsequent research using the SRT paradigm has resulted in somewhat faster, and presumably more accurate, estimates of IHTT: 2.0 msec (Stefano, Morelli, Marzi & Berlucchi, 1980), 3.3 and 2.1 msec (Berlucchi, Heron, Hyman, Rizzolatti & Umilta, 1971), 2.5 msec (Berlucchi, Crea, DiStefano & Tassinari, 1977), and 1.5 msec (Anzola, Bertoloni, Buchtel & Rizzolatti, 1977). In a review of the literature, Bashore (1981) concluded that SRTs could indeed provide good, reliable measures of IHTT.

Savage et al. (1988) recently attempted to confirm Witelson's hypothesis of faster IHTT in left-handers with the SRT estimate of IHTT, described above. The purpose was to test specifically whether the differences observed in degree of lateralization between the two handedness populations might be accounted for by faster communication between the hemispheres of left-handers. The hypothesis stated that sinistrals, who are consistently less lateralized than dextrals, should have faster IHTT estimates. Finger oscillation data (Halstead, 1947) were also collected, in order to get a more pure index of motor performance, and to test for any left hemisphere motor difficulties among left-handers (Reitan & Wolfson, 1985a).

Although the IHTT estimate from Savage et al. (1988) of 2.88 msec was consistent with previous studies (Anzola et al., 1980;

Berlucchi et al., Berlucchi et al., 1977; Stefano et al., 1980), the
results of the study did not support the stated hypothesis. There
was no indication that sinistrals had faster IHTT estimates. There
were, however, indications of differences in intrahemispheric
processing between dextrals and sinistrals. A model was developed to
account for the observed results of the SRT procedure. This model is
depicted in Figure 1.

Insert Figure 1 about here

Looking at Figure 1, the reader will note that sinistrals are
somewhat faster over all conditions. For example, while the fastest
mean response of right-handers was 221.36 msec, the slowest response
for left-handers was only 219.47. Thus, the slowest response for
left-handers was still somewhat faster than the fastest response for
right-handers, although this difference was not significant. The
most efficient responses for dextrals were, to no surprise, those
initiated with the right hand. Interestingly, however, both the
fastest and slowest responses for the sinistral group were right-
handed responses.

At first view, the results appear to be both surprising and
somewhat confusing. For example, when comparing the ipsilateral and
contralateral responses in each hand, the difference between means
should equal the overall IHTT estimate for that handedness group, as
the only difference between the two conditions is the necessity for
interhemispheric transfer. In this study, the overall IHTT estimates

were 2.73 for dextrals and 3.04 for sinistrals. The authors found, however, that the right hand IHTT estimates were lower than expected for dextrals (.29 msec), and higher for sinistrals (6.89 msec). Conversely, the left hand IHTT estimates were higher for dextrals (4.73 msec), and lower for sinistrals (-.82 msec). Savage et al. explained the discrepant results by hypothesizing that right-handers had a right hemisphere visual processing advantage, while left-handers had a similar left hemisphere advantage. In right-handers, the right hemisphere superiority was canceling out IHTT estimates in right hand responses, and inflating IHTT in left hand responses. Among left-handers, the left hemisphere superiority was inflating right hand IHTT estimates, and nullifying left hand estimates. This interpretation explains the variable IHTT estimates for the two hands.

Thus, upon closer inspection a meaningful model emerged. According to this model, right-handers have a right hemisphere visual processing advantage, but this advantage is masked by a stronger right hemisphere/left hand motor disadvantage. Conversely, the data for left-handers were consistent with a left hemisphere visual processing advantage and only a slight left hemisphere/right hand motor advantage. Dextrals are, therefore, very highly lateralized to the left hemisphere for motor functions, and moderately lateralized to the right hemisphere for visual processing. Sinistrals, on the other hand, are more diffusely lateralized for motor functions, but moderately lateralized to the left hemisphere for visual processing. Thus, the authors concluded that sinistrals are less highly

lateralized for motor functions, but oppositely lateralized for visual processing tasks. These results call into question the expectation of global differences in degree of lateralization between dextrals and sinistrals, as left-handers appeared to be no less lateralized in their processing of visual information.

As previously discussed, these intrahemispheric processing differences were believed to be confounding the estimates of IHTT. In other words, the SRT paradigm estimates were confounded by an interaction between hemisphere of processing and response hand. This interaction is apparent in the discrepant IHTT estimates from the right and left hands of dextrals (.29 msec, 4.73 msec) and sinistrals (6.89 msec, -.82 msec). Superior stimulus processing in one hemisphere violates the assumption of equal processing, which is the basis of the SRT paradigm. Thus, not only were there no indications of IHTT differences between the two handedness groups on the SRT tasks, but the very validity of this IHTT paradigm was called into question.

VEP Estimates of IHTT

IHTT can also be estimated using a visual evoked potential (VEP) paradigm. This first became apparent as researchers noted that latencies of VEP peaks were generally shorter for sites over the hemisphere contralateral to the field of stimulation (the directly stimulated hemisphere); for example, see Andreassi, Okamura, and Stern (1975). Conversely, latencies were longer for sites over the ipsilateral hemisphere (the indirectly stimulated hemisphere). Andreassi et al. (1975) proposed that the VEPs in the indirectly

stimulated hemisphere did not occur until stimulation crossed over the corpus callosum, and that the latency difference between the two sites represented the time required for this process (IHTT). The rational for this paradigm is also based on an assumption of equal processing between the hemispheres. Although Andreassi et al. described the above process, and collected data supporting it, they did not actually perform calculations of IHTT using this procedure.

At least one attempt has since been made to directly estimate IHTT using a VEP paradigm (Rugg, Lines, & Milner, 1984). The technique is similar in many ways to the SRT paradigm, except that VEP data are simultaneously collected from two homologous sites over the left and right hemispheres, while stimuli are presented in the left and right visual fields. Latencies are then calculated between stimulus onset and a consistently identified peak, such as N160 (Rugg et al., 1984). As noted above, the latencies of the hemisphere contralateral to the stimulus field (which is directly stimulated) are shorter than those of the indirectly stimulated ipsilateral hemisphere (Andreassi, et al., 1975; Ledlow, Swanson, & Kinsbourne, 1978; Rugg & Beaumont, 1978; Rug et al., 1984). The actual IHTT estimate is calculated by subtracting the average latency for the directly stimulated hemisphere from the latency of the indirectly stimulated hemisphere.

Rugg et al. (1984) used this method to estimate IHTT between occipital and central areas of the cortex in a GO/NOGO choice reaction time task. Their estimate of IHTT at occipital recording sites was 15.7 msec. They also went back to three previous studies

(Andreassi et al., 1975; Ledlow, Swanson, & Kinsbourne, 1978; Rugg & Beaumont, 1978) which did not actually estimate IHTT, but provided data with which to make the calculations. All three studies recorded VEP data from homologous occipital regions, and reported the data as a function of visual field of stimulus presentation. Using this method of calculating IHTT, the four studies produced estimates ranging from 14 to 19 msec. It is important to note, for the purposes of the current review, that none of the above VEP studies included left-handers. This paradigm has not yet been used to examine differences between dextrals and sinistrals.

Discrepancies Between SRT and VEP Paradigms

Looking at these estimates of IHTT, an immediate discrepancy appears between the VEP and SRT paradigms: The average estimate for the SRT paradigm is approximately 3 msec (Anzola et al., 1980; Berlucchi et al., 1977; Berlucchi et al., 1971; Savage et al., 1988; Stefano et al., 1980), while the estimate using the VEP paradigm is approximately 16 msec (Andreassi et al., 1975; Ledlow et al., 1978; Rugg & Beaumont, 1978; Rugg et al., 1984). This difference is very substantial, and must, therefore, be resolved.

What then, is responsible for this discrepancy? Rugg et al. (1984) suggested that the disagreement between the two paradigms can be accounted for by differences in IHTT at different regions of the corpus callosum. They based their hypothesis on Milner and Lines (1982), who proposed that information is transmitted across the commissures centrally much faster than it is posteriorly. If this is in fact the case, then the SRT estimates of IHTT are actually

estimating central IHTT, since this information crosses over much faster. Rugg et al. tested this hypothesis, using the VEP paradigm described above, and interpreted the results as supporting the proposed IHTT differences at different functional regions of the corpus callosum. Their estimates of IHTT were 14 msec and 4 msec, for occipital and central sites, respectively.

Intrahemispheric Confounding

Although the above interpretation of the data is reasonable, an alternate explanation is also tenable, based upon the model of Savage et al. (1988). Rugg et al. (1984) estimated IHTT using the N160 peak, which means that the peak occurred approximately 160 msec after stimulus presentation, ample time for confounding of the estimates by the intrahemispheric processing differences proposed by Savage et al. (1988). In other words, the VEP IHTT estimates might also be confounded by intrahemispheric processing differences, and thus be no more accurate than the SRT estimates.

In an earlier review of the literature, Rugg (1983) explains the reasoning on which the VEP estimates of IHTT are based. In support of the paradigm, he states that any processing which might influence differences in reaction time occurs only after callosal transfer has already taken place. Thus, it is presumably only callosal transfer which is reflected by the differences in peak latencies. What he seems to be saying is that VEP IHTT estimates could not be affected by cerebral processing differences, such as those observed by Savage et al. (1988). Callosal transfer is, after all, a fast process, ranging in both paradigms between 2.5 and 19 msec. Even 19 msec

seems somewhat insignificant when one considers it in light of a 200 to 600 msec reaction time.

This argument does not, however, alter the susceptibility of VEP estimates to confounding by processing differences. The VEP and SRT paradigms both depend on the assumption of equal processing of simple stimuli between the hemispheres, as was originally proposed by Poffenberger (1912). The current author believes that this assumption may be a weakness in both paradigms. While the stimulus certainly arrives later to the indirectly stimulated hemisphere, subsequent processing of that stimulus may not necessarily be equal to that of the directly stimulated hemisphere.

An example would be helpful in illustrating this point. Assume, for example, that the left hemisphere of right-handers is slower than the right hemisphere at visual processing, as proposed by Savage, et al. (1988). This slower left hemisphere processing will, therefore, subtract from the IHTT estimates of right visual field presentations. For instance, stimuli presented in the right visual field are initially projected to the left hemisphere, and represented in the right hemisphere only after crossing over the corpus callosum. In dextrals, however, it is proposed that this directly stimulated left hemisphere processes information more slowly, which results in a longer peak latency for that hemisphere. This increased latency of the directly stimulated hemisphere will then decrease the IHTT estimate when it is subtracted from the latency of the indirectly stimulated hemisphere. The estimate acquired by this method is thereby confounded by intrahemispheric processing differences.

Therefore, it is at least conceivable that IHTT confounding could be occurring in the VEP paradigm.

VEP Generators

This argument is strengthened upon consideration of the actual generators of the VEP peak components. The term "generator" refers to the area of the brain responsible for the activity reflected in the EEG and the averaged VEP. Averaging EEG immediately after presentation of a visual stimulus results in a characteristic waveform with certain expected components, or peaks. These peaks may be referred to according to their sequential order (e.g., P1 or N1), or according to their latency post-stimulus (e.g., P100 or N160). In addition, the actual waveforms may vary according to the nature of the stimulus. One commonly used stimulus is the reversed checkerboard pattern (e.g., Jeffreys and Axford, 1972a and 1972b). Reliable VEPs may also be elicited from more simple stimuli, however, such as unpatterned light flashes (e.g., Rugg et al., 1984). Figure 2 depicts a prototypical VEP waveform, elicited from cross stimuli (+) presented during an SRT task similar to Savage et al. (1988). This waveform includes the two most prominent early peaks, P100 and N160.

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Insert Figure 2 about here

_____

It is generally accepted that all components of the occipitally recorded VEP result from activity in the visual cortex, since they can also be recorded from intracranial depth electrodes directly on

or within the occipital lobe (Allison, Matsumiya, Goff, & Goff, 1977; Goff, Allison, & Vaughan, 1978; Vaughan, 1982).

Isolation of the specific generators within the visual cortex is more difficult, however. Vaughan (1982) describes three basic approaches to answering this question of neural generators. The first approach is called the scalp topography approach. This procedure attempts to identify neural generator locations based on changes in VEP peaks, as a function of site of recording and type of evoking stimulus. The second approach is a brain lesion approach, and examines the effects of brain lesions in particular areas of the visual cortex. The third procedure uses depth electrodes to record directly from the visual cortex. Vaughan (1982) proposes that a combination of the three approaches is the most appropriate means for locating generators, as each approach has certain limitations associated with it.

The majority of the studies into neural generators of VEP use some modification of the scalp topography approach (e.g. Jeffries & Axford, 1972a; Jeffries & Axford, 1972b; Previc, 1988). Most topography studies are inherently eclectic, however, since they must rely on data from other approaches in order to make their inferences. For example, scalp topography researchers have noted that stimulation of a particular portion of the visual field (e.g. a particular half-field, or quadrant) selectively activates a specific region of the visual cortex (Vaughan, 1982). They examine these changes in VEP peak components at different scalp sites, and make inferences concerning underlying generators, based on their knowledge of the

functional anatomy of the visual cortex. This information, however, comes from data produced by brain lesion and intracranial measurement studies. It, therefore, seems that the modern topography studies are, by their very nature, combinations of the three approaches described by Vaughan (1982).

Jeffreys and Axford (1972a; 1972b) used a scalp topography paradigm to locate generators of VEP to patterned flashes. They focused on the two earliest VEP peaks, which they labeled CI and CII. CI occurred in the 65-80 msec range, and is also referred to as P1. CII was in the 90-100 msec latency range, and is often referred to as N1. Using the topographical paradigm, described above, the authors concluded that CI and CII were generated in different areas of the visual cortex. Specifically, they proposed that CI was generated in the striate cortex, while CII was generated in the extrastriate cortex. The striate cortex is located in Brodmann's area 17, and is most commonly referred to as the primary visual receptive cortex (Reitan & Wolfson, 1985b). The extrastriate cortex is located in Brodmann's areas 18 and 19, and is better known as the secondary visual association cortex (Reitan & Wolfson, 1985b). Thus, Jeffreys and Axford (1972a; 1972b) concluded that the generators of P1 and N1 are located in the primary visual receptive cortex and the secondary visual association cortex, respectively.

There is a problem, however, with an over-simplistic interpretation of the above data. Vaughan (1982) points out that concurrent processing in the primary and secondary visual areas is taking place whenever VEP data are collected. Because these areas

are also contiguous, it is impossible to isolate a single generator for any particular component peak. A conservative approach, therefore, leads one to the conclusion that it is actually groups of generators, possibly in different areas of the visual cortex, which are responsible for any particular VEP peak.

Despite this need for caution, there seems to be a general consensus that P1 is generated from activation of the primary visual cortex (Goff et al., 1978; Jeffreys & Axford, 1972; Previc, 1988). Vaughan (1982) describes activation within the cortex as originating in the primary receptive cortex, and later spreading to more secondary areas. As previously noted, when taking a conservative approach, it is prudent to interpret topographical studies in terms of groups of generators. Using this approach, therefore, it can be concluded that the "earlier" peaks (those with latencies in the 40 to 80 msec range) are generated in more primary group areas, and "later" peaks (those with latencies greater than 80 msec) in more secondary group areas.

Reitan and Wolfson (1985b) describe the functions of the primary visual receptive cortex as involving very simple processing, such as the presence or absence of light. The secondary visual association cortex is, by comparison, involved in more complex functions of visual processing (Reitan & Wolfson, 1985b). These functions include visual object recognition, recognition of significance, and the relation of current visual information to past visual experience. Consequently, one can also conclude that VEP components beyond 80 msec, which are generated by both primary and secondary areas of the

visual cortex, are more susceptible to confounding by intrahemispheric processing differences. The N160 peak of Rugg et al. (1984) is one of these later "primary and secondary processing components," and presumably more susceptible to confounding by intrahemispheric processing differences.

This line of reasoning is further strengthened by a recent study which focused on the types of processing associated with VEP peak components. Kramer, Sirevaag, and Hughes (1988) recorded VEP data while subjects engaged in a continuous monitoring task and an arrow discrimination task, either separately or simultaneously. Using this paradigm, they examined the effects of increased difficulty within a single task, as well as increased difficulty resulting from the introduction of a second, simultaneous task. The authors found that N160 amplitudes and latencies changed with increased difficulty within a single task, but not from the introduction of dual task demands. N190 and P300, on the other hand, changed with both manipulations. Kramer et al. concluded that N160 reflects the distribution of attention to the different spatial locations of a single task. They also concluded that N190 represents the allocation of general perceptual resources, both within and between tasks, on the basis of processing priorities. Finally, they proposed that P300 provides a measure of perceptual and central processing resources.

Thus, all peaks from N160 and beyond appear to reflect relatively complex cortical processing (i.e. attentional processes). As early as N160, there is evidence of activity beyond simple visual processing (as one would expect from primary generators) to more

complex processing (as one would expect from secondary generators). It is, therefore, concluded that the study of Kramer et al. (1988) is consistent with the previous conclusions of this review, concerning VEP generators and complexity of processing.

Confounding in Previous VEP Studies

Finally, support for IHTT estimate confounding, as well as the model of Savage et al. (1988), is provided by close examination of the data of Rugg et al. (1984) and Andreassi et al. (1975). A specific pattern of results would be expected in both studies of right-handers, based on the Savage et al. model of intrahemispheric processing differences. The first prediction is that the mean peak latencies should be longer for directly stimulated left hemisphere sites (O1 electrode location) than for directly stimulated right hemisphere sites (O2 electrode location) among the right-handed subjects used in the study. Secondly, the actual estimates of IHTT from the occipital sites should be shorter when the stimulus is presented in the right visual field. This result is expected because the longer N160 latency of the directly stimulated left hemisphere should deflate IHTT estimates when it is subtracted from the latency of the indirectly stimulated right hemisphere.

This pattern of results is present in the data of Rugg at al. (1984), and fulfills both of the expectations stated above. The N160 latency data for Rugg et al. (1984) are summarized in Table 1.

Insert Table 1 about here

The mean N160 latency for the left hemisphere, when directly stimulated, is 155.5 msec, while the mean latency of the right hemisphere, under the same condition, is 151.5 msec. This 4 msec difference would presumably provide an estimate of the proposed right hemisphere advantage. Savage et al. (1988) estimated the right hemisphere advantage in right-handers to be 2.22 msec. The means are, therefore, in the direction hypothesized by Savage et al., with the left hemisphere demonstrating longer latencies. The confounding effects of processing speed are also apparent, and the second expectation supported, when one looks at the estimates of IHTT for each visual field. The right visual field estimate is faster (13 msec) than the left visual field estimate (18 msec). Thus, while the results can legitimately be interpreted as supporting the hypothesis of Rugg et al. (1984), it also appears likely that at least the occipital estimates are confounded by intrahemispheric processing differences.

Support for the Savage et al. (1988) model also comes from close inspection of the data of Andreassi et al. (1975). These authors used several paradigms to look at differences in VEPs at varying lateral stimulation eccentricities. As stated previously, this study did not directly calculate IHTT estimates. Thus, the current author calculated IHTT and meaningful means from the paradigm most similar to Rugg et al. (1984) and Savage et al. (1988). These data are presented in Table 2. As is apparent to the reader, Andreassi et al. (1974) included data for three different peaks: P1, N2, and P2. These peaks occur at roughly 100, 150, and 250 msec, respectively.

Thus, N2 corresponds roughly to N160, which is the peak used by Rugg et al. (1984).

Insert Table 2 about here

As was the case for the Rugg et al. (1984) data, all expectations of the Savage et al. (1988) model are supported. For instance, the mean latencies for the left hemisphere, when directly stimulated, are 129, 177, and 268 msec, while the mean latencies for the directly stimulated right hemisphere are only 108, 164, and 258 msec. In this study, the estimates of right hemisphere advantage would thus be 21, 13, and 10 msec. The resulting IHTT estimates are also in the direction hypothesized by the current author. The IHTT estimates are 11, 11, and -7 msec for the right visual field presentations, and 25, 23, and 8 msec for left visual field presentations. These estimate discrepancies among the different peaks are consistent with the proposed confounding by intrahemispheric differences, as the Savage et al. model predicts different estimates of IHTT at different points along the VEP. The reader will also immediately notice the negative, and thus invalid, IHTT estimate for the right visual field presentation at P2. It is reasonable to conclude that, after 250 msec, confounding has become so severe that one cannot even calculate a legitimate estimate of IHTT.

There is another very interesting pattern of results in both studies (Andreassi et al., 1975; Rugg et al., 1984). As previously

stated, there are 4 msec (Rugg et al., 1984) and 13 msec (Andreassi et al., 1975) advantages in the directly stimulated right hemispheres. When looking at the same data, however, it becomes apparent that the right hemisphere advantages disappear in the indirect conditions of both studies. This raises an intriguing question: Why is there this discrepancy between the direct and indirect differences of the two hemispheres? The discrepancy can also be explained by differential hemispheric processing. The slower left hemisphere increases left hemisphere times in the direct condition, while it increases right hemisphere times in the indirect condition. In other words, the stimulation of the right hemisphere is delayed by the slower processing of the left hemisphere. Conversely, the left hemisphere receives stimulation earlier from the comparatively faster right hemisphere. This "reversal" of effects acts to decrease the hemispheric asymmetries in the indirect condition.

This confounding of both the direct and indirect conditions is also apparent in the discrepant IHTT estimates of each hemisphere in the Rugg et al. (1984) and Andreassi et al. (1975) studies. These estimates should presumably equal the overall IHTT estimate, as the only difference between direct and indirect conditions would be the need for interhemispheric transfer in the latter condition. Looking at the data in Tables 1 and 2, however, the reader will note that this is not the case. In Rugg et al. (1984), the IHTT estimate for the left hemisphere is 14 msec, while the same estimate in the right hemisphere is 17 msec. Meanwhile, in Andreassi et al. (1975), the

IHTT estimates are 10 and 24 msec, for the left and right hemispheres, respectively. Thus, in both studies the hemispheres are generating unique estimates of IHTT. The estimates of the left hemisphere are being deflated, while those of the right hemisphere are similarly inflated.

Berlucchi et al. (1971) and Milner and Lines (1982) have proposed that, in reaction time studies, visual information is completely processed in the directly stimulated hemisphere, and a motor message ultimately relayed across the corpus callosum. The VEP data from Rugg et al. (1984) and Andreassi et al. (1975) suggest that at least some partial processing of the stimulus has occurred in the directly stimulated hemisphere prior to callosal transfer. The signal arriving at the indirectly stimulated hemisphere is, therefore, different in some fundamental way: It has been affected by the intrahemispheric processing abilities of the directly stimulated hemisphere. In the indirect condition, the faster right hemisphere is being slowed by the delayed signal from the slower left hemisphere, while the left hemisphere is getting the benefit of faster processing in the right hemisphere.

In summary, all of the studies reviewed above are consistent with the conclusions of Savage et al. (1988). First, confounding is possible, considering the location of N160 generators in both primary and secondary areas of the visual cortex. Secondly, IHTT estimates using the VEP paradigm may be confounded by intrahemispheric processing differences, as was also the case for the SRT studies. Both paradigms are based on an equal processing assumption, which is

not supported by careful inspection of the data from previous studies. Finally, differential intrahemispheric processing, in the direction of Savage et al. (1988), has been established, at least for right-handers. Specifically, VEP data from previous studies (Andreassi et al., 1975; Rugg et al., 1984) are consistent with a right hemisphere visual processing advantage for dextrals.

The problem of contamination of later peaks suggests that an earlier peak, such as P1 (Allison, et al., 1977; Goff et al., 1978) might be less contaminated by intrahemispheric differences. As previously stated, this "early" peak, in the 40 to 80 msec range, should primarily represent activity of the primary visual cortex and, therefore, be less contaminated by intrahemispheric differences. Use of this peak is not without problems, however, as the earlier peaks are more difficult to consistently identify (Allison, et al., 1977). This is, in fact, the very reason Rugg et al. (1984) chose to use N160. They were unable to attain reliable P50 and P100 peaks. It thus appears that neither the SRT nor the VEP paradigms, as they have been applied in the past, are ideal to use in estimating "true" IHTT.

Conclusions

The current review of the literature has produced several conclusions regarding the cerebral organization differences responsible for handedness. The study of handwriting posture differences among sinistrals does not appear to be a productive avenue of study, as these differences do not necessarily relate to underlying cerebral organization. Left-handers are, however, more diffusely lateralized than right-handers for many functions, and

these differences do relate to CNS organization. Left-handedness does not appear to be the result of a pathological process for the majority of the population, and the more diffuse lateralization may even give sinistrals an advantage on certain tasks, such as those involving visual-motor skills. These differences in degree of lateralization have not been demonstrated to relate to increased interhemispheric communication of left-handers, but instead the IHTT estimates themselves appear to be confounded by intrahemispheric processing differences. Finally, there appear to be asymmetries between left- and right-handers in the intrahemispheric processing of visual stimuli, in addition to the previously noted decreased lateralization of other functions, such as motor and verbal. Specifically, dextrals are hypothesized to possess a visual processing advantage in the right hemisphere, while sinistrals demonstrate a similar left hemisphere advantage. It is also concluded that these intrahemispheric processing differences provide an important focus for future studies into the CNS organization of the two handedness groups.

The Dissertation Proposal

The aim of the literature review was to provide the rational for the current doctoral dissertation. The purposes of the dissertation will now be outlined. First, it will attempt to demonstrate intrahemispheric processing asymmetry differences between dextrals and sinistrals for visual stimuli, within the SRT paradigm of Savage et al. (1988). In other words, an endeavor will be made to validate the model of Savage et al. (1988) with a VEP procedure. Second, this

study will attempt to provide further support for the proposed confounding of IHTT estimates from the SRT and VEP paradigms. Although both the Rugg et al. (1984) and the Andreassi et al. (1975) data support IHTT confounding, neither study was conducted within a SRT paradigm. If the study can demonstrate confounding within a combined SRT-VEP paradigm, it would further explain the discrepancies observed in IHTT estimates of previous studies.

Finally, specific hypotheses, which have been generated by the current review, will be discussed in detail. These hypotheses are summarized in Table 3.

Insert Table 3 about here

The first stated purpose is to demonstrate the intrahemispheric processing asymmetries of left- and right-handers, in the direction proposed by Savage et al. (1988). Three hypotheses are, thereby, generated for each handedness group. On the SRT task, dextrals will show the same pattern of results as summarized in Figure 1, from the Savage et al. study. Right-handers will also demonstrate increased mean VEP peak latencies for directly stimulated left hemisphere scalp measurements compared to directly stimulated right hemisphere measurements. Dextrals will not, however, show a significant difference between the two hemispheres in the indirect condition. These results are expected because the slower processing of the left hemisphere should affect estimates in both the direct condition and, as previously explained, the indirect condition.

Sinistrals are expected to demonstrate a somewhat different pattern of results. Again, they will show the same SRT results as summarized in Figure 1. Sinistrals will also have longer mean VEP peak latencies for directly stimulated right hemisphere scalp measures when compared to directrly stimulated left hemisphere measures. They are expected to show no such differences between the hemispheres in the indirect condition. As was the case with right-handers, this pattern is expected because of the confounding effects of the slower hemisphere in both conditions. The only difference is that slower processing is now predicted to be in the right hemisphere. Finally, when comparing VEP latencies of the two handedness groups on the direct measurement condition, it will be demonstrated that sinistrals are faster than dextrals in the left hemisphere, but slower than dextrals in the right hemisphere. This pattern should result from the hypothesized left hemisphere advantage of sinistrals, and the corresponding right hemisphere advantage of dextrals.

The second stated purpose of the proposed study is to partially explain the SRT-VEP conflict in IHTT estimates by showing that both paradigms are confounded by intrahemispheric processing differences between the hemispheres. The reader will, of course, note that support for the first purpose will, by default, provide support for the second. Nonetheless, two hypotheses are generated which should specifically demonstrate IHTT confounding. First, VEP IHTT estimates will be faster for right visual field presentations among dextrals and left visual field presentations among sinistrals, presumably

reflecting the different intrahemispheric processing advantages of each group. Second, VEP IHTT estimates will be faster in the left hemisphere of dextrals and in the right hemisphere of sinistrals. This expectation is based on the confounding influences of the slower hemisphere in both the direct and indirect conditions.

It should be noted that all of the above predictions involving VEP latency data are based on the use of N160 as the peak of comparison. As previously explained, however, an earlier peak such as P100, should be less confounded by intrahemispheric processing differences. The proposed study will directly test this assumption of decreased confounding using P100, providing that the peak can be consistently identified in all subjects. If this early peak is less affected by intrahemispheric processing differences, then a different pattern of results would be expected. Specifically, while a significant difference between direct and indirect conditions is hypothesized (indirect times should still be affected by IHTT), the latencies should not vary as a function of hemisphere of processing or handedness of the subject. Furthermore, if it can be demonstrated that P100 is less contaminated by processing differences, then the estimates of IHTT derived from this peak should be more accurate.

Method

Subjects

The Dean Laterality Preference Schedule (Dean, 1978) was given to 500 Introductory Psychology students at Oklahoma State University as a screening device for selection of subjects. The 20 most highly lateralized males in the dextral and sinistral groups were then

solicited for participation in the study, which resulted in a total of 40 subjects. All subjects were required to have normal vision or vision corrected to normal by glasses. In addition, subjects were screened for a history of significant head injury or recent use of potentially sedating prescription medication. Subjects received extra credit and five dollars for participation in this study.

Material and Apparatus

The Dean test is a paper and pencil test, consisting of 49 items in which the subject selects responses on a five point Likert scale (1=left always, 2=left mostly, 3=both equally, 4=right mostly, 5=right always) on 49 questions. The individual scores can, therefore, range from 49 (left always on all items) to 245 (right always on all items). Lateral preference is assessed on the hands, arms, feet, legs, eyes, and ears.

During the SRT task, the subject's head was maintained at a uniform distance of 50 cm (nasion to computer screen) by requiring the subject to keep his head against the head rest of a reclining chair. This distance was measured again, after data collection, in order to ensure that the subject had not moved his head. The stimuli for the SRT/VEP task were presented by an Apple II computer. The stimulus was a cross (+), measuring 17 mm by 17 mm, and subtending $1.9°$ of the visual angle. The stimulus was presented $5.6°$ to the left or right of a central fixation point for a duration of 12 msec. The luminous intensity was measured at 42 cd/m^2 . The interstimulus interval, or foreperiod duration, varied randomly between three and five seconds in order to prevent anticipatory responses by the

subject.

Gold-plated disk electrodes were used to record EEG, which were amplified with bandpasses of 1-100 Hz with 60 Hz notch filters. An IBM PC computer was responsible for digitization of the EEG data, collection of reaction times, and controlling the display of the Apple II computer.

Procedure

Subjects were seated in an electrically shielded room. Following the acquisition of informed consent, the subject's eyes were covered by single use eye patches, so that he could begin dark adaptation. Electrodes were then affixed at O1, O2, A1, and A2 according to the international 10-20 system. O1 and O2 were referenced to linked earlobes (A1 and A2), and the forehead served as ground. Impedances were kept at 5 Kohms or less, and were checked at the beginning and the end of the procedure. Following electrode attachment, the lights were turned off and the eye patches removed. Each subject was given a total of at least 30 minutes dark adaptation.

Following dark adaptation, the experimenter read instructions to the subject over an intercom. Each subject was instructed to keep both eyes on the fixation point, and to respond with a button press from the thumb of the designated hand as soon as possible after the stimulus flash. The subject was instructed to blink only between stimulus presentations. The visual field (left or right) of stimulus presentation was varied randomly in order to prevent anticipatory eye movements. The subject was initially given 10 practice trials with

each hand. The computer program then continued, breaking after blocks of 50, until 100 valid trials were collected from each hand. The starting hand was counterbalanced between subjects according to odd or even subject number. Data were discarded, and the trial replaced, based upon the following two criteria: Eye movements (horizontal and vertical), which were monitored in two designated channels; and reaction times less than 160 msec, or greater than 496 msec, which are presumably reflective of anticipatory or inattentive responses.

The EEG was digitized and stored 12 msec prior to stimulus presentation. Recording then continued for another 504 msec, for a total of 516 msec. The EEG was sampled at 2000 Hz (two times per msec).

Reaction time data were averaged from 50 valid trials (based on the criteria described above) for each of the four possible response conditions: left hand ipsilateral (LIL), left hand contralateral (LCL), right hand ipsilateral (RIL), and right hand contralateral (RCL). EP data were averaged from the same valid trials, but stored under a different organizational scheme, based on direct or indirect hemispheric stimulation. The four trial conditions in the VEP data were left hemisphere direct (LHD), left hemisphere indirect (LHI), right hemisphere direct (RHD), and right hemisphere indirect (RHI). Data were averaged from 100 trials to create the waveform in each VEP condition.

VEP Wave Form Quantification

Two peaks were of interest in the current study: P100 and N160.

P100 was defined as the point of greatest positivity between 88 and 140 msec, while N160 was defined as the point of greatest negativity between 130 and 195 msec. The minimum definition of a positive or negative "peak" was at least two consecutively equal points. If a "peak" was actually a flat plateau, the midpoint of the plateau was taken as the peak; or if only two points were equal, the first point was used. Finally, if two peaks of equal positivity or negativity occurred within the acceptable latency range, the earlier peak was used.

In order for a subject's data to be used in the study, he had to generate at least an acceptable N160. As expected, more subjects produced acceptable N160s than P100s. If a subject did not generate at least an acceptable N160, his data were discarded and another subject selected. On the basis of N160 requirements, data were discarded for one dextral and two sinistrals, and additional subjects solicited to ensure 20 subjects in each laterality group. Based on P100 requirements, six sinistrals did not produce acceptable P100s. Three dextrals also did not produce adequate P100s, but an additional three subjects were randomly discarded in order to balance the two groups in the P100 measure. Thus, while N160 analyses were conducted with 20 subjects in each laterality group, the P100 analyses only included 14 subjects in each group.

Analyses

A 2 (Laterality) X 2 (Response Hand) X 2 (Visual Field) mixed design analysis of variance was conducted on the reaction time data in order to provide an initial overall test of significance and to

provide appropriate mean square error terms for subsequent planned comparisons using Dunn's multiple comparison procedure (Kirk, 1982). Specific directional hypotheses were predicted a priori (see Figure 1). Among right-handers, it was predicted that right hand responses would be significantly faster than left hand responses, and that left visual field responses would be faster than right visual field responses. Furthermore, the LIL responses would be significantly faster than the LCL responses, but there would be no significant difference between RIL and RCL conditions. Left-handers were predicted to show no significant difference between the means of right hand and left hand responses, but they were predicted to produce faster right visual field responses than left visual field responses. The RIL responses were predicted to be significantly faster than the RCL responses, but the LIL and LCL conditions were not expected to be statistically different.

In each average VEP, P100 and N160 were measured. In addition, IHTT estimates were derived by subtracting mean direct latencies from mean indirect latencies for each visual field and recording site. The VEP latency data were subjected to two separate analyses, according to the component peak of the waveform. Specifically, a 2 (Laterality) X 2 (Recording Site) X 2 (Visual Field) analysis of variance was conducted for each of the two VEP peaks (P100 and N160). Once again, specific directional hypotheses were predicted a priori (see Table 3), and were tested using Dunn's multiple comparison procedure. The reader should note that all following hypotheses concern the use of N160 unless otherwise specified. Among dextrals,

it was predicted that the right hemisphere would be significantly faster than the left hemisphere in the direct condition, while the two hemispheres would be statistically equal in the indirect condition. Among sinistrals, it was predicted that the left hemisphere would be faster than the right in the direct condition, but the two hemispheres would be equal in the indirect condition. In addition, the mean left hemisphere latency of sinistrals would be shorter than the mean latency of the same hemisphere of dextrals. Conversely, the mean right hemisphere latency of dextrals would be faster than the mean right hemisphere latency of sinistrals.

When testing the VEP N160 IHTT data, it was predicted that the mean IHTT estimate from the right visual field would be significantly faster than the mean from the left visual field for dextrals. Among sinistrals, however, the mean IHTT estimate of the left visual field would be faster than the mean of the right visual field. The IHTT data were also tested by hemisphere, and it was predicted that, among right-handers, the mean IHTT estimate from the left hemisphere would be significantly smaller than the mean estimate from the right hemisphere. Finally, it was predicted that the IHTT estimate of the right hemisphere would be significantly faster than the estimate of the left hemisphere in left-handers.

As previously stated, a separate analysis was performed on the P100 latency data. A different pattern of results was hypothesized in the comparisons of the P100 data. First, a significant difference was predicted between direct and indirect conditions in both handedness groups. No significant difference was predicted, however,

between the left and right hemispheres in the direct condition of dextrals or sinistrals. Finally, no significant difference was predicted between dextrals and sinistrals in the direct condition.

Results

Planned Comparisons

Planned comparisons of the SRT data with Dunn's multiple comparison procedure supported all stated hypotheses among right-handers, and all but one among left-handers. These data are summarized in Table 4.

Insert Table 4 about here

Right hand responses of dextrals were faster than left hand responses, $tD(2,38)=2.25$, $p<.05$, and left visual field responses were faster than right visual field responses, $tD(2,38)=2.59$, $p<.05$. LIL responses of dextrals were faster than LCL responses, $tD(4,38)=5.01$, $p<.05$, and RIL responses and RCL responses were statistically equal, $tD(4,38)=.98$, $p>.05$. Among left-handers, right hand responses were statistically equal to left hand responses, $tD(2,38)=.78$, $p>.05$, and RIL responses were faster than RCL responses, $tD(4,38)=3.33$, $p<.05$. Two hypotheses were not supported among left-handers, however, as right visual field responses were not faster than left visual field responses, $tD(2,38)=.42$, $p>.05$, and LIL responses and LCL responses were not statistically equal, $tD(4,38)=2.37$, $p<.05$; LIL responses were faster than LCL responses.

Dunn's planned comparisons supported only two hypotheses in the

VEP N160 data, both involving predicted non-significant differences. These data are summarized in Table 5.

Insert Table 5 about here

Among dextrals, RHD latencies were not significantly faster than LHD latencies, $\underline{t}D(4,38)=.25$, $\underline{p}>.05$, but RHI latencies were equal to LHI latencies, $\underline{t}D(4,38)=.99$, $\underline{p}>.05$. Among sinistrals, LHD latencies were not significantly faster than RHD latencies, $\underline{t}D(4,38)=.73$, $\underline{p}>.05$, but LHI and RHI latencies were statistically equal, $\underline{t}D(4,38)=.47$, $\underline{p}>.05$. Finally, left hemisphere latencies of sinistrals were not faster than left hemisphere latencies of dextrals, $\underline{t}D(2,38)=.54$, $\underline{p}>.05$; nor were right hemisphere latencies of right-handers faster than those of left-handers, $\underline{t}D(2,38)=.13$, $\underline{p}>.05$.

Similarly, with the VEP N160 IHTT data, the only hypotheses supported were those involving predicted non-significant differences. These data are summarized in Table 6.

Insert Table 6 about here

Among dextrals, left hemisphere IHTT estimates were not faster than right hemisphere IHTT, $\underline{t}D(2,38)=.92$, $\underline{p}>.05$, nor were right visual field IHTTs significantly faster than left visual field IHTTs, $\underline{t}D(2,38)=.66$, $\underline{p}>.05$. Among sinistrals, right hemisphere IHTT estimates were not faster than left hemisphere estimates, $\underline{t}D(2,38)=.20$, $\underline{p}>.05$, nor were left visual field IHTTs significantly

faster than right visual field IHTTs, $\underline{t}D(2,38)=1.07$, $\underline{p}>.05$. Finally, the predicted non-significant difference between the overall IHTT estimates of left- and right-handers was supported, $\underline{t}D(2,38)=.18$, $\underline{p}>.05$.

The final set of planned comparisons involved the P100 data, and these data are summarized in Table 7.

Insert Table 7 about here

Among right-handers, direct latencies were not significantly shorter than indirect latencies, $\underline{t}D(3,26)=1.60$, $\underline{p}>.05$, and LHD latencies and RHD latencies were statistically equal, $\underline{t}D(2,26)=1.78$, $\underline{p}>.05$. Among left-handers, direct latencies were shorter than indirect latencies, $\underline{t}D(3,26)=2.27$, $\underline{p}<.05$, but LHD latencies were not equal to RHD latencies, $\underline{t}D(2,26)=2.80$, $\underline{p}<.05$. Finally, direct responses of left- and right-handers were statistically equal, $\underline{t}D(3,26)=1.80$, $\underline{p}>.05$, as predicted.

Post-Hoc Comparisons

Post-hoc comparisons were conducted on the SRT and VEP data in order to assess trends in the data not tested in the planned Dunn's tests. Mean reaction times for all conditions of the SRT paradigm are presented in Table 8. The SRT data were analyzed in a 2 (Laterality) x 2 (Response Hand) x 2 (Visual Field) mixed design analysis of variance procedure.

Insert Table 8 about here

No significant main effects were indicated for laterality,
$F(1,38)=.62$, $p>.05$, response hand, $F(1,38)=1.08$, $p>.05$, or visual
field, $F(1,38)=2.36$, $p>.05$. A significant laterality by response
hand interaction was indicated, $F(1,38)=4.59$, $p<.05$, however, as was
a laterality by visual field interaction, $F(1,38)=4.51$, $p<.05$. These
interactions are depicted in Figure 3.

Insert Figure 3 about here

Finally, a very large interaction was also indicated between response
hand and visual field conditions, $F(1,38)=23.63$, $p<.0001$, which
reflects effects of IHTT. This interaction is represented in Figure
4.

Insert Figure 4 about here

Post-hoc comparisons of the above interactions were completed,
using the Student-Newman-Keuls multiple range statistic (Kirk, 1982).
In the laterality by response hand interaction, comparisons indicated
that left hand responses of dextrals were significantly slower than
all responses of sinistrals. In the laterality by visual field
interaction, comparisons indicated that all responses of left-handers
were faster than all responses of right-handers. This finding is

interesting, considering that a significant main effect for laterality was not indicated in the primary analysis. This discrepancy can be explained by the known characteristics of the mixed design ANOVA. In this design, one sacrifices statistical power on the main effect in exchange for increased sensitivity in interaction analyses (Kirk, 1982). Thus, in this design, the laterality by visual field test is more powerful than the main effects analysis, and picks up the significantly faster responses of left-handers. Finally, post-hoc comparisons of the response hand by visual field indicated that LCL responses were significantly slower than all other conditions. Also, looking at Figure 4, one can see the effects of IHTT reflected in this interaction.

Mean latencies for the VEP N160 paradigm are presented in Table 9. The N160 data were analyzed in a 2 (Laterality) x 2 (Recording Site) x 2 (Visual Field) mixed design analysis of variance procedure.

Insert Table 9 about here

No significant main effects were indicated for laterality, $F(1,38)=.02$, $p>.05$, recording site, $F(1,38)=1.51$, $p>.05$, or visual field, $F(1,38)=.27$, $p>.05$. As with the SRT data, a significant recording site by visual field interaction was found, $F(1,38)=43.07$, $p<.0001$, again reflecting a very robust IHTT effect. This interaction is represented in Figure 5.

Insert Figure 5 about here

Subsequent analysis of the interaction using the Newman-Keuls procedure indicated that both direct conditions (RHD and LHD) were shorter than both indirect conditions (RHI and LHI). This indicates that IHTT estimates were not confounded by intrahemispheric differences in the VEP N160 paradigm.

The actual VEP N160 IHTT estimates were subjected to two separate analyses: 2 (laterality) x 2 (recording site); and 2 (laterality) x 2 (visual field) mixed design analyses of variance. Neither analysis indicated significant main effects for laterality, $F(1,38)=.03$, $p>.05$, recording site $F(1,38)=.27$, $p>.05$, or visual field, $F(1,38)=1.51$, $p>.05$. Also, no significant interactions were indicated for laterality by recording site, $F(1,38)=.63$, $p>.05$, or laterality by visual field, $F(1,38)=.08$, $p>.05$.

Finally, the P100 data were also subjected to a 2 (laterality) x 2 (recording site) x 2 (visual field) mixed design analysis of variance. This analysis indicated no significant main effects for laterality, $F(1,26)=1.48$, $p>.05$, or recording site, $F(1,26)=1.53$, $p>.05$. A significant main effect was indicated, however, for visual field of stimulus presentation, $F(1,26)=7.45$, $p<.01$, with left visual field presentations resulting in shorter P100 latencies than right visual field presentations. Finally, a significant recording site by visual field interaction was also found, $F(1,26)=15.06$, $p<.001$, again reflecting effects of IHTT. This interaction is presented in Figure 6.

Insert Figure 6 about here

Subsequent post-hoc comparisons indicated that RHD latencies were significantly faster than all other conditions. Results are similar to the N160 data, but IHTT effects appear to be confounded by the strong visual field main effect.

Subsequent Analyses

Further analyses were conducted on the SRT and VEP data in order to clarify the previous analyses. SRT and VEP N160 estimates of IHTT were compared in a 2 (laterality) x 2 (method) mixed design analysis of variance. A significant main effect was indicated for method of estimation, $F(1,38)=8.08$, $p<.01$, but not for laterality, $F(1,38)=.42$, $p>.05$. Thus, the VEP N160 method generated significantly longer estimates of IHTT (6.56 msec) than the SRT method (3.00 msec), but neither estimate varied as a function of laterality. The SRT IHTT estimates were then subjected to two separate analyses: 2 (laterality) x 2 (response hand); and 2 (laterality) x 2 (visual field) mixed design analyses of variance. As was the case with N160 IHTTs, no main effects were indicated for laterality, $F(1,38)=.72$, $p>.05$, response hand, $F(1,38)=2.36$, $p>.05$, or visual field, $F(1,38)=1.08$, $p>.05$. Handedness of the subject, however, was found to influence IHTT estimates in laterality by response hand, $F(1,38)=4.51$, $p<.05$, and laterality by visual field, $F(1,38)=4.59$, $p<.05$, interactions. These two interactions are represented in Figure 7.

Insert Figure 7 about here

Post-hoc analysis of the interactions using the Newman-Keuls procedure did not indicate any significant differences between the means, despite the presence of significant interactions. This results from inflated error terms in both interactions, due to high variances in IHTT estimates within each condition. Nonetheless, Figures 3 and 7 reveal clear effects of response hand and visual field, particularly among right-handers.

Because the SRT and N160 methods of estimating IHTT provided significantly different estimates, it was decided to determine if the two methods were related. A Pearson product-moment correlation coefficient was calculated between the mean SRT and VEP N160 estimates of IHTT for each subject. The two measures were not related, $r(38)=-.15$, $p>.05$. Pearson r coefficients were also calculated between mean SRTs and mean VEP N160s for each subject, and again the two measures were not related, $r(38)=.05$, $p>.05$. Finally, correlation coefficients were calculated between all conditions of the SRT and VEP N160 paradigms. These correlations are listed in Table 10.

Insert Table 10 about here

Examination of Table 10 quickly reveals that all correlations between conditions of the same estimation method were significant ($p<.01$),

while all correlations between conditions of different methods were not significant (p>.05). Thus, SRT and N160 estimates of IHTT were not related, nor were the reaction times and N160 latencies themselves related.

This general procedure was repeated, adding P100 data to the analyses of methods of estimating IHTT. The reader should be reminded that six subjects from each laterality group were dropped in all analyses including P100. The overall estimate of IHTT for the P100 data was 4.08 msec. A 2 (laterality) x 3 (method) mixed design analysis of variance was conducted on remaining data. No significant main effects were indicated for laterality, $F(1,28)$=.52, p>.05, or method, $F(1,28)$=.69, p>.05. Interestingly, even previously significant differences between SRT and N160 IHTT estimates disappeared when twelve subjects were dropped from the analysis. Correlations were also calculated between N160 and P100 means, and SRT and P100 mean estimates of IHTT for each subject. No significant relationship was found between N160 and P100 estimates of IHTT, $r(26)$=.05, p>.05, nor between SRT and P100 methods, $r(26)$=-.03, p>.05.

Finally, a "laterality index" was calculated for each subject by taking the absolute differences of individual scores on the Dean test from 147 (the Dean score for a completely ambidextrous person). Thus, a higher laterality index score represents a more highly lateralized person in either direction. Comparison of the two groups with an independent t-test indicated that left-handers (mean laterality index = 41.35, SD=26.50) in this experiment were less

lateralized than right-handers (mean laterality index = 77.05, SD=7.51), $\underline{t}$(38)=5.80, $\underline{p}$<.001. In addition, note the large differences between the standard deviations of each group, with left-handers showing greater variance in their Dean test scores.

Discussion

The SRT data are consistent with the previous Savage et al. (1988) results for right-handers, and all planned hypotheses were supported in this group (see Table 4). Dextrals showed the predicted 5.99 msec right hand advantage and 3.69 msec left visual field advantage, both of which are clearly represented in Figure 3. These significant response hand and visual field effects amplify ipsi/contralateral effects (IHTT) in the left hand (6.16 msec) and cancel them out in the right hand (-1.21 msec). Overall, therefore, the SRTs of dextrals appear to be consistently influenced by two factors: The hemisphere which is initially stimulated, and the hand which ultimately responds.

The SRT data of the left-handers are only partially consistent with the Savage et al. (1988) study, as only two of the four predictions were supported (see Table 4). Sinistrals showed the predicted equality between right and left hand responses, as well as the expected ipsi/contralateral effects in their right hand. The predicted right visual field advantage and, therefore, confounding of ipsi/contralateral effects in the left hand, was not demonstrated, however. Left-handers showed only a non-significant .59 msec right visual field advantage. The laterality x visual field interaction is plotted in Figure 3. Clearly, sinistrals did not show the large

visual field effects of dextrals, and ipsi/contralateral effects in the left hand were not confounded by visual field effects. In the original study, left-handers demonstrated visual field advantages opposite those of right-handers, which resulted in equal ipsilateral and contralateral responses in their left hand. In this study, however, left-handers were less lateralized than right-handers on the SRT task, regardless of response hand or visual field. Simple effects analyses of the laterality x response hand interaction indicated that left hand responses of dextrals were slower than both left and right hand responses of sinistrals. Analyses of the laterality x visual field interaction indicated that all responses of left-handers were faster than all responses of dextrals. Overall, therefore, sinistrals responded faster than dextrals, and demonstrated no confounding effects of response hand or visual field (they were less lateralized).

It is interesting that all of the planned SRT hypotheses were supported among right-handers but not among left-handers. This lack of consistency between the left-handers of the current study and the Savage et al. (1988) study might be explained by the variability of the left-handed population. Comparison of Dean scores between the two studies confirms that the "left-handed" groups were different. As previously discussed, a "laterality index" can be calculated for each subject by subtracting his score from 147, and taking the absolute value of that difference. In the first Savage et al. study, right-handers obtained a mean laterality index of 74.63, while left-handers obtained a mean index score of 29.13. In the current study,

the mean index for dextrals was 77.05 and the mean index for sinistrals was 41.35. Thus, the right-handers' scores are similar between the two studies (74.63 and 77.05), while the left-handers' scores are different (29.13 and 41.35). The sinistral group of the current study appears to be more highly lateralized (left) than the group from the previous study, which is comparatively more ambidextrous. There is no such difference between right-handers, and their results are consistent between the two studies. It is, therefore, concluded that the failure to replicate results between sinistrals of the two studies reflects a fundamental difference in their degree of lateralization. It may be more difficult to find consistently lateralized groups of left-handers, and this problem will need to be addressed in future studies. Results may otherwise continue to vary between different handedness studies.

The SRT data are, therefore, interpreted to be consistent with the earlier study of Savage et al. for right-handers, but not for left-handers. In the VEP N160 data, however, only two a priori hypotheses were supported, and both involved predicted non-significance (see Table 5). In fact, the most notable feature of the N160 data is the total absence of laterality, hemisphere, or visual field effects. Neither the N160 latencies, nor their derived IHTT estimates, varied significantly as a function of hemisphere of generation or visual field of presentation. Additionally, dextrals and sinistrals produced similar VEP N160s, and their derived IHTT estimates (6.36 msec and 6.71 msec) were also similar (see Table 9). Thus, the consistent SRT differences between the two groups were not

reflected in the N160 VEPs. The only significant effect in the N160 data was a very strong, and non-confounded, IHTT effect (see Figure 5).

The SRT and VEP N160 methods of IHTT estimation provided significantly different estimates of IHTT: 3.00 msec for the SRT method, and 6.54 msec for the N160 method. Interestingly, the SRT IHTT estimate of 3.00 msec is exactly equal to the mean IHTT estimate from previously reviewed studies (Anzola et al., 1980; Berlucchi et al., 1977; Berlucchi et al., 1971; Savage et. al., 1988; Stefano et al., 1980). There are, nonetheless, certain problems with this estimate, as predicted in the Introduction of the current study. For instance, comparison of individual means in the response hand x visual field interaction (see Figure 4), which reflects IHTT, found that LCL (left hand-right visual field) responses were significantly slower than all other conditions, including RCL (right hand-left visual field) responses. In addition, RCL responses were statistically equal to both ipsilateral conditions. When the SRT IHTT estimates are analyzed, one finds significant laterality x visual field and laterality x response hand interactions (see Table 8, and Figure 7). In fact, the IHTT estimates for the LVF and right hand conditions of right-handers are actually negative. Examination of mean IHTTs for individual subjects in this study found that nine subjects produced negative mean IHTTs (6 right-handers and 3 left-handers). These findings are anatomically inconsistent. In Figure 7 one can see the effects of visual field and response hand among the IHTT estimates of right-handers, but these differences were not

statistically significant. The problem is the extremely variable SRTs, and thus IHTTs, of the SRT paradigm. Note the large standard deviations in Table 8: It is very difficult to produce significant between-group differences when within-cell variances are so large.

Another problem with the SRT IHTT estimates is their inconsistency with human anatomical findings. Saron and Davidson (1989) point out that only 10% of the callosal fibers in humans are myelinated, and of sufficient diameter, to produce IHTTs as fast as 3 msec. It, therefore, appears unlikely that IHTT in humans could be as fast as 3 msec. In addition, Saron and Davidson (1989) reported results from a previous study (Swadlow, Waxman, & Rosene, 1978) in which direct cortical measurement of interhemispheric conduction in rhesus monkeys estimated IHTT at 7 msec. Thus, although the SRT paradigm produces consistent grand mean IHTTs among many different studies, the estimates may be confounded by response hand and visual field effects among right-handers, extreme variability in both groups, and inconsistency with known anatomical and physiological data.

This apparent confounding of the SRT IHTT estimates does not invalidate the overall SRT paradigm, however. Left- and right-handers consistently differ on this measure, and these differences are believed to reflect real underlying variations in cerebral organization. It is this difference in hemispheric processing which confounds attempts to estimate IHTT with the SRT method. Therefore, the very presence of IHTT confounding demonstrates the SRT paradigm's sensitivity to group differences in brain organization. The current

study only calls into question the accuracy of IHTT derived from the method, not the paradigm itself.

By comparison, the N160 method of IHTT estimation in the current study produced very robust and non-confounded IHTT estimates (see Table 9 and Figure 5). Analyses of N160 IHTT found no significant effects for handedness, hemisphere, or visual field. As previously noted, the only significant interaction in the N160 data was the very large hemisphere x visual field effect, as represented in Figure 5. Thus, the predicted confounding of N160 IHTT estimates by intrahemispheric visual processing differences was not demonstrated. An important requirement for valid IHTT estimates in a VEP paradigm is equal latencies between directly stimulated hemispheres: Note that RHD (157.46) and LHD (156.99) are statistically equal. Simple effects analyses also found that both direct conditions were faster than both indirect conditions, and that the indirect conditions were equal. Thus, N160 IHTT estimates do not appear to be significantly affected by anything other than direct vs indirect presentations. Furthermore, examination of mean N160 IHTT estimates among individual subjects indicated no negative estimates: Every subject produced a reasonable direct/indirect effect, in the anatomically predicted direction. Also, the reader is reminded that direct cortical measurement of IHTT in rhesus monkeys was 7 msec (Swadlow, et al., 1978), which is consistent with the 6.54 msec estimate from the current study.

Figures 4 and 5 allow a direct comparison of IHTT estimates between the SRT and N160 paradigms. A line is drawn to illustrate

the ipsi/contralateral and direct/indirect effects of the two
methods. Ideally, these lines should have zero slope and be
parallel. Note the differences in slope between the two methods:
The SRT method shows a clear visual field effect on the contralateral
line, while the N160 direct and indirect lines have less slope and
are closer to parallel. This provides further evidence that the VEP
N160 paradigm in this study produced reliable non-confounded
estimations of IHTT, while the SRT paradigm did not. The predicted
confounding of N160 IHTT estimates did not occur, and the overall
estimate of 6.54 msec appears to be a more accurate estimate of IHTT
than the 3.00 msec estimate from the SRT procedure.

This now brings the discussion to the P100 data. Analysis of
the P100 VEP data supported three of five predictions, two involving
predicted non-significance (see Table 7). The P100 paradigm
generated an overall IHTT estimate 4.08 msec. As with the N160 data,
the estimates did not vary by laterality or hemisphere. There was,
however, a significant main effect for visual field. The P100 IHTT
estimate of 4.08 msec is interesting, because it falls between the
SRT estimate of 3.00 msec and the N160 estimate of 6.54 msec. The
current author, however, has little confidence in the P100 data for
several reasons, some which have already been discussed. As noted in
the Method section, six left-handers and three right-handers did not
produce acceptable P100s, even though they produced good N160s.
Three right-handed subjects were then randomly discarded from all
analyses involving P100 in order to balance subject numbers, which
further confounded interpretation. In addition, the P100 IHTT

estimate of 4.08 msec has the same problem as the SRT estimate of 3.00 msec, that is, the lack of correspondence with known anatomical structures in humans. It appears unlikely that human callosal transfer could be that fast (Saron & Davidson, 1989).

The P100 IHTT estimates are also confounded by a significant main effect for visual field. This results in a left hemisphere IHTT estimate of 0.64 msec and a right hemisphere IHTT of 7.50 msec, and a left visual field estimate of 5.46, compared to a right visual field estimate of 2.68. As noted with the N160 data, a fundamental requirement for accurate IHTT estimates in a VEP paradigm is that the direct conditions of the two hemispheres be equal. Examination of Figures 5 and 6 reveals a non-significant difference between direct conditions in the N160 data (.47 msec), but a statistically significant difference in the P100 data (4.82 msec). Thus, the P100 estimates appear to be confounded by hemisphere and visual field effects, and the IHTT estimate of 4.08 is believed to be questionable. The reader should also note that this confounding does not reflect predicted patterns of cerebral lateralization, as was the case with the SRT data. These problems with P100, however, may be confined to the current study. Saron and Davidson (1989) found that P100 provided accurate estimates of IHTT. In fact, they proposed that P100 provided a more accurate estimate of IHTT than N160, because N160 has both striate (primary visual cortex) and extrastriate (visual association cortex) generators. Overall, however, results of the current study indicate reliable, non-confounded IHTT estimates from the VEP N160 paradigm, but not from

the SRT or VEP P100 paradigms. Thus, the predicted confounding of IHTT estimates was demonstrated for the SRT and P100 methods, but not for the N160 method. Differences in P100 results between the two studies may be partially accounted for by differences in the visual stimuli. The current study used a 17 mm by 17 mm cross, while Saron and Davidson (1989) used an 8.4 cm by 6.3 cm checkerboard. The larger stimulus size, increased light-dark contrast, and presence of additional lines and angles may result in more efficient stimulation of the visual cortex in the Saron and Davidson paradigm.

Another interesting outcome of the current study is the difference between the mean VEP N160 IHTT of this study (6.54 msec) and estimates from previous VEP studies (approximately 16 msec). One reason for this discrepancy might be the nature of the reaction time tasks in which the VEPs were collected. Previous studies did not use a SRT paradigm to present the visual stimuli. For instance, Rugg et al. (1984) used a GO/NOGO choice reaction time task, while Andreassi at al. (1975) merely asked subjects to count while the stimuli were presented. In fact, Rugg et al. (1984) noted that they were unable to get reliable N160s from subjects using a SRT paradigm. This was not a problem for the current study, which produced acceptable N160s in 40 of 43 subjects. Another potential factor to account for different IHTT estimates is the relatively slow sampling rate of the previous studies, such as Rugg et al. (1984), who used a 3 msec sampling rate. A 3 msec sampling rate allows for a great deal of variability in IHTT estimates. The more recent study of Saron and Davidson (1989) used a SRT paradigm and a .4 msec sampling rate,

which is comparable to the .5 msec sampling rate and SRT paradigm of the present study. Saron and Davidson produced a much lower overall N160 IHTT estimate of 7.9 msec, which is comparable to the current study's estimate of 6.54 msec. These data suggest that the apparent VEP intrahemispheric processing differences of Rugg et al. (1984) and Andreassi et al. (1975) may have been the result of task differences or increased measurement error. It appears that VEP estimates of IHTT are becoming increasingly accurate as measurement error is decreased and the task paradigms are perfected.

In summary, the N160 IHTT estimates of the current study appear to be reliable, non-confounded, and consistent with known human anatomy and animal studies. Anatomically, visual fibers cross almost exclusively through the posterior fifth section of the corpus callosum, known as the splenium (Saron & Davidson, 1989). Thus, the VEP N160 paradigm is most likely estimating transmission of visual sensory information across the splenium. The fact that the current study found no significant differences in N160 IHTT between dextrals and sinistrals provides evidence against faster splenium conduction of sensory information among sinistrals. Results are consistent with Kertesz et al. (1988), who found no differences in callosal size between left- and right-handers on MRI. Kertesz et al. also failed to find any correlation between callosal size and degree of lateralization. Results of the current study and previous studies, therefore, suggest that there are no differences in splenium IHTT between dextrals and sinistrals. Callosal size, IHTT, and degree of lateralization may not be causally related (Kertesz et al., 1988).

Another important finding of the present study is the lack of relation between SRT and VEP results. When a correlation coefficient was calculated for the mean SRT and VEP N160 estimates of IHTT, they were not found to be significantly related. The two methods, therefore appear to produce different, and unrelated, estimates of IHTT. In addition, the mean SRTs and N160s for each subject also failed to correlate significantly. Finally, correlation coefficients between all conditions of the SRT and N160 paradigms are listed in Table 10. There are no significant correlations among any of the conditions between the two different methods, although correlations among conditions within the same method are highly, and significantly, correlated. Thus, the two paradigms produced independent latencies as well as unrelated IHTT estimates. Saron and Davidson (1989) also found that SRT and VEP methods of IHTT estimation were not significantly correlated.

Several factors might account for the apparent independence of the two paradigms. One possible factor, as discussed above, involves the problems with the SRT IHTT estimates, which appear to be confounded by visual field and response hand effects, particularly in right-handers. Since the N160 IHTTs are apparently not subject to the same confounding, one would not necessarily expect them to be related to estimates highly influenced by hemispheric differences. Alternatively, Rugg et al. (1984) proposed that SRT and VEP provide measures of IHTT at different functional regions of the corpus callosum. Specifically, they proposed that the SRT method provides an estimate of IHTT of motor information, while the VEP method

provides an estimate of IHTT of visual information. They further proposed that anteriorly conducted motor information was transferred more rapidly (approximately 3 msec) than posteriorly conducted visual sensory information (approximately 16 msec). Saron and Davidson (1989) seem to agree with this explanation, proposing that the lack of correlation between the two methods reflects the complexity and heterogeneity of the transfer of different types of information (motor vs sensory) in different callosal regions (anterior vs posterior).

Confounding of the SRT IHTT estimates and the proposed differences in callosal transmission are not the only possible explanations for the absence of significant correlations between the SRT and VEP latencies. None of the conditions between the SRT and N160 paradigms were significantly related, although all correlations between conditions of the same paradigm were significant (see Table 10). The differences between the two groups in SRT are believed to result from real underlying differences in cerebral organization, but they are not reflected in VEPs. Therefore, it appears that SRT and VEP latencies reflect fundamentally different aspects of information processing.

One way to account for the independence of the two methods might be to consider the tremendous amount of processing potentially occurring during the intervening period between N160 and the motor response. As previously discussed, the VEP N160 peak is believed to reflect activity of the visual cortex, in areas 17 (the primary visual receptive cortex) and 18 and 19 (the visual association

cortex). N160, therefore, appears to be a good measure of activity in the visual cortex, including the initial stimulation of the primary visual cortex and secondary processing of the stimulus. By comparison, SRT is a very late behavioral process, occurring at approximately 250 msec post-stimulus. Even "simple" reaction times involve many complex cortical and peripheral processes. Therefore, early cortical (VEP N160) and late behavioral (SRT) processes will not necessarily be related, because so many individual and group differences can occur during the intervening period: In this case, the time period would be approximately 160 msec to approximately 250 msec, a difference of 90 msec. Following this "sequential" line of reasoning, differences in brain organization between left- and right-handers might also occur during this 90 msec latency window.

The current author believes, however, that a purely sequential explanation of cortical processing differences is probably overly simplistic. An alternate explanation might provide a more viable account for the independence of SRT and VEP latencies, as well as differences in brain organization between dextrals and sinistrals. This explanation takes into consideration differences between the primarily sequential process of sensory conduction along the visual pathway, and the more complex parallel processing of the cerebral cortex (Reitan & Wolfson, 1985b). Between the retina and the visual cortex, the visual system conducts sensory information along a discrete sequential pathway. In the SRT paradigm, electromagnetic energy from the visual stimulus excites the retina of the eye, causing a photochemical reaction, which in turn generates the initial

membrane potential. Direct projections from the retina form the optic nerve, and the nasal hemiretinae projections then cross at the optic chiasm, forming the left and right optic tracts. The fibers of each optic tract then synapse in the lateral geniculate body of the thalamus, forming the geniculocalcarine tract. Finally, this tract terminates at the optic radiations, which project into area 17 of the occipital lobe, the primary visual receptive cortex. Therefore, the processes set in motion after retinal excitation, up to the point of stimulation of the primary visual cortex, occur sequentially. One sequential process is always highly dependent on the previous process, as its sequence cannot begin until it is initiated by the parent process.

After initial cortical stimulation, however, many simultaneous and parallel processes are set in motion, as activation spreads out from the primary visual receptive cortex to other areas of the cortex. Unlike the initial visual pathway, information processing in the cortex is not a primarily sequential process from one discrete stage, and area of the brain, to another. Instead, many processes act simultaneously, and presumably independently, following initial activation of the cortex. These independent processes will not necessarily be reflected in occipitally recorded N160 latencies, even though they potentially have profound effects on SRTs. In addition, the fact that left- and right-handers produce similar VEPs does not preclude the possibility that group differences could occur before 160 msec. For instance, IHTT presumably takes only approximately 7 msec. Therefore, by 160 msec post-stimulus, many areas of the cortex

are certainly activated, even though their activity may not be reflected in occipitally recorded VEPs. This explanation, therefore, accounts for the lack of relation between SRTs and VEPs. The fact that these two measures are unrelated speaks to the complexity of brain processes, which can occur either in sequence (the receptive mechanisms along the initial visual pathway), or simultaneously and independently (the central processing mechanisms in the cerebral cortex).

Although this study cannot isolate a precise 90 msec time window for group differences, it can define more conservative upper and lower limits where these differences must, by process of elimination, occur. It has already been noted in the Introduction that dextrals and sinistrals do not differ in speed of peripheral sensory conduction (Tan, 1985). Thus, it seems unlikely that differences in SRT result from peripheral conduction of the cortical message to the muscles. This, therefore, sets a reasonable upper limit: Differences most likely take place around the cortical initiation of the motor response, or earlier.

As previously discussed, all visual processes from retinal excitation to stimulation of the primary visual cortex occur primarily in a sequential fashion, through known pathways. This initial sequential processing also allows one to define the lower limit of dextral-sinistral differences. Differences in this sequential process should be reflected in N160 latencies, because the time of initial cortical stimulation would vary: One sequential process is dependent on its parent process. Based on the N160

results of this study, dextrals and sinistrals probably do not differ in the speed of input mechanisms along their initial visual pathways.

Thus, the current study has narrowed down conservative upper and lower limits, between which, differences in brain organization likely occur. Differences between left- and right-handers, by process of elimination, presumably occur somewhere between the earliest responses of the visual cortex and the cortical initiation of the motor response. Although these differences are not necessarily confined to the 90 msec latency window between N160 and SRT, some additional conclusions can be made, based on knowledge of the human VEP. It has already been noted that N160 appears to be a good measure of activity in the visual cortex, including the primary and associative areas. The fact that left- and right-handers produce similar N160 latencies suggests that between-group differences do not occur during primary and secondary visual processing. Thus, results of the current study do not support the hypothesized lateralized differences in visual processing between left- and right-handers. Instead, differences most likely occur during complex tertiary processing, in which various sensory modalities are integrated, a "decision" made to respond, and a response ultimately initiated in the motor strip of the posterior frontal cortex. As previously discussed, many processes might be set in motion before 160 msec post-stimulus. Therefore, even these tertiary processes could conceivably begin before N160.

Although the accuracy of the SRT IHTT estimates have been called into question, the SRT differences between right- and left-handers

provide for the development of a useful model. Based on N160 results, dextrals and sinistrals do not appear to differ in primary and secondary processing in the visual cortex. Another explanation, therefore, seems more plausible, assuming the generally accepted principle of complete processing in the initially activated hemisphere (e.g., Berlucchi et al., 1971; Milner & Lines, 1982).

On the SRT task (see Figure 3), right-handers demonstrated advantages of 5.99 msec for right hand responses and 3.69 msec for left visual field responses. Among right-handers, therefore, the left hemisphere appears to be more efficient at initiating a motor response than the right hemisphere, while the right hemisphere seems to have an advantage over the left hemisphere for complex tertiary information processing. By comparison, left-handers did not demonstrate any significant response hand or visual field effects on the SRT task, with only a 2.07 msec left hand advantage and a negligible visual field difference (.59 msec). Therefore, the left-handers from the current study appear to have a non-significant right hemisphere advantage for motor control, and no apparent hemispheric advantage for integrative tertiary processing. It should be noted that these specific interpretations depend upon acceptance of complete processing in the initially activated hemisphere, as well as the validity of N160 as a measure of activity in the visual cortex. The reader is also reminded that left-handers of the current study were different from those of the previous study (Savage et al., 1988) on measures of SRT and lateralization. Regardless, however, it seems most likely that differences in brain organization between the two

handedness groups appear during complex tertiary processing and cortical initiation of the motor response. Left-handers appear to be less lateralized for these functions than right-handers, which is consistent with previously reviewed literature (e.g., Fennell, 1986; McKeever, 1986; Miller, 1983; Tankle & Heilman, 1982).

In conclusion, differences between dextrals and sinistrals do no appear to be the result of faster IHTT in the splenium of the corpus callosum, despite somewhat inconsistent evidence of larger callosi in left-handers. Differences in peripheral nerve conduction have also been ruled out by previous studies. In addition, the well established differences in SRT between dextrals and sinistrals are probably not the result of differences in stimulus input to the cortex, nor initial primary and secondary processing in the visual cortex. Instead, differences in brain organization, as reflected in the SRT procedure, probably occur during complex tertiary cortical processing, in which several modalities (e.g., visual, tactile, and motor) and cortical areas (e.g., occipital, parietal, frontal) are integrated, and a motor response cortically initiated. These processes can occur simultaneously and independently, and do not appear to be reflected in occipitally recorded VEPs.

The independence of the SRT and VEP measures speaks to the complexity of the human brain, particularly the cerebral cortex, as it carries out many tasks simultaneously and independently. The current author believes that handedness is also a very complex process, and that it is unlikely a "single mechanism" will ever be isolated to account for handedness. It appears that the brain

organization of a minority of sinistrals might result from some type of brain insult. However, many patterns of impairment can exist which ultimately lead to lateralization of behavior in brain damaged individuals. The current general consensus in the scientific literature is that lateral dominance is a naturally occurring phenomenon for the vast majority of left-handers. Even in this normal group, however, it is probably unlikely that a single cortical mechanism will ever be isolated to completely account for lateral dominance. Instead, "handedness" is most likely the end result of very complex cortical processes, which often operate independently, and ultimately determine where an individual lies along a continuum of lateralization.

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Table 1

Mean N160 Latencies (msec) for Visual Field and Hemisphere, and IHTT

Estimates (msec) for Each Visual Field

	Left Hemisphere (O1)	Right Hemisphere (O2)	IHTT Estimate by VF
Right Visual Field	155.5 (Direct)	168.5 (Indirect)	13
Left Visual Field	169.5 (Indirect)	151.5 (Direct)	18
IHTT estimate by hemisphere	14	17	

Table 2

Mean P1, N2, and P2 Latencies (msec) for Visual Field and Hemisphere, and IHTT Estimates (msec) for Each Visual Field and Electrode Site

		Left Hemisphere (O1)	Right Hemisphere (O2)	IHTT Estimate by VF and Peak
Right Visual Field	P1	129	140	11
	N2	177	188	11
	P2	268	261	-7
		(Direct)	(Indirect)	
Left Visual Field	P1	133	108	25
	N2	187	164	23
	P2	266	258	8
		(Indirect)	(Direct)	
IHTT Estimate by Hemisphere and Peak	P1	4	32	
	N2	10	24	
	P2	-2	3	

Table 3

Summary of the Hypotheses for the Proposed Study, Broken Down

According to the Purposes of the Study

Purpose 1 - Demonstrate intrahemispheric processing asymmetry
        differences between dextrals and sinistrals

    Dextrals - 1. See Figure 1
               2. Mean VEP peak latencies of the direct
                  condition greater for left hemisphere
                  measurements
               3. Mean VEP peak latencies of the indirect
                  condition equal between the hemispheres

    Sinistrals - 1. See Figure 1
                 2. Mean VEP peak latencies of the direct
                    condition greater for right hemisphere
                    measurements.
                 3. Mean VEP peak latencies of the indirect
                    condition equal between the hemispheres

    Between Groups - 1. The left hemisphere of sinistrals
                        faster than the left hemisphere of
                        dextrals in the direct condition

                     2. The right hemisphere of dextrals faster
                        than the right hemisphere of sinistrals
                        in the direct condition

Purpose 2 - Resolve SRT-VEP differences by demonstrating
        confounding of both estimates by intrahemispheric
        processing asymmetries

    1. VEP IHTT estimates faster for right visual field
       presentations among dextrals and left visual field
       presentations among sinistrals

    2. VEP IHTT estimates faster in the left hemisphere of
       dextrals and the right hemisphere of sinistrals

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Table 4

Hypotheses for Planned Comparisons of the SRT Data, for Each

Laterality Group, With Means of Each Condition in Parentheses

	Prediction	Significance Level	Outcome
Dextrals			
	1. Rt hand < Lft hand (243.42) (249.41)	p<.05	Supported
	2. LVF < RVF (244.57) (248.26)	p<.05	Supported
	3. LIL < LCL (246.33) (252.49)	p<.05	Supported
	4. RIL = RCL (244.03) (242.82)	p>.05	Supported
Sinistrals			
	1. Rt hand = Lft hand (241.51) (239.44)	p>.05	Supported
	2. RVF < LVF (240.18) (240.77)	p>.05	Rejected
	3. RIL < RCL (239.46) (243.57)	p<.05	Supported
	4. LIL = LCL (237.97) (240.90)	p<.05	Rejected

Table 5

Hypotheses for Planned Comparisons of the VEP N160 Data, for Each

Laterality Group, With Means of Each Condition in Parentheses

	Prediction	Significance Level	Outcome
Dextrals			
	1. RHD < LHD (157.25) (157.75)	p>.05	Rejected
	2. RHI = LHI (164.85) (162.88)	p>.05	Supported
Sinistrals			
	1. LHD < RHD (156.23) (157.68)	p>.05	Rejected
	2. LHI = RHI (163.20) (164.13)	p>.05	Supported
Between Groups			
	1. L Hem Sin < L Hem Dex (159.72) (160.32)	p>.05	Rejected
	2. R Hem Dex < R Hem Sin (161.05) (160.91)	p>.05	Rejected

Table 6

Hypotheses for Planned Comparisons of the VEP N160 IHTT Data, for

Each Laterality Group, With Means of Each Condition in Parentheses

	Prediction	Significance Level	Outcome
Dextrals			
	1. LHem IHTT < RHem IHTT (5.13) (7.60)	p>.05	Rejected
	2. RVF IHTT < LVF IHTT (7.10) (5.63)	p>.05	Rejected
Sinistrals			
	1. RHem IHTT < LHem IHTT (6.45) (6.98)	p>.05	Rejected
	2. LVF IHTT < RVF IHTT (5.53) (7.90)	p>.05	Rejected
Between Groups			
	1. IHTT Dex = IHTT Sin (6.36) (6.71)	p>.05	Supported

Table 7

Hypotheses for Planned Comparisons of the VEP P100 Data, for Each

Laterality Group, With Means of Each Condition in Parentheses

	Prediction	Significance Level	Outcome
Dextrals			
	1. Direct < Indirect (114.70) (118.06)	p>.05	Rejected
	2. LHD = RHD (116.57) (112.83)	p>.05	Supported
Sinistrals			
	1. Direct < Indirect (118.49) (123.27)	p<.05	Supported
	2. LHD = RHD (121.43) (115.54)	p<.05	Rejected
Between Groups			
	1. Dir Dex = Dir Sin (114.70) (118.49)	p>.05	Supported

Table 8

Mean SRTs and Estimated IHTT for all Conditions by Handedness,

Response Hand, and Visual Field

	L Hand-LVF (LIL)	L Hand-RVF (LCL)	R Hand-LVF (RCL)	R Hand-RVF (RIL)
Dextrals				
	246.33 SD=28.63	252.49 SD=26.32	242.82 SD=24.50	244.03 SD=24.55
Sinistrals				
	237.97 SD=21.19	240.90 SD=22.97	243.57 SD=24.50	239.46 SD=26.27

IHTT Estimates

		Left Hand	Right Hand	IHTT by Visual Field
RVF	Dex	252.49	244.03	8.46
	Sin	240.90	239.46	1.44
	Overall	246.70	241.75	4.95
		(Contralateral)	(Ipsilateral)	
LVF	Dex	246.33	242.82	−3.51
	Sin	237.97	243.57	5.60
	Overall	242.15	243.20	1.05
		(Ipsilateral)	(Contralateral)	
IHTT by Hand	Dex	6.16	−1.21	2.48
	Sin	2.93	4.11	3.52
	Overall	4.55	1.45	3.00

Table 9

Mean VEP N160s and Estimated IHTT for all Conditions by Handedness, Hemisphere, and Visual Field

	L Hem-LVF (LHI)	R Hem-LVF (RHD)	L Hem-RVF (LHD)	R Hem-RVF (RHI)
Dextrals				
	162.88 SD=8.94	157.25 SD=10.85	157.75 SD=9.60	164.85 SD=8.63
Sinistrals				
	163.20 SD=9.05	157.68 SD=8.16	156.23 SD=10.83	164.13 SD=8.49

IHTT Estimates

		Left Hemisphere (01)	Right Hemisphere (02)	IHTT by Visual Field
RVF	Dex	157.75	164.85	7.10
	Sin	156.23	164.13	7.90
	Overall	156.99 (Direct)	164.49 (Indirect)	7.50
LVF	Dex	162.88	157.25	5.63
	Sin	163.20	157.68	5.52
	Overall	163.04 (Indirect)	157.47 (Direct)	5.57
IHTT by	Dex	5.13	7.60	6.37
Hem	Sin	6.97	6.45	6.71
	Overall	6.05	7.02	6.54

Table 10

Correlations Between all Conditions of SRT and VEP N160 Paradigms

	SRT Conditions				VEP N160 Conditions			
	LIL	LCL	RCL	RIL	LHI	RHD	LHD	RHI
LIL	---	.95 p<.01	.86 p<.01	.84 p<.01	.06 ns	-.13 ns	-.03 ns	-.04 ns
LCL		---	.84 p<.01	.87 p<.01	.05 ns	-.04 ns	.03 ns	.01 ns
RCL			---	.96 p<.01	.08 ns	.01 ns	.06 ns	.04 ns
RIL				---	.08 ns	.07 ns	.09 ns	.07 ns
LHI					---	.63 p<.01	.47 p<.01	.66 p<.01
RHD						---	.66 p<.01	.69 p<.01
LHD							---	.65 p<.01
RHI								---

Figure Caption

Figure 1. Illustration of the theoretical model of Savage et al.

(1988), with response pathways in order from fastest to slowest, for

right- and left-handers.

RIL = Right Hand Ipsilateral   RCL = Right Hand Contralateral
LIL = Left Hand Ipsilateral   LCL = Left Hand Contralateral

1 = Very Fast   2 = Fast   3 = Slow   4 = Very Slow
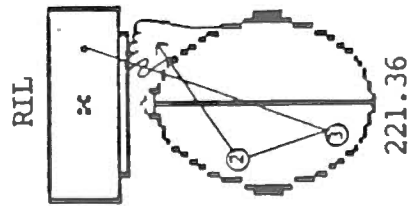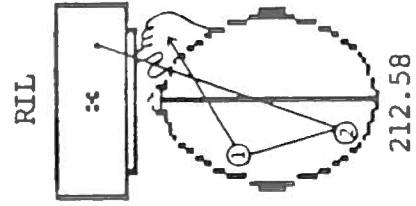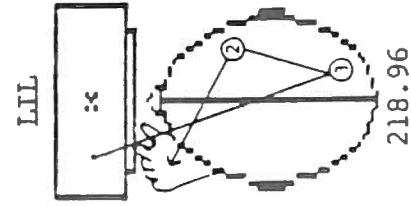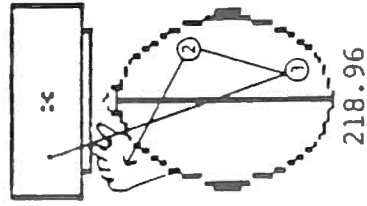
RIL   RCL   LIL   LCL

221.36   221.65   225.65   230.38

RIGHT-HANDERS

RIL   LCL   LIL   RCL

212.58   218.14   218.96   219.47

LEFT-HANDERS
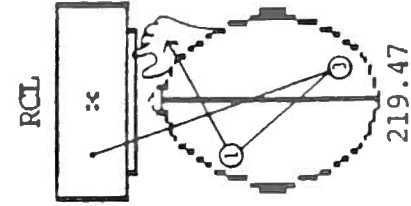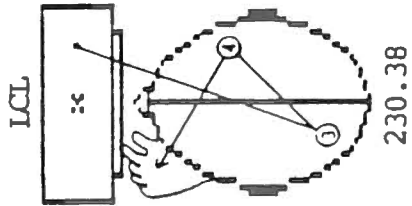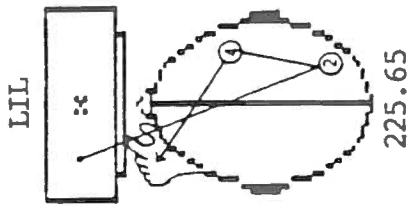
Figure Caption

Figure 2. Illustration of a prototypical VEP, elicited from cross

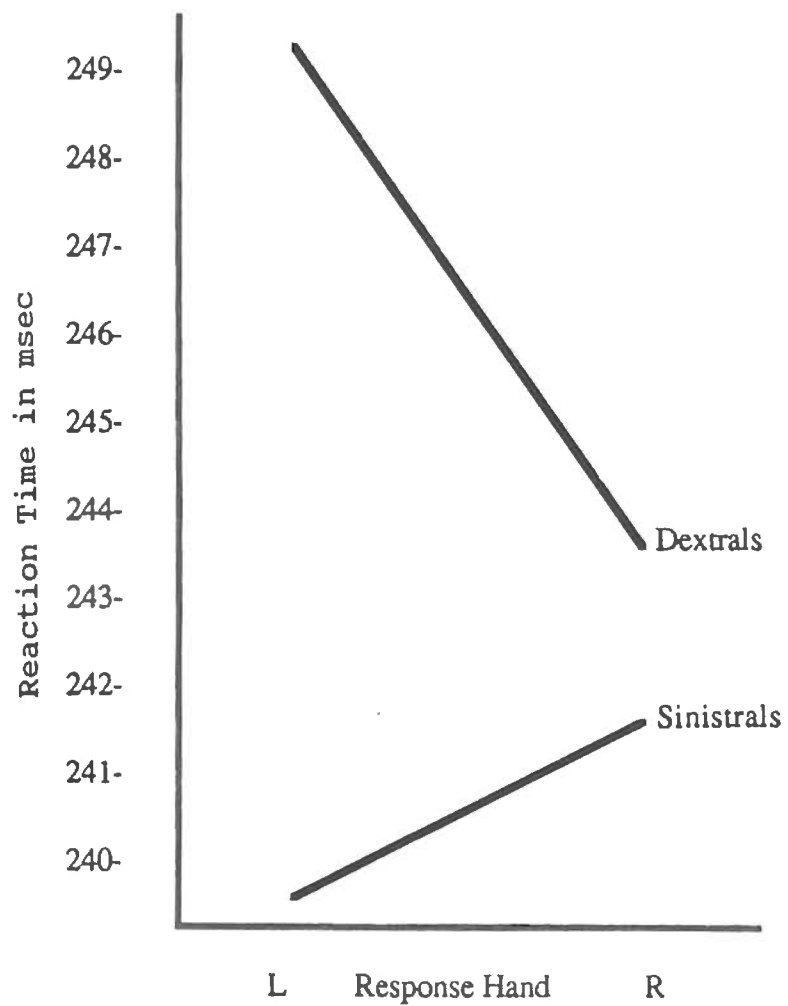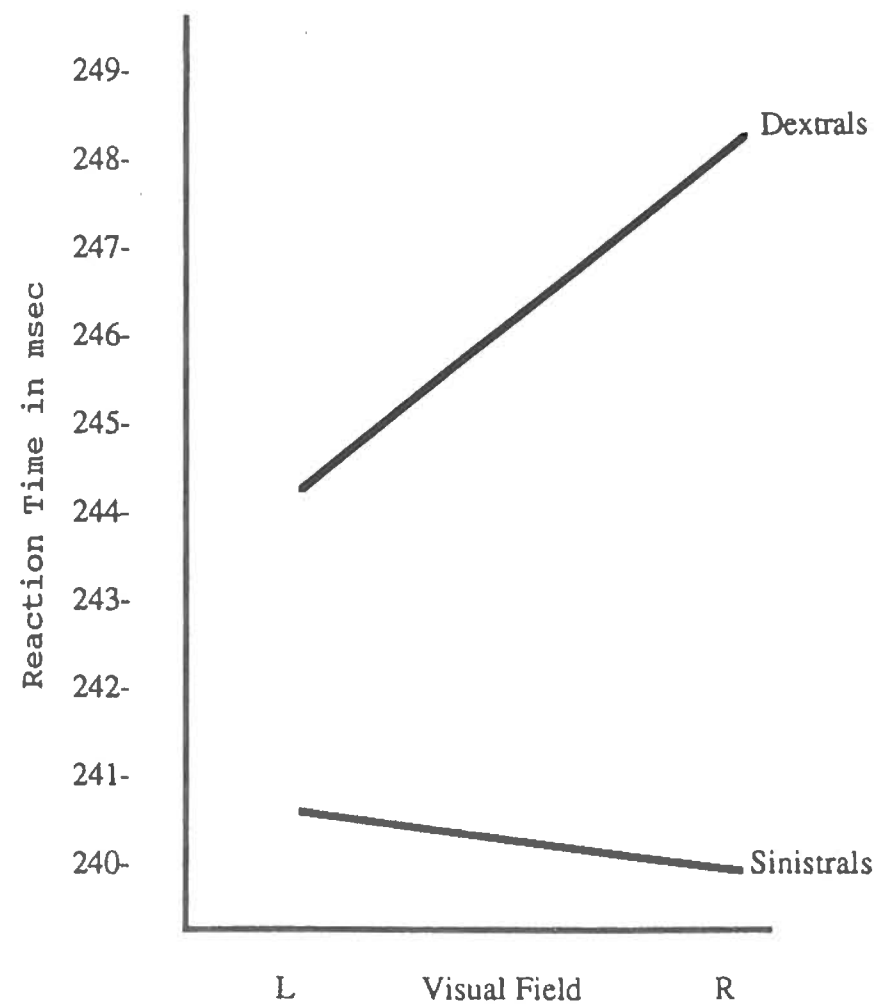(+) stimuli, in an SRT paradigm similar to Savage et al. (1988).

P100

N160

Stimulus
Onset

0   50   100   150

Latency in msec

PROTOTYPICAL VEP
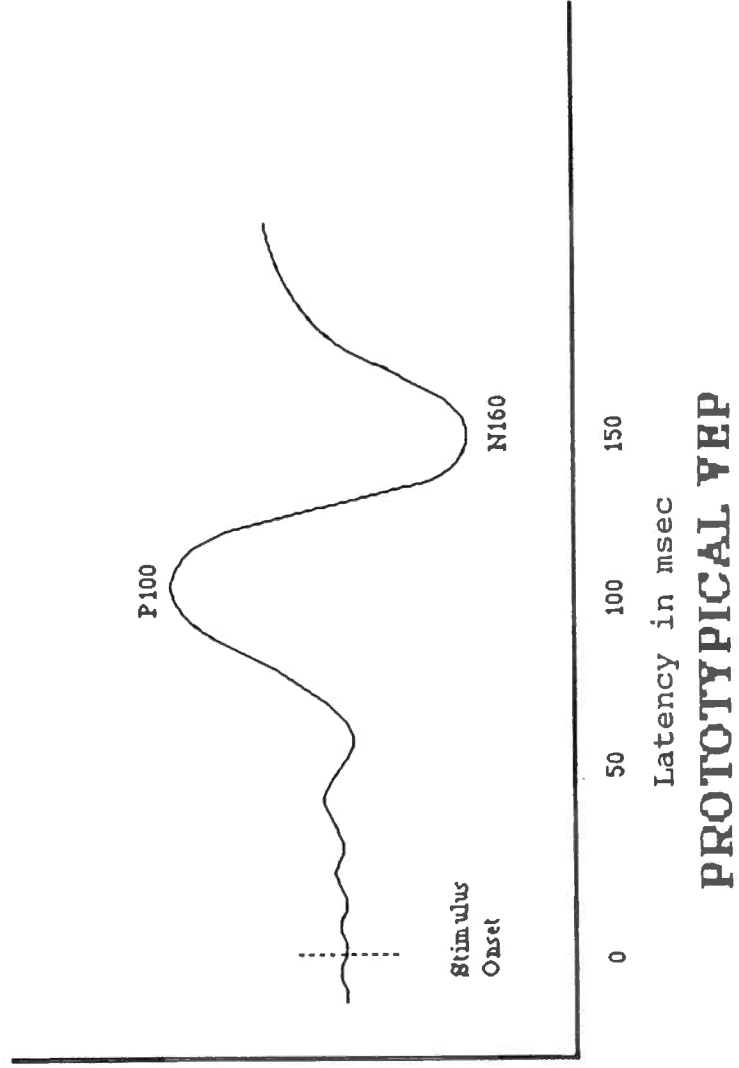
Figure Caption

Figure 3. Laterality x response hand and laterality x visual field

interactions from the SRT data.

LAT X RH

LAT X VF

Figure Caption

Figure 4. Response hand x visual field interaction from the SRT

data, with lines drawn to depict contralateral and ipsilateral

effects. This interaction illustrates the effects of IHTT in the SRT
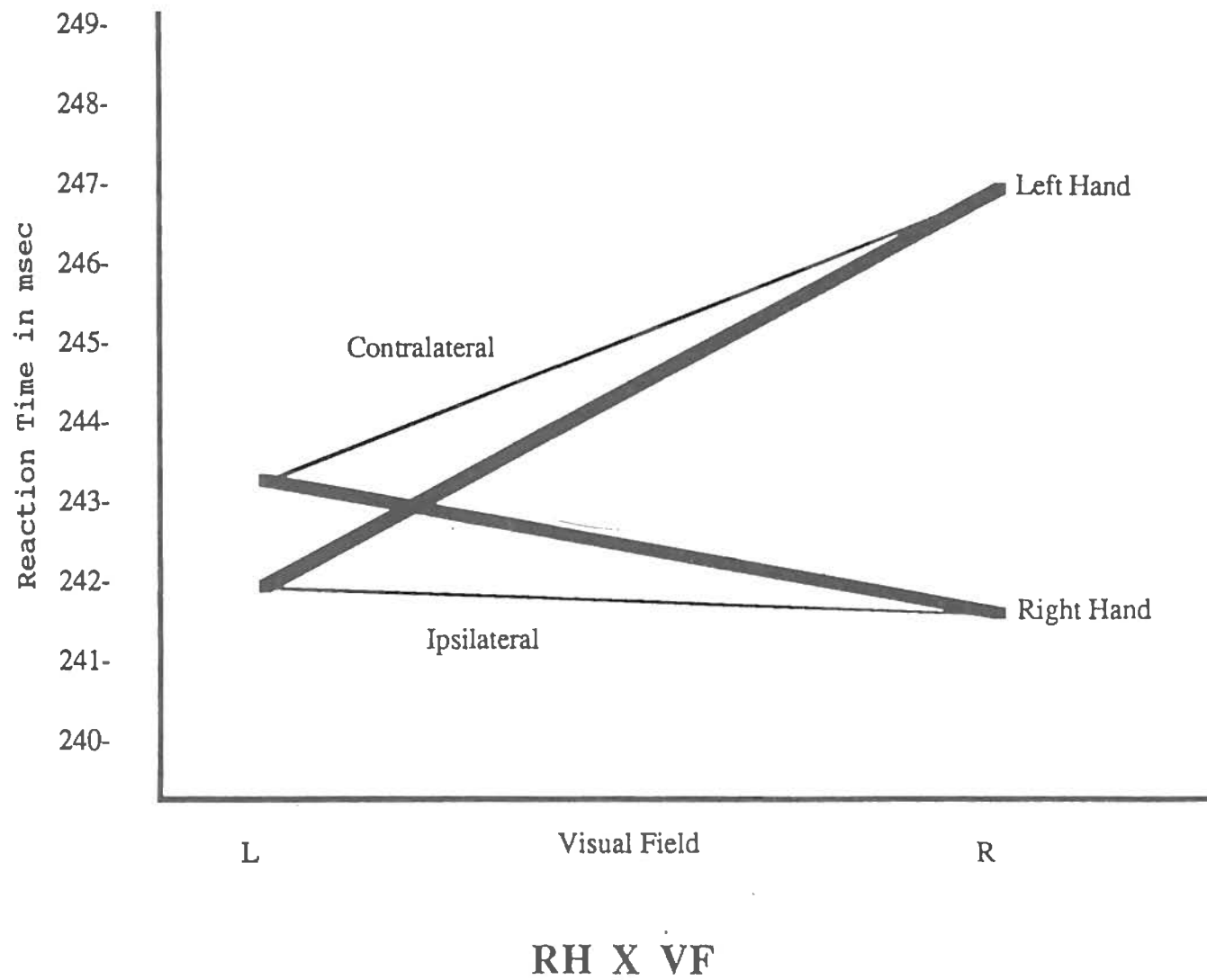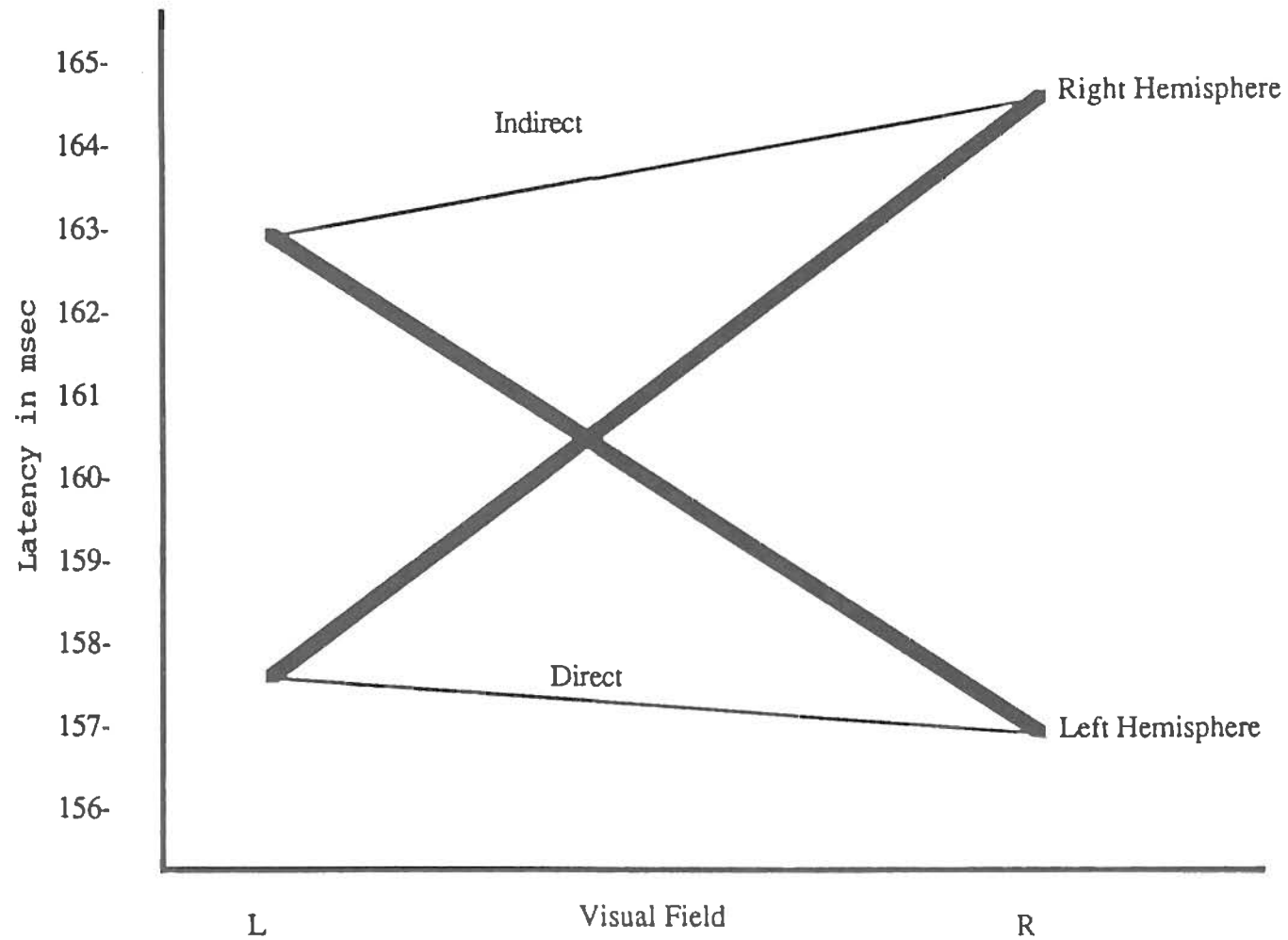
paradigm.

RH X VF

Figure Caption

Figure 5. Hemisphere x visual field interaction from the VEP N160 data, with lines drawn to depict indirect and direct effects. This interaction illustrates the effects of IHTT in the VEP N160 paradigm.

Figure axes: Latency in msec (y-axis, 156 to 165); Visual Field (x-axis, L to R). Lines labeled Indirect, Direct, Right Hemisphere, Left Hemisphere.
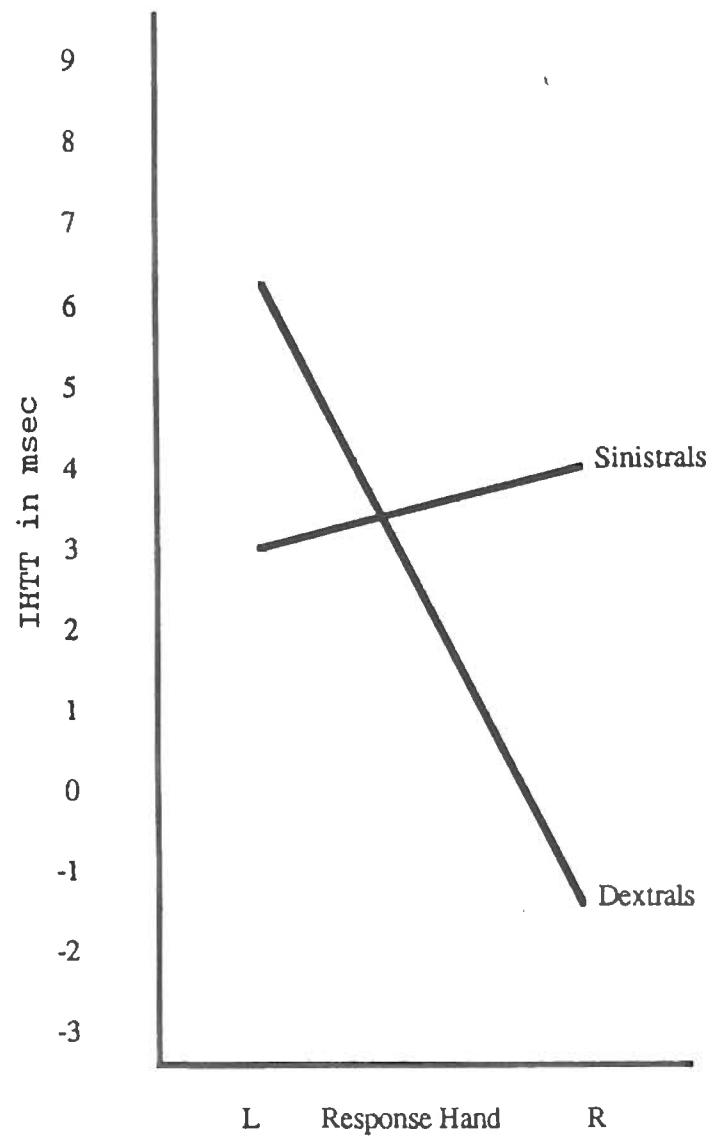
HEM X VF

Figure Caption

Figure 6. Hemisphere x visual field interaction from the VEP P100 data, with lines drawn to depict indirect and direct effects. This interaction illustrates the effects of IHTT in the VEP P100 paradigm.
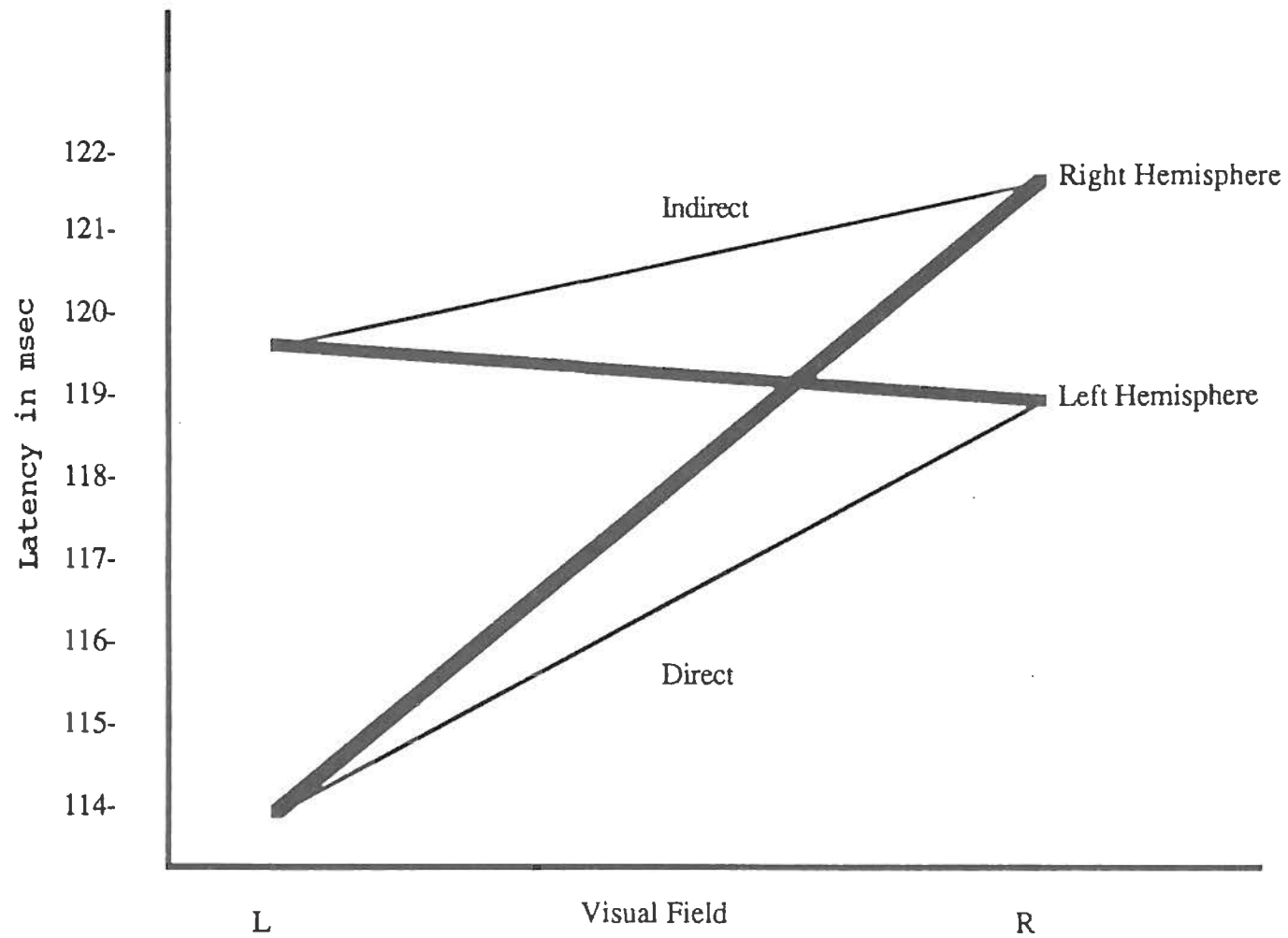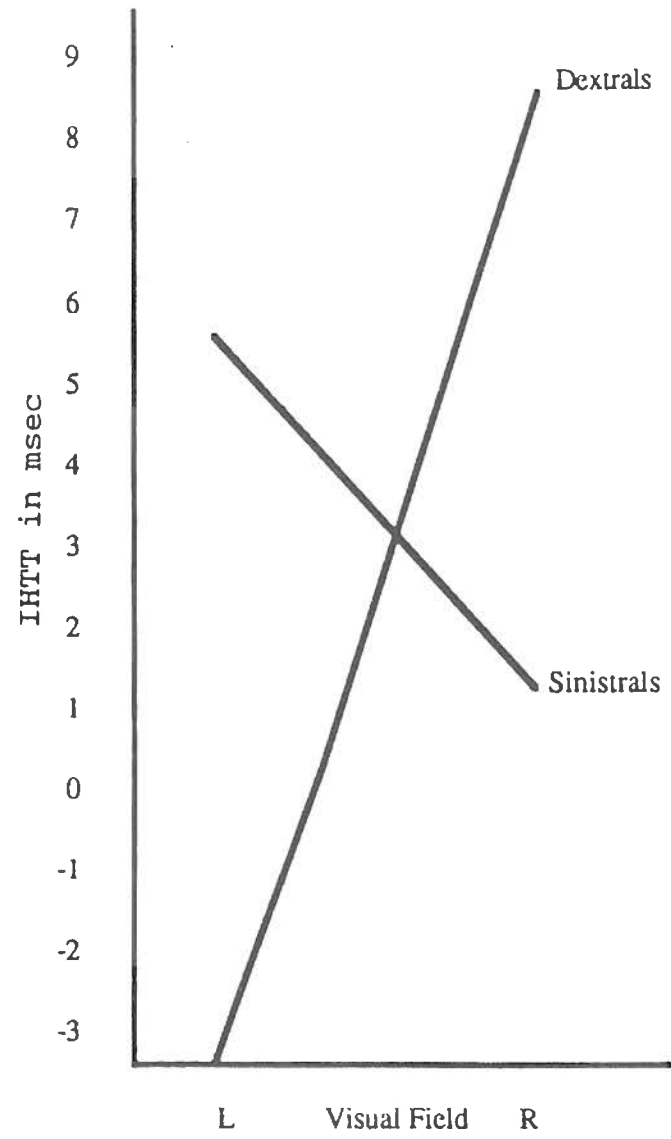
HEM X VF

Figure Caption

Figure 7. Laterality x response hand and laterality x visual field

interactions from the SRT IHTT data.

LAT X RH

LAT X VF

VITA

Cary R. Savage

Candidate for the Degree of

Doctor of Philosophy

Thesis: INFORMATION PROCESSING DIFFERENCES IN DEXTRALS AND
         SINISTRALS

Major Field: Clinical Psychology

Biographical:

    Personal Data: Born in Fort Worth, Texas, December 8, 1962, the
        son of Roy E. and Kay Savage.

    Education: Graduated from Gregory-Portland Senior High School,
        Portland, Texas, in December, 1980; received Bachelor of
        Arts degree in Psychology from University of Northern
        Colorado in June, 1986; received Master of Science degree
        in Psychology from Oklahoma State University in May, 1988;
        completed requirements for the Doctor of Philosophy degree
        at Oklahoma State University in July, 1991.

    Professional Experience:
        Clinical: Psychological Associate, Psychological Services
            Center, Oklahoma State University, August, 1987 to
            May, 1989; Therapist, Marriage and Family Counseling
            Service, Oklahoma State University, June, 1988 to
            August, 1989; Therapist, Family Mental Health Center,
            Tulsa, Oklahoma, August, 1988 to August, 1989;
            Administrative Assistant, Psychological Services
            Center, Oklahoma State University, May, 1989 to June,
            1990; Clinical Fellow in Psychology, Harvard Medical
            School/Massachusetts General Hospital, Boston,
            Massachusetts, July, 1990 to present.
        Teaching: Teaching Assistant, Department of Psychology,
            Oklahoma State University, August, 1986 to August,
            1988.