Cerebral asymmetries in processing language and time

by

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Abstract

Initially it was thought that only `higher functions' are lateralized, but investigators have recently been noting very `low-level' perceptual asymmetries. Some have speculated that these low-level asymmetries underlie hemispheric specialization for higher functions such as language processing. Experiments 1 and 2 tested this hypothesis by administering tests of low-level temporal asymmetries in the visual (1) and auditory (2) modalities, concurrent with a dichotic-listening test of linguistic laterality. As predicted, individuals demonstrated significant left hemisphere advantages (LHAs) on both the visual and auditory temporal tasks, and in both cases, these LHAs correlated significantly with linguistic asymmetries. A recent theory by Ringo et al. (1994) claims that the evolutionary pressure favouring hemispheric specialization came from a lateralized system's relative superiority at processing stimuli requiring fine temporal precision. This theory would then predict that individuals with greater interhemispheric transmission times (IHTTs) would exhibit greater lateralization for time critical tasks such as language processing. Experiment 3 provided support for the prediction that longer IHTT's from the right to left hemisphere in the auditory modality are associated with greater left hemispheric specialization for linguistic perception. Experiment 4 tested two predictions. The first prediction, that preferred hand for throwing (but not preferred hand for writing) would be associated with linguistic lateralization, was only supported by individuals who normally write with their right hand. The second prediction, that complementarity of functional asymmetries should not be causal in nature, was also supported. There was a weak positive association between what are normally right and left hemispherically dominated tasks. Taken together, these results support the position that the brain is lateralized to facilitate temporal processing.

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Although Phil Bryden never got to see these experiments completed, I will forever wonder what he would have thought of them. Getting to know him profoundly altered the way I think about designing experiments, interpreting the experimental literature, what a student-advisor relationship should be like, what makes a for a successful scholarly conference, and how to combine an academic career with a happy life.

Dedication

To Phil Bryden
1934 - 1996

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General Introduction: We know what is lateralized, but we don't know why

We have been actively studying hemispheric specialization for well over a hundred years. Although we have learned a great deal about anatomical and functional asymmetries across species, we know very little about the possible causes of such deviations from symmetry. What adaptive advantage is provided by lateralization? Why is it subject to individual variation? To what degree is hemispheric specialization uniquely human? What developmental mechanism leads to lateralization?

The present document will examine the possibility that hemispheric specialization arose as a consequence of increasing interhemispheric axonal conduction delay (ICD), coupled with an increasing need for high temporal precision at the behavioural level. The theory requires that one abandon the traditional assumption that hemispheric asymmetry is related to behavioural complexity. "Deviations from bisymmetry have attracted interest because they characterize the representation of many higher mental functions" (Hiscock & Kinsbourne, 1995, p. 535), but this does not necessarily imply the claim of Luria (1973), that the more abstract a function is, the more its cerebral basis is asymmetric.

More recently, it has become clear that hemispheric specialization is not uniquely human, and it is not restricted to "higher functions". "It is no longer tenable to view brain lateralization as an exclusively, or even primarily human attribute" (Hiscock & Kinsbourne, 1995, p. 563). Further, robust "lower-level" cerebral asymmetries have been demonstrated for very simple temporal tasks in the visual, auditory, and somatosensory modalities (see Nicholls, 1996, for a review). Therefore, cerebral specialization can influence the processing of all stimuli, regardless of their complexity.

There is increasing speculation that low-level temporal asymmetries might underlie some hemispheric specializations for "higher functions". Tallal et al. (1993) claim that "Processes that have been interpreted to be hemispherically specialized for speech may in fact be specialized, more generally, for the analysis of rapidly changing acoustic information....we suggest that it is the temporal requirement, not the requirement for verbal analysis per se, underlying the observed REA for speech." (pg. 38 and pg. 41). After reviewing competing theories about the potential causes and nature of hemispheric specialization, I will describe tests of this claim.

A successful theory of the cause of functional cerebral asymmetry has some daunting criteria to satisfy. McManus (1985) provides a list of these criteria, which include (1) the ability to account for parent-child concordance rates for handedness (2) the ability to account for the low handedness concordance rate between MZ twins (3) the ability to account for differences in the prevalence of left-handedness between different cultural/genetic populations and generations, (4) compatibility with other known mechanisms of inherited asymmetries, and (5) biological integrity (consistency). To these criteria, Laland et al. (1995) added that such a theory must have (6) the ability to explain the finding that all human societies are (and presumably have been) predominantly right-handed, and (7) the ability to "explain how the processes that underlie handedness could have come into existence" (Laland et al., 1995, p. 435). To these criteria, I add these two: The successful theory should also account for (8) the well known sex differences in the laterality literature, such as the finding that males are more likely to be left-handed than females (Gilbert & Wysocki, 1992), and (9) the associations between left-handedness and various special populations.

Theories about the cause of laterality

When researching the potential causes of laterality, one encounters a wealth of theories, with widely varying perspectives on the problem. Some assume that laterality is learned, and that an exclusively "environmental" explanation can account for the phenomenon. Others take a strictly biological perspective, not recognizing any role played by the environment. Still others integrate the two perspectives within an ontogenetic or phylogenetic context. The following section will critically review the theories that have been popular over the last century. For an excellent review of earlier theories, see Harris (1980).

A. Environmental/Psychosocial Theories

1. Jackson's (1905) "Parental Pressure" Theory

Some authors have claimed that handedness is entirely determined by the environment of a child, and that this effect is in no way influenced by biological factors. For example, the "Parental Pressure" theory posited that most humans are right-handed because their parents were right-handed and parents tend to pressure their infants into conforming to their own handedness pattern. Jackson (1905) asserted that a child's handedness is (initially) completely flexible, and that any given child can be right-handed, left-handed, or even ambidextrous given the appropriate environment. Because of this flexibility, Jackson (1905) claimed that all children should be taught to use either hand interchangeably.

Much more recently, the "extreme" position that the direction of handedness is determined exclusively by environmental asymmetries was supported through a series of comparative studies (Collins, 1970; Collins, 1975). Mice do not normally demonstrate population-level motoric biases to one side or the other. However, after forcing mice to feed through a glass tube against a right wall, Collins (1970) found that 90% of the mice would feed with their right paws (a figure that approximates the handedness distribution in humans, who also live in a "right-handed" world). Further, subsequent breeding studies have revealed that **direction** of paw preference does not seem to be influenced by genetics, but one can breed for **degree** of paw preference (Collins, 1985; Signore, Chaoui, Nosten-Bertrand, Perez-Diaz, & Marchaland, 1991).

2. Blau's (1946) Psychodynamic Theory

Within a psychoanalytic framework, Abram Blau (1946) also argued that a child's handedness was the result of his/her environmental circumstances. Left-handedness was claimed to be the result of "emotional negativism", having no biological basis whatsoever.

Problems with Environmental/Psychosocial theories:

(1) Handedness runs in biological families, regardless of the handedness of those parenting the child. Adoption studies have shown that the handedness of a child is more closely related

to that of the biological parent than that of the adoptive parent (Carter-Saltzman, 1980; Hicks & Kinsbourne, 1976).

(2) Left-handedness has persisted across the centuries (see Coren & Porac, 1977). If handedness is determined by environmental influences, why would it persist against violent opposition for so many years?

(3) All siblings in a given family do not exhibit uniform handedness (even identical twins), despite very similar (if not identical) environmental circumstances (see McManus, 1980).

(4) The newborn fetus exhibits structural asymmetries in the brain's hemispheres, long before any parental "environmental" influence could have taken place (see Previc, 1991).

(5) This theory does not suggest an impetus behind the population-level right-handedness that we see today, it merely proposes a mechanism for the maintenance of this right-handed bias.

B. Genetic Theories

Genetic theories of lateralization do not necessarily "compete" with the developmental and evolutionary theories discussed here, because they address a different level of explanation of cerebral asymmetries. Genes code for the production of proteins, not "behavioural traits".

Therefore, even if lateralization is entirely controlled by genetic processes and we successfully identified all genes relevant to its expression, we still would not necessarily know what developmental mechanisms are critical, or why lateralization is advantageous to the individual. Similarly, isolating the genes responsible for the growth of feathers in birds would not be informative about why feathers are adaptive. Even if the developmental theories of Previc (1991, 1996) or Geschwind et al. (1985a; 1985b; 1985c; 1987) prove to be completely correct (these theories are discussed in the next section), it is quite possible that the mechanisms they propose are controlled through the expression of genes.

Nevertheless, some of the more "environmental" theories discussed above do not acknowledge any biological contribution to the determination of direction of handedness (Blau, 1946; Collins, 1985; Jackson, 1905). There is considerable evidence that handedness is under some sort of genetic control, and discussing the theories here is important in proving that lateralization is biologically, rather than strictly environmentally determined.

There is little doubt that handedness runs in families, but the extent to which this effect is due to environmental pressure (parents purposefully or accidently teaching their children to be right- or left-handed) is unclear. According to a recent meta-analysis by McManus and Bryden (1992), two right-handed parents have a 9.5% chance of having a left-handed child. The chances rise to 19.5% if one parent if left-handed (and this effect appears to be driven primarily by left-handed mothers), and 26.1% of the children from two left-handed parents are also left-handed. Taken alone, these statistics do not necessitate a "genetic" conclusion, for the effect could be driven entirely by parental pressure. However, genetic arguments become much more convincing when one notes that even adoption studies suggest that handedness is under genetic control. The handedness of adopted children is more likely to follow that of their biological parents than of their adopted parents (Carter-Saltzman, 1980; Hicks & Kinsbourne, 1976).

There is even some evidence concerning the potential location of the gene (or genes) that could code for handedness. Same-sex siblings are more likely to be concordant for handedness than are opposite-sex siblings. Based on this finding, Corballis, Lee, McManus, and Crow (1996) concluded that "the genetic locus for handedness is in an X-Y homologous region of the sex chromosomes" (p. 67).

1. Simple Mendelian Recessive Gene Theories

Most early genetic theories proposed that handedness is a recessive trait, following the laws of Mendelian genetics (Chamberlain, 1928; Falek, 1959; Hudson, 1975; Jordan, 1911; Jordan, 1922; Newman, 1931; Ramaley, 1913; Rife, 1940; Schott, 1931; Trankell, 1955; see Hardyck, 1977, for a review). However, the pattern of inheritance followed by left-handedness appears to be far too complex for this type of genetic model. Specifically, the proportion of left-handed children born of one or two left-handed parents is too low to support such a simple model. As a result, more recent genetic theories have postulated an element of "chance" within the genetic model, or proposed a two gene-locus mechanism for the expression of handedness. The following sections will review the four most popular current genetic theories of handedness and cerebral lateralization (See Corballis, 1997b).

2. McManus's (1985) Model

The McManus (1985) model proposes that hand preference is controlled by two alleles at one gene locus. However, the model is not quite like the simple Mendelian dominant/recessive theories described above. The *D* allele codes for 'dextrality', and instead of the second allele coding for 'sinistrality', the *C* allele codes for 'chance' determination of handedness (defined in terms of hand preference). The model postulates that the incidence of right-handedness is determined additively within the model, wherein 100% of *DD* homozygotes will be right-handed, compared with 75% of *CD* heterozygotes and 50% of *CC* homozygotes. Therefore, "chance" determination of handedness is only linked to the *C* allele.

3. Annett's (1972) Right Shift Model

Like McManus's (1985) model, the Annett (1972) 'Right Shift' model also proposes that handedness is controlled by two alleles at one gene locus. However, Annett's model differs from McManus's in that inheritance of the 'Right Shift' (RS) gene biases an individual towards superior right-hand skill, not preference. In the absence of the RS gene, the individual will not necessarily be biased towards left-hand skill, but instead, handedness will be determined randomly. Because of this assumption of "chance" handedness in the absence of the RS gene, Annett's (1972) theory can also provide a plausible account of the relative number of left-handed children born of the four possible combinations of right- and left-handed parents (Annett, 1974; Annett, 1983; Annett, 1985; but see McManus & Bryden, 1992, for a review and meta-analysis).

4. Klar's "RGHT" (1996) Model

Klar's (1996) genetic model attracted a great deal of media attention (provoking national headlines such as "Lefties missing gene"), but it offers very few differences from the Annett (1985) RS theory and McManus's (1985) theory described above. Like both Annett (1985) and McManus (1985), Klar (1996) also claims that handedness is coded by two alleles at one gene locus, which he names 'RGHT'. The two possible alleles are "R" for right-handed, and "r" for random handedness. Therefore, half of individuals homozygous for the "r" allele will be left-handed, half will be right-handed, and all heterozygotes will be right-handed.

As with the other two single-gene theories, the Klar (1996) theory must accurately predict the prevalence of left-handed children from parents with the four possible handedness combinations. Annett (1985) defines handedness in terms of hand skill, McManus (1985) defines handedness in terms of hand preference, but Klar (1996) defines hand preference according to a preference test published by Rife (1940) in which individuals are considered right-handed iff (if and only if) the acts of throwing a ball, using a spoon, sawing, sewing, shooting marbles, bowling, cutting with a knife, cutting with scissors, hammering, and writing are **all** performed **only** with the right hand. If an individual performs any of these activities with the left hand or either hand, he or she is considered left-handed. Although Klar (1996) claims that "some investigators in this field (see, e.g., Annett, 1985) seem to agree that the best criteria and definition are those adopted by Rife (1940)" (p. 59-60), it is my experience that most investigators define handedness according to scores on "hand preference" inventories, such as the Edinburgh handedness inventory (Oldfield, 1971), the Lateral Preference Inventory (Porac & Coren, 1981), or the Waterloo Handedness

Questionnaire (Steenhuis & Bryden, 1989). Unlike Rife's (1940) measure, these tests require that a person demonstrate an average bias to the left side over a number of the items (not just one) before they are defined as left-handed.

Using Rife's (1940) relatively "liberal" criteria for left-handedness (or "stringent" criteria for right-handedness), it is not surprising that Klar (1996) finds much higher prevalence of left-handedness in the offspring of two left-handed parents than the 26.1% reported in the meta-analysis by McManus and Bryden (1992). Instead, Klar (1996) reports that 78% (7 out of 9) of the children born of two left-handed parents in their sample were left-handed, according to Rife's (1940) measure. Rife (1940) reported that 50% of the children of two left-handed parents would also be left-handed, a result very similar to those of Annett (1974; 1983) who used performance measures to define handedness. Therefore, defining handedness according to hand skill or using Rife's (1940) stringent preference measure can produce data that conform more closely to the predictions of Klar's (1996) genetic theory.

Although Klar (1996) appears to be using an outdated measure of handedness, the most significant contribution that he made to this area of research was the presentation of handedness data that spanned three generations. This type of data is **essential** for testing these single-gene theories. By examining the handedness of both one's parents and grandparents, it is then possible to determine with certainty whether an individual is heterozygous or homozygous for the dominant "dextral" allele, be it Annett's (1985) "RS factor", McManus's (1985) "*D*" allele, or Klar's (1996) "*R*" allele.

5. Levy and Nagylacki's (1972) Two Gene-Locus Model

A relatively more complex model was proposed by Levy and Nagylacki (1972), who proposed that the complex interactions between handedness and the cerebral lateralization of higher functions must depend on more than one genetic locus. They proposed a model in which one genetic locus determines which hemisphere is dominant for higher functions (such as language), and another locus determines whether manual motor control is ipsilateral or contralateral to the language-dominant hemisphere. The position that laterality is specific to "higher functions" has not been borne out by recent experimental evidence, as discussed more thoroughly in a later section.

Furthermore, as reviewed by Corballis (1997a), this theory cannot explain the relatively low concordance of handedness among twins (reviewed by McManus, 1980). Although the authors later claimed that twinning produces complications that make twin studies inappropriate for evaluating genetic theories of lateralization (Nagylaki & Levy, 1973), it seems extremely unlikely that these complications alone could completely eliminate genetic influences on cerebral lateralization, if such influences do exist.

Problems with genetic theories:

(1) It is very difficult to evaluate (and therefore falsify) genetic theories of lateralization. With the exception of adoption studies, it is very difficult to separate environmental effects from genetic effects.

(2) Different theorists define handedness according to different criteria. For example, Annett (1972) defines handedness in terms of relative hand skill whereas McManus (1985) defines it in terms of hand preference.

(3) Genes code for the production of proteins, not 'behaviours'. Although genes *could* be the mechanism of lateralization, that is uninformative regarding <u>why</u> lateralization provides an adaptive advantage.

C. Anatomical Theories

The anatomical asymmetries exhibited by the brain pale in comparison to those found in other internal organs. The leftward displacement of the heart is arguably the most dramatic asymmetry, but even "paired" organs such as the lungs, kidneys, ovaries, and testes exhibit obvious and reliable lateralization (Bisazza, Rogers, & Vallortigara, 1998; Bogaert, 1997; Gerendai & Halasz, 1997; McCarthy & Brown, 1998). Some have claimed that these asymmetries are causally related to cerebral asymmetries.

1. Thomas Carlyle's "Sword and Shield" Theory

According to Hardyck and Petrinovich (1977) and Corballis (1980), the "Sword and Shield" theory was first put forward by Sir Thomas Carlyle. Carlyle claimed that handedness had its origins in early warfare, when the combatants who held their sword in the right hand and shield in their left (and therefore better protected their heart) were more likely to survive in battle. The greater mortality of the left-handers in battle, then, is proposed as the mechanism driving the higher prevalence of right-handedness today.

This theory is still popular today, and although it is appealing in its simplicity, the theory is also fraught with problems:

(1) Right-handedness was the norm far before the bronze age, suggested by the hunting style of Australopithecus (Dart, 1949), stone implements constructed by Peking Man (Black, Young, Pei, & de Chardin, 1933), paintings of hands by Cro-Magnon (Magoun, 1966), examination of North American aboriginal art (Brinton, 1896), the hand used for skilled activities depicted in paintings in the tombs of Beni Hasan and Thebes between 2500 B.C. and 1500 B.C. (Dennis, 1958), and large-scale studies of ancient artworks (Coren & Porac, 1977). In all of these studies, the estimated distribution of hand preference is similar to the prevalence we observe today.

(2) The theory predicts that men would be more likely to be right-handed than women (because, after all, they were usually the ones fighting with swords). The data indicate the opposite - males are more likely to be left-handed than are females, by a ratio of 5:4 (Gilbert & Wysocki, 1992).

(3) Those very rare cases of *situs inversus*, in which asymmetries including the heart and other

organs are reversed from left to right, do not exhibit left-handedness more frequently than normals (Cockayne, 1938; Torgerson, 1950; Wilson, 1872). For example, in a sample of 160 people with the anomaly, Torgerson (1950) found that 6.9% were left-handed.

(4) The heart is really not displaced to the left very much - its location is quite central. Therefore, the selective pressure favouring protection of the left side would be weak, resulting in handedness ratios that are slightly biased towards right-handedness. It seems unlikely that the very different prevalence of left-/right-handedness (10%/90%) could be driven by such a weak effect.

2. Salk's (1966) "Parent Holding Baby" Theory

A less popular theory (also cardiac in origin) claims that humans developed population level right-handedness as a result of our attempts to comfort our young. More specifically, the theory claims that most women (and presumably men) could most effectively comfort infants if they were cradled in the parent's left arm, keeping the head of the baby closest to the parent's heart (the sound of a heartbeat is known to soothe infants, see Salk, 1973) and leaving the parent's right hand free to perform more complex tasks. Because the right hand would benefit from more practice than the left with highly skilled unimanual manipulations, right-handedness could have become the norm. This theory is not without *some* empirical support. Salk (1966) found that both right-handed and left-handed women usually hold neonates with their left arm.

Although this theory correctly predicts the greater prevalence of right-handedness among females (who traditionally perform more of the child-rearing duties), it also has some serious flaws. Perhaps its most serious shortcoming is its assumption that a left-sided carrying arrangement would have more influence on the handedness of the parent than it would on that of the child. Because carrying an infant with one's left hand leaves the infant's left hand free (assuming the infant's head is lateral, not medial with respect to the parent, and because handedness is usually established between 3 and 5 years of age, (Gessell & Ames, 1947) (long before child-bearing age!), this leftward carrying arrangement should have much greater influence on the handedness exhibited by the child than that by the parent. Further, the direction of this influence should favour left-handedness, not right-handedness. A further weakness of this theory is its failure to account for the apparent dissociation between humans and other primates in terms of handedness. Given the anatomical similarities between all primates (particularly with reference to cardiac location), why do only humans show strong population level right-handedness?

D. Developmental Theories

Developmental theories of cerebral lateralization have an advantage over environmental, anatomical, and genetic theories in that they often incorporate influences from all of these factors. Further, these theories also help account for the fact that infants are lateralized (structurally at least, if not functionally) at birth.

1. Geschwind and Galaburda's (1987) "Triadic" theory

The Geschwind-Galaburda theory (G-G theory) is cited hundreds of times each year and is implicitly accepted in much of the literature. In its most simplified form, the theory claims that elevated levels of testosterone are responsible for deviations from the "normal dominance pattern" (i.e. right-handed with left-hemispheric linguistic dominance and right-hemispheric visuo-spatial dominance). The wide appeal of the theory is attributable both to the charismatic manner in which Geschwind popularized the theory, as well as its ability to account for a vast number of previously unrelated and inexplicable correlations.

These correlations include a number of reliable sex-differences in the literature, such as a higher prevalence of left-handedness in males (Gilbert & Wysocki, 1992; Oldfield, 1971), higher prevalence of immune disorders in males, higher prevalence of language disorders in males (Taylor, 1974), the well established cognitive sex differences, such as male superiority in visuo-spatial and mathematical tasks and female superiority in linguistic tasks (Benbow & Stanley, 1980; Mann, Sasanuma, Sakuma, & Masaki, 1990), and the different maturational rates of the sexes (females tend to mature faster than males) (Taylor, 1969). Further, there are a number of neuroanatomical sex differences in the literature (see Bishop & Wahlsten, 1997).

The G-G (1987) theory also attempts to explain the relation between behavioural laterality and developmental disorders. There is a higher prevalence of left-handers in those with Down Syndrome (Pipe, 1988), autism (Pipe, 1988; Soper et al., 1986), stuttering (Christensen & Sacco, 1989; Dellatolas, Annesi, Jallon, Chavance, & Lellouch, 1990; Records, Heimbuch, & Kidd, 1977), dyslexia (Eglinton & Annett, 1994; Strehlow et al., 1996; Tonnessen, Lokken, Hoien, &

Lundberg, 1993), skeletal malformations (Geschwind & Behan, 1982), immune diseases (Geschwind & Behan, 1982; Tonnessen et aL, 1993), mental retardation (Geschwind & Behan, 1982; Morris & Romski, 1993; Soper, Satz, Orsini, Van Gorp, & Green, 1987), migraine headaches (Geschwind & Behan, 1982; but cf. Hering, 1995), allergies (Coren, 1994b; Geschwind & Behan, 1982; but cf. Bulman-Fleming, Bryden, & Wyse, 1996), Crohn's disease (Geschwind & Behan, 1982; Persson & Ahlbom, 1988; Searleman & Fugagli, 1987; but cf. Meyers & Janowitz, 1985), and eczema (see Hécaen, 1984, for a review, but cf. Bishop, 1986, and Stanton, Feehan, Silva, & Sears, 1991).

However, left-handers are also over-represented among groups of people with superior "right hemispheric" skills, such as divergent thinkers (Coren, 1995), architects (Gotestam, 1990; Peterson, 1979; Peterson & Lansky, 1977), engineers, musicians (Gotestam, 1990; but cf. Hering, Catarci, & Steiner, 1995; Oldfield, 1969), lawyers (Schachter & Ransil, 1996), and students in the visual arts (Peterson, 1979). The G-G (1987) theory also attempts to account for the prevalence of these individuals.

The G-G (1987) theory centres on the hormone testosterone. This hormone can affect the growth of many tissues, and has an inhibitory effect on the growth of immune structures such as the thymus gland. Testosterone is also capable of changing the structure of specific nuclei in the hypothalamus and limbic system. Testosterone also has major effects on the development of other neural tissue, because sex hormone receptors are widely dispersed in the brain (Gorski, Harlan, Jacobson, Shryne, & Southam, 1980).

According to the G-G (1987) theory, if effective testosterone levels are higher than normal during pregnancy due to genetic factors, increased sensitivity to testosterone, the presence of a male co-twin, or an anomalous endocrine environment during pregnancy, this increase in testosterone levels is responsible for a myriad of consequences. These consequences include masculinization, early puberty, general growth retardation, a smaller left-hemisphere, post-pubertal thymus suppression, abnormal neural crest development, and atypical metabolism.

More central to the theory is testosterone's ability to produce a condition termed "Anomalous Dominance" through its delay of left-hemispheric growth. Anomalous Dominance can be characterized by left-handedness, right-hemispheric language dominance, left-hemispheric visuo-spatial dominance, or reduced degree of handedness, language dominance, or visuo-spatial dominance. By slowing down the growth of the left hemisphere, testosterone somehow results in a disruption of the "normal" cortical architecture of the left-hemisphere. Further, because of the left-hemispheric growth delay, G-G (1987) propose that the right hemisphere compensates for this growth delay, and corresponding regions of the right hemisphere develop more quickly. This compensatory growth is the mechanism proposed by G-G (1987) to account for the over-representation of left-handed people in "right-hemispheric" vocations. This effect is also presumed responsible for left-handers' relative superiority at mathematics, visual arts, athletics, and music.

The testosterone theory also accounts for the correlation between handedness and immune disorders. Because elevated testosterone levels are said to be responsible for both immune disorders and anomalous dominance, this relation is responsible for the correlation between the two.

Some problems with the G-G theory:

(1) The theory does not explain why testosterone only slows the growth of the left hemisphere (and not the right as well) in the neonate. Possible mechanisms include greater testosterone receptor density in the left hemisphere, or greater sensitivity of the receptors there, but the authors do not present any evidence suggesting the plausibility of either mechanism.

(2) Some direct tests of the model have failed to support the G-G theory. For example, a study by Grimshaw, Bryden, and Finegan (1995) measured prenatal testosterone levels (in amniotic fluid), and compared these levels to the behavioural indicators of lateralization (like handedness and language lateralization) in the same children 10-15 years later. The results were exactly the opposite of what would be predicted by the G-G theory - children with high levels of prenatal testosterone were <u>more</u> likely to be right-handed and have left-hemispheric language lateralization.

(3) Many of the correlational studies on which the theory has been based have not been successfully replicated, such as those that associate left handedness with a number of diseases.

(4) The theory does not provide any insight into the phylogenetic differences in the prevalence of population-level asymmetries. Assuming that lower primates are subject to the same

hormonal influences, why do they not exhibit similar population-level lateral biases?

2. The "Pathological Left-handedness" theory

As reviewed by Peters (1995), the "pathological left-handedness" (PLH) theory must be subclassified into three variants. The first and most extreme variant is that proposed by Bakan et al. (1973) who claimed that right-handedness is the norm, and that left-handedness is always the result of some sort of injury. A second, and less extreme variant is that proposed by Satz and his colleagues (also see Dellatolas et al., 1993; Satz, 1972; Satz, Orsini, Saslow, & Henry, 1985), who maintain that sometimes left-handedness is normal, and sometimes it is pathological. A third, and even less extreme variant, is the position that left-handedness itself might not be pathological, but it serves as a marker for other pathologies (Coren & Halpern, 1991; Geschwind & Behan, 1982; Geschwind & Galaburda, 1985c; Kinsbourne, 1988; Manoach, 1994).

Supporting the position that left-handedness might be caused by birth stress, there is a higher prevalence of left-handedness among groups of infants who appear (as assessed by indirect measures) to have been exposed to stressors (see Table1).

Table 1: Associations between indirect measures of stressors and elevated prevalence of left-handedness.

Condition / Group	**Reference(s)**
babies with low birthweight	(O'Callaghan, Burn, Mohay, Rogers, & Tudehope, 1993; Powls, Botting, Cooke, & Marlow, 1996; Ross, Lipper, & Auld, 1992; Ross, Lipper, & Auld, 1987; Saigal, Rosenbaum, Szatmari, & Hoult, 1992; Segal, 1989)
babies with low APGAR scores	(Schwartz, 1988; but cf. Olsen, 1995)
offspring of smoking mothers	(Bakan, 1991; but cf. Olsen, 1995)
perinatal birth stress	(Bakan et al., 1973; but cf. Ehrlichman, Zoccolotti, & Owen, 1982; van Strien, Bouma, & Bakker, 1987)
premature birth	(Ross et al., 1992; Ross et al., 1987)

Supporting the 2nd and 3rd variant of the theory (that left-handedness might be pathological or serve as a marker for other pathologies), there is a higher prevalence of left-handedness among people with a number of pathological conditions (see Table 2).

Table 2: Associations between elevated prevalence of left-handedness and pathological conditions or circumstances that could lead to pathology.

Condition / Group	**Reference(s)**
albinism	(Murdoch & Reef, 1986)
alcoholics	(Bakan, 1973; Biro & Novotny, 1991; London, 1987; London, 1989; London, Kibbee, & Holt, 1985; McNamara, Blum, O'Quin, & Schachter, 1994; Nasrallah, Keelor, & McCalley Whitters, 1983)
allergies	(Coren, 1994; Geschwind & Behan, 1982; Geschwind & Behan, 1984; but cf. Gilger, Pennington, Green, Smith, & Smith, 1992; Pennington, Smith, Kimberling, Green, & Haith, 1987; Smith, 1987; Steenhuis, Bryden, & Schroeder, 1993; but cf. van Strien, Bouma, & Bakker, 1987; Bulman-Fleming, Bryden, & Wyse, 1996)
autism	(Boucher, 1977; Colby & Parkison, 1977; Geschwind, 1983; Gillberg, 1983; Laxer, Rey, & Ritvo, 1988; Leboyer, Osherson, Nosten, & Roubertoux, 1988; Lewin, Kohen, & Mathew, 1993; Pipe, 1988; Soper et al., 1986; Tsai, 1982; but cf. Barry & James,

	1978; Boucher, Lewis, & Collis, 1990)
autoimmune thyroid disease	(Wood & Cooper, 1992)
breast cancer	(Kramer, Albrecht, & Miller, 1985; London, 1989; London & Albrecht, 1991)
children with hydrocephalus	(Lonton, 1976)
cerebral palsy	(Galliford, James, & Woods, 1964; Keats, 1965)
coronary artery disease	(Lane et al., 1994)
criminality	(Ellis & Ames, 1989; but cf. Hare & Forth, 1985)
criminals	(Lombroso, 1903)
Crohn's disease	(Geschwind & Behan, 1982; Persson & Ahlbom, 1988; Searleman & Fugagli, 1987; but cf. Meyers & Janowitz, 1985)
deafness	(Arnold & Askew, 1993; Bonvillian, Orlansky, & Garland, 1982)
delinquency	(Ellis & Ames, 1989; Gabrielli & Mednick, 1980; but cf. Feehan, Stanton, McGee, Silva, & Moffitt, 1990)
depression	(Bruder et al., 1989; but cf. Clementz, Iacono, & Beiser, 1994; Moscovitch, Strauss, & Olds, 1981)
Down Syndrome	(Lewin, Kohen, & Mathew, 1993; Pipe, 1988)
dyslexia	(Annett & Kilshaw, 1984; Bemporad & Kinsbourne, 1983; Eglinton & Annett, 1994; Geschwind, 1983; Strehlow et al., 1996; Tonnessen et al., 1993)
early onset Alzheimer's disease	(Seltzer, Burres, & Sherwin, 1984)
eczema	(see Hecaen, 1984, for a review, but cf. Bishop, 1986; Smith, 1987; Stanton, Feehan, Silva, & Sears, 1991)
epilepsy	(Lewin et al., 1993)
epileptic schizophrenia	(Oyebode & Davison, 1990)
immune disorders	(Geschwind, 1983; Geschwind & Behan, 1982; Tonnessen et al., 1993)
learning disabled children	(Geschwind & Behan, 1982; but cf. Gilger, Pennington, Green, Smith, & Smith, 1992)
mental retardation	(Geschwind & Behan, 1982; Lucas, Rosenstein, & Bigler, 1989; Morris & Romski, 1993; Soper et al., 1987)
migraine headaches	(Bishop, 1986; Geschwind, 1983; Geschwind, 1984; Geschwind & Behan, 1982; Guidetti, Moschetta, Ottaviano, Seri, & Fornara, 1987; but cf. Hering, 1995; van Strien et al., 1987)
myasthenia gravis	(Geschwind & Behan, 1982; but cf. Bryden, McManus, & Bulman-Fleming, 1994; Cosi, Citterio, & Pasquino, 1988; McManus, Naylor, & Booker, 1990)
post-traumatic stress disorder	(Spivak, Segal, Mester, & Weizman, 1998)
prisoners	(Andrew, 1978)
psychoticism	(Clementz, Iacono, & Beiser, 1994; Taylor & Amir, 1995)
Rett syndrome	(Olsson & Rett, 1986)

schizophrenia	(Manoach, Maher, & Manschreck, 1988; Piran, Bigler, & Cohen, 1982; Taylor & Amir, 1995, but cf. David, Malmberg, Lewis, Brandt, & Allebeck, 1995; Shimizu, Endo, Yamaguchi, Torii, & Isaki, 1985)
severe sleep apnea	(Hoffstein, Chan, & Slutsky, 1993a)
skeletal malformations	(Geschwind & Behan, 1982)
sleep difficulties	(Coren & Searleman, 1987; but cf. Hoffstein, Chan, & Slutsky, 1993b)
smoking	(Harburg, 1981; Harburg, Feldstein, & Papsdorf, 1978; London, 1989)
strabismus	(Holman & Merritt, 1986; Lessell, 1986; Niederlandova, 1967)
students who worry too much	(Dillon, 1989; but cf. Mueller, Grove, & Thompson, 1993)
stuttering	(Christensen & Sacco, 1989; Dellatolas et al., 1990; Geschwind, 1983; Hatta & Kawakami, 1994; Records et al., 1977; but cf. Webster & Poulos, 1987)
thyroid disorders	(Geschwind & Behan, 1982)
ulcerative colitis	(Bryden et al., 1994a; Geschwind & Behan, 1982)

Also supporting the position that left-handedness might be pathological or serve as a marker for other pathologies, some have claimed that left-handers have decreased life expectancy as compared to right-handers (Aggleton, Kentridge, & Neave, 1993; Coren, 1994a; Coren & Halpern, 1991; Coren & Halpern, 1993; Rogerson, 1993). However, quite a number of studies have either failed to replicate the finding (Fudin, Renninger, Lembessis, & Hirshon, 1993; Hicks, Johnson, Cuevas, Deharo, & Bautista, 1994; Persson & Allebeck, 1994; Wolf & Cobb, 1991), or taken issue with the methodology used to support the "elimination hypothesis" (Harris, 1993; Hugdahl, Satz, Mitrushina, & Miller, 1993; Lembessis & Fudin, 1994).

Coren (1989) attempted to account for the longevity differences he found by proposing a mechanism for the decreased longevity. He claimed that left-handers are more prone to accident-related injuries. These claims of increased accident rates among left-handers (the "clumsy hypothesis") have also garnered mixed support. Some studies find relatively elevated accident rates (Aggleton, Bland, Kentridge, & Neave, 1994; Coren, 1989; Graham & Cleveland, 1995; Graham, Dick, Rickert, & Glenn, 1993; MacNiven, 1994; Taras, Behrman, & Degnan, 1995; Wright, Williams, Currie, & Beattie, 1996) whereas others do not (Merckelbach, Muris, & Kop, 1994; Peters & Perry, 1991). Others have even suggested that it is not left-handers who exhibit elevated accident rates, but it is actually those with "mixed" handedness (Hicks, Pass, Freeman, Bautista, & Johnson, 1993).

There are some serious problems with all three variants of the PLH model:

(1) The birthing process (and the amount of money and technology available to support it) varies tremendously between cultures, but the prevalence of left-handedness between cultures is remarkably similar. One would expect greater prevalence of left-handedness among those cultures that experience relatively more "stressful" births.

(2) The prevalence of left-handedness has not decreased across time, despite marked improvements in medical science. Now that obstetricians are provided with much better training and technology, according to the PLH theory one would expect the prevalence of left-handedness to decrease. In fact, the prevalence of left-handedness appears to be increasing, if it has changed at all (Brackenridge, 1981).

(3) The presence of direct birth stressors (such as anoxia) have not been linked to left-handedness (Ehrlichman et al., 1982; see Previc, 1996, for a review).

(4) Left-handedness has often been linked with various professional groups and groups of the intellectually "gifted" (see Table 3).

Table 3: Professional and Intellectually "gifted" groups associated with higher prevalence of left-handedness.

Group	Reference(s)
architects	(Gotestam, 1990; Peterson, 1979; Peterson & Lansky, 1977)
children of professional parents	(Annett, 1978)
children with superior mathematical ability	(Annett & Manning, 1990; Benbow, 1988)
creative thinkers	(Coren, 1995; Newland, 1981)
divergent thinkers	(Coren, 1995)
gifted children	(Hicks & Dusek, 1980)
lawyers	(Schachter & Ransil, 1996)
musicians	(Gotestam, 1990; but cf. Hering et al., 1995; Oldfield, 1969)
professional baseball players	(McLean & Cuirczak, 1982)
students of the visual arts	(Mebert & Michel, 1980; Peterson, 1979)
the intellectually precocious	(Benbow, 1986)

3. Previc's (1991, 1996) "Vestibular-Monoaminergic" theory

Previc's theory is much less well known than the other developmental theories. Whereas the G-G (1987) theory focuses on a possible chemical mechanism for creating functional lateralization, Previc (1991, 1996) proposes a more "mechanical" model. The central claim of his theory is that all facets of human laterality can be traced back to asymmetrical influences in the prenatal environment. One of the strengths of Previc's theory is the fact that it accounts for the dissociation between perceptual and motoric laterality, whereas this dissociation is a weakness of the G-G (1987) model. Further, Previc (1991, 1996) takes a comparative perspective, noting the differential prevalence of these asymmetrical influences between humans and non-human primates.

Fetal position is paramount to this theory. Although fetal position is relatively flexible throughout the first two trimesters of pregnancy, during the final trimester, two-thirds of fetuses are confined to the leftward fetal position, with their right side facing out (Taylor, 1976). This effect is probably caused by the asymmetric intrauterine environment. Torsion of the uterus extends backward and toward the right of midline because of the encroachment of the bladder and rectum (Taylor, 1976). Fetal position could also be influenced by placental site. Most anterior placentas are located on the right side of the uterus (Hoogland & de Haan, 1980). These factors probably contribute to the prevalence of leftward fetal position during the final trimester.

Previc (1991, 1996) postulates separate mechanisms to account for motoric lateralization and perceptual lateralization. Perceptual lateralization of non-prosodic language is dominated by the left-hemisphere in 95% of right-handers and 70% of left-handers (Rasmussen & Milner, 1977). Conversely, perception of the prosodic components of speech are usually lateralized to the right hemisphere (Bryden & MacRae, 1988). If one examines the critical frequencies necessary for discriminating between different phonemes and the frequencies that distinguish prosodic speech, those frequencies below 1000Hz are most important for prosody, music, and environmental sounds. Frequencies greater than 1000Hz are critical for distinguishing between speech features such as second and third formant transitions (see Deutsch, 1985).

Given that the left hemisphere (and right ear) is superior at processing linguistic stimuli and the right hemisphere (and left ear) is superior at processing prosody, the critical difference between these types of stimuli might be the relative frequencies of the stimuli. The left hemisphere might simply be better at processing stimuli of high frequency. Previc (1991, 1996) attributes this effect to cranio-facial asymmetries in humans. Just as 2/3 of all fetuses remain in the leftward position during the third trimester, 2/3 of all humans display a slight enlargement of the left portion of their face (Kirveskari & Alanen, 1989). Cranio-facial asymmetries restrict the motion of the mandible, which can result in partial occlusion and hearing loss (see Arlen, 1985).

Perhaps more importantly, the fetus usually has the right ear facing out during the final trimester, causing asymmetries in auditory experience. There is some experimental evidence suggesting that fetuses can hear language sounds in utero and recognize those sounds. In sum, the lateralization of language perception may be a function of both asymmetrical auditory experience, as well as the physical constraints on the left side of the face.

Previc (1991, 1996) proposes an entirely different mechanism for the lateralization of motor functions. The vestibular experience of the fetus during the final trimester is also asymmetrical. During normal walking, people usually spend more time in the acceleratory phase (although the rate of acceleration is less) than the deceleratory phase (Smidt, Arora, & Johnston, 1971). When the fetus is confined to the leftward position, the acceleratory component of the maternal walk is registered as rightward movement, producing asymmetric shear forces in utero. Previc (1991, 1996) supports his claim that there are asymmetric shear forces in the human uterus by citing work that describes the twisting pattern of ovarian tumours. Left- and right-sided tumorous bodies resting in ovarian fluid twist in opposite directions (Selheim, 1929). The same forces that cause these twisting patterns could have an asymmetrical effect on the development of the vestibular system of the fetus.

There is considerable evidence that the left otolith dominates over the right in 2/3 of the population. There is a rightward deviation of the body axis in most people, while 25% demonstrate a leftward tilt and 12% do not appear to show any significant deviation (Kohen-Raz, 1986). Further, there is a prevalence of dextral turning in the normal population, and after unilateral damage to the vestibular system, people prefer to turn towards the involved side (Peiterson, 1974). According to Previc (1991, 1996), these findings support his theory that asymmetrical vestibular stimulation during development produces behavioural motor asymmetries later in life.

One strength of Previc's (1991, 1996) approach over that of the G-G (1987) model is his comparative/evolutionary perspective. Claiming that there is no convincing evidence of strong handedness or lateralization of higher functions in non-human primates or other mammals (although this is a matter of vigorous debate), Previc (1991, 1996) attributes this lack of functional laterality to differences in fetal position between humans (that are bipedal) and other non-bipedal mammals. The typical fetal position in non-human primates is one in which the fetus' spine is parallel to that of the mother's and the fetal head is also in line with that of the mother, as opposed to the perpendicular orientation exhibited by humans during the last trimester. As a consequence of this fetal orientation, non-human fetuses might not experience asymmetrical shearing in utero, and subsequently do not develop strong handedness and lateralization of higher functions.

In sum, Previc (1991, 1996) claims that all lateralized behaviours can be traced back to asymmetric shear forces in the prenatal environment. Sensory lateralization (especially hearing) develops as a consequence of asymmetrical auditory experience (2/3 of fetuses have the right-ear facing out during the last trimester) and possible conductive hearing loss from having part of the left-ear occluded from larger left-facial structures. Motoric lateralization is said to arise from the asymmetrical vestibular experience resulting from shear forces during maternal walking.

In a more recent formulation of his theory, Previc (1996) also postulates a role for monoamines in the incidence of nonright-handedness. Specifically, he claims that nonright-handedness is associated with impaired noradrenergic function, and to a lesser extent, impaired serotonergic function. Given these associations, Previc (1996) proposes that vestibular projections to the locus coeruleus (which produces norepinephrine) and raphe nucleus (which produces serotonin) are critical for the lateralization of motor dominance and mono-aminergic activity.

Problems with the Previc (1991, 1996) theory:

(1) Perhaps the most daunting failure of the Previc (1991, 1996) theory is some of the statistical data used to support it. 2/3 of all fetuses are confined to the leftward fetal position. So, the theory would predict that 1/3 of all babies would be left-handed. In fact, the prevalence of left-handedness is much lower than that - namely 10-13%, a far cry from the 33% predicted by Previc.

(2) Another problem with Previc's (1991, 1996) theory is his attempted explanation of the dissociation between motoric and sensory lateralization of function. An example of the dissociation is the lack of perfect relation between handedness and linguistic hemispheric dominance. Although Previc (1991, 1996) proposes different mechanical rationales for these two types of lateralization, both the asymmetrical auditory experience and asymmetrical shear forces on the vestibular system are presumably caused by fetal position. Unless a fetus can be positioned in such a manner that allows asymmetrical

stimulation of the vestibular system in one direction while allowing the opposite pattern of asymmetrical auditory stimulation, dissociations between motoric and perceptual laterality should not occur.

(3) Previc's claim that fetal position at birth is related to functional laterality has not always been borne out by experimental evidence. For example, Searleman found that left-handedness was not related to birth position, but to birth stress (Searleman, Porac, & Coren, 1989). Goodwin found that fetal position was not related to head-turning or reaching behaviours (Goodwin & Michel, 1981). Vles also found that fetal position was not related to handedness (Vles, Grubben, & Hoogland, 1989).

(4) Other problems with the Previc (1991, 1996) theory concern the causal mechanisms he proposes between asymmetrical vestibular stimulation and future motor laterality. There is no direct evidence to suggest that handedness is causally related to vestibular lateralization.

4. Corballis and Morgan's (1978) "Maturational Gradient" theory

Based on the classic embryological studies of Spemann and Falkenberg (1919), Corballis and Morgan (1978) proposed that many asymmetries (including cerebral ones) are the result of a more "global" left-right maturational gradient, coded in the cell cytoplasm rather than the genes. This gradient favours earlier development of the left side, and this pattern will only be reversed if the leading side is damaged or restricted. Both right-handedness and left-hemispheric language dominance are assumed to be manifestations of this gradient, in which the larger and earlier developing left hemisphere dominates these tasks.

Although appealing in its simplicity, the "Maturational Gradient" theory is not supported by anatomical studies revealing that the right hemisphere develops before the left, as revealed through both structural (Best, 1988) and functional imaging (Chiron et al., 1997).

In the mature adult, it is the right hemisphere that is larger and heavier (Gur et al., 1991) (see Table 4 and Table 5). Further, as mentioned previously, cases of *situs inversus* do not exhibit left-handedness more frequently than normals (Cockayne, 1938; Torgerson, 1950; Wilson, 1872).

Table 4. Post-mortem differences in weight between the hemispheres.

Source	N	Left Hemisphere	Right Hemisphere	Right-Left Difference
Broca (1875)	19	530.84g	531.31g	0.47g
see Henderson (1986)	18	574.39g	575.83g	1.44g
Crichton-Browne (1880)	18 males	616.1g	618.2g	2.1g
	18 females	556.7g	558.0g	1.3g
Braune (1891)	100	549.7g	551.2g	1.5g
Weighted Averages		**557.8g**	**559.3g**	**1.4g**

Table 5. Mean hemispheric volume +/- standard deviation

Source	N	Left Hemisphere	Right Hemisphere	Z
Kelsoe et al. (1988)	14	392 +/- 89.8cm^3	402 +/- 89.8 cm^3	0.045
Weis et al. (1989)	29	534.4 +/- 50.6cm^3	538.2 +/- 49.2cm^3	0.076
Gur et al. (1991)	23 male	575.46 +/- 47.74cm^3	580.69 +/- 47.03cm^3	0.055
	20 female	529.28 +/- 57.89cm^3	532.76 +/- 59.42cm^3	0.059
Kertescz et al. (1990)	50 male	88.59 +/- 7.05	90.39 +/- 6.46	0.266
	53 female	81.02 +/- 7.16	82.90 +/- 6.92	0.267
Heckers et al. (1991)	23	531.1+/- 79.8cm^3	546.6 +/- 75.0cm^3	0.200
Salerno et al (1992)	17	544 +/- 61cm^3	545 +/- 58cm^3	0.017
	18	548 +/- 117cm^3	551+/-112cm^3	0.026
Murphy et al. (1993)	19	36.9 +/- 0.89	37.2 +/- 0.89	0.337
Weighted Average				**0.167**

5. The "Developmental Instability" theory

The "Developmental Instability" (DI) theory is most commonly associated with Yeo and Gangestad (Gangestad & Yeo, 1994; Yeo, Gangestad, & Daniel, 1993; Yeo, Gangestad, Thoma, Shaw, & Repa, 1997), but a similar account is described by Markow (1992). The theory differs from most genetic theories of lateralization, in that it proposes that variations in functional/anatomical asymmetries are outcomes of DI. DI is characterized by reduced canalization, or even incorrect expression of a genetic sequence as a result of pathogens, toxins, or mutations. According to the theory, people with disturbances in laterality should also show both minor physical anomalies (MPAs), and fluctuating asymmetry (FA). MPAs include features such as wide-spaced eyes (hypertelorism), multiple hair whorls, and low-set ears (see Waldrop & Halverson, 1971). FAs are individual variations (greater than one standard deviation from the population mean) in bilateral symmetry in physical features. FAs are measured by taking bilateral measurements of features such as ear length, elbow width, hand width, and foot breadth.

Support for the theory comes from the relation between measures of DI and functional lateralization. In a recent study, (Yeo et al., 1997), individuals with greater DI composite scores exhibited more "atypical lateralization scores", not just in the opposite direction from normal asymmetries, but also more severe deviations than normal in the predicted direction. The theory is also attractive in that it provides a relatively simple account for the association between atypical laterality and developmental disorders such as skeletal malformations (Geschwind & Behan, 1982). The theory also helps account for the fact that a child's handedness is more likely to be concordant with that of the mother than the father (see McManus & Bryden, 1992, for a review).

With respect to the current model, offspring would be influenced by the degree of DI in both parent's genes, but also by the mother's DI during fetal development.

Problems with the DI theory:

(1) According to McManus (1985), the principal problem with the DI theory "is that *none* of its variance can ever be genetically controlled (hence the name: the asymmetry fluctuates randomly from generation to generation)" (McManus, 1985). There is clearly a genetic influence on cerebral lateralization, and the DI theory cannot account for this influence.

(2) Even if the DI theory proves useful for describing individual differences in cerebral lateralization, the theory is not informative about population-level asymmetries. If symmetry is the norm, why are 90% of all people right-handed and left-hemispheric dominant for language?

6. The "Vanishing Twins" theory

Despite its popular appeal, (there was a recent special on "The Learning Channel" about this very topic, as well as an article in "The New Yorker"), references to the "Vanishing twins" theory are very rare in the academic literature. The theory ties two previously unrelated phenomena together into an explanatory model: the mirror-imaging that is occasionally seen in twins, and the fact that the majority of pregnancies initially diagnosed with multiple gestations only produce one viable child (see Landy, Keith, & Keith, 1982). Taken together, some have argued that all left-handers (approximately 13% of the population, see Gilbert & Wysocki, 1992) once had a twin, but only one embryo survived the full term. By the same logic, it is also claimed that the other half of the "surviving twins" (another 13% of the population) should be right-handed.

Tracking the source of this theory has proven to be very difficult. Some attribute it to Charles Boklage for his comment that "the numbers are such that it is entirely possible that every nonrighthander in the world is a product of twin embryogenesis" (Boklage, 1997, personal communication). However, he has never published this theory in any scientific journal, and he appears to have mixed feelings about the position, "I don't think of vanishing twins as a 'cause' of lefthandedness..." but "I have no reason even to dilute that idea, let alone to retract it" (Boklage, 1997). Others, such as Wright (1995), have claimed that the theory was suggested by Luigi Gedda of Rome's Gregor Mendel Institute (no reference given). Although Gedda has certainly completed studies of the mirror-imaging phenomenon in twins (Gedda, Brenci, Franceschetti, Talone, & Ziparo, 1981; Gedda et al., 1984), I have not found any published report to substantiate the claim that he attributes left-handedness to the vanishing twin phenomenon.

The "vanishing twins" theory certainly has **some** empirical support. Approximately 1/80 (1.25%) of all births are twins (Jeanty, Rodesch, Verhoogen, & Struyven, 1981), and of those, approximately 1/3 are mono-zygotic (MZ). However, many more than 1.25% of all pregnancies have multiple gestations before 6 weeks. Because ultrasonic scanners keep getting better with time (achieving higher resolution), early estimates indicated that multiple gestations were relatively rare. In a classic study by Levi, 1.7% of pregnancies in a sample of 6990 (Levi, 1976) showed evidence of multiple gestations. A few years later, Varma estimated the prevalence to be slightly higher, 2.0% in a sample of 1500 (Varma, 1979). More recent estimates range between 3.3% to 5.4% (Landy, Weiner, Corson, Batzer, & Bolognese, 1986), and 2.3% in a sample of 5000 pregnancies (Blumenfeld et al., 1992).

Of these multiple gestations, how many fetuses survive? Levi (1976) reported that a shocking 71% of the multiple gestations "disappeared", meaning that most pregnancies ended in births of singletons. In a review of the literature, Landy et al. (1982) reported a 43%-78% disappearance rate before 6 weeks. More recently, in a sample of 88 multiple gestations, Blumenfield et al. (1992) reported a 49% disappearance rate. Therefore, the viability of multiple gestations does not appear to be very high. Approximately 3% of all pregnancies have multiple gestations before six weeks, and less than half of these pregnancies result in multiple births (which approximates the 1.25% prevalence of twinning among viable births).

The second phenomenon invoked in the "vanishing twins" theory of handedness is the "mirror-imaging" phenomenon, described in Newman's (1928) classic paper. Different investigators have employed different criteria for defining mirror-imaging. In extremely rare cases, complete situs inversus is reported in one twin (Gedda et al., 1984). Most commonly, dental abnormalities are reported as evidence of mirror-imaging, but other physical markers such as hair whorls, fingerprints, and facial dysmorphologies have also been used. Others have employed more "functional measures" of mirror-imaging, including handedness (Boklage, 1981), EEG (Meshkova, 1992), or patterns of sleep difficulties (Golbin, Golbin, Keith, & Keith, 1993). Golbin et al. (1993) also discuss "medical mirroring", exhibited through a history of opposite dental or skin lesions, or even opposite tendencies in blood pressure and blood sugar, and "psychological mirroring", exhibited through opposite temperament, interests, and sexual orientation.

Estimates of the prevalence of mirror-imaging in MZ twins are usually higher than those for dizygotic (DZ) twins (but see Meshkova, 1992, for a possible exception with EEG data). Using measures of lateral preference, Gedda et al. (1981) reported that mirror imaging was present in approximately 15% of MZ pairs and 8% of DZ pairs. A slightly greater disparity between MZ and DZ twins was reported by Golbin et al. (1993), wherein 22% of MZ twins exhibited some signs of mirroring compared to only 9% of DZ twins. However, these authors appear to have employed slightly more liberal criteria, including "anatomical", "functional", "medical", and "psychological" mirroring in their analysis.

Given the data on the viability of multiple gestations and estimates of the prevalence of mirror imaging among twins, one can evaluate Boklage's claim that "the numbers are such that it is entirely possible that every nonrighthander in the world is a product of twin embryogenesis" (Boklage, 1997, personal communication). Approximately 13% of the North American population is left-handed (Gilbert & Wysocki, 1992). Assuming that left-handed fetuses are just as viable as right-handed fetuses, for every left-hander that is the survivor of a "right-handed, vanished twin", there should also be a right-hander that survived a "left-handed, vanished twin". Even if all twins exhibited mirror imaging, for Boklage's statement to be correct, 26% (13%+13%) of all pregnancies would need to have multiple gestations at one point to account for the current prevalence of left-handedness. This value is far greater than the current estimates of 3%. Further, only 15% of twins surviving to term exhibit mirror imaging. Taking this value into account, the prevalence of multiple gestations would have to be far greater than 26% for the "vanishing twins theory of handedness" to account for a majority of all left-handers, never mind all of them.

Despite its apparent inability to account for the prevalence of left-handedness, the theory is consistent with a number of other findings. Left-handedness is more common among twins (Coren, 1994c; Davis & Annett, 1994), and both twinning and handedness appear to run in families. Further, the theory also predicts an association between left-handedness and relatively "harsher" uterine environments, resulting in only one "twin" surviving to term. As previously reviewed, left-handedness is associated with low APGAR scores (Schwartz, 1988; but cf. Olsen, 1995), premature birth (Ross et al., 1992; Ross et al., 1987), skeletal malformations (Geschwind & Behan, 1982), and low birth weight (O'Callaghan et al., 1993; Powls et al., 1996; Saigal et al., 1992; Segal, 1989).

Despite the fact that these associations are consistent with the "vanishing twins" theory of handedness, they are just as consistent with the "pathological left-handedness" theory. Evidence for vanishing twins theory of handedness is tenuous at best.

E. Evolutionary Theories

Although some evolutionary theories focus on potential benefits of lateralization in general (and sometimes right-handedness in particular), others have tabled the "suggestion that the left-handed represent an evolutionary retrogression (Levy, 1969; Miller, 1971; Nebes, 1971) - a phylogenetic step backward" (Hardyck & Petrinovich, 1977, p. 386). Some theories attempt to account for the interspecies laterality effects (MacNeilage, 1991), whereas others simply focus on the advantage that cerebral lateralization might provide for tool- and language-using humans.

1. Corballis (1991)

The most commonly accepted evolutionary theory of handedness (described by Corballis, 1991) proposes that handedness and language are lateralized to the same hemisphere because they both require similar fine motor control. Motor innervation of both hands and feet is primarily under the control of the contralateral hemisphere, and the hemisphere that is usually preferred for skilled motoric activities has been assumed to be responsible for language (which also requires fine motoric activation). The theory states that as early hominids learned to make and use more and more sophisticated tools, they developed more skilled motor control, lateralized to the left hemisphere. This practice with fine-motor sequences predisposed the left hemisphere to take on subsequent language functions, which also require very fine motor control. A similar view was put forward by Kimura and Archibald (1974), who claimed that left speech lateralization developed from manual asymmetry, perhaps through the left-hemisphere's superiority for controlling sequences of rapid movements.

There are some problems with this evolutionary scenario.

(1) Why is the left hemisphere usually (90% of the time) primarily responsible for both skilled unimanual activities and linguistic processing? The theory gives a cogent account

of why both language and handedness should be dominated by one hemisphere (within the individual), but why not the right hemisphere for half of all individuals and the left for the others.

(2) Left-handers do not necessarily demonstrate the opposite (i.e. right-hemispheric) pattern of language dominance, as is predicted by the theory.

(3) "Apes do not speak, point, or babble. Thus the tight relation between hand use and speech does not compel belief in speech origin through tool use or gesture" (Hiscock & Kinsbourne, 1995, p. 561).

(4) Language lateralization appears to be more related to lateral preference for ballistic tasks (such as kicking and throwing) than for fine-motor tasks such as writing and manipulating tools (Day & MacNeilage, 1996; Elias & Bryden, 1998).

2. MacNeilage's (1991) "Postural Origins" theory

MacNeilage (1991) proposed that the first evolutionary step in hemispheric specialization was a left-hand, right-hemispheric visuospatial specialization for unimanual predation. The postural demands of unimanual predation then lead to a right-side, left-hemispheric specialization for postural support. Because the respiratory and phonatory components of language production are influenced by postural factors, and facial and whole-body communicative gestures played a principal role in early communication, the left hemisphere might have been predisposed for language functions (MacNeilage, 1991).

Some problems with this evolutionary scenario:

(1) Instead of proposing that the left hemisphere has some special properties that predispose it to dominate fine-motor unimanual activities and linguistic functions, this theory proposes that the right hemisphere has special properties predisposing it to dominate visuo-spatial tasks. Why did the right hemisphere become specialized for spatial tasks?

(2) The theory assumes a causal relation between left-hemispheric language and right-hemispheric lateralization for spatial abilities. Experimental data do not support such a relation. Certainly, most people are right-hemispheric dominant for spatial abilities (about 70%) and left-hemispheric dominant for language (almost 90%), but there are many people who have the same hemisphere (right or left) dominating both their language and spatial abilities (Bulman-Fleming & Bryden, 1997).

(3) The theory predicts that the lateralization of postural control and lateralization of linguistic processing should be localized within the same hemisphere. Day and MacNeilage (1996) support this claim with evidence that language lateralization varies with preferred foot for kicking. In similar study, Elias and Bryden (1998) also found that

language lateralization varies with footedness, but the foot-preference items that correlated significantly with the measures of linguistic laterality were: smoothing sand at the beach, kicking a ball at a target, stomping on a bug, and picking up a marble with one's toes. All of these items assess preference for the foot manipulating an object, not the foot providing balance or postural support during the action. Further, it is the opposite foot that provides postural support during these activities, suggesting that lateralization of postural control is usually localized to the opposite hemisphere from that dominating linguistic processing.

3. The Interhemispheric Conduction Delay Hypothesis

Most evolutionary theories of cerebral lateralization involve the construction of specific scenarios, wherein some adaptive function/behaviour can be better supported or elaborated by a lateralized neural system. For example, the adaptive value of a superior communication system or the ability to manipulate tools is obvious, and these functions are plausible candidates for the selection pressures favouring laterality. However, instead of constructing such a scenario, the evolutionary theory proposed by Ringo, Doty, Demeter, and Simard (1994) suggests that laterality provides a much more *general* advantage to organisms with relatively large brains. They propose that "specialization comes about because the temporal delay in conducting nerve impulses back and forth between the two hemispheres is simply too long in many instances to permit interhemispherically integrated neuronal computations" (Ringo et al., 1994, p. 331).

Ringo et al. (1994) support this argument by comparing the time required for interhemispheric communication to the temporal specificity required for tasks that normally exhibit functional lateralization. They estimate that 175mm is the average length of callosal fibres in humans, and that the average conduction speed is about 6.5 m/sec (the calculations of average conduction speed are heavily dependent on data from electrophysiological studies of conduction velocities in macaques). Using these values, Ringo et al. (1994) calculated that the average interhemispheric transmission would be almost 30 msec.

For tasks that do not require great temporal precision, an interhemispheric conduction delay (ICD) of 30 msec might be tolerable. Indeed, for tasks *without any* time limits, ICD would be irrelevant. However, some tasks appear to require temporal precision greater than 30 msec. Further, an ICD of 30 msec would become more serious for processing beyond the primary sensory stage because "there, smaller slower fibers must carry the interhemispheric communication. Such delays would become particularly burdensome if the processing required multiple transits of the callosum" (Ringo et al., 1994, p. 336).

Consider the physical limitations on processing linguistic stimuli with a bilaterally symmetrical system with an average ICD of 30 msec. "Elementary speech sounds (vowels and consonants) are temporal patterns whose components may last 50-200 msec" (Miller, 1996, p. 5). The "just-noticeable-difference" for a single phonetic segment is in the order of 10-25 msec (Miller, 1996). The temporal precision required for language production appears to be even greater. Gracco and Abbs (1986) had normal participants pronounce the word "sapapple" repeatedly and studied the timing of movement patterns of the upper lip, lower lip, and jaw. Within each participant, the timing was highly consistent and very small differences were critical during pronunciation. For example, there was a 23msec interval between onset of movements of the upper and lower lip. Timing of the coordination between jaw movements and lower lip movements required even more precision, in the order of 12 msec. Studies of facial EMG during normal speech have produced similar results. Leanderson, Person, and Ohman (1970, as cited in Miller, 1996) found that EMG latencies when participants pronounced the 'p' consonant showed system differences in timing of 10-15 msec, dependent on which vowel was adjacent to the consonant. Could a bilateral system with an ICD of 30 msec support such temporal precision?

Skilled unimanual behaviours appear to require even greater temporal precision than that required for human linguistic processing. Consider the temporal precision required when making a relatively simple throw. Calvin (1983) calculates that the 'launch window' (time during which a thrown object can be released and still successfully hit the target) is substantially below Ringo et al.'s (1994) estimated ICD of 30 ms. Assuming a target of a 20cm diameter bucket at a distance of 4m, thrown by someone with a 40 cm elbow-to-hand radius, with the elbow 120 cm above the target, the launch window is 6-7 msec. Calvin (1983) argues that the selection pressure favouring encephalization and lateralization of function was primarily due to the adaptive advantage of accurate throwing during hunting and warfare.

The Ringo et al. (1994) theory shares some of the same weaknesses as the other theories:

(1) Although the theory offers a plausible explanation about *why* lateralization provides an adaptive advantage, it does not explain population-level asymmetries. Why is the left hemisphere the one that dominates linguistic processing for 90% of the population? The Ringo et al. (1994) theory simply predicts that one hemisphere or the other should

dominate.

(2) The theory does not address the relation between linguistic lateralization and handedness. As it is presently formulated, the theory would predict independence between lateralization for various functions.

(3) The theory does not address the sex difference in the handedness literature, nor is it informative about the correlations between atypical lateralization and various conditions discussed previously.

Relation between the lateralization of fine timing and lateralization of higher functions

Although currently there is no satisfactory account of the phylogeny and ontogeny of cerebral lateralization, the position that laterality arose to enhance temporal processing is gaining support. Functional cerebral asymmetries have traditionally been reported only for higher functions, such as linguistic processing, spatial relations, and facial recognition. Luria (1973) claimed that the more abstract a function is, the more its cerebral basis is asymmetric. Recently investigators have been noting functional asymmetries for much "lower" perceptual tasks (see Nicholls, 1996, for a review).

In the visual modality, a left-hemisphere advantage (LHA) has been reported for critical flicker fusion (Goldman, Lodge, Hammer, Semmes, & Mishkin, 1968), temporal ordering of stimuli (Carmon & Nachshon, 1971; Swisher & Hirsh, 1972), perception of simultaneity

(Corballis, 1996; Efron, 1963; Umiltà, Stadler, & Trombini, 1973), two-flash fusion (Nicholls, 1994a), and inspection time (Elias, Bulman-Fleming, & McManus, 1998b; Nicholls & Atkinson, 1993; Nicholls & Cooper, 1991; but cf. Sadler & Deary, 1996). In the auditory modality, LHA's have been reported for the perception of temporal order (Mills & Rollman, 1980), non-linguistic rhythms (Natale, 1977; Robinson & Solomon, 1974), duration discrimination (Mills & Rollman, 1979), offset of tones (Emmerich, Pitchford, Joyce, & Koppell, 1981), and gap detection (Brown & Nicholls, 1997; Vroon, Timmers, & Tempelaars, 1977; but cf. Efron, Yund, Nichols, & Crandall, 1985). There is even some evidence of tactile LHA's (Bakker & Van der Kleij, 1978; Hammond, 1981; Nachshon & Carmon, 1975; Nicholls & Wheelan, 1998; but cf. Clark & Geffen, 1990). These reports of tactile LHA's are particularly important because with this methodology, it is possible to avoid confounding the effects of hemispace with those of hemispheric asymmetries (a concern raised by Clark & Geffen, 1990; Geffen, Mason, Butterworth, McLean, & Clark, 1996). Nicholls and Whelan (1998) found that the LHA demonstrated some reduction for midline hand placements, but this effect was only present in the error data, and not in the RT or response-bias data. Therefore, hemispace appears to have very weak effects (if any) on these tactile hemispheric asymmetries (Nicholls & Wheelan, 1998).

These low-level temporal asymmetries may underlie some hemispheric specializations for "higher functions". Tallal et al. (1993) supports "the view that a left-hemispheric specialization for speech initially developed through evolution as a specialization for processing and producing sensory and motor events that occur in rapid succession" (p. 27). Tallal also asserts that "a basic temporal processing impairment in language-impaired children underlies their inability to integrate sensory information that converges in rapid succession in the central nervous system" (Tallal et al., 1993, p. 27). Tallal's claims are supported by findings such as that of Wolff (1993) that dyslexics exhibit impairments in low-level temporal tasks. Demonstrating that the temporal processing deficit is specific to people with language disabilities, Watson (1993) found evidence of impaired temporal processing in students with reading disabilities, but no impairment emerged in a group of math-disability students.

Mills and Rollman (1979) administered an auditory duration-discrimination task to normal participants and found a Right Ear Advantage (REA) for durations of 50 msec or less. Because the temporal discriminations required to identify phonemes are also in 50 msec range (Minifie, 1973), Mills and Rollman (1979) interpreted this result as evidence that the left hemisphere is generally specialized for tasks that require fine temporal processing, including language perception and production.

Schwartz and Tallal (1980) performed a similar study wherein they hypothesized that the REA for speech in the dichotic-listening paradigm was caused by a more general left-hemisphere advantage for temporal processing. Schwartz and Tallal (1980) prepared two sets of consonant-vowel (CV) stimuli using the syllables /ba/, /da/, and /ga/. In one set, the formant transition lasted 40 msec, and in the other set, the transition lasted 80 msec. Participants exhibited a highly significant REA for the rapidly (40 msec) changing stimuli, but no ear advantage emerged for the 'slowly' (80 msec) changing stimuli.

Similar evidence can be found in studies of patients with acquired brain damage. Tallal and Newcombe (1978) studied a group of men with missile wounds to the left or right hemisphere to determine whether damage to the right or left hemisphere selectively disrupts temporal processing. Damage to the left (but not the right) hemisphere caused a selective impairment in the participants' ability to respond correctly to two tones with short (but not long) interstimulus intervals (ISIs). Therefore, rapidly changing *non*-verbal information processing can be impaired by left-hemisphere damage in adults.

More recently Belin, Zilbovicus, Crozier, Thivard, Fontaine, Masure, and Samson (1998) monitored asymmetry of cerebral activation using PET while participants were stimulated with rapid (40 msec) or extended (200 msec) frequency transitions. Although the slower frequency transitions produced bilateral auditory cortex activation, the rapidly changing transitions produced a left-biased asymmetry in activation. The authors interpret this result as indicating that "such functional asymmetry in temporal processing is likely to contribute to language lateralization from the lowest levels of cortical processing" (Belin et al., 1998, p. 536).

If low-level temporal processing asymmetries underly hemispheric asymmetries for 'higher functions' such as linguistic processing, individual participants who exhibit left hemisphere advantages (LHAs) for low-level temporal processing should also exhibit LHA's for linguistic processing. Experiments 1 and 2 were designed to test this claim. Assuming that there is a relation between lateralized temporal processing and linguistic lateralization, Experiment 3 tests the ICD theory more directly. Directional ICDs for different types of information (auditory and visual) will be compared to the degree of linguistic laterality exhibited by the individuals. Finally, Experiment 4 will test two predictions of the ICD theory. First, it will test Calvin's (1983) version of the theory that predicts that linguistic lateralization should vary with preferred hand for throwing. Second, it will test the position that the nature of complementary hemispheric specialization should not be causal in nature.

Experimental Section

Prediction 1: Low-level temporal asymmetries should underlie linguistic asymmetries

A number of authors have detected LHA's for temporal processing and related these processing asymmetries to the left hemisphere's superiority at processing linguistic stimuli (Belin et al., 1998; Mills & Rollman, 1979; Mills & Rollman, 1980; Schwartz & Tallal, 1980; Tallal et al., 1993; Tallal & Newcombe, 1978). Similarly, Calvin (1983) asserted that the left hemisphere typically contains a "generalized temporal processor", which first evolved to support fine-motor activities such as throwing, later predisposing the area to subserve the fine-motor requirements of spoken language. Nicholls (1996) has recently published a series of experiments that demonstrate a low-level left-hemisphere (LH) advantage for temporal processing. If the left hemisphere's superiority at linguistic processing is caused by its more general superiority at temporal processing, individuals with LH advantages for low-level temporal tasks should also demonstrate LH advantages on a linguistic task.

Experiment 1

This experiment seeks to evaluate linguistic asymmetries using the Fused Dichotic Words Test (FDWT) developed by Wexler and Halwes (1983), and visual temporal asymmetries using a lateralized visual-inspection-time (IT) task described by Nicholls and Cooper (1991) and Nicholls and Atkinson (1993). The inspection-time task was first described by Vickers (1970; 1979) and is based on the "accumulator" model of perception and decision-making. This model suggests that there are absolute temporal limitations on an individual's rate of assimilation of stimuli from the environment. To measure the rate at which stimuli could be assimilated, Vickers (1970; 1979) developed a task in which the stimuli (referred to as "pi" figures), consisting of an inverted U-shaped figure with one "leg" shorter than the other, were presented and participants were required to judge which leg was shorter (see Figure 1). By varying the exposure duration of the pi figure and examining the relative performance of a subject at the different durations, one can obtain a measure of "inspection time", defined as the exposure duration at which a subject can correctly identify the shorter leg on 90% of the stimulus presentations.

Nicholls and Cooper (1991) modified the original IT task to allow separate presentations of the pi stimulus to the left visual field (LVF) and right visual field (RVF). They found that pi stimuli presented to the RVF were processed significantly more quickly than those presented to the LVF, as revealed by overall accuracy as well as separate estimates for IT for each visual field. Out of concern that the RVF advantage on the task might be related to the potentially categorical nature of the task, Nicholls and Atkinson (Nicholls & Atkinson, 1993) further modified the IT task, varying the difficulty of the task (but not the categorical nature of the judgements) by varying exposure duration (time task) or the degree to which one line was shorter than the other (length task), in effect making the categorical part of the task more difficult. Therefore, the temporal and categorical components of the IT could be examined separately. Nicholls and Atkinson (1993) found a significant RVF-LHA for the time task, but no such asymmetry for the length task. Therefore, the RVF advantage on the task does not appear to be related to the categorical judgements it requires.

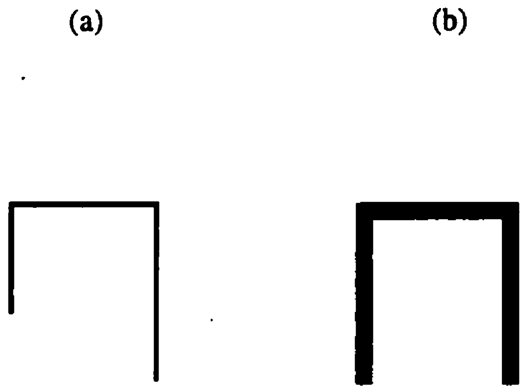

Figure 1. The pi stimulus (a) and its backward mask (b).

However, other investigators have failed to replicate the RVF-LHA for IT (Nettelbeck, Hirons, & Wilson, 1984; Sadler & Deary, 1996). The Sadler and Deary (1996) study differed from that of Nicholls and Cooper (1991) and Nicholls and Atkinson (1993) in a number of respects. Sadler and Deary (1996) presented pi stimuli tachistoscopically (rather than using a computer monitor), used a modified masking stimulus (in an attempt to reduce apparent movement effects), employed a wider range of stimulus onset asynchronies (SOAs), tested participants over a period of five days (as opposed to one day of testing), and required verbal (rather than button-press) responses at the participant's leisure, not recording reaction time. Contrary to their hypothesis that the RVF-LHA would disappear with practice, they found no evidence of an RVF-LHA on the initial testing days, but a non-significant RVF-LHA emerging by day 5. It is unclear which differences between the two versions of the bilateral IT tasks could be responsible for the discrepancy between the results of these studies.

The present study seeks to investigate the possible relation between performance asymmetries on a visual inspection-time task and linguistic lateralization as measured by the Fused Dichotic Words Test (FDWT) developed by Wexler and Halwes (Wexler & Halwes, 1983). We chose the FDWT as a test of linguistic laterality because it has performed very well in validation studies (Zatorre, 1989), and serves as a rapid, inexpensive, and non-invasive test. The lateralized IT paradigm described by Nicholls and Cooper (1991) and Nicholls and Atkinson (Nicholls & Atkinson, 1993) was chosen because a cross-modal (i.e. auditory performance compared with visual performance) comparison would be less vulnerable to potential confounds of two tasks testing the same modality (such as higher sensitivity of one ear affecting two auditory tasks). Studies of low-level temporal asymmetries in the visual modality are also preferable because the visual system demonstrates greater initial contralaterality in its projections than does the auditory system. The RVF-LHA reported for the IT paradigm does not seem to be related to the potentially categorical nature of the task (Nicholls & Atkinson, 1993), and other studies of visual temporal asymmetries have found that attentional biases do not mediate the RVF-LHA (Nicholls, 1994a).

The goals of this experiment were twofold: First, I wanted to attempt a replication of the Nicholls and Cooper (1991) and Nicholls and Atkinson (1993) result that there are visual asymmetries in IT, in light of a recent failure to replicate the result (Sadler & Deary, 1996). Second, if I found evidence for a RVF advantage on the task, I wanted to investigate its relation with linguistic asymmetries. Because the methodology of our inspection-time task was closely modeled after that described by Nicholls and Cooper (1991) and Nicholls and Atkinson (1993), I expected to replicate their results. Further, I expected that the RVF-LHA on the visual IT would be significantly positively correlated with linguistic asymmetries on the dichotic-listening task. Because language laterality appears to vary with both hand preference (Lake & Bryden, 1976; Rasmussen & Milner, 1977) and foot preference (Day & MacNeilage, 1996; Elias & Bryden, 1998), I recruited participants with consistently right or consistently left lateral preferences. I expected that left-handed, left-footed participants would be less likely than right-handed, right footed participants to exhibit a RVF-LHA on the IT task.

Method

Participants: 51 undergraduate students participated in this experiment for six dollars remuneration or course credit. The data from 11 participants had to be removed from the analysis because they could not complete the inspection-time task significantly above chance performance. Therefore, the data from 40 participants were included in the analysis. Participants were selectively recruited to include an equal number of males and females within an equal number of left-handers and right-handers. Further, only individuals who were consistently right-handed and right-footed or both left-handed and left-footed were recruited for the experiment. All participants were students at the University of Waterloo, and had normal hearing and normal or corrected-to-normal vision at the time of the experiment.

Materials: To confirm the consistency and direction of an individual's hand and foot preferences (participants initially indicated their lateral preferences for hand and foot by answering three screening questions about prefered hand for writing and throwing and preferred foot for kicking a ball), all participants completed the "Waterloo Handedness Questionnaire - Revised" (WHQ-R) and the "Waterloo Footedness Questionnaire - Revised" (WFQ-R). Both questionnaires are listed in Elias et al. (1998a) and in Appendices U and V.

Language lateralization was assessed using the FDWT developed by Wexler & Halwes (Wexler & Halwes, 1983). The test consists of 15 dichotic pairs of rhyming single-syllable words (e.g. coat/goat) that vary only in the initial phoneme. Stimuli were natural speech signals that were digitized on a PDP-2/24 computer and recorded on audio cassette by T. Halwes at Precision Neurometrics. The tape was played on a Sony Professional Walkman (model WM-D6C) through JVC (model HA-D500) earphones with circumaural cushions. Each stimulus pair was presented four times in each of two possible stimulus arrangements (Stimulus A in left ear or Stimulus A in right ear) for a total of 120 trials. Four blocks of 30 trials were presented, and earphones were reversed after the first and third blocks to control for mechanical defects in the testing equipment. Test trials were preceded by 30 monaural practice trials in which each stimulus was presented once to each ear. During the testing, participants indicated which word they heard by circling it from among four possibilities presented in pseudo-random order on an answer sheet: the word in the left ear, the word in the right ear, and two rhyming distractors.

The inspection-time task was very similar to that employed by Nicholls and Atkinson (1993). The test was administered via an IBM compatible 386/SX computer, interfaced with a Magnavox CM9039 Color VGA Monitor. At a viewing distance of 50cm (held constant by employing a chin rest), the pi figures occupied 2.3 degrees of visual angle in width and 3.0 degrees in height. The shorter "leg" of the pi figure occupied 1.3 degrees of visual angle. The stimuli were displayed in black against a white background.

500 msecs before each trial, a central fixation cross measuring 0.5 degrees of visual angle was presented. The pi figures were presented randomly on either the left or right side of the fixation cross, with the nearest leg 2.3 degrees from the central point, and the outer leg a further 2.3 degrees away. The pi figure was presented for 40, 60, 80, 100, or 120 msecs, after which a similar backward mask with both legs of equal length was presented. A new trial was initiated 1000 msecs after the subject responded. Figure 1 shows the pi stimulus and the backward mask.

Each subject completed 196 trials of this task, divided unequally between the 5 different exposure durations: 28 trials at 40 msecs, 28 trials at 60 msecs, 56 trials at 80 msecs, 56 trials at 100 msecs, and 28 trials at 120 msecs. Pilot testing using the exposure durations (20 to 100 msecs) employed by Nicholls and Atkinson (1993) indicated that exposure times of both 20 msec and 40 msec were vulnerable to floor effects, so to avoid the possibility of a large number of participants performing at chance on the task, the exposure durations used by Nicholls and Atkinson (Nicholls & Atkinson, 1993) were increased by 20 msecs for the present study. Twice as many trials were presented at the 80 and 100 msec durations because pilot testing indicated that they were the least vulnerable to floor and ceiling performance effects. The testing sessions were broken up into 7 blocks of 28 trials. Within each block, representative proportions of the possible combinations of stimulus duration, side of the shorter leg on the pi figure, and side of presentation were included. These three parameters were randomized within each block to prevent the participants from being able to predict the location and type of the next trial.

Participants responded by pressing one of four keys on a keyboard, with their index and middle fingers of each hand, using two keys on their right side for stimuli that fell in their right visual field and vice versa for stimuli presented to their left visual field. Using this spatially mapped arrangement, when responding correctly, participants pressed the key that corresponded to the location of the shorter leg of the pi figure.

Prior to beginning the test, participants were instructed to keep the chin firmly in the chin rest, and that they should be very careful to keep their eyes fixed on the cross in the middle of the screen to maximize their performance, because the side of presentation was randomized. Accuracy of response, rather than response speed, was emphasized to the subject. Participants were encouraged to take breaks between blocks to facilitate concentration, and short cartoons were presented between blocks. The IT task took between 15 and 20 minutes to complete.

Procedure: To enable the recruitment of an equal number of participants from each handedness/footedness group and sex, a screening questionnaire was administered to 600 undergraduate students. Participants who could not complete the visual inspection-time task significantly above chance were replaced with someone from the same handedness, footedness, and sex group. First, each participant completed the WHQ-R, followed by the WFQ-R. Then, 120 trials of the FDWT were completed. After completion of the dichotic task, participants performed the inspection-time task. The entire testing procedure took approximately 45 minutes.

Scoring and Analysis: The FDWT data were scored using a log-linear analysis procedure described by Grimshaw, McManus, and Bryden (1994), which calculates a laterality index (λ*) controlling for effects of stimulus dominance (the λ* index is analogous to the λ index described by Bryden and Sprott 1981). Ear advantages are calculated by fitting a model that includes every relevant effect except the 'response' × 'stimulus arrangement' interaction (one would include main effects of 'stimulus pair', 'response', 'stimulus arrangement', and the 'stimulus pair' × 'stimulus arrangement' interaction) and note the likelihood ratio chi-square test statistic. Next, one must fit a second model that includes every effect in the first model in addition to the 'response' × 'stimulus arrangement' interaction. In this way, the parameter estimates provided for each subject's 'response' by 'stimulus arrangement' interaction provide an index of lateralization that is unbounded, approximately normally distributed, unconstrained by accuracy, and that controls for the effects of stimulus dominance. Positive λ* scores are indicative of a right-side advantage, and negative scores indicate left-side advantages.

The first (practice) block of the inspection-time task was not scored, but the data from the remaining 6 blocks were scored using the λ index described by Bryden and Sprott (1981). The

λ index = $\log_e$ [(right hits × left misses) / (left hits × right misses)]. This index is unbounded, approximately normally distributed, and unconstrained by accuracy. In addition to scoring the inspection-time data with the λ index, it was also scored in terms of percent correct and median time for each SOA within each visual field.

Results

Inspection-time task: The accuracy data on the inspection-time task were analyzed using a repeated-measures ANOVA, with within-subjects variables of visual field (left or right) and duration of exposure (40, 60, 80, 100, or 120 msecs), and between-subjects variables of hand/foot preference (left or right) and sex (male or female). There was a significant main effect of visual field (see Figure 2), with participants more accurately detecting the shorter leg in the RVF, $F(1,36) = 4.38$, $p = .043$. There was also a significant main effect of exposure duration in which longer stimulus presentations were identified more accurately, $F(4,33) = 45.36$, $p < .001$. Surprisingly, there was also a significant main effect of sex: males were significantly more accurate than females across the 5 exposure durations, $F(1,36) = 5.79$, $p = .021$. There were no significant interactions between any of the variables.

Despite the non-significant interaction between sex and visual field of presentation, $F(1,36) < 1$, the possibility that the two groups might differ in the strength of visual-field asymmetry warranted investigation because the laterality data of the two groups could be confounded by the significant differences in performance (see Bryden & Sprott, 1981). Therefore, a log-odds ratio laterality index was calculated for each individual. Although males

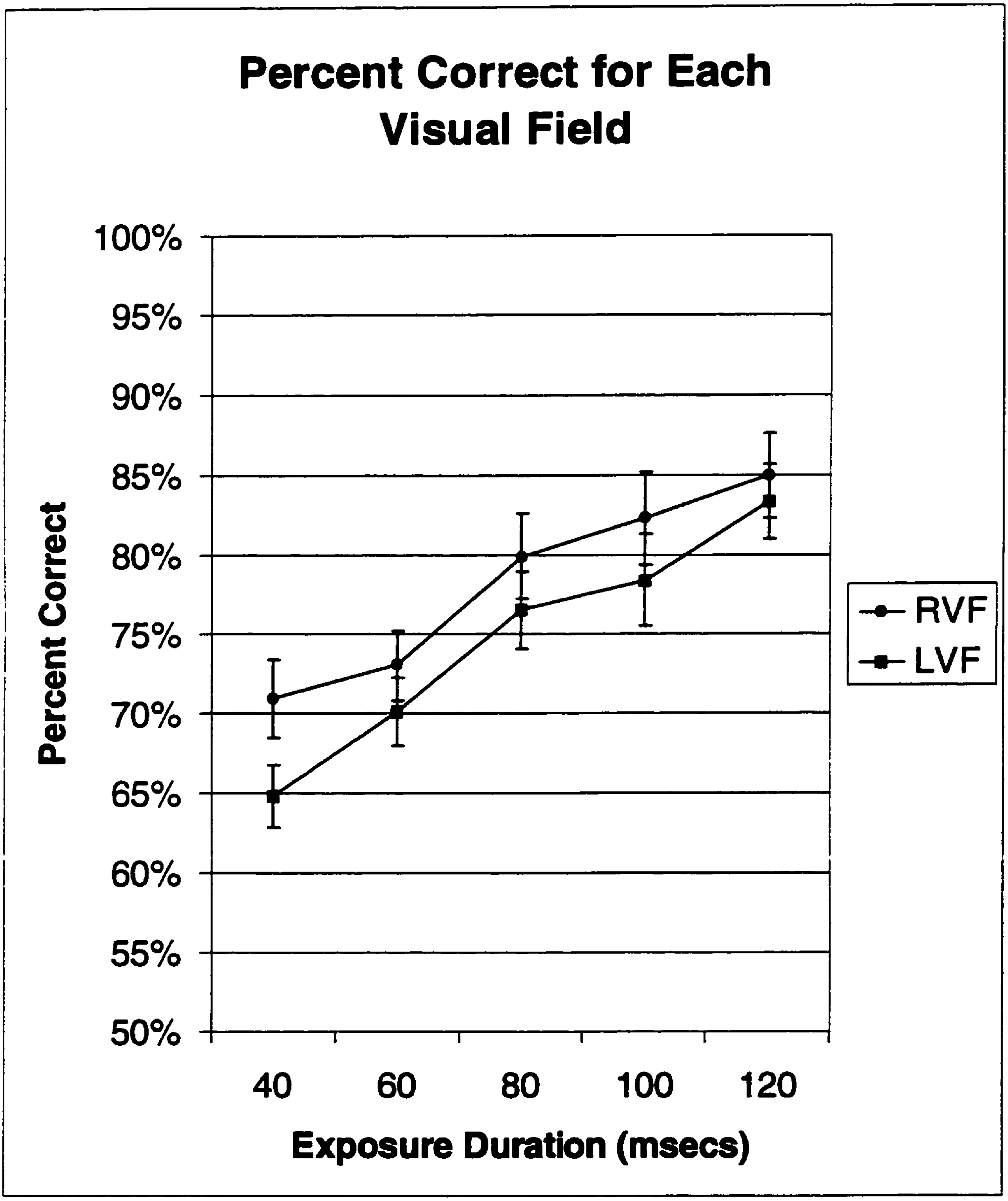

Figure 2. Percent correct for pi presentations to RVF and LVF across the 5 SOA's.

tended to exhibit slightly greater RVF advantages than females, this effect was not significant, $t(38) = 0.54$, $p = .596$.

The reaction time (RT) data did not reveal any visual-field asymmetry, $F(1,36) < 1$ (see Figure 3), and the sex difference noted in the accuracy data did not reach significance, $F(1,36) = 2.71$, $p = .11$. The only significant effect in RT was one of exposure duration, $F(4,33) = 39.16$, $p < .001$, wherein participants responded faster to longer exposures of the pi figure.

Dichotic-listening task: As expected, most participants (30/40) exhibited right-ear advantages (REA's) on the FDWT. Although left-handed left-footed participants tended to exhibit lower λ^* scores (indicating a smaller REA) than right-handed right-footed participants, this effect was non-significant, $F(1,39) < 1$, and there was no sex effect or interaction between these variables.

Tests of Association Between the two Tasks: As hypothesized, λ^* scores on the FDWT and the inspection-time task were significantly positively correlated (see Figure 4), $r = .306$, $p = .028$ (one tailed). However, because the correlation of interest is that between the latent variables of inspection time and dichotic listening, and the correlation above is based on measured values (incorporating measurement error), the correlation must be disattenuated for error. Split-half reliability of the inspection-time task in the present experiment was $r = .482$. The FDWT has proven considerably more reliable in our laboratory, demonstrating split-half reliability of $r = .823$. Therefore, after disattenuation, the correlation increases to $r = .486$.

To further investigate the relation between performance on these two tests, participants

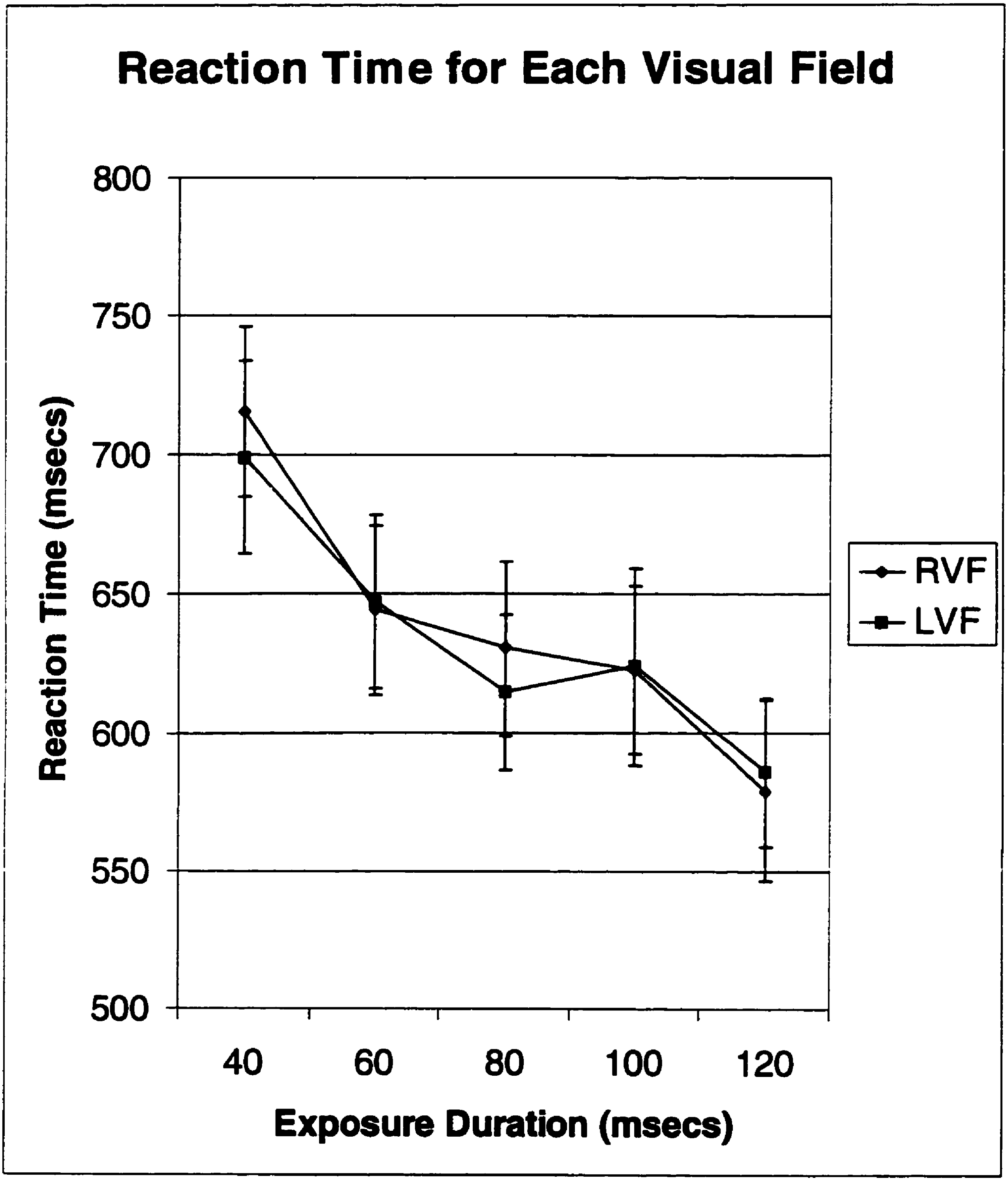

Figure 3. Reaction Time for pi presentations to RVF and LVF across the 5 SOA's.

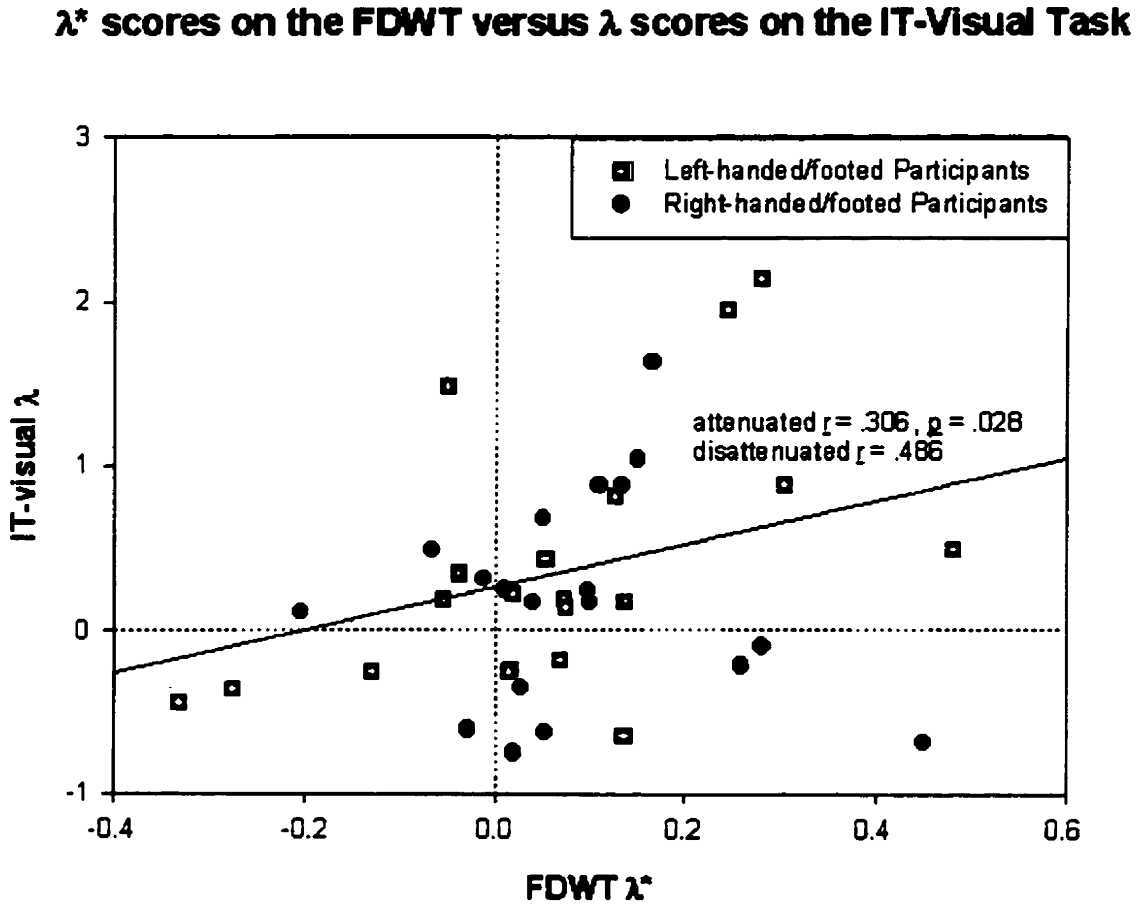

Figure 4. Scatterplot of λ^* scores on the FDWT versus λ scores on the inspection time task.

were classified as either left- or right-hemisphere advantaged (LHA or RHA) on each task to enable odds-ratio testing. Strictly speaking, if both tests are measuring the same underlying process, no individual should exhibit an LHA on one task and an RHA on another. In other words, given that an individual exhibits an REA (LHA) on the FDWT, the odds of his or her also showing an LHA (as opposed to an RHA) on the inspection-time task should be high whereas these odds given an RHA on the FDWT should be very low. The ratio of the former odds to the latter, then, should be high. The natural log of an odds ratio is easily tested for significance using a z-test (Bryden, McManus, & Bulman-Fleming, 1994b). For the present data, after dichotomizing participants' scores on both measures, the resulting odds ratio was not significant. Thus, individuals were no more likely to show an LHA on the inspection-time task if they had shown an LHA on the dichotic task than if they had shown an RHA on the dichotic task. The odds ratio, then, although >1 as would be predicted, is not significant.

Discussion

The present study provides clear support for the claim that low-level temporal asymmetries are related to linguistic asymmetries. Similar to the results of Nicholls and Cooper (1991) and Nicholls and Atkinson (1993), analysis of our data revealed a significant RVF-LHA for a lateralized visual inspection-time task, and this visual processing asymmetry was significantly correlated with linguistic asymmetry measured with the dichotic-listening paradigm.

Although the correlation between these two tests may seem low ($r = .306$ before disattenuation, $r = .486$ after disattenuation), it becomes more impressive when one considers the strength of cross-modal correlations between visual and auditory linguistic laterality tests reported in the literature. Despite the fact that these tests are meant to tap similar (if not identical) processes, many investigators have failed to find any significant positive correlation between these measures, and some have even found weak negative correlations (Bryden, 1965; Bryden, 1973; Fennell, Bowers, & Satz, 1977a; Fennell, Bowers, & Satz, 1977b; Kim & Levine, 1992; Moscovitch, 1979). On those occasions when significant positive correlations are obtained between the measures, they are usually rather low. For example, Hines and Satz (1974) found modest correlations, which were only significant in their right-handed participants (r= .39). Conversely, Dagenbach (1986) found significantly larger cross-modal correlations for his left-handed participants (r= .302) than for his right-handed participants (r= -.138). In light of the relatively poor relation between visual half-field tests of linguistic laterality and dichotic-listening tasks, the significant positive correlation between inspection-time asymmetries and laterality scores on the FDWT in the present study provides evidence that the two tasks could be relying on a common process.

The absence of a clear RVF-LHA in the RT data despite a significant effect on accuracy is puzzling, but not unprecedented. There is no evidence of a speed/accuracy tradeoff in the present study. The discrepancy between the accuracy and RT results may be due to decreased power in studying reaction time, because of much greater individual variation. Alternatively, the effect could have been mediated by the experimental instructions, because accuracy, not response speed, was stressed to the participants as the critical part of the task.

I predicted that there would be significant effects of lateral preference in the RVF-LHA exhibited in the inspection-time task. Although the two lateral preference groups differed in the predicted direction, this effect did not approach statistical significance. Similarly, the left-handed left-footed participants exhibited non-significantly weaker REA's than the right-handers on the dichotic task. The present study may not have had enough power to detect differences between the handedness groups.

The sex difference in accuracy on the IT was unexpected. Although some authors have suggested that IT is significantly related to intelligence (Brand & Deary, 1982; Chaiken, 1993; Nettelbeck, 1987; Zhang, 1991), it seems unlikely that the males participating in this study were significantly more intelligent than the females. The physical nature of the task might be more to blame for the sex difference. When completing the task, participants have to quickly press buttons in response to rapidly flashing stimuli on a computer screen, a task not entirely unlike playing a video game. Because males seem to be more likely to be well practiced at such games and performance on the inspection-time task improves significantly with practice (Sadler & Deary, 1996), the greater practice experienced by males on similar tasks might account for the observed sex difference in the present study.

Given that visual asymmetries as measured with the inspection-time paradigm appear to be related to linguistic asymmetries, this suggests the possibility that other low-level temporal asymmetries will exhibit a similar relatedness.

Experiment 2

Although a significantly positive relation between visual temporal asymmetries and linguistic asymmetries was found in Experiment 1, the cross-modal nature of the comparison could have weakened the relation between the two tasks. Experiment 2 seeks to compare *auditory* temporal asymmetries with auditory asymmetries in linguistic perception. The relation between auditory temporal asymmetries and linguistic asymmetries will be tested using the FDWT developed by Wexler and Halwes (1983) as the linguistic task, and the auditory gap-detection task described by Brown and Nicholls (1997) as the low-level auditory temporal task.

The position that there are low-level auditory asymmetries is still contentious. Vroon et al. (1977) presented monaural 3-second bursts of broad-band white noise, half of which were interrupted by gaps of silence (1-4msecs in length) at various locations within the burst (1.0, 1.5, or 2.0 seconds after onset of the noise). They found evidence for a strong REA on the task. Efron et al. (1985), conducted a similar study, in which half of the monaural narrow-band bursts of noise (200-400Hz) 300 msecs in length were interrupted by gaps of silence of 2-7 msecs. Efron et al. (1985) found no evidence of an REA on the task. Most recently, Brown and Nicholls (1997), presented monaural bursts of white noise, 300 msecs in length, half of which were interrupted by gaps of silence, 2-8 msecs in length. In addition to varying gap length, they also varied gap location and variability. In keeping with the results of Vroon et al. (1977), Brown and Nicholls (1997) found strong evidence for an REA on the gap-detection task, and this effect did not appear to depend on gap location or the variability of gap location.

There were two goals for the second experiment. First, I wanted to attempt a replication of the Vroon et al. (1977) and Brown and Nicholls (1997) finding that there are low-level auditory asymmetries in gap detection, given the fact that Efron et al. (1985) failed to replicate the effect. Second, if I found evidence for an REA on the gap-detection task, I wanted to investigate its possible relation with linguistic asymmetries. Linguistic asymmetries were measured with the Fused Dichotic Words Test (FDWT) developed by Wexler and Halwes (1983). Because the methodology of the gap-detection task was closely modeled after that described by Brown and Nicholls (1997), I expected to replicate their results. Further, I expected that the REA-LHA on the visual IT would be significantly positively correlated with linguistic asymmetries on the dichotic-listening task. Because language laterality appears to vary with both hand preference (Lake & Bryden, 1976; Rasmussen & Milner, 1977) and foot preference (Day & MacNeilage, 1996; Elias & Bryden, 1998), I recruited participants with consistently right or consistently left lateral preferences. I also expected that left-handed left-footed participants would be less likely to exhibit a REA-LHA on the gap-detection task.

Method

Participants: 48 undergraduate students participated in this experiment for six dollars remuneration or course credit. Participants were selectively recruited to include an equal number of males and females within an equal number of left-handers and right-handers. Further, only individuals who were consistently right-handed and right-footed or both left-handed and left-footed were recruited for the experiment. All participants were students at the University of Waterloo, and had normal hearing and normal or corrected-to-normal vision at the time of the experiment.

Materials: All participants completed the WHQ-R and the WFQ-R (both questionnaires are listed in Elias et al., 1998a, or see Appendices U and V).

Dichotic-listening Task: Language lateralization was assessed using the same dichotic test (the FDWT) employed in experiment one.

Gap-detection Task: The gap-detection task was closely modeled after the test described by Brown and Nicholls (1997). It was administered with an Apple Macintosh 7100 computer, delivering monaural broad-band bursts of white noise at an intensity of 70 dB SPL through JVC (model HA-D500) earphones with circumaural cushions. The bursts of noise were either continuous (the "no gap" condition), or interrupted by a brief period of silence (the "gap" condition - See Figure 5). Gap location, gap position, and gap duration were varied. Within a block, only one gap duration (2, 3, 4, or 5 msecs) was presented, but gap position varied within each block. The gaps were located in one of three positions: early (after 75msecs), middle (after 150msecs), or late (after 225msecs).

Participants completed a total of 288 trials of the task. Before starting the experimental trials, participants completed 48 practice trials of increasing difficulty to familiarize themselves with the task. The remaining 240 experimental trials were divided into four blocks of 60 trials, with rest periods between blocks. Gap length was blocked, but within each block, equivalent proportions of the three gap positions and two possible sides of presentation were delivered in

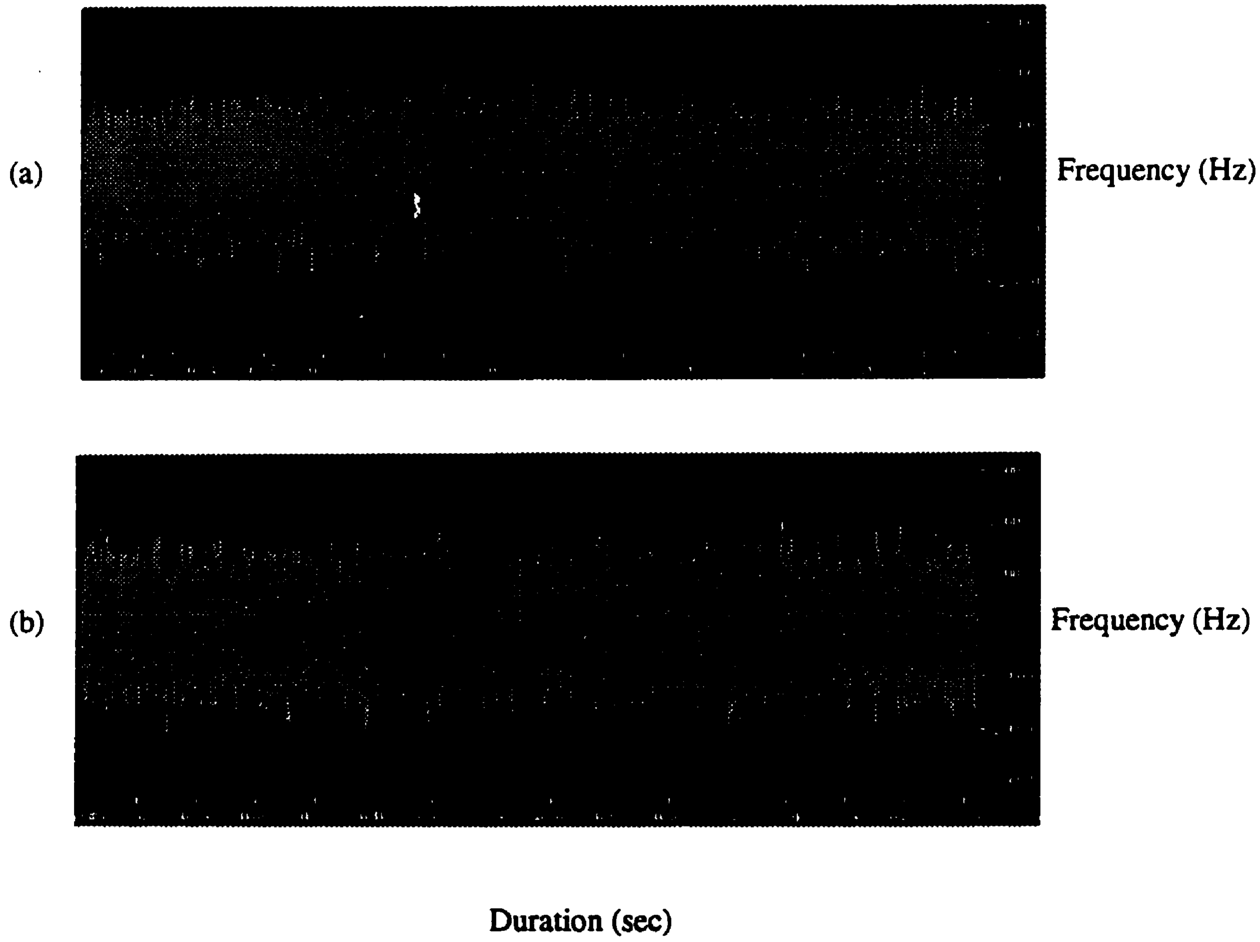

Figure 5. Diagram of two examples of the auditory stimuli used in the gap-detection task. The first diagram (a) depicts a 300 msec burst of continuous (no gap) noise, whereas the second diagram (b) depicts a 300 msec burst of noise interrupted by a 5 msec gap of silence.

randomized order. Half of all noise bursts presented contained a gap of silence. Order of presentation of the four experimental blocks was randomized, and one participant from each handedness group completed the test using one of the 24 possible orderings of the 4 blocks.

Before starting the task, each participant was informed that there would be two types of trials: One in which a continuous burst of noise was presented, and one in which the noise burst was interrupted by a brief gap of silence. They were also informed that half of all stimulus presentations would contain a gap, and that some testing blocks would be more difficult than others. Participants responded on a keyboard, pressing one key to indicate the presence of a gap and another to indicate the absence of a gap. In order to control for motor biases between the hands and between response fingers, half of all subjects responded with their non-dominant hand and half responded with their dominant hand. Within these four groups, half of all participants indicated the presence of a gap by pressing a button with their index finger, and half of the participants indicated the presence of a gap with their middle finger.

Procedure: To enable the recruitment of an equal number of participants from each handedness/footedness group and sex, a short screening questionnaire was administered to 600 undergraduate students. During the testing sessions, each participant first completed the WHQ-R, followed by the WFQ-R. Then, 120 trials of the FDWT were completed. After completion of the dichotic task, participants performed the gap-detection task. The entire testing procedure took approximately 45 minutes.

Scoring and Analysis: The dichotic-listening data were scored using the same procedure described for experiment 1. The auditory gap-detection data were scored for percentage error by summing all misses for the "gap" trials with the number of false positives among the "no gap" trials, and dividing the resulting value by 60, the total number of trials of that type. The RT data were scored by averaging RT's correctly identified "gap" trials. Because only correctly identified gap durations were included in the analysis and the number of correctly identified gaps varied between participants, the RT data were subjected to a recursive outlier-removal procedure described by Van Selst and Jolicoeur (1994). A measure of response bias towards indicating "gap" or "no-gap" responses was calculated by subtracting the number of "no gap" responses from the number of "gap" responses within each stimulus presentation condition (ear and duration of gap), regardless of whether the response was correct or not. Therefore, positive bias scores indicate that a participant was more likely to produce "gap" responses than "no-gap" responses within a given condition. For the purposes of comparing the gap-detection data to the dichotic-listening data, the accuracy data for the gap-detection task were also scored using the index described by Bryden and Sprott (1981).

Results

Dichotic-listening task: As expected, most participants (36/48) exhibited REAs on the FDWT. Two participants did not demonstrate any asymmetry on the task, and 10 demonstrated LEAs. Although left-handed left-footed participants tended to exhibit lower λ scores (indicating a smaller REA) than right-handed right-footed participants, this effect was non-significant, $\underline{F}(1,44) = 1.53$, $\underline{p} = .222$. There was a significant sex difference in the dichotic-listening scores, with males demonstrating stronger REA's than females, $\underline{F}(1,44) = 5.67$, $\underline{p} = .022$.

Gap-Detection task: The accuracy data on the gap-detection task were analyzed using a repeated-measures ANOVA, with within-subjects variables of side of presentation (left or right) and gap length (2, 3, 4, or 5 msecs), and between-subjects variables of hand/foot preference (left or right) and sex (male or female). There was a significant main effect of gap length, $\underline{F}(1,132) = 265.28$, $\underline{p} < .001$ (see Figure 6), with participants more accurately detecting the longer gaps of silence. There was also a significant main effect of side of presentation, $\underline{F}(1,44) = 11.07$, $\underline{p} = .002$, with participants more accurately detecting gaps of silence presented to the right ear. These main effects were qualified by a significant interaction between the factors of gap length and side of presentation, $\underline{F}(3,132) = 16.72$, $\underline{p} <.001$. Accuracy of gap detection varied depending on side of presentation for gaps that were 3 msecs in length, $\underline{t}(1,47) = 5.87$, $\underline{p} < .001$, but the difference was not significant at any other gap lengths. There were no significant interactions between any of the other variables.

The RT data for the gap-detection task were more problematic to analyze than the accuracy data. Only the RT's for the correct gap identifications were included in the analyses. However, during the blocks of trials in which gap durations were very short (i.e. 2 or 3msecs), some individuals never correctly identified the presence of a gap, always signaling that there was no gap present. Therefore, when analyzing the group RT data, some individuals' cells were empty, resulting in a corresponding loss of degrees of freedom for some analyses.

The RT data on the gap-detection task were also analyzed using a repeated-measures ANOVA, similar to that employed for the accuracy data. The main effect of gap length was

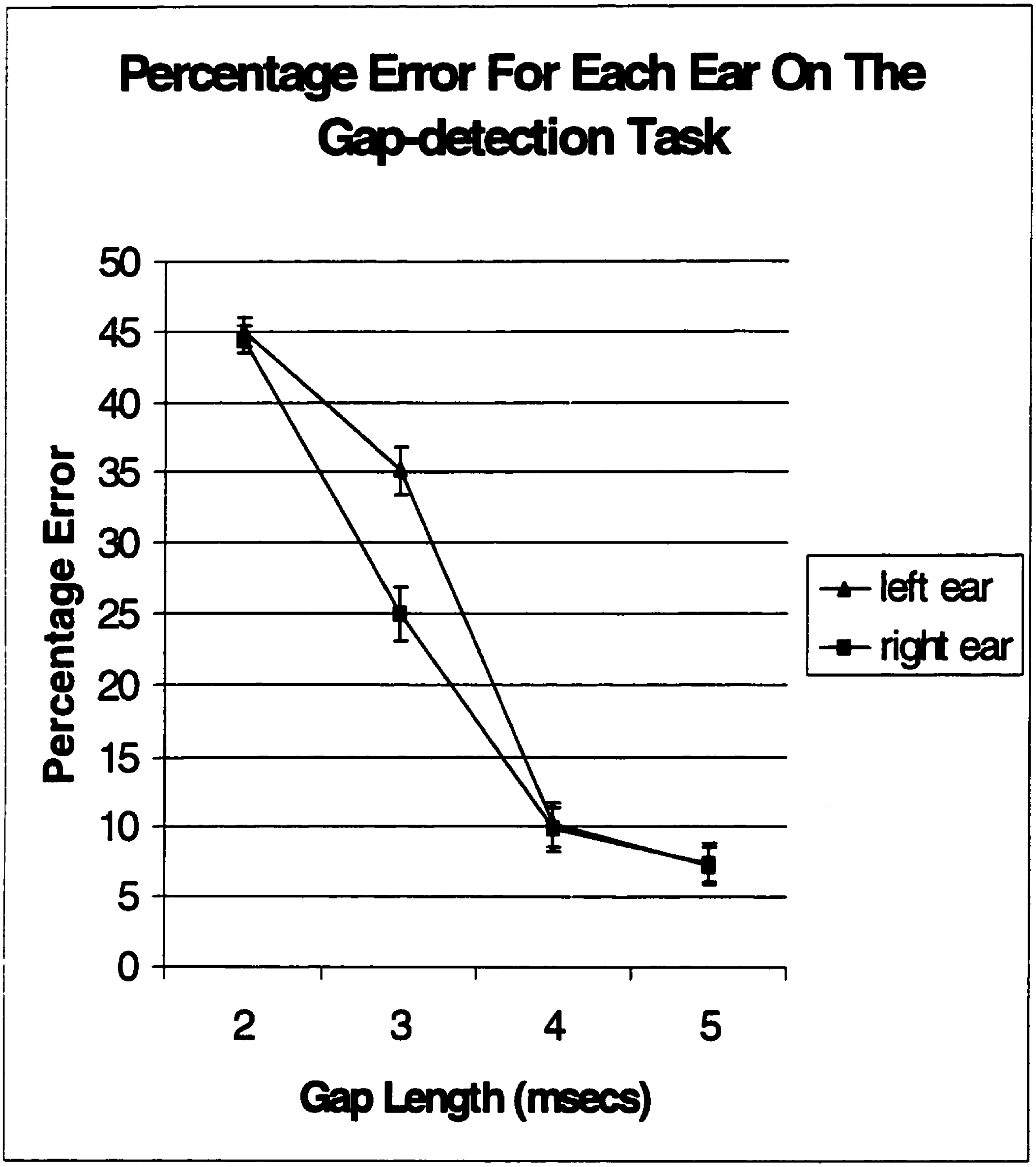

Figure 6. Percentage error for gaps presented to the right or left ear across the 4 gap lengths.

highly significant, *F*(3,63) = 7.91, *p* < .001, and the main effect of side of presentation approached significance, *F*(1,21) = 3.90, *p* = .061. However, with the RT data, the interaction between these two variables was not significant, *F*(3,63) = 1.10, *p* = .355 (see Figure 7). Paired t-tests revealed that the differences in RT were not significant at a gap length of 2msecs, *t*(24) = 1.53, *p* = .139, but the differences were significant at gap lengths of 3msecs, *t*(43) = 2.90, *p* = .006, and 4msecs, *t*(47) = 2.34, *p* = .024. The effects of the other variables did not reach significance, and there were no interactions between the variables.

Response bias towards indicating “gap” or “no-gap” responses was calculated by subtracting the number of “no gap” responses from the number of “gap” responses, within each stimulus presentation condition (ear and duration of gap), regardless of whether the response was correct or not. Therefore, positive bias scores indicate that a participant was more likely to produce “gap” responses than “no-gap” responses within a given condition. The response bias data were analyzed with a repeated-measures ANOVA, similar to that employed for the accuracy data. There was a highly significant main effect of gap duration, *F*(3,132) = 185.42, *p* < .001, in which longer gap durations were associated with higher (more positive) bias scores (see Figure 8). There was also a significant main effect of side of presentation, *F*(1,44) = 9,71, *p* = .003, wherein presentations to the right ear were associated with higher bias scores. These main effects were qualified by their interaction, *F*(3,132) = 6.94, *p* < .001. Pairwise comparisons revealed that the difference in bias scores between the two sides of presentation was significant for 3 msec gaps, *t*(47) = 4.28, *p* <.001, but no other inter-pair differences were significant (although the difference for 5 msec gaps approached significance, *t*(47) = 1.72, *p* = .093, one-tailed).

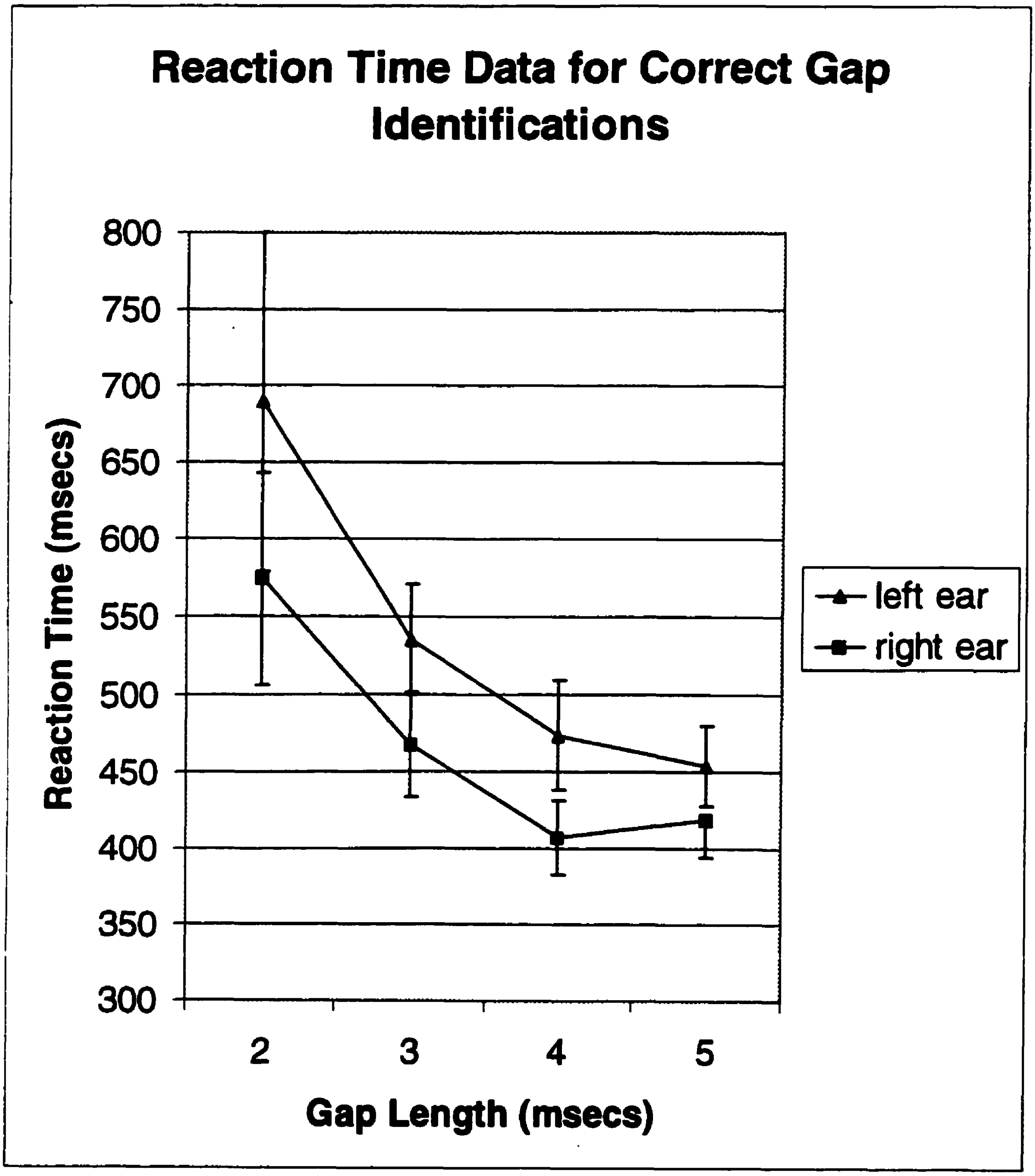

Figure7. Group mean RT data for correctly identified gaps across the four gap lengths.

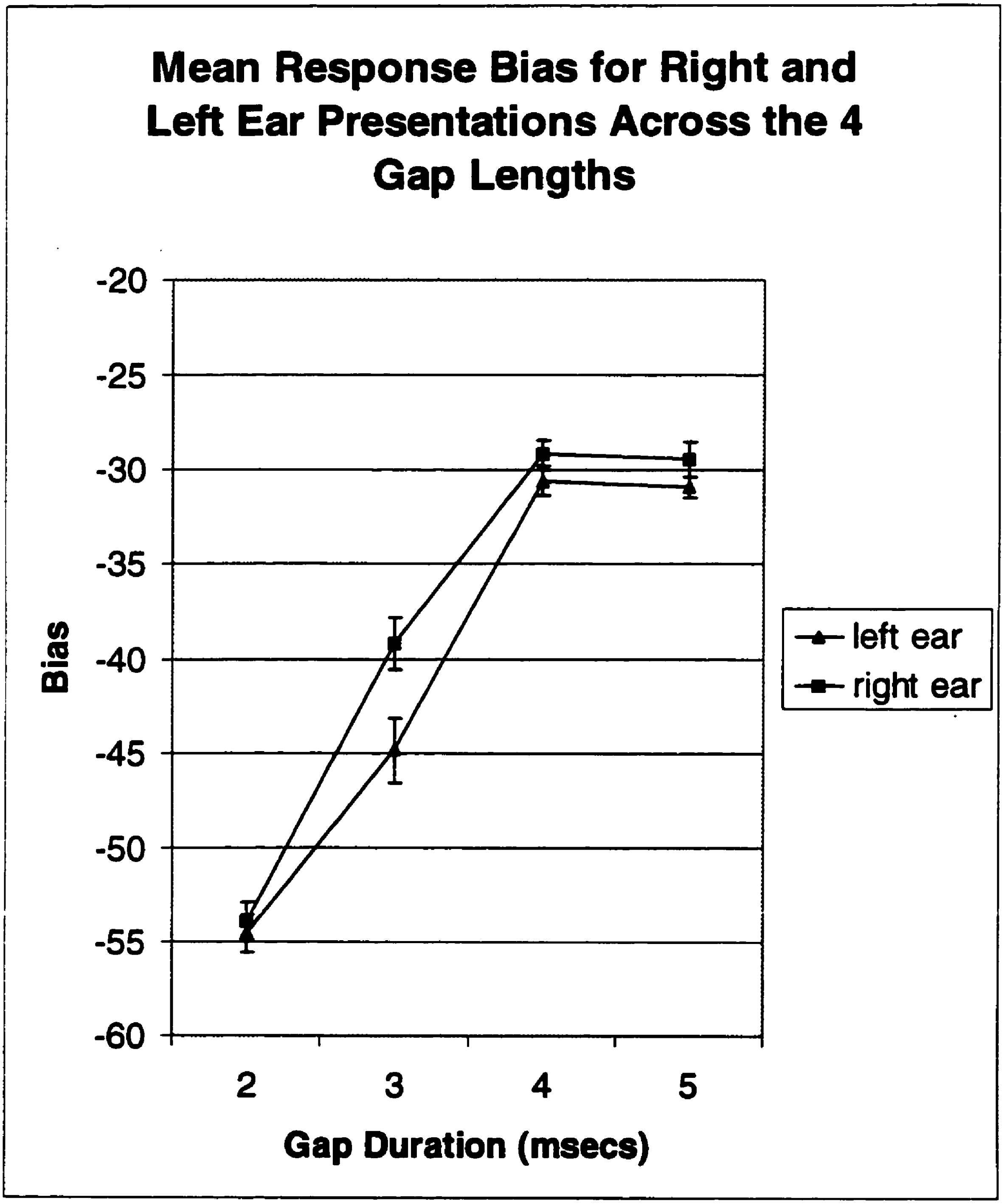

Figure 8. Group mean response bias data for gaps across the four possible gap lengths.

Tests of Association Between the two Tasks: As hypothesized, λ^* scores on the FDWT and λ scores on the auditory gap-detection task were significantly positively correlated (see Figure 9), $r = .307$, $p = .017$ (one tailed) before disattenuation. Split-half reliability of the gap-detection task in the present experiment was $r = .525$. The FDWT has proven considerably more reliable in our laboratory, demonstrating split-half reliability of $r = .823$. Therefore, after disattenuation, the correlation increases to $r = .467$.

To further investigate the relation between performance on these two tests, participants were classified as either left- or right-hemisphere advantaged (LHA or RHA) on each task to enable odds-ratio testing. Strictly speaking, if both tests are measuring the same underlying process, no individual should exhibit an LHA on one task and an RHA on another. For the present data, 39 of 48 participants' scores could be dichotomized on both measures, and the resulting odds ratio was not significant. Thus, individuals were no more likely to show an LHA on the dichotic task than if they had shown an RHA on the gap-detection task. The odds ratio, then, although >1 as would be predicted, is not significant.

Discussion

The present study provides clear support for the claim that low-level temporal asymmetries are related to linguistic asymmetries. Like the results of Vroon et al. (1977) and Brown and Nicholls (1997), I found evidence for a significant REA-LHA for a gap-detection task, and this processing asymmetry was significantly correlated with linguistic asymmetry measured with the dichotic-listening paradigm.

λ* scores on the FDWT versus λ scores on the Gap-detection Task

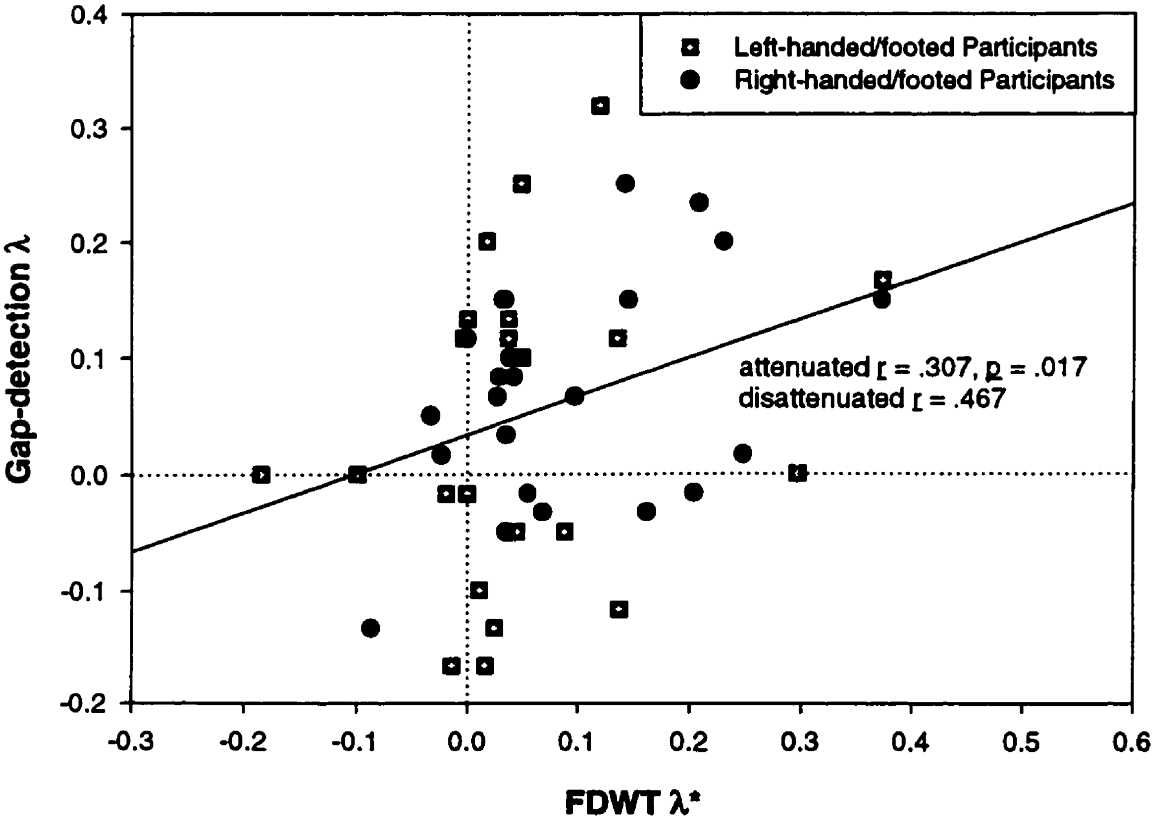

Figure 9. Scatterplot of λ* scores on the FDWT versus λ scores on the gap detection task.

Although the correlation between these two tests seems low ($r = .307$ before disattenuation, and $r = .467$ after disattenuation), it becomes more impressive when one considers the strength of correlations between different dichotic-listening tests that are meant to measure the same underlying process. Generally, dichotic-listening tests demonstrate reasonably good test-retest reliability. The FDWT has a test-retest correlation of $r = 0.85$ (Wexler & Halwes, 1983), and other tests tend to show test-retest correlations between $r = 0.35$ and $r = .90$ (see Fennell et al., 1977a; Fennell et al., 1977b; Hines, Fennell, Bowers, & Satz, 1980; Hugdahl & Hammar, 1997).

However, scores between **different** linguistic dichotic-listening tests usually do not correlate very highly, and sometimes the correlations are even negative. For example, in our own laboratory, we found that scores on the FDWT test related quite poorly to scores on the linguistic component of the Emotional Words Test (described by Bryden & MacRae, 1988), resulting in a (nonsignificant) correlation of $r = 0.16$ (Bryden & Bulman-Fleming, 1995). Wexler and Halwes (1985) also failed to find any significant correlation between two linguistic dichotic-listening tests when they compared scores on a Consonant-Vowel-Consonant (CVC) dichotic-listening test to Vowel-Consonant-Vowel (VCV) and Consonant-Vowel (CV) test, even though the set of distinguishing phonemes was identical for both tests. Jäncke, Steinmetz, and Volkman (1992) administered seven different dichotic listening tests to the same participants and found that most of the tests were reasonably reliable (correlations between 0.75 and 0.88 for all tests except Morse-code recall), but the majority of intertest correlations were not significantly positive, and many were even negative. Reports of reasonably strong positive correlations between different dichotic tests are rare. However, Kim and Levine

(1992) compared the results from a test of spoken words to those from a test of spoken digits, and found a significantly positive correlation of $r = 0.47$. In light of the relatively poor relation between scores on different dichotic-listening tests that are meant to be measuring the same underlying process, the present correlation between FDWT scores and auditory gap-detection provides clear evidence that the two tasks might be relying on a common process.

I predicted that there would be significant handedness/footedness effects in the REA-LHA exhibited in the gap-detection task. Although the two handedness groups differed in the predicted direction, this effect did not approach statistical significance. Similarly, the left-handers also exhibited non-significantly weaker REA's on the dichotic task. The present study might not have had enough power to detect differences between the handedness groups.

The significant sex difference in the dichotic-listening data was unexpected, but not unprecedented. Significant sex-differences are relatively rare in the dichotic-listening literature, but when present, they usually indicate stronger lateralization of function in males. In a recent survey of this literature by Hiscock, Inch, Jacek, Hiscock-Kalil, & Kalil (1994), they found that when significant sex differences in dichotic-listening performance were reported (according to the strict criteria set by Hiscock et al., 1994), 9 of the 11 reports indicated greater functional specialization in males. However, the vast majority of investigations fail to find any significant sex difference in either direction (Hiscock et al., 1994; Hiscock & Mackay, 1985).

Given that low-level temporal auditory asymmetries as measured with the visual inspection-time paradigm (Elias et al., 1998b), and now an auditory gap-detection task appear to be related to linguistic asymmetries, this invites the question of whether other low-level temporal asymmetries will exhibit a similar relatedness.

Prediction 2: Longer ICD's should be associated with greater linguistic lateralization.

It appears as though the left hemisphere's relative superiority at temporal processing might underlie its superiority at linguistic processing. According to the Ringo et al. (1994) ICD theory of cerebral lateralization, longer interhemispheric delays should *cause* greater hemispheric specialization for time-critical tasks. More specifically, longer ICDs from the right hemisphere to the left hemisphere should be associated with greater left-hemispheric linguistic lateralization. ICD can be estimated using a simple reaction-time (SRT) paradigm. Using a within-subjects design, individuals with greater ICDs from the right hemisphere to the left hemisphere should exhibit greater left-hemispheric linguistic lateralization.

Experiment 3

Since Poffenberger's (1912) classic experiment, it has become quite popular to estimate interhemispheric transfer time (IHTT) using an SRT paradigm. By subtracting the amount of time a participant takes to respond to visual stimuli in the field ipsilateral to the responding hand (a task which does not require interhemispheric transfer) from the time the participant takes to respond to contralateral stimuli (a task which **does** require interhemispheric transfer), one can estimate IHTT. This difference between RT to contralateral or "crossed" stimuli and ipsilateral or "uncrossed" stimuli is typically referred to as the "crossed-uncrossed difference (CUD).

Using this technique, the CUD in normal participants has typically been estimated to be between 2-5ms (Braun, 1992; see Bashore, 1981, for a review). Participants with either a congenitally absent (Clarke & Zaidel, 1989; Milner, 1982; Milner, Jeeves, Silver, Lines, & Wilson, 1985) or surgically severed callosum (Clarke & Zaidel, 1989; Sergent & Myers, 1985) exhibit much longer CUDs. Over a hundred papers have questioned whether the CUD truly reflects IHTT, and although it is clear that CUDs do not correspond to IHTT in a simple and direct manner, they do provide investigators with a practical and non-invasive mechanism to study interhemispheric transfer. Investigators monitoring evoked potentials to lateralized visual stimulation have also typically reported significantly positive CUDs, but the length of the difference has typically been longer (i.e. 11-15msec) than those reported using simple RT procedures (Brown, Larson, & Jeeves, 1994).

Although much less popular, the CUD method of measuring IHTT has also been employed in the auditory modality. Broman, Rudel, Helfgott, and Kriger (1985) administered both a visual and auditory CUD test to a group of dyslexic children and normals. Unlike the results typical of most visual studies, Broman et al. (1985) did not find a hand × side of presentation interaction in either group of participants. This could be due to the relatively small number of trials administered in each condition (40), or because the Poffenberger (1912) paradigm is not well suited to the auditory modality. Because each ear sends projections to each hemisphere, interpretation of CUDs in the auditory modality is even more complicated than that of CUDs in the visual modality. More recently, Bjorklund and Lian (1993) had participants perform a unimanual auditory two-choice RT task, in which the participants pressed a button on their left or right side depending where they heard the tone. Using this technique, Bjorklund and Lian found a significant CUD, estimating IHTT to be 16msecs, which is considerably higher than the estimate resulting from visual studies.

Recent work with the Poffenberger paradigm has focused on asymmetries in callosal conduction velocity. Meta-analyses of the RT CUD literature (Marzi, Bisiacchi, & Nicoletti, 1991) as well as the evoked potential IHTT literature (Brown et al., 1994) have found significant experiment-wise predominance of faster right-hemisphere-to-left-hemisphere transmission. This effect has usually been linked with the left hemisphere's superiority at processing linguistic stimuli and other stimuli requiring fine temporal processing.

The present experiment seeks to investigate the relation between IHTT and linguistic lateralization. The ICD theory of cerebral lateralization claims that longer IHTT's should result in greater functional lateralization for time-critical tasks. Given that IHTT appears to be faster from the right hemisphere to the left hemisphere, it is predicted that transfer time from the right hemisphere to the left will be significantly related to linguistic lateralization, but transfer of information in the opposite direction should not demonstrate a similar relatedness. Although I will measure CUDs in both the visual and auditory modalities, the predicted relation should be most prominent in the auditory modality.

Method

Participants: 40 undergraduate students participated in this experiment for six dollars remuneration or course credit. Participants were selectively recruited to include an equal number of males and females within an equal number of left-handers and right-handers. All participants were students at the University of Waterloo, and had normal hearing and normal or corrected-to-normal vision at the time of the experiment.

Materials: To measure the consistency and direction of an individual's hand and foot preferences, all participants completed the WHQ-R and the WFQ-R (see Appendices U and V).

Dichotic-listening Task: Language lateralization was assessed using 240 trials of the FDWT developed by Wexler and Halwes (1983). Details of the test were provided in the method section of Experiment 1. Unlike the procedure for Experiments 1 and 2, the audio samples were delivered by an IBM compatible Pentium 200 computer through a 16-bit soundcard to JVC (model HA-D610) earphones with circumaural cushions. During the testing, participants indicated which word they heard by pressing one of four numbered keys corresponding to four possibilities presented in pseudo-random order on the computer screen for each trial: the word in the left ear, the word in the right ear, and two rhyming distractors.

Visual Unimanual SRT Task: The visual SRT task was loosely modeled on the classic Poffenberger (1912) paradigm. The experiment was administered via the same IBM compatible Pentium 200 computer, interfaced with an ADI Microscan 4V 15" monitor. The stimuli consisted of black squares (subtending 1 degree of arc) presented on a white background, presented at an eccentricity of 8 degrees of arc (to either the left or right side) from the centre of the screen for 30 msec. Viewing distance and eccentricity was held constant by employing a metal chin rest, 50cm from the screen.

At the initiation of each trial, a fixation cross measuring 0.5 degrees of visual angle was presented in the middle of the screen. To prevent participants from anticipating the presentation of the visual stimulus, the time between the presentation of the fixation cross and the lateralized square varied randomly, with the SOA lasting for 1.0 second, 1.5 second, 2.0 seconds, or 2.5 seconds. Within each block of trials, the side of presentation was also randomized. Participants responded to the stimuli by pressing a button on a symmetrical mouse with their index finger.

Four blocks of 32 trials were presented, preceded by 32 practice trials. Within each testing block, 4 trials of each SOA (1.0, 1.5, 2.0, and 2.5 seconds) were presented to each visual field. Participants responded with their left hand for the first block, right hand for the second block, left hand for the third block, and right hand for the fourth block. Viewing distance and eccentricity were held constant by employing a metal chin rest, 50cm from the screen. Participants were given short periods of rest between each block.

Auditory Unimanual SRT Task: The auditory SRT task was administered using the same computer equipment and headphones described in the two sections above. The stimuli consisted of 5 msec 1000Hz square wave pulses presented at 63dB (SPL).

At the initiation of each trial, the message (get ready) appeared on the computer screen to warn participants of the beginning of the next trial. To prevent participants from anticipating the presentation of the auditory stimulus, the time between the presentation of the warning and the lateralized sound varied randomly, with the SOA lasting for 1.0 second, 1.5 second, 2.0 seconds, or 2.5 seconds. Within each block of trials, the side of presentation was also randomized. Participants responded to the stimuli by pressing a button on a symmetrical mouse with their index finger.

Four blocks of 32 trials were presented, preceded by 32 practice trials. Within each testing block, 4 trials of each SOA (1.0, 1.5, 2.0, and 2.5 seconds) were presented to each ear. Participants responded with their right hand for the first block, left hand for the second block, right hand for the third block, and left hand for the fourth block. Participants were given short periods of rest between each block.

Procedure: To enable the recruitment of an equal number of participants from each handedness group and sex, a screening questionnaire was administered to 3000 undergraduate students. During the testing session, each participant first completed 240 trials of the FDWT. Then, they completed the WHQ-R, followed by the WFQ-R. Then, the 160 trials of the visual unimanual SRT task were completed, followed by 160 trials of the auditory unimanual SRT task. The entire testing procedure lasted between 45 minutes and 1 hour.

Scoring and Analysis: The FDWT data were scored using the λ^* log-linear analysis procedure described by Grimshaw et al. (1994).

The visual and auditory SRT tasks were scored after removing all trials containing outlier responses, defined as RTs that were 3 standard deviations above or below the participant's mean RT within that condition (response hand, laterality of the stimulus, and modality of presentation). This resulted in an exclusion of 1.4% of the trials. After these trials were excluded, mean RTs within each condition were calculated.

Results

Dichotic-listening task: As expected, most participants (36/38) exhibited right-ear advantages (REA's) on the FDWT. Participants' $\lambda*$ scores did not vary significantly with handedness, footedness, eyedness, or sex.

Unimanual SRT Task: The SRT tasks were analyzed with a repeated measures ANOVA with the between-subjects variables of sex (male or female) and handedness (left or right) and the within-subjects variables of modality of stimulus (visual or auditory), side of presentation (left or right), and response hand (left or right). There was a significant main effect of stimulus modality, $F(1, 34) = 159.18$, $p <.001$, wherein auditory stimuli elicited faster responses than visual stimuli. As is usually reported in experiments using this paradigm, there was also a significant interaction $F(1,34) = 4.70$, $p = .037$, between response hand and side of presentation. When stimuli were presented to the same side as the responding hand, reaction time were faster than when stimuli were presented contralateral to the responding hand (see Figure 10).

There was also a significant interaction in RTs between the modality of the stimulus and side of presentation, $F(1,34) = 6.08$, $p = .019$. Stimuli presented to the right ear elicited faster responses than stimuli presented to the left ear, but stimuli presented to the RVF elicited slower responses than stimuli presented to the LVF (see Figure 11). The other significant two-way interaction was between response hand and sex, $F(1,34) = 5.14$, $p = .030$. Males generally responded more quickly with their left hand, whereas females generally responded more quickly

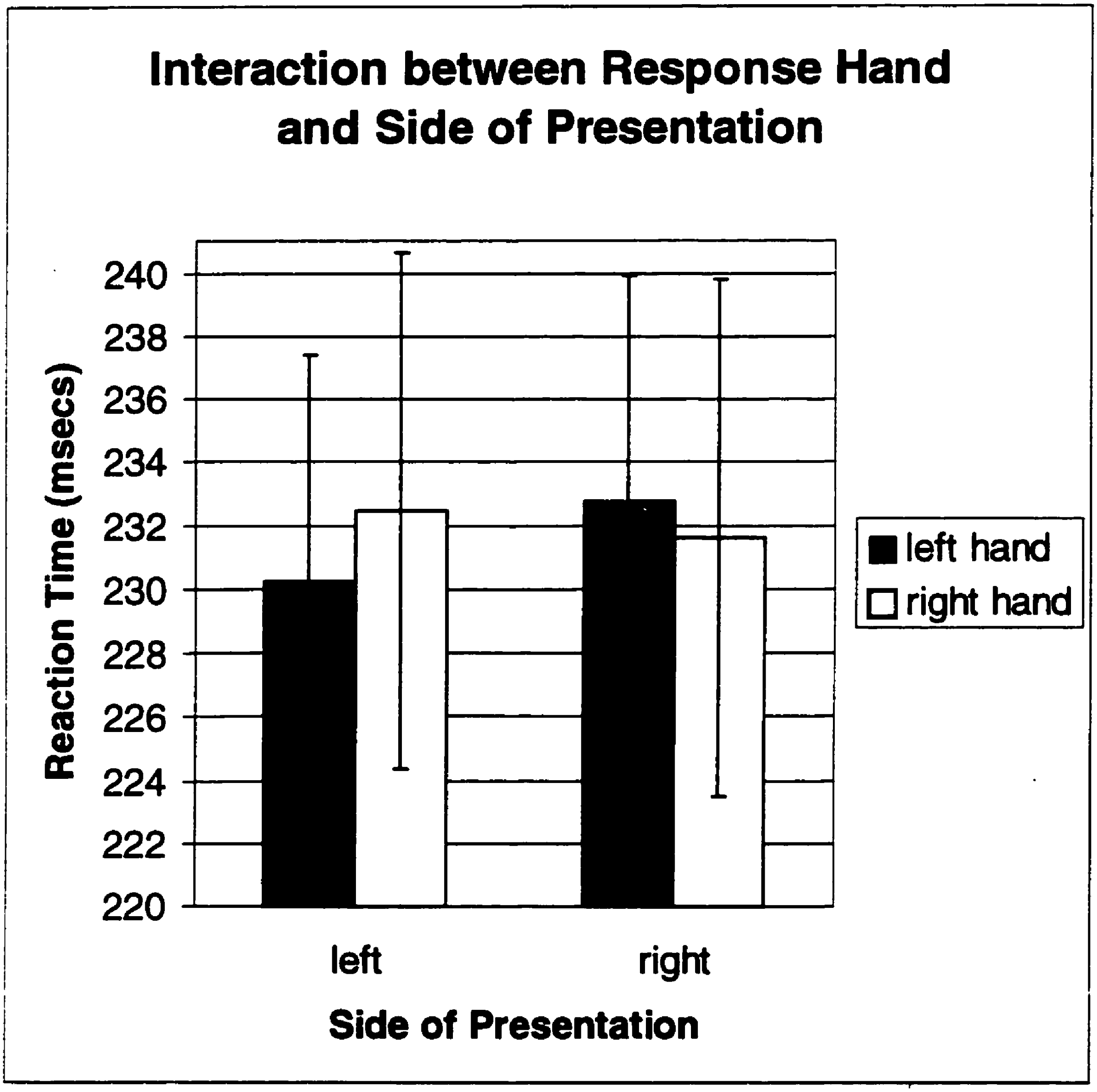

Figure 10. Response hand by side of presentation interaction in reaction time. Values are means +/- SEM.

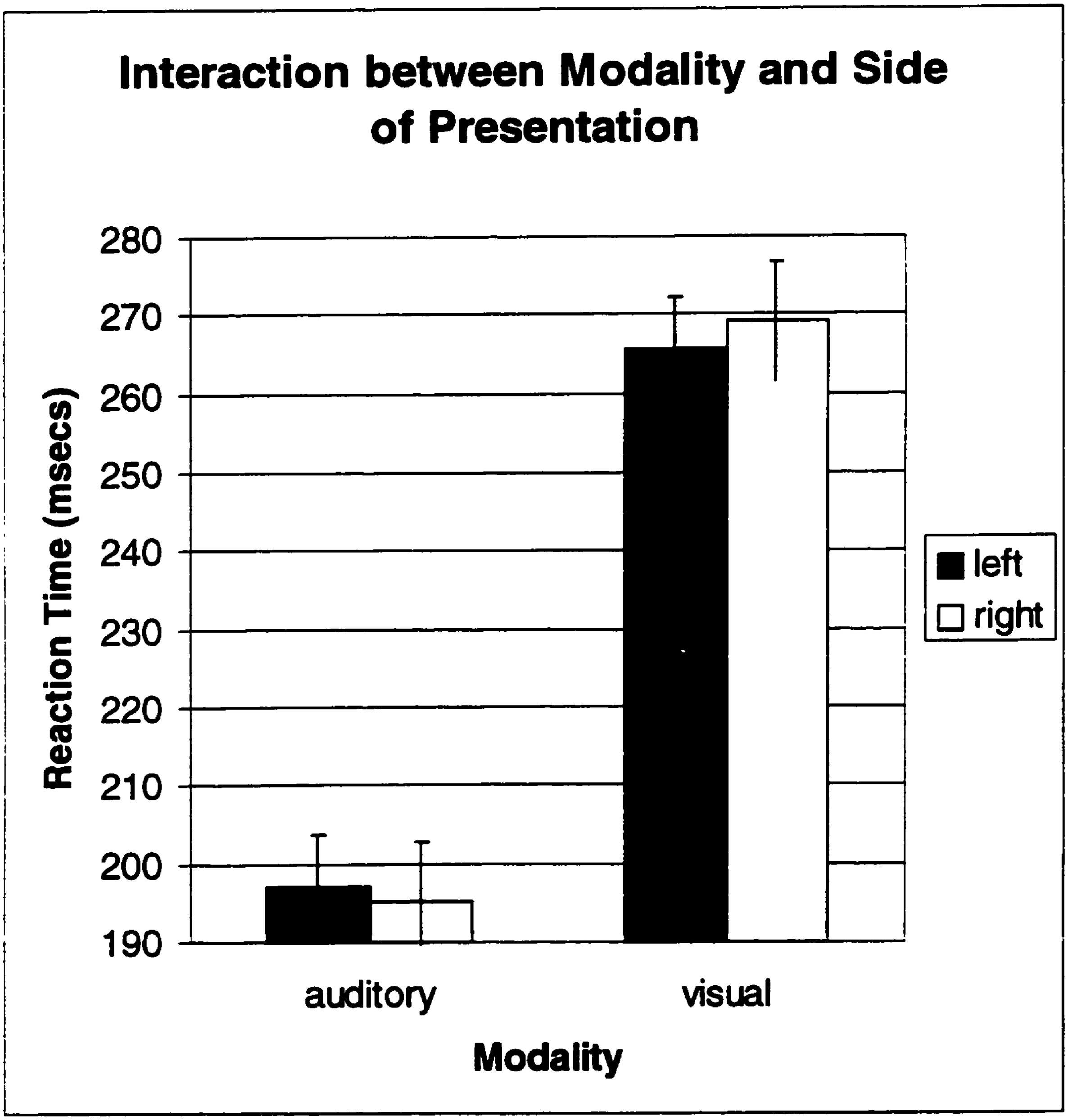

Figure 11. Modality by side of presentation interaction in reaction time. Values are means +/- SEM.

with their right hand (see Figure 12).

Tests of Association Between the two Tasks: It was predicted that the rate of transfer of auditory information from the right to the left hemisphere would be related to the direction and degree of linguistic laterality. To test this prediction, directional CUDs were calculated within each modality, holding response hand constant. CUDs for left hand responses therefore indicated rates of transfer from the left hemisphere to the right, and vice versa. These calculations resulted in four CUDs for each participant: Auditory right→left, auditory left→right, visual right→left, and visual left→right. These CUDs were then correlated with each participant's λ^* scores on the FDWT (see Table 6).

Table 6. Correlations between directional CUDs and FDWT λ^* scores.

CUD	**Auditory L → R**	**Auditory R → L**	**Visual L → R**	**Visual R → L**
r with λ^*	-.183, p = .136	.354, p = .015*	.168, p = .157	.195, p = .120

* significant at the α =.05 level (all tests are 1-tailed)

As predicted, CUDs for auditory information transfer from the right to left hemisphere were significantly positively correlated with increasing REA's/left-hemispheric specialization for language, but no other directional CUDs correlated with linguistic lateralization.

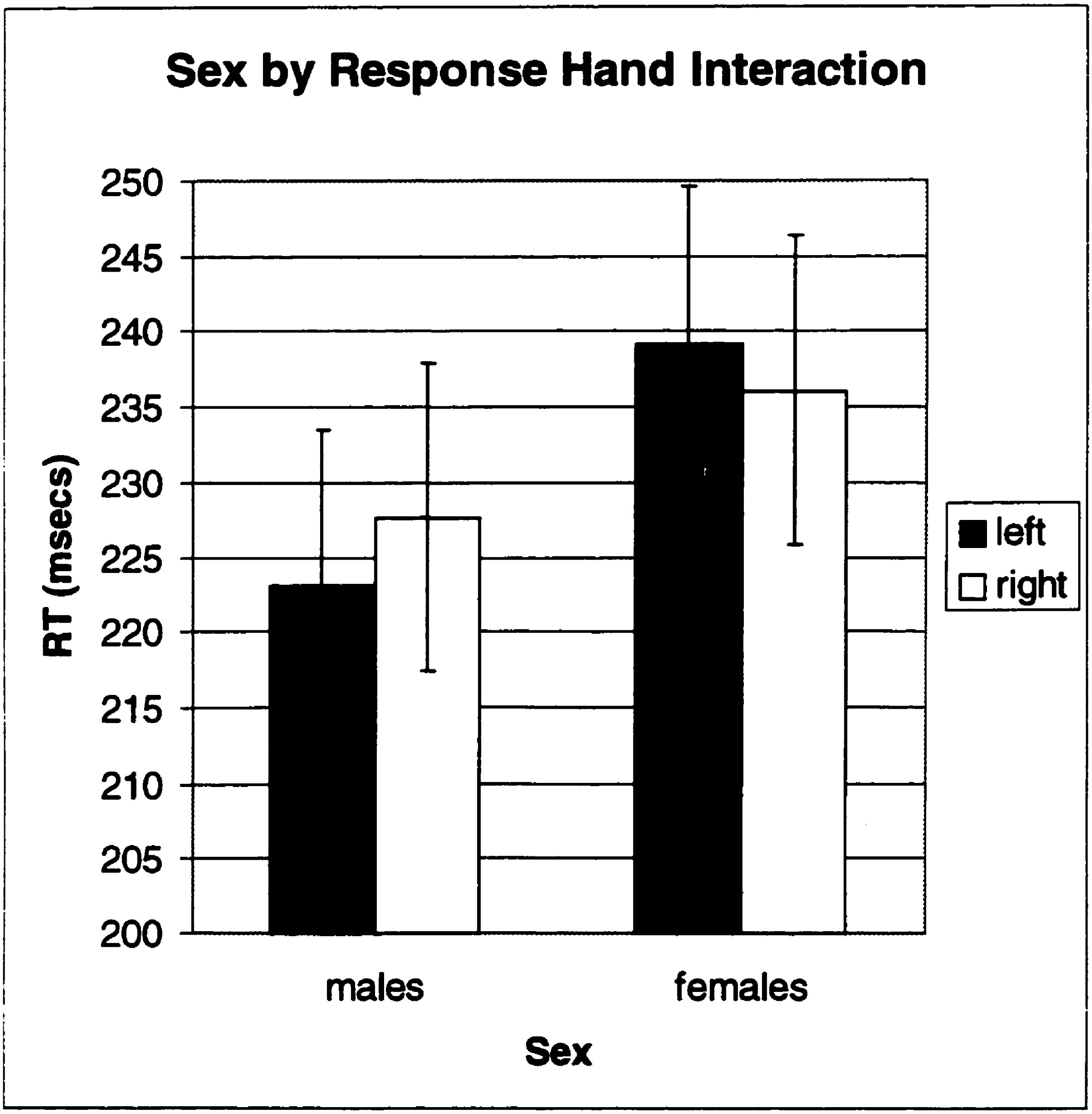

Figure 12. Interaction between sex and response hand in reaction times. Value are means +/- SEM.

Discussion

In addition to replicating the classic Poffenberger (1912) effect (in which reaction times to stimuli ipsilateral to the responding hand were shorter than those for stimuli contralateral to the responding hand) in **both** visual and auditory modalities, the present experiment demonstrated a significantly positive relation between the asymmetries in IHTT and linguistic lateralization.

As predicted, after examining modality and direction of transmission reflected in the CUDs, only the rate of auditory information transfer from the right hemisphere to the left hemisphere correlated significantly with dichotic-listening scores (see Table 6). This result supports the position of Ringo et al. (1994) that hemispheric specialization for time-critical tasks is critically dependent on the length of delay between the hemispheres for the task.

The main effect of stimulus modality, wherein auditory stimuli elicited faster responses than visual stimuli is not an uncommon effect in the literature. For example, the mean RTs for participants performing an auditory gap-detection task were considerably shorter (between 400 and 625 msec on average) than the latencies of participants performing a similar task in the visual modality (for which RTs were between 600-700 msec) (Brown & Nicholls, 1997; Nicholls, 1994b).

There was also a two-way interaction in RT between stimulus modality and side of presentation. Participants responded more quickly to auditory stimuli presented to the right ear, and to visual stimuli presented to the left visual field. This result was not surprising, because normals are usually superior at identifying temporal patterns in auditory stimuli presented to the right ear (Brown & Nicholls, 1997; Mills & Rollman, 1979; Mills & Rollman, 1980; Tallal et al., 1993), but are also better at visuo-spatial tasks presented to the LVF-RH, particularly if the stimuli are of relatively high spatial frequency (Christman, Kitterle, & Hellige, 1991; Kitterle, Hellige, & Christman, 1992; Proverbio, Zani, & Avella, 1997).

The other significant two-way interaction was between response hand and sex, wherein males generally responded more quickly with their left hand, but females generally responded more quickly with their right hand. One possible explanation for this effect could be related to males generally being more experienced with playing video games. Most video-game controllers have buttons or joysticks on the right side for "directional control" during the game and buttons on the left side of the controller which typically must be pressed repeatedly and rapidly. Such an arrangement allows for the right hand to control the more "fine motor control" tasks, whereas the left hand is more involved in rapidly repeating actions. Because the males probably had more practice with these controllers, this could have predisposed them to respond more quickly during a simple signal-detection task with their left hand.

Given that half of the females were right-handed and half were left-handed, why would they as a group respond more quickly with their right hand? Perhaps this too is the result of a practice effect, but not one related to video games. Female left-handers are far more likely than the right-handers to regularly use their non-dominant hand for controlling a computer mouse (a modified computer mouse was used to collect the reaction-time data in this experiment). Therefore, the group of participants might have had more practice pressing the buttons on a mouse using their right hand than using their left.

The central issue addressed in this experiment is the relation between IHTT/CUD and linguistic lateralization. As predicted, only the rate of information transfer from the right hemisphere to the left hemisphere correlated significantly with dichotic-listening scores (see Table 6). This result supports the position of Ringo (1994) that hemispheric specialization for time-critical tasks is dependent on the length of delay between the hemispheres for the task.

Prediction 3: Linguistic lateralization should vary with throwing hand

Calvin (1983) claims that the evolutionary pressure favouring encephalization was driven by adaptive gains from accurate throwing. "Enhanced throwing skill could have produced a strong selection pressure for any evolutionary trends that provided additional timing neurons. This enhanced timing circuitry may have developed secondary uses for language reception and production." (Calvin, 1983, pg. 121). Given his claim that linguistic processing relies on some of the same lateralized neural architecture which subserves unimanual throwing, one would predict that linguistic lateralization should vary with preferred hand for throwing.

Experiment 4

A tremendous amount of experimental work has attempted to identify reliable behavioural predictors of cerebral lateralization. When attempting to predict language laterality, preferred handedness has been the most popular predictor, but there is a general consensus that hand preference alone is a relatively weak predictor (Day & MacNeilage, 1996; Elias & Bryden, 1998; Lake & Bryden, 1976; Lee, Loring, Newell, & Meador, 1994; Rasmussen & Milner, 1977; Searleman, 1980; Strauss, 1986; Subiriana, 1969). Levy and Reid (Levy, 1984a; Levy, 1984b; 1976; 1978) claimed that taking writing hand posture into account could increase the predictive power of handedness, but most subsequent work has failed to replicate this effect (Peters & McGrory, 1987; Strauss, Wada, & Kosaka, 1984; Volpe, Sidtis, & Gazzaniga, 1981; but cf. Duckett, Gibson, & Salama, 1993) or taken issue with the methodology employed by Levy and Reid (Buchtel & Rueckert, 1984).

Our group, and others, have recently uncovered several complexities involving the interrelations among handedness, footedness, eyedness and throwing arm, which suggest that an understanding of the complete 'laterality phenotype' of an individual is important when attempting to understand individual differences in brain lateralization. It has been shown that writing hand and throwing hand have different distributions, with left-writing right-throwers being relatively common whereas right-writing left-throwers being quite rare, comprising less than 2% of the population (Coren, Augustyn, & Peters, 1994; Gilbert & Wysocki, 1992; Peters & Pang, 1992). These two handedness indicators (writing and throwing) are independent predictors of eye dominance (McManus, Porac, Bryden, & Boucher, 1996). Furthermore, although we have information on the prevalence of left-footedness (Gentry & Gabbard, 1995; Porac & Coren, 1981; Reiss & Reiss, 1997), we know very little about how footedness relates to these other variables. Foot dominance has recently been shown to be a better predictor of language lateralization (Day & MacNeilage, 1996; Elias & Bryden, 1998; Searleman, 1980; Watson, Pusakulich, Hermann, Ward, & Wyler, 1993) and of the perception of the emotional content of language (Elias et al., 1998a) than either writing hand or general handedness.

Studies that attempt to compare the degree to which various lateral preferences vary with cerebral lateralization are complicated by a number of factors. Perhaps most importantly, most people (particularly right-handers) are relatively consistent in their lateral preferences. Most right-handers (95%) are also right-footed (Coren, Augustyn, & Peters, 1993; Day & MacNeilage, 1996; Peters, 1995; Peters & Pang, 1992) and right-eyed (66%) (Bourassa, Bryden, & McManus, 1996). Therefore, when a right-handed individual demonstrates left hemispheric dominance for language, how can one determine whether that is related to hand dominance, foot dominance, or eye dominance? An experimental strategy that can help solve this problem is to selectively recruit and test individuals with unusual combinations of lateral preferences.

For example, Day and MacNeilage (1996) expanded on the findings of Searleman (1980) and Strauss (1986) by selectively recruiting participants with both "crossed" and "uncrossed" preferences for hand and foot. Most people have uncrossed lateral preferences in that they prefer the foot ipsilateral to their preferred hand. However, between 1.5% and 6% of right-handed adults appear to prefer their left foot. The prevalence of crossed lateral preference is higher in left-handed individuals, wherein between 20% and 50% prefer their right foot (Augustyn & Peters, 1986; Brown & Taylor, 1988; Chapman, Chapman, & Allen, 1987; Coren et al., 1993; Day & MacNeilage, 1996; MacNeilage, 1991; Peters & Durding, 1979). Unlike Searleman (Searleman, 1980) and Strauss (Strauss, 1986), Day and MacNeilage (Day & MacNeilage, 1996) found that degree of ear advantage varied significantly with both handedness and footedness. However, when the data were analyzed only in terms of direction of ear advantage, footedness was the only significant predictor.

This result is complicated by a number of other reports, which link throwing hand, preferred eye, and writing hand to the lateralization of higher functions. Further, those individuals with "crossed" lateral preferences (for example, left-handed and right-footed) tend to prefer throwing with the hand contralateral to their writing hand (Peters, 1995; Peters & Durding, 1979). Therefore, it may not be the footedness of these participants that is predicting patterns of cerebral lateralization, but their preferred throwing hand.

The present study was designed to test Calvin's (1983) theory that linguistic laterality relies on the same lateralized neural architecture that subserves throwing. If Calvin (1983) is correct, this could account for some of the discrepancies in the literature. Assessment of one's preferred hand for throwing is often included in handedness inventories (Bryden, 1977; Coren et al., 1993; Oldfield, 1971; Steenhuis & Bryden, 1989), but studies rarely examine throwing hand independently of one's preferred hand writing. Further, there do not appear to be any published studies where participants were selectively recruited based on unusual combinations of lateral preferences (such as those who write with their right hand and throw with their left) and subsequently administered a test of language lateralization. In order to test Calvin's (1983) hypothesis, individuals with unusual "lateral preference phenotypes" were recruited (see Table 7 for details on the lateral preferences of the sample) and administered tests of linguistic and prosodic lateralization.

Method

Participants: 47 undergraduate students participated in this experiment for six dollars remuneration or course credit. Participants were selectively recruited to include individuals with unusual laterality phenotypes, such as those who prefer to write with their right hand but throw with their left (see Table 7). To accomplish this selection, a small screening questionnaire was administered to approximately 3500 undergraduates, asking which hand they preferred for writing, which hand they preferred for throwing, and which foot they preferred for kicking. I attempted to include data from every possible combination of these three factors.

All participants were students at the University of Waterloo at the time of the experiment.

Materials: All participants completed two questionnaires: The WHQ-R and the WFQ-R (see Appendices U and V).

Linguistic Dichotic Task: Linguistic lateralization was assessed using the 240 trials of the FDWT (details about the test were provided in the method section of Experiment #1). The tape was played on a Sony Professional Walkman (model WM-D6C) through JVC (model HA-D500) earphones with circumaural cushions. During the testing, participants indicated which word they heard by circling it from among four possibilities presented in pseudo-random order on an answer sheet: the word in the left ear, the word in the right ear, and two rhyming distractors.

Prosodic Dichotic Task: Lateralization of emotional perception was assessed using the Emotional Words Test (EWT) described by Bryden and MacRae (1988). The test consists of a stimulus set of the words "power", "bower", "dower", and "tower" spoken by a male speaker in happy, sad, angry, and neutral emotional tones, producing a total of 16 different tokens. When appropriate tokens had been selected, each token was digitized on a modified PDP-11/40 computer, edited to a common length of 500ms, equalized in intensity, and stored. Each item was then paired dichotically with every other item that differed in both affective tone and verbal content, to produce 144 different stimulus pairs with aligned onset times. These pairs were recorded on an audio cassette in a random sequence for presentation through earphones at an average intensity of 75dB. Each stimulus pair was separated by a 3 s intertrial interval, with a 10 s break after each block of 18 trials. The stimuli were played on the same apparatus described above and test trials were preceded by 16 practice trials in which each affective and phonetic stimulus was paired once and presented binaurally. During the testing, participants indicated whether or not they heard the emotional target (a word spoken in an "angry" tone) by circling "Yes" or "No" on a sheet of paper.

Procedure: Every participant was given all tests in one sitting. First, each participant completed the WHQ-R, followed by the WFQ-R. Then, the 240 trial FDWT was completed. After completing the FDWT, subjects completed the EWT. This ordering of the dichotic tasks was chosen because the EWT is clearly dichotic to the participant (because both the words and prosody differ between the ears on a given trial), but most participants cannot detect the dichotic nature of the FDWT. The entire testing procedure took approximately 45 minutes.

Scoring and Analysis: All lateral preference questionnaire data were scored as follows: Responses of (a) left-always, (b) left-usually, (c) equal, (d) right-usually, (e) right-always were scored on a scale from -2 to 2. The FDWT data were scored using the λ^* procedure described by Grimshaw et al. (1994), and the EWT data were converted to λ values (Bryden & Sprott, 1981).

Results

Linguistic Dichotic-listening task: The data from the linguistic dichotic-listening task (FDWT) were analyzed with step-wise multiple regression, with the dependent variable of subjects' λ^* lambda scores and the independent variables of hand preference for writing, hand preference for throwing, foot preference, eyedness, and sex. There was a significant effect of the interaction between hand preference for writing and hand preference for throwing, $B = .325$, $t = 2.353$, $p = .023$, but no other variables or interactions accounted for a significant amount of variance in linguistic lateralization. This interaction was caused by a significant difference ($t(19) = 2.036$, $p = .023$) in lambda scores between individuals who preferred to write and throw with their right hand (demonstrating strong REA's on the task) and those who preferred to write with their right hand but throw with their left (demonstrating weaker REA's on average). Individuals who preferred to write with their left hand did not demonstrate significantly different ($t(26) = .165$, $p = .870$) λ^* scores between the two "throwing hand" groups (see Figure 13).

Prosodic Dichotic-listening task: The data from the prosodic dichotic-listening task (EWT) were also analyzed with step-wise multiple regression, with the dependent variable of participants' λ lambda scores and the independent variables of hand preference for writing, hand preference for throwing, foot preference for kicking, eyedness, and sex. There was a significant effect of the interaction between eyedness and sex, $B = .322$, $t = 2.31$, $p = .025$, but no other variables or interactions accounted for a significant amount of variance in emotional lateralization. The interaction was caused by a significant difference ($t(21) = 3.51$, $p = .002$)

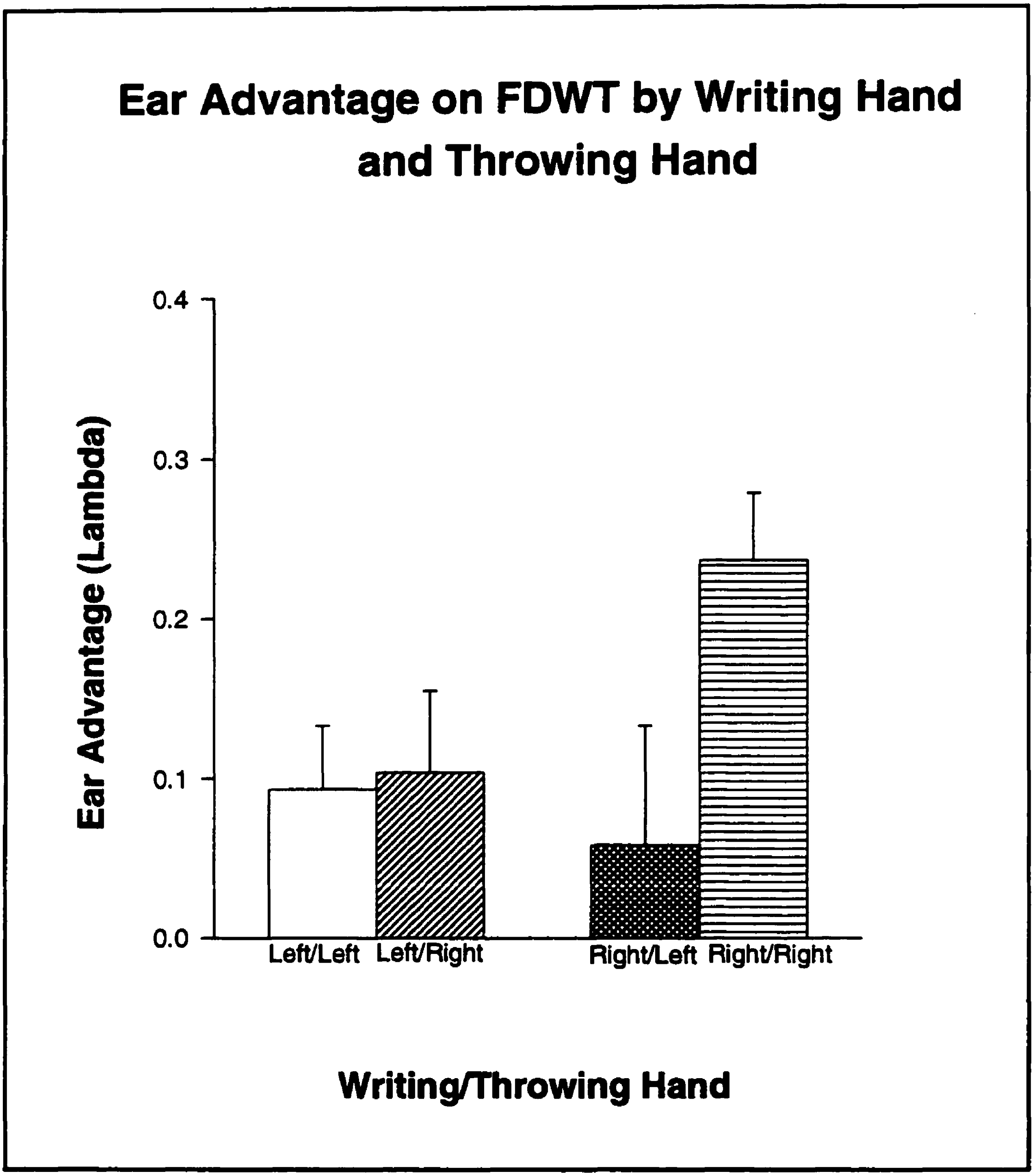

Figure 13. λ* ear advantage scores of the four writing hand/throwing hand groups.

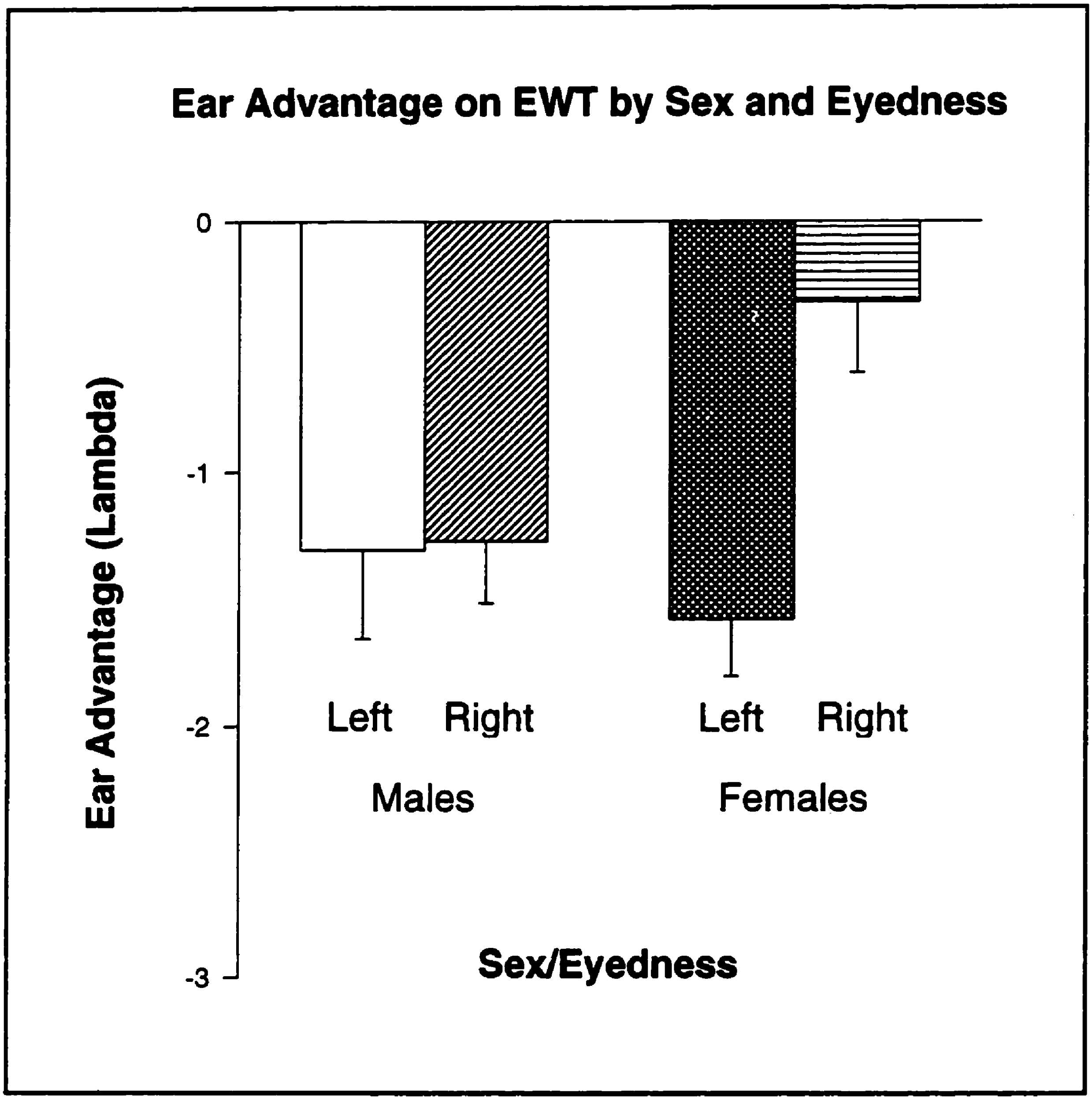

Figure 14. Lambda scores on the EWT for each sex/eyedness group.

between λ scores of females with left eyedness as compared to those with right eyedness. Males did not demonstrate any significant difference (*t*(23) = .089, *p* = .930) between the eyedness groups (see Figure 14).

Table 7: Classification of Participants by Writing Hand, Throwing Hand, and Foot Preference

	Left-Writers		Right-Writers	
Foot Preference	Throwing Hand			
	Left	Right	Left	Right
Left	13	0	2	5
Right	6	9	3	9

Discussion

The present study found some tentative evidence in support of Calvin's (1983) "throwing hypothesis". Preferred hand for throwing was a significant predictor of ear-advantage scores on the FDWT for individuals who prefer to write with their right hand, but no such effect was present in those individuals who preferred to write with their left hand. Individuals who write with their right hand and throw with their left are extremely rare, comprising less than 2% of the general population (Coren et al., 1994; Gilbert & Wysocki, 1992; Peters, 1995). However, as many as 40% of left-handers appear to prefer to throw with their right hand (Coren et al., 1994; Gilbert & Wysocki, 1992; Peters, 1995; Peters & Pang, 1992). Therefore, the throwing hand X writing hand interaction observed in the present study was largely driven by individuals with very rare laterality phenotypes, and generalizing these results to the general population might not be appropriate.

Curiously, there was no evidence of preferred foot significantly predicting ear advantages on a linguistic task in this sample of individuals with rare laterality phenotypes, despite a number of recent reports that footedness does predict linguistic laterality (Day & MacNeilage, 1996; Elias & Bryden, 1998; Searleman, 1980; Watson et al., 1993). This study's failure to replicate this result could be partially attributable to the nature of the sample, composed almost exclusively of individuals with rare combinations of lateral preferences.

There was also no evidence in the present study that preferred hand for throwing or preferred foot predict prosodic lateralization, contrary to a recent report that laterality of emotional perception varies with footedness (Elias et al., 1998a). Instead, there was a significant effect of the interaction between eyedness and sex, in which there was no difference in the λ scores of the male eyedness groups, but right-eyed females exhibited weaker LEAs than all other groups tested. This result is particularly puzzling because most females are right-eyed, and females generally do not exhibit weaker LEAs on the EWT than those exhibited by males (Bryden & MacRae, 1988; Bulman-Fleming & Bryden, 1994; Elias et al., 1998a). However, the participants in this study were not administered the EWT in order to test Calvin's (1983) throwing hypothesis. Instead, these participants were given tests of both linguistic and prosodic lateralization to test a prediction of Ringo's (1994) ICD theory, which is reviewed in the next section.

Prediction 4: Complementarity of cerebral function should not be causal in nature

According to Ringo et al.'s (1994) ICD theory, the lateralization of tasks that require very fine temporal discrimination (such as verbal functions) and the lateralization of tasks requiring much less temporal specificity (such as spatial functions) should not be causally related. Instead, "slow communication causes functional neuronal networks to form mainly intrahemispherically...Our hypothesis does not indicate why, at a population level, the right hemisphere usually performs best in one type of task and the left in another... It is interesting to note that our hypothesis is compatible with the challenging finding of Bryden and colleagues (Bryden, 1986) that there appears to be statistical independence in the hemispheric distribution of different lateralized functions." (Ringo et al., 1994, p. 336). Therefore, the complementarity of verbal and non-verbal functions should **not** be causally related.

Experiment 4 (revisited)

Complementarity of cerebral function (the notion that each hemisphere subserves complementary functions) is the prototypical pattern of brain organization. The idea that the right hemisphere is specialized to perform nonverbal processing because the left-hemisphere preferentially deals with language processing is referred to as 'causal complementarity' (Bryden, Hecaen, & DeAgostini, 1983). Despite the lack of empirical evidence that complementarity is causal in nature, the assumption of causal complementarity underlies some models of the development of cerebral laterality (Corballis & Morgan, 1978; MacNeilage, 1991).

Bryden articulated two alternative scenarios in addition to causal complementarity (Bryden, 1990; Bulman-Fleming & Bryden, 1997). His 'statistical-complementarity' model is one in which the processes by which lateralization of various functions occur are independent of one other, and his 'bias' model posits underlying anatomical asymmetries as heavily influencing behavioural asymmetries. Each of these models predicts a different correlation between tasks tapping right- and left-hemisphere functions. The causal model predicts a negative correlation, the statistical model a lack of correlation, and the bias model, a positive correlation.

There have been relatively few systematic investigations into the nature of complementary hemispheric specialization (Bryden, 1986; Bryden, 1990; Bryden et al., 1983; Bulman-Fleming & Bryden, 1997). This might in part be due to the fact that most investigations of hemispheric asymmetry involve tests of either left- or right-hemispheric dominance, but individuals are rarely given tests of <u>both</u> left- and right-hemispherically dominated functions. Fortunately, there are some exceptions to this trend. (Alter, Rein, & Toro, 1989; Bryden, 1986; Bryden et al., 1983; Bulman-Fleming & Bryden, 1994; Kim & Levine, 1991; Ley & Bryden, 1982; McGlone & Davidson, 1973; Murray, 1985; Segalowitz & Plantery, 1985; Sidtis, 1982; Vrbancic, 1989). From these studies. It appears as though 25-50% of the population exhibit causal complementarity. The remainder of the population might have cerebral specialization determined randomly (Bulman-Fleming & Bryden, 1997), which is compatible with the ICD theory of cerebral lateralization proposed by Ringo et al. (Ringo et al., 1994). According to the ICD, laterality per se should be advantageous, but the direction of the lateral dominance is irrelevant.

I report here the testing of 47 individuals selectively recruited because of their atypical laterality phenotypes, because recent work has suggested the importance of preferences other than writing hand to patterns of hemispheric specialization (Day & MacNeilage, 1996; Elias & Bryden, 1998; Elias et al., 1998a; Searleman, 1980; Watson et al., 1993)

Method

The same sample and corresponding data presented in the previous experimental section was included in the analyses below. Because tests of what is normally a left-hemisphere dominated function (linguistic processing) and right-hemispheric function (prosodic/emotional perception) were administered to the same individuals, this data set allows further investigation into the nature of complementary hemispheric specialization.

Results

As expected, most participants (39/47 = 83%) exhibited right-ear advantages (REA's) on the linguistic dichotic task, and left-ear advantages (LEA's) (38/47 = 81%) on the prosodic dichotic task. Two participants did not exhibit any ear advantage on the EWT (for subsequent analyses, one of these subjects was added to the REA group and one was added to the LEA group). There was a significant positive correlation between lambda scores on the FDWT and the EWT (*r* =.308, *p*=.033). Most subjects (33/47 = 70%) exhibited the typical pattern of left-hemispheric linguistic dominance and right-hemispheric prosodic dominance, but none of the

Individuals' Laterality Scores on FDWT versus EWT

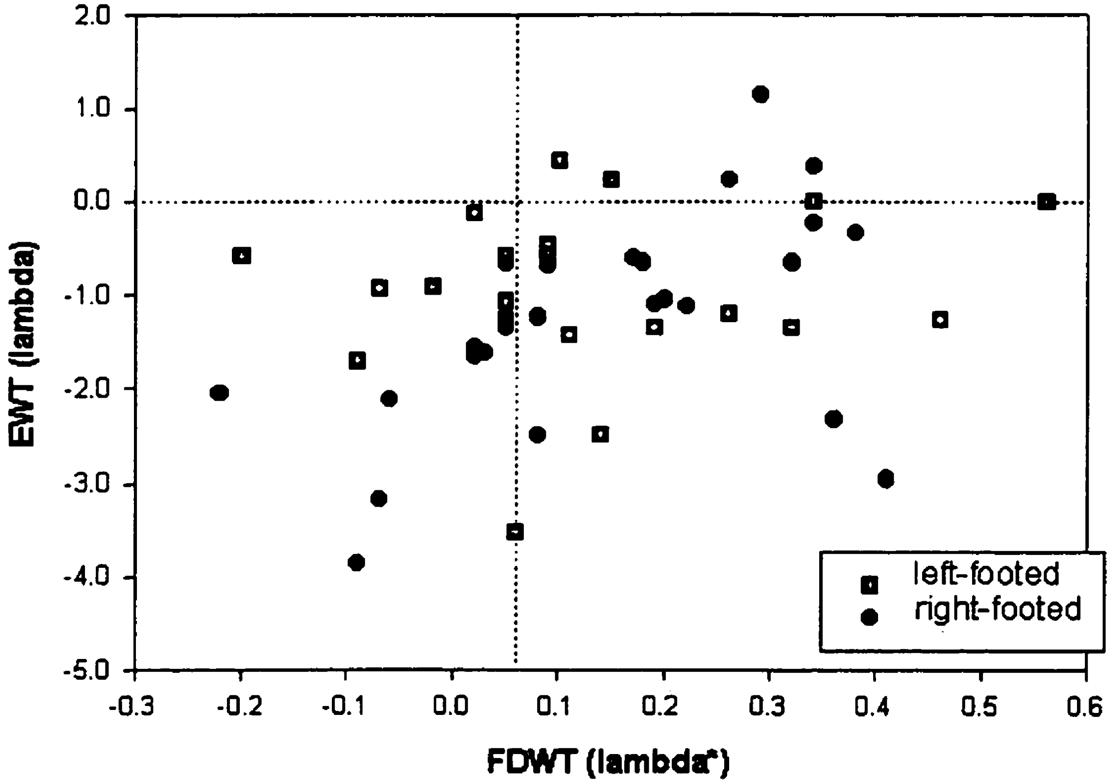

Figure 15. Individuals' lambda* scores on the linguistic dichotic-listening task (FDWT) versus lambda scores on the prosodic task (EWT). Positive values are indicative of REA's.

subjects exhibited the reverse pattern of hemispheric dominance. Instead, 9/47 (19%) of the subjects exhibited right-hemisphere dominance for both tasks, whereas 5/47 (11%) exhibited left-hemisphere dominance for both tasks.

To investigate whether an individual's pattern of linguistic and prosodic lateralization was related to his or her lateral preferences or sex, I compared the correlations between the FDWT and EWT lambdas for each sex, handedness (writing and throwing), footedness, and eyedness group. The correlations were generally very similar between the respective groups (ranging between $r = .246$ and $r = .327$), except for the two footedness groups. Lambda scores correlated strongly for right-footed participants, $r = .517$, $p = .008$, but not for left-footed participants, $r = .133$, $p = .564$, and the difference between the two correlations was highly significant by the Fisher r to z transformation ($z = 4.29$, $p < .001$).

Discussion

In the present experiment there was a significant positive correlation between laterality scores on the linguistic and the prosodic dichotic-listening tasks. The majority of the participants exhibited the "normal" cerebral dominance pattern (left-hemispheric linguistic dominance and right-hemispheric prosodic dominance), but no participants exhibited the opposite pattern of cerebral dominance. Instead, subjects with "atypical" patterns of cerebral dominance appeared to exhibit a bias to process both types of information in either one hemisphere or the other.

The positive association between lateralization of linguistic and prosodic perception varied with the lateral preferences of the subjects. Right-footed participants exhibited a significant positive correlation between the dichotic tasks and left-footed participants did not. The finding that preferred foot may be a factor that differentiates patterns of cerebral lateralization is compatible with other recent studies that have shown footedness to be a better predictor of both the lateralization of linguistic and of affective aspects of language processing (Elias & Bryden, 1998; Elias et al., 1998).

General Discussion

This series of experiments was designed to investigate the possibility that hemispheric asymmetries in linguistic processing are related to much "lower-level" temporal asymmetries, or possibly even caused by the need for very fine temporal processing. The first two experiments are qualitatively different than those that follow in that they were designed to assess the abilities of each hemisphere separately. Very simple temporal stimuli (auditory or visual) were presented unilaterally, and in both cases the left hemisphere was usually superior at performing low-level temporal processing, as well as the linguistic processing. Instead of assessing processing within a particular hemisphere, the third experiment related the speed with which information could be transferred from one hemisphere to the other to the degree to which an individual appeared to demonstrate linguistic lateralization. As predicted, the longer that it took auditory information to pass from the right hemisphere to the left, the greater the degree of linguistic lateralization. In search of what might have provided the evolutionary pressure for superior temporal processing, Calvin's (1983) conjecture that gains in throwing accuracy led to lateralization of function (and subsequent linguistic skills) was tested with individuals with unusual combinations of lateral preferences. The prediction that preferred hand for throwing (but not preferred hand for writing) would be associated with linguistic lateralization, was only supported by individuals who normally write with their right hand. The prediction that complementarity of functional asymmetries should not be causal in nature was also supported. Instead of finding the negative association between what are normally right and left hemispherically dominated tasks (as would be predicted by the causal complementarity model), there was a weak positive association.

Given the results of Experiments 1 and 2, it might seem ambitious to claim that linguistic asymmetries and low-level temporal asymmetries have a common origin. In Experiment 1, the correlation between laterality indices on the two tasks was only $\underline{r} = .306$ before disattenuation and $\underline{r} = .486$ after disattenuation. Similarly, in Experiment 2, the correlation between laterality indices on the temporal task and the linguistic task was $\underline{r} = .307$ before disattenuation and $\underline{r} = .467$ after disattenuation. Could these temporal tasks and linguistic task be measuring a common process?

The low correlations between the temporal tasks and the linguistic task become much more impressive when one compares them to the correlations one typically obtains when comparing two different tests of linguistic laterality. Despite relatively impressive test-retest reliability (between 0.75 and 0.88 according to Jäncke et al., 1992) **different** linguistic dichotic-listening tests that purport to measure the extent to which language is lateralized usually do not correlate significantly, and sometimes the correlations are even negative. From my review of the literature, the **highest** correlation between two dichotic-listening tests was $\underline{r} = 0.47$, reported by Kim and Levine (1992).

Cross-modal comparisons (such as the comparison made in Experiment 1 between visual temporal asymmetries on the IT task and linguistic asymmetries on the FDWT) typically yield even lower correlations. Despite the fact that these tests are meant to tap similar (if not identical) processes, many investigators have failed to find any significant positive correlation between visual and auditory measures of linguistic lateralization (Bryden, 1965; Bryden, 1973; Fennell et al., 1977a; Fennell et al., 1977b; Kim & Levine, 1992; Moscovitch, 1979). From my review of the literature, the **highest** correlation between a visual and auditory test of linguistic laterality was $r = .39$, reported by Hines and Satz (1974). Given these trends in the literature, the cross-modal correlation of $r = .306$ (before disattenuation) in Experiment 1 and the within-modal correlation of $r = .307$ in Experiment 2 become more impressive.

Experiment 3 investigated the relation between the length of IHTT and linguistic lateralization. Although the Poffenberger (1912) paradigm is almost exclusively administered in the visual modality, both visual and auditory versions of the task were presented, concurrent with a dichotic-listening test of linguistic laterality. As predicted, only the rate of auditory information transfer from the right hemisphere to the left hemisphere correlated significantly with dichotic-listening scores, supporting the position of Ringo (1994) that hemispheric specialization for time-critical tasks is dependent on the length of delay between the hemispheres for the task.

The fourth experiment sought to test two theoretically independent predictions through the administration of both linguistic and prosodic tests of lateralization to individuals with unusual combinations of lateral preferences. First, it served as a test of Calvin's (1983) "throwing hypothesis". Preferred hand for throwing was a significant predictor of ear-advantage scores on the FDWT for individuals who prefer to write with their right hand, but no such effect was present in those individuals who preferred to write with their left hand.

Second, Experiment 4 served as a test of Ringo's conjecture that complementarity of hemispheric specialization should *not* be causal in nature. The causal complementarity model posits that one hemisphere is specialized for processing a particular type of stimuli (prosodic stimuli for example) *because* the other hemisphere is specialized for processing different stimuli (such as linguistic stimuli). Such a model then predicts that when one gives the same individuals tests of right- and left-hemispheric function concurrently, laterality indices on the two tasks should be negatively correlated. In Experiment 4, there was a significant positive correlation between laterality scores on the linguistic and the prosodic dichotic-listening tasks. The majority of the participants exhibited the "normal" cerebral-dominance pattern (left-hemispheric linguistic dominance and right-hemispheric prosodic dominance), but no participants exhibited the opposite pattern of cerebral dominance. Instead, subjects with "atypical" patterns of cerebral dominance appeared to exhibit a bias to process both types of information in either one hemisphere or the other.

Given these results, can one conclude that hemispheric specialization for linguistic processing is caused by low-level temporal asymmetries, and that the evolutionary pressure favouring lateralization of function was caused by gains in temporal processing? No. Although some of this recent evidence points in that direction, there is clearly a tremendous amount of variance in the laterality literature that is unaccounted for by the temporal theories proposed by Mills and Rollman (1979), Calvin (1983), Tallal et al. (1993), and Ringo et al. (1994). Consider all the criteria that a successful theory of the cause of functional cerebral asymmetry must satisfy (according to McManus, 1985 and Laland et al., 1995):

(1) The ability to account for parent-child concordance rates for handedness

(2) The ability to account for the low handedness concordance rate between MZ twins

(3) The ability to account for differences in the prevalence of left-handedness between different cultural/genetic populations and generations

(4) Compatibility with other known mechanisms of inherited asymmetries

(5) Biological integrity (consistency)

(6) The ability to explain the finding that all human societies are (and presumably have been) predominantly right-handed

(7) The ability to "explain how the processes that underlie handedness could have come into existence" (Laland et al., 1995, p. 435)

(8) The well known sex differences in the laterality literature, such as the finding that males are more likely to be left-handed than females

(9) The associations between left-handedness and various special populations

The position that cerebral asymmetries are rooted in temporal asymmetries (particularly the conjecture provided by Ringo et al., 1994) satisfies the 7th criterion particularly well, describing what evolutionary advantage could be provided by lateralizing neural architecture that must perform fine temporal computations. An argument could also be made for Ringo et al.'s (1994) theory satisfying the 4th and 5th criteria, but none of the temporal theories provides any useful insights regarding either the inheritance of patterns of cerebral asymmetry, the cultural variation in cerebral asymmetries, the question of why most people are <u>right</u>-handed (the theory describes why handedness would be adaptive, but not the consistency in its direction), the existence of sex differences in functional lateralization, or the associations between left handedness and various populations from architects to albinos.

Given these shortcomings, should we reject the notion that gains in temporal processing capacity led to lateralization of higher functions such as linguistic processing? No. It is entirely possible that the theories of the cause of hemispheric specialization reviewed in the introductory section of this document are simply addressing different levels of explanation. Consider the study of genetics. Even if one can successfully isolate the genes responsible for the growth of feathers in birds, one has learned nothing about why feathers are adaptive. Lateralization of function appears to be influenced by genetics, by the (pre- and post-natal) environment, and by the evolutionary forces that have been selecting for it over the course of centuries. Gains in proficiency for temporal processing appears to be one of those forces.

Appendix A: Experiment 1: Individual Participant Data for Accuracy

								Percent Correct					
				left gap					right gap				
ID	Sex	Hand/Foot	FDWT	L-40ms	L-60ms	L-80ms	L-100ms	L-120ms	R-40ms	R-60ms	R-80ms	R-100ms	R-120ms
1	F	L	0.07	0.71	0.82	0.86	1.00	1.00	0.86	0.68	0.92	0.86	1.00
2	M	L	0.02	0.64	0.75	0.79	0.93	0.86	0.64	0.71	0.81	0.79	0.71
3	F	L	-0.13	0.50	0.79	0.79	0.64	0.71	0.50	0.54	0.77	0.71	0.79
4	F	L	0.13	0.64	0.36	0.64	0.71	0.64	0.29	0.50	0.50	0.21	0.43
5	F	L	0.24	0.64	0.71	0.89	0.93	0.93	0.86	0.96	1.00	1.00	1.00
6	F	L	0.30	0.64	0.64	0.79	0.93	0.79	0.79	0.86	0.85	1.00	0.93
7	M	L	-0.04	1.00	0.96	0.89	0.79	1.00	0.86	1.00	0.93	1.00	0.93
8	F	L	0.13	0.64	0.50	0.43	0.57	0.50	0.71	0.64	0.66	0.79	0.79
9	F	R	-0.07	0.43	0.46	0.54	0.36	0.79	0.64	0.68	0.48	0.64	0.79
10	M	L	-0.05	0.57	0.71	0.86	1.00	0.93	0.93	0.86	1.00	1.00	1.00
11	F	L	0.07	0.71	0.82	0.86	0.79	0.71	0.71	0.75	0.82	0.93	1.00
12	F	R	0.03	0.43	0.61	0.39	0.71	0.71	0.36	0.50	0.45	0.50	0.50
13	F	L	-0.28	0.64	0.54	0.71	0.64	0.71	0.50	0.61	0.54	0.57	0.50
14	F	R	0.45	0.57	0.82	0.93	1.00	0.79	0.57	0.64	0.81	0.79	0.79
15	F	R	0.11	0.57	0.54	0.54	0.50	0.50	0.79	0.57	0.74	0.86	0.86
16	M	R	0.01	0.64	0.86	0.82	0.93	1.00	0.86	0.75	0.92	1.00	0.93
17	M	R	-0.03	0.79	0.89	0.96	1.00	1.00	0.64	0.79	0.96	1.00	1.00
18	F	R	0.05	0.57	0.75	0.79	0.86	0.86	0.79	0.79	0.85	1.00	1.00
19	M	R	0.26	0.79	0.86	1.00	0.86	0.93	0.93	0.75	0.85	1.00	1.00
20	F	R	0.04	0.64	0.64	0.64	0.50	0.86	0.50	0.68	0.77	0.57	0.86
21	F	R	0.10	0.64	0.75	0.79	0.79	0.93	0.86	0.71	0.78	0.93	0.86
22	M	L	0.02	0.57	0.61	0.68	0.50	0.93	0.86	0.61	0.77	0.57	0.71
23	M	L	0.28	0.71	0.75	0.82	0.86	0.79	0.93	0.96	1.00	0.93	1.00
24	M	L	0.01	0.71	0.82	0.89	1.00	0.93	0.57	0.79	0.93	0.93	0.93
25	M	L	0.07	0.50	0.68	0.79	0.64	0.86	0.64	0.68	0.81	0.86	0.64
26	F	R	-0.20	0.36	0.64	0.57	0.50	0.64	0.57	0.54	0.48	0.79	0.71
27	M	R	0.15	0.64	0.79	0.71	0.79	1.00	0.86	0.86	0.96	0.86	1.00
28	M	R	0.28	0.71	0.82	0.89	0.93	1.00	0.79	0.71	0.96	0.93	0.93
29	M	R	-0.01	0.50	0.50	0.54	0.50	0.57	0.64	0.57	0.55	0.57	0.71
30	M	R	0.10	0.71	0.61	0.75	0.79	0.71	0.79	0.68	0.74	0.79	0.86
31	M	R	0.02	0.64	0.68	0.71	0.79	0.93	0.50	0.50	0.62	0.64	0.57
32	M	R	0.16	0.64	0.57	0.75	0.79	0.93	0.79	0.89	0.96	1.00	1.00
33	F	L	0.14	0.79	0.82	0.93	0.93	0.86	0.71	0.89	0.93	0.93	0.93
34	F	R	0.13	0.86	0.82	1.00	1.00	1.00	0.86	0.96	1.00	1.00	1.00
35	F	R	0.05	0.79	0.79	0.93	0.93	0.86	0.79	0.71	0.74	0.71	0.93
36	M	L	0.48	0.71	0.75	0.89	0.86	0.93	0.79	0.79	0.92	1.00	1.00
37	M	L	-0.33	0.79	0.79	0.93	0.93	0.86	0.71	0.71	0.85	0.86	0.86
38	M	L	-0.05	0.71	0.68	0.75	1.00	1.00	0.64	0.79	0.89	0.79	1.00
39	F	L	0.05	0.50	0.50	0.50	0.43	0.50	0.71	0.64	0.48	0.64	0.57
40	M	R	0.16	0.64	0.64	0.68	0.79	0.93	0.64	0.96	0.96	1.00	1.00
		overall mean	0.07	0.65	0.70	0.77	0.78	0.83	0.71	0.73	0.80	0.82	0.85

Appendix B: Experiment 1: ANOVA Table for Accuracy

Tests of Within-Subjects Effects

Measure: MEASURE_1

Sphericity Assumed

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
SIDE	.129	1	.129	4.384	.043	4.384	.531
SIDE * SEX	7.623E-04	1	7.623E-04	.026	.873	.026	.053
SIDE * HFPREF	2.486E-03	1	2.486E-03	.084	.773	.084	.059
SIDE * SEX * HFPREF	3.439E-04	1	3.439E-04	.012	.915	.012	.051
Error(SIDE)	1.061	36	2.947E-02				
DURATION	1.409	4	.352	45.357	.000	181.426	1.000
DURATION * SEX	2.764E-02	4	6.909E-03	.889	.472	3.558	.278
DURATION * HFPREF	4.639E-02	4	1.160E-02	1.493	.207	5.972	.454
DURATION * SEX * HFPREF	9.066E-03	4	2.266E-03	.292	.883	1.167	.114
Error(DURATION)	1.119	144	7.768E-03				
SIDE * DURATION	2.129E-02	4	5.323E-03	.775	.543	3.101	.244
SIDE * DURATION * SEX	3.802E-02	4	9.506E-03	1.384	.242	5.538	.423
SIDE * DURATION * HFPREF	2.350E-02	4	5.876E-03	.856	.492	3.423	.268
SIDE * DURATION * SEX * HFPREF	9.995E-03	4	2.499E-03	.364	.834	1.456	.131
Error(SIDE*DURATION)	.989	144	6.866E-03				

[a] Computed using alpha = .05

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Intercept	233.724	1	233.724	1547.749	.000	1547.749	1.000
SEX	.874	1	.874	5.786	.021	5.786	.648
HFPREF	1.657E-02	1	1.657E-02	.110	.742	.110	.062
SEX * HFPREF	6.635E-03	1	6.635E-03	.044	.835	.044	.055
Error	5.436	36	.151				

[a] Computed using alpha = .05

Appendix C: Experiment 1: Individual Participant Data for Reaction Time

									Reaction Time				
				left gap					right gap				
ID	Sex	Hand/Foot	FDWT	L-40ms	L-60ms	L-80ms	L-100ms	L-120ms	R-40ms	R-60ms	R-80ms	R-100ms	R-120ms
1	F	L	0.07	833.07	829.89	681.25	794.00	612.00	764.71	745.86	725.47	669.43	604.43
2	M	L	0.02	432.00	465.25	548.89	452.86	564.57	674.43	726.46	489.57	654.14	464.93
3	F	L	-0.13	505.43	487.79	458.07	476.21	479.29	460.50	447.71	453.51	424.14	400.36
4	F	L	0.13	1541.14	1283.00	1215.43	1427.43	1082.21	1257.07	1243.25	1251.63	1121.21	1149.29
5	F	L	0.24	434.00	412.61	405.04	397.07	364.93	461.64	401.43	375.66	379.86	349.36
6	F	L	0.30	776.64	659.29	699.86	660.14	625.07	662.86	606.82	733.51	789.86	619.29
7	M	L	-0.04	496.43	495.21	465.25	516.86	448.14	562.57	565.32	499.01	455.64	511.36
8	F	L	0.13	563.79	506.86	533.96	533.14	588.57	586.64	519.04	531.47	443.21	465.21
9	F	R	-0.07	959.71	939.82	808.86	936.71	899.50	965.71	938.71	884.31	883.21	829.86
10	M	L	-0.05	472.79	467.36	493.11	412.79	454.07	507.21	468.96	389.88	393.07	383.36
11	F	L	0.07	616.29	671.71	653.00	636.64	501.07	1034.29	811.93	860.76	623.71	716.14
12	F	R	0.03	691.79	598.29	648.11	742.14	692.14	724.93	566.96	723.09	685.29	674.00
13	F	L	-0.28	535.36	446.36	444.18	374.79	527.64	477.93	378.11	385.06	404.86	395.86
14	F	R	0.45	576.50	609.14	474.54	531.07	588.36	576.14	476.75	545.28	513.57	445.57
15	F	R	0.11	699.00	575.82	583.79	588.00	537.43	850.00	833.89	837.23	927.86	1067.07
16	M	R	0.01	584.57	529.39	455.82	423.64	435.50	573.36	509.57	677.37	548.00	513.93
17	M	R	-0.03	459.86	400.54	342.54	338.43	286.21	508.07	416.57	356.18	389.21	304.64
18	F	R	0.05	750.50	975.21	783.36	959.79	726.64	826.50	699.21	824.04	781.57	680.14
19	M	R	0.26	354.79	281.07	275.79	281.86	261.21	315.93	277.04	228.62	253.43	215.00
20	F	R	0.04	559.57	548.57	522.86	577.71	552.43	583.64	608.32	538.52	572.79	577.79
21	F	R	0.10	638.93	604.18	593.61	517.86	510.29	617.29	581.86	618.64	614.36	583.79
22	M	L	0.02	1172.57	1018.79	962.50	1226.21	921.29	1064.29	942.50	1001.71	985.57	1015.29
23	M	L	0.28	756.07	776.36	676.07	698.86	677.29	853.21	712.71	574.73	617.36	500.14
24	M	L	0.01	728.79	716.43	642.96	657.79	535.57	748.86	558.25	557.40	546.21	513.43
25	M	L	0.07	777.50	787.07	785.96	629.43	706.14	859.29	835.25	805.99	857.29	730.21
26	F	R	-0.20	997.29	921.18	941.96	861.50	927.64	886.29	927.11	882.79	875.79	943.57
27	M	R	0.15	778.36	873.82	777.21	717.07	514.07	880.07	739.36	623.59	764.00	554.00
28	M	R	0.28	914.07	674.43	735.96	685.14	724.86	711.79	740.46	622.77	626.21	602.50
29	M	R	-0.01	421.93	491.61	474.86	530.29	419.00	483.71	430.50	474.31	562.21	432.43
30	M	R	0.10	647.00	614.71	632.18	585.64	598.36	683.14	632.57	661.20	612.64	595.93
31	M	R	0.02	764.57	531.46	563.93	570.71	579.79	570.07	555.71	567.60	589.93	591.86
32	M	R	0.16	747.14	534.61	529.29	495.43	409.93	717.93	517.75	441.13	402.00	344.57
33	F	L	0.14	894.29	777.14	689.61	704.79	694.64	848.57	878.82	748.92	740.43	700.00
34	F	R	0.13	704.86	689.36	556.00	531.29	535.79	714.29	679.57	645.60	566.93	536.86
35	F	R	0.05	675.43	756.14	641.39	671.86	704.64	968.71	624.86	739.19	775.71	673.36
36	M	L	0.48	627.93	501.54	478.50	443.07	616.00	653.57	626.79	494.56	428.36	414.00
37	M	L	-0.33	860.50	712.93	730.04	744.07	636.57	874.21	882.00	756.61	731.64	669.29
38	M	L	-0.05	632.93	584.86	576.04	499.43	515.43	614.07	596.07	602.79	609.43	470.50
39	F	L	0.05	633.93	591.68	559.14	619.86	560.07	768.00	551.00	633.40	669.79	567.71
40	M	R	0.16	742.86	539.61	534.36	496.07	409.71	719.93	493.71	440.66	402.00	345.21
		overall mean	0.07	699.00	647.03	614.38	623.69	585.60	715.29	643.72	630.09	622.30	578.81

Appendix D: Experiment 1: ANOVA Table for Reaction Time

Tests of Within-Subjects Effects

Measure: MEASURE_1

Sphericity Assumed

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
SIDE	1680.809	1	1680.809	.111	.741	.111	.062
SIDE * SEX	8287.426	1	8287.426	.545	.465	.545	.111
SIDE * HFPREF	1018.565	1	1018.565	.067	.797	.067	.057
SIDE * SEX * HFPREF	17436.586	1	17436.586	1.147	.291	1.147	.181
Error(SIDE)	547199.2	36	15199.978				
DURATION	672160.8	4	168040.2	39.158	.000	156.632	1.000
DURATION * SEX	34827.063	4	8706.766	2.029	.093	8.116	.596
DURATION * HFPREF	5441.544	4	1360.386	.317	.866	1.268	.120
DURATION * SEX * HFPREF	33924.320	4	8481.080	1.976	.101	7.905	.583
Error(DURATION)	617952.2	144	4291.335				
SIDE * DURATION	9740.770	4	2435.193	.610	.656	2.440	.197
SIDE * DURATION * SEX	31834.140	4	7958.535	1.993	.099	7.973	.587
SIDE * DURATION * HFPREF	18713.657	4	4678.414	1.172	.326	4.687	.361
SIDE * DURATION * SEX * HFPREF	7950.450	4	1987.612	.498	.737	1.991	.166
Error(SIDE*DURATION)	574931.5	144	3992.580				

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Intercept	1.62E+08	1	1.62E+08	500.083	.000	500.083	1.000
SEX	875714.2	1	875714.2	2.707	.109	2.707	.360
HFPREF	108205.3	1	108205.3	.334	.567	.334	.087
SEX * HFPREF	667070.9	1	667070.9	2.062	.160	2.062	.287
Error	11647214	36	323533.7				

a. Computed using alpha = .05

Appendix E: Experiment 1: ANOVA Table for FDWT data

Tests of Between-Subjects Effects

Dependent Variable: FDWT

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Corrected Model	.104[b]	3	3.465E-02	.194	.900	.581	.083
Intercept	1.307	1	1.307	7.300	.010	7.300	.748
HFPREF	4.543E-02	1	4.543E-02	.254	.618	.254	.078
SEX	4.494E-03	1	4.494E-03	.025	.875	.025	.053
HFPREF *SEX	5.402E-02	1	5.402E-02	.302	.586	.302	.083
Error	6.445	36	.179				
Total	7.855	40					
Corrected Total	6.549	39					

[a] Computed using alpha = .05

[b] R Squared = .016 (Adjusted R Squared = -.066)

Appendix F: Experiment 2: Individual Participant Data for Accuracy

	hand/				left				right			
ID	foot	Sex	Eye	FDWT	al2ms	al3ms	al4ms	al5ms	ar2ms	ar3ms	ar4ms	ar5ms
1	L	F	L	0.044	43.33	26.67	6.67	6.67	50.00	33.33	0.00	10.00
2	L	F	L	-0.019	46.67	36.67	10.00	0.00	50.00	26.67	16.67	3.33
3	L	F	R	0.050	43.33	20.00	6.67	3.33	36.67	6.67	0.00	10.00
4	L	F	L	0.024	43.33	23.33	0.00	0.00	50.00	36.67	0.00	6.67
5	L	F	L	0.048	50.00	46.67	16.67	10.00	46.67	10.00	10.00	6.67
6	L	F	L	0.037	53.33	36.67	0.00	3.33	46.67	23.33	0.00	0.00
7	L	F	R	-0.014	40.00	43.33	13.33	3.33	53.33	43.33	6.67	30.00
8	L	F	L	0.017	46.67	30.00	3.33	0.00	26.67	6.67	6.67	0.00
9	L	F	L	-0.185	36.67	30.00	6.67	6.67	40.00	30.00	6.67	3.33
10	L	F	L	-0.099	43.33	43.33	13.33	16.67	50.00	30.00	16.67	20.00
11	L	F	L	0.044	53.33	53.33	10.00	23.33	50.00	40.00	16.67	13.33
12	L	F	L	0.000	50.00	40.00	6.67	6.67	50.00	13.33	13.33	0.00
13	L	M	R	0.137	40.00	36.67	43.33	6.67	50.00	33.33	50.00	16.67
14	L	M	R	0.088	36.67	10.00	0.00	0.00	53.33	0.00	0.00	3.33
15	L	M	R	0.135	50.00	26.67	3.33	10.00	50.00	10.00	3.33	3.33
16	L	M	R	-0.004	50.00	50.00	3.33	0.00	50.00	30.00	0.00	0.00
17	L	M	L	0.297	40.00	40.00	10.00	0.00	50.00	30.00	6.67	3.33
18	L	M	L	0.016	26.67	66.67	0.00	0.00	50.00	66.67	10.00	0.00
19	L	M	L	0.045	33.33	36.67	20.00	6.67	50.00	23.33	23.33	10.00
20	L	M	R	0.011	33.33	30.00	0.00	0.00	40.00	33.33	3.33	6.67
21	L	M	R	0.037	50.00	30.00	3.33	6.67	50.00	13.33	0.00	0.00
22	L	M	R	0.373	46.67	46.67	16.67	3.33	36.67	26.67	16.67	0.00
23	L	M	L	0.000	43.33	13.33	6.67	6.67	33.33	30.00	6.67	3.33
24	L	M	R	0.119	50.00	46.67	30.00	30.00	46.67	33.33	13.33	0.00
25	R	F	L	0.035	43.33	33.33	0.00	0.00	43.33	20.00	6.67	0.00
26	R	F	R	0.029	26.67	33.33	10.00	10.00	40.00	6.67	10.00	6.67
27	R	F	L	-0.033	46.67	40.00	3.33	0.00	50.00	30.00	0.00	0.00
28	R	F	R	0.055	40.00	16.67	0.00	0.00	36.67	23.33	0.00	0.00
29	R	F	R	0.373	43.33	43.33	3.33	3.33	40.00	13.33	6.67	3.33
30	R	F	R	0.248	46.67	20.00	3.33	0.00	46.67	16.67	3.33	0.00
31	R	F	R	0.097	50.00	46.67	6.67	30.00	50.00	40.00	10.00	20.00
32	R	F	R	-0.086	43.33	23.33	3.33	3.33	50.00	33.33	13.33	3.33
33	R	F	R	0.035	40.00	23.33	0.00	0.00	33.33	36.67	3.33	0.00
34	R	F	R	-0.001	36.67	30.00	16.67	6.67	36.67	13.33	16.67	0.00
35	R	F	L	0.027	50.00	36.67	13.33	10.00	50.00	16.67	3.33	26.67
36	R	F	L	0.068	56.67	43.33	3.33	3.33	50.00	36.67	13.33	13.33
37	R	M	R	0.042	50.00	36.67	20.00	3.33	43.33	16.67	30.00	3.33
38	R	M	R	0.204	53.33	43.33	10.00	20.00	36.67	43.33	6.67	43.33
39	R	M	R	0.032	50.00	43.33	0.00	3.33	40.00	26.67	0.00	0.00
40	R	M	L	0.028	46.67	23.33	13.33	3.33	46.67	13.33	3.33	6.67
41	R	M	R	0.038	50.00	43.33	13.33	0.00	50.00	23.33	10.00	3.33
42	R	M	R	0.143	53.33	43.33	23.33	6.67	43.33	20.00	10.00	3.33
43	R	M	R	-0.023	50.00	50.00	53.33	36.67	46.67	50.00	50.00	40.00
44	R	M	R	0.231	50.00	33.33	10.00	16.67	30.00	16.67	10.00	13.33

45	R	M	R	0.162	36.67	6.67	10.00	6.67	40.00	10.00	3.33	13.33
46	R	M	R	0.145	43.33	30.00	10.00	13.33	36.67	16.67	10.00	3.33
47	R	M	R	0.208	50.00	36.67	13.33	16.67	33.33	13.33	20.00	3.33
48	R	M	L	0.033	53.33	43.33	16.67	6.67	50.00	33.33	6.67	0.00

Appendix G: Experiment 2: ANOVA Table for Accuracy

Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
SIDE	704.167	1	704.167	11.072	.002	11.072	.902
SIDE * LPREF	72.338	1	72.338	1.137	.292	1.137	.181
SIDE * SEX	72.338	1	72.338	1.137	.292	1.137	.181
SIDE * LPREF * SEX	150.000	1	150.000	2.359	.132	2.359	.324
Error(SIDE)	2798.380	44	63.600				
DURATION	89798.495	3	29932.832	265.280	.000	795.839	1.000
DURATION * LPREF	250.926	3	83.642	.741	.529	2.224	.205
DURATION * SEX	505.093	3	168.364	1.492	.220	4.476	.387
DURATION * LPREF * SEX	192.940	3	64.313	.570	.636	1.710	.165
Error(DURATION)	14894.213	132	112.835				
SIDE * DURATION	1772.685	3	590.895	16.718	.000	50.154	1.000
SIDE * DURATION * LPREF	156.829	3	52.276	1.479	.223	4.437	.384
SIDE * DURATION * SEX	10.532	3	3.511	.099	.960	.298	.068
SIDE * DURATION * LPREF * SEX	197.222	3	65.741	1.860	.139	5.580	.474
Error(SIDE*DURATION)	4665.509	132	35.345				

Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Intercept	203811.2	1	203811.2	662.218	.000	662.218	1.000
LPREF	1.852	1	1.852	.006	.939	.006	.051
SEX	444.907	1	444.907	1.446	.236	1.446	.217
LPREF * SEX	402.894	1	402.894	1.309	.259	1.309	.201
Error	13541.898	44	307.770				

[a] Computed using alpha = .05

Appendix H: Experiment 2: Individual Participant Data for Reaction Time

					left reaction times (msec)				right reaction times (msec)			
ID	hand/ foot	Sex	Eye	FDWT	rtl2ms	rtl3ms	rtl4ms	rtl5ms	rtr2ms	rtr3ms	rtr4ms	rtr5ms
1	L	F	L	0.044	815.50	616.71	445.60	339.86	N/A	630.20	430.47	364.92
2	L	F	L	-0.019	270.00	426.17	429.71	334.33	N/A	372.57	386.10	329.21
3	L	F	R	0.050	360.50	454.33	467.86	317.27	443.00	416.62	464.27	392.77
4	L	F	L	0.024	843.00	574.63	382.53	603.60	N/A	644.75	376.33	433.80
5	L	F	L	0.048	219.00	316.00	365.80	375.25	444.50	312.46	441.25	639.64
6	L	F	L	0.037	N/A	694.00	662.80	591.36	871.33	465.18	371.47	479.40
7	L	F	R	-0.014	240.20	304.50	285.00	310.73	283.50	287.50	347.20	252.14
8	L	F	L	0.017	398.50	399.25	374.67	250.73	428.44	343.23	375.60	261.53
9	L	F	L	-0.185	1283.50	656.09	476.21	699.00	464.00	674.67	585.69	549.27
10	L	F	L	-0.099	2020.00	1023.20	1409.55	636.91	930.00	1396.56	872.45	891.64
11	L	F	L	0.044	N/A	N/A	900.50	822.33	N/A	1159.00	536.40	534.18
12	L	F	L	0.000	234.00	233.33	265.86	280.77	N/A	339.33	246.33	261.13
13	L	M	R	0.137	306.75	388.50	242.47	307.00	362.00	399.67	282.87	331.50
14	L	M	R	0.088	797.25	640.50	368.60	642.73	N/A	548.40	324.67	508.80
15	L	M	R	0.135	N/A	307.77	236.00	304.36	N/A	386.07	325.47	278.79
16	L	M	R	-0.004	N/A	N/A	523.47	392.07	N/A	354.83	318.93	334.80
17	L	M	L	0.297	848.67	905.75	610.46	833.00	N/A	503.83	563.73	891.27
18	L	M	L	0.016	747.14	N/A	335.13	535.47	N/A	373.50	330.20	424.53
19	L	M	L	0.045	1219.00	452.60	504.67	445.80	N/A	443.25	473.20	467.73
20	L	M	R	0.011	1445.20	1132.67	792.93	660.73	1117.33	971.17	596.79	585.20
21	L	M	R	0.037	N/A	1111.67	564.86	621.43	N/A	624.55	583.73	508.67
22	L	M	R	0.373	761.00	469.50	659.31	274.00	1237.75	363.50	617.21	396.93
23	L	M	L	0.000	260.50	345.00	373.31	497.85	241.60	298.70	361.00	297.20
24	L	M	R	0.119	556.50	251.50	203.11	308.09	236.50	178.00	197.50	272.00
25	R	F	L	0.035	249.00	482.60	367.07	306.93	599.00	490.00	347.79	310.33
26	R	F	R	0.029	278.86	359.11	247.73	359.07	323.00	399.50	261.27	328.00
27	R	F	L	-0.033	218.00	545.00	327.27	314.80	N/A	405.50	375.93	374.60
28	R	F	R	0.055	1334.67	719.60	512.13	411.73	671.20	668.13	429.40	392.20
29	R	F	R	0.373	2043.67	805.00	816.57	715.00	1306.50	612.93	720.23	661.64
30	R	F	R	0.248	685.00	541.10	446.93	445.60	516.50	484.10	464.53	462.13
31	R	F	R	0.097	N/A	462.00	436.54	708.86	N/A	518.67	415.00	604.56
32	R	F	R	-0.086	904.50	473.56	453.86	431.93	N/A	339.60	367.45	362.00
33	R	F	R	0.035	502.00	612.63	429.60	619.93	432.00	740.17	448.67	540.20
34	R	F	R	-0.001	356.75	314.22	315.90	459.08	552.40	286.07	407.82	508.00
35	R	F	L	0.027	N/A	569.50	321.31	443.87	N/A	709.60	256.87	270.47
36	R	F	L	0.068	N/A	1001.50	590.20	774.20	966.00	564.00	453.00	567.79
37	R	M	R	0.042	413.00	533.75	252.79	342.00	456.00	473.40	217.69	328.21
38	R	M	R	0.204	677.00	738.33	521.69	362.79	544.00	374.07	936.80	503.13
39	R	M	R	0.032	N/A	540.00	482.80	406.93	528.33	352.14	376.27	306.87
40	R	M	L	0.028	1271.00	545.25	460.00	496.14	1170.00	439.27	341.47	417.64
41	R	M	R	0.038	588.00	668.00	494.54	540.00	949.00	471.25	396.07	399.53
42	R	M	R	0.143	N/A	257.00	236.25	185.54	222.83	185.22	203.92	209.64
43	R	M	R	-0.023	N/A	N/A	1364.00	591.14	733.00	849.00	524.75	493.93

44	R	M	R	0.231	466.00	285.17	164.48	209.25	278.43	211.55	163.62	180.69
45	R	M	R	0.162	137.25	295.50	392.40	251.07	130.33	318.75	202.14	168.17
46	R	M	R	0.145	386.50	279.14	272.83	205.58	231.20	219.33	194.36	206.21
47	R	M	R	0.208	N/A	270.00	421.83	133.91	218.60	183.67	124.25	156.36
48	R	M	L	0.033	N/A	544.00	530.33	693.21	N/A	520.40	500.73	641.73

Appendix I : Experiment 2: ANOVA Table for Reaction Time

Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
SIDE	109266.4	1	109266.4	3.904	.061	3.904	.470
SIDE * LPREF	52.297	1	52.297	.002	.966	.002	.050
SIDE * SEX	72.016	1	72.016	.003	.960	.003	.050
SIDE * LPREF * SEX	7.024	1	7.024	.000	.988	.000	.050
Error(SIDE)	587693.7	21	27985.414				
DURATION	1393679	3	464559.7	7.907	.000	23.720	.986
DURATION * LPREF	34683.900	3	11561.300	.197	.898	.590	.085
DURATION * SEX	11478.043	3	3826.014	.065	.978	.195	.061
DURATION * LPREF * SEX	63299.904	3	21099.968	.359	.783	1.077	.117
Error(DURATION)	3701626	63	58755.966				
SIDE * DURATION	83540.959	3	27846.986	1.103	.355	3.310	.284
SIDE * DURATION * LPREF	26644.088	3	8881.363	.352	.788	1.056	.115
SIDE * DURATION * SEX	141295.5	3	47098.490	1.866	.144	5.598	.461
SIDE * DURATION * LPREF * SEX	14504.711	3	4834.904	.192	.902	.575	.084
Error(SIDE*DURATION)	1590142	63	25240.355				

[a] Computed using alpha = .05

Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Intercept	48339278	1	48339278	99.231	.000	99.231	1.000
LPREF	84133.429	1	84133.429	.173	.682	.173	.068
SEX	392279.6	1	392279.6	.805	.380	.805	.137
LPREF * SEX	57747.453	1	57747.453	.119	.734	.119	.062
Error	10229874	21	487136.9				

[a] Computed using alpha = .05

Appendix J: Experiment 2: Individual Participant Data for Response Bias

				left				right			
ID	hand/foot	sex	eye	2ms	3ms	4ms	5ms	2ms	3ms	4ms	5ms
1	L	F	L	-56	-46	-26	-30	-60	-50	-30	-34
2	L	F	L	-58	-44	-28	-30	-60	-46	-40	-32
3	L	F	R	-56	-42	-30	-28	-52	-34	-30	-32
4	L	F	L	-56	-44	-30	-30	-60	-36	-30	-26
5	L	F	L	-56	-58	-40	-36	-54	-32	-36	-30
6	L	F	L	-58	-48	-30	-32	-50	-32	-30	-30
7	L	F	R	-14	-4	-30	-32	-26	-28	-34	-44
8	L	F	L	-54	-40	-28	-30	-38	-34	-26	-30
9	L	F	L	-52	-28	-30	-30	-54	-36	-34	-28
10	L	F	L	-52	-44	-38	-36	-56	-36	-36	-34
11	L	F	L	-58	-58	-36	-40	-60	-54	-40	-38
12	L	F	L	-56	-54	-30	-34	-60	-34	-22	-30
13	L	M	R	-56	-38	-28	-28	-60	-54	-34	-30
14	L	M	R	-52	-36	-30	-30	-58	-30	-30	-28
15	L	M	R	-60	-22	-28	-28	-60	-28	-28	-32
16	L	M	R	-60	-60	-28	-30	-60	-48	-30	-30
17	L	M	L	-54	-50	-32	-30	-60	-48	-26	-28
18	L	M	L	-46	-60	-30	-30	-60	-52	-24	-30
19	L	M	L	-46	-48	-18	-26	-60	-44	-16	-24
20	L	M	R	-60	-38	-30	-30	-60	-30	-30	-28
21	L	M	R	-60	-48	-32	-30	-60	-38	-30	-30
22	L	M	R	-58	-54	-28	-32	-52	-42	-24	-30
23	L	M	L	-56	-38	-34	-34	-50	-32	-30	-28
24	L	M	R	-52	-46	-36	-28	-54	-26	-26	-30
25	R	F	L	-56	-50	-30	-30	-56	-42	-30	-30
26	R	F	R	-46	-34	-24	-24	-46	-30	-24	-26
27	R	F	L	-58	-54	-28	-30	-60	-48	-30	-30
28	R	F	R	-54	-40	-30	-30	-48	-44	-30	-30
29	R	F	R	-52	-36	-32	-32	-50	-26	-34	-32
30	R	F	R	-54	-38	-32	-30	-54	-40	-28	-30
31	R	F	R	-60	-58	-34	-44	-60	-54	-32	-42
32	R	F	R	-56	-40	-32	-28	-60	-50	-38	-32
33	R	F	R	-54	-44	-30	-30	-50	-44	-28	-30
34	R	F	R	-52	-36	-40	-34	-48	-26	-36	-30
35	R	F	L	-60	-52	-30	-24	-60	-40	-28	-14
36	R	F	L	-56	-56	-28	-28	-56	-52	-26	-26
37	R	M	R	-56	-52	-22	-28	-56	-40	-20	-32
38	R	M	R	-46	-16	-32	-22	-48	-8	-26	-4
39	R	M	R	-60	-56	-30	-32	-54	-46	-30	-30
40	R	M	L	-58	-44	-26	-32	-58	-38	-28	-30
41	R	M	R	-56	-56	-30	-30	-52	-44	-24	-28
42	R	M	R	-58	-56	-28	-34	-40	-42	-32	-32
43	R	M	R	-60	-60	-54	-40	-50	-56	-12	-10
44	R	M	R	-56	-46	-32	-32	-44	-36	-32	-30
45	R	M	R	-52	-30	-24	-26	-54	-36	-32	-34
46	R	M	R	-56	-44	-36	-34	-48	-32	-28	-32
47	R	M	R	-60	-52	-34	-36	-50	-34	-30	-32
48	R	M	L	-58	-56	-20	-30	-60	-50	-26	-30

Appendix K : Experiment 2: ANOVA Table for Response Bias

Tests of Within-Subjects Effects

Measure: MEASURE_1
Sphericity Assumed

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
SIDE	518.010	1	518.010	9.709	.003	9.709	.862
SIDE * LPREF	137.760	1	137.760	2.582	.115	2.582	.349
SIDE * SEX	128.344	1	128.344	2.406	.128	2.406	.329
SIDE * LPREF * SEX	78.844	1	78.844	1.478	.231	1.478	.221
Error(SIDE)	2347.542	44	53.353				
DURATION	38635.031	3	12878.344	185.422	.000	556.266	1.000
DURATION * LPREF	138.615	3	46.205	.665	.575	1.996	.187
DURATION * SEX	320.448	3	106.816	1.538	.208	4.614	.398
DURATION * LPREF * SEX	195.448	3	65.149	.938	.424	2.814	.252
Error(DURATION)	9167.958	132	69.454				
SIDE * DURATION	366.865	3	122.288	6.943	.000	20.829	.976
SIDE * DURATION * LPREF	43.615	3	14.538	.825	.482	2.476	.225
SIDE * DURATION * SEX	21.365	3	7.122	.404	.750	1.213	.129
SIDE * DURATION * LPREF * SEX	34.698	3	11.566	.657	.580	1.970	.185
Error(SIDE*DURATION)	2324.958	132	17.613				

Tests of Between-Subjects Effects

Measure: MEASURE_1
Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Intercept	586406.3	1	586406.3	4195.058	.000	4195.058	1.000
LPREF	.260	1	.260	.002	.966	.002	.050
SEX	21.094	1	21.094	.151	.700	.151	.067
LPREF * SEX	14.260	1	14.260	.102	.751	.102	.061
Error	6150.542	44	139.785				

[a] Computed using alpha = .05

Appendix L: Experiment 2: ANOVA Table for FDWT Data

Tests of Between-Subjects Effects

Dependent Variable: LSTAR

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
SEX	6.033E-02	1	6.033E-02	5.671	.022	5.671	.644
LPREF	1.633E-02	1	1.633E-02	1.534	.222	1.534	.228
SEX * LPREF	1.727E-02	1	1.727E-02	1.624	.209	1.624	.238
Error	.468	44	1.064E-02				
Total	.788	48					
Corrected Total	.562	47					

[a] Computed using alpha = .05

Appendix M: Experiment 3: Individual Participant Data for Reaction Time to Visual Stimuli

				Visual						
				left hand response		right hand response				
ID	Sex	Hand	FDWT	LVF	RVF	LVF	RVF	V-crossed	V-uncrossed	difference
1	M	L	0.33	236.59	268.50	259.06	264.75	263.78	250.67	13.11
2	M	L	0.36	249.27	251.43	295.65	270.90	273.54	260.08	13.45
3	M	L	0.26	236.84	241.06	247.91	252.63	244.48	244.73	-0.25
4	M	L	0.34	218.19	220.44	238.63	243.84	229.53	231.01	-1.48
5	M	L	0.17	239.22	257.87	263.22	250.40	260.54	244.81	15.74
6	M	L	0.32	390.17	424.44	407.39	402.32	415.92	396.24	19.67
7	M	L	0.09	206.88	211.35	251.00	247.03	231.18	226.95	4.22
8	M	L	0.16	287.41	280.28	265.59	263.47	272.94	275.44	-2.50
9	M	R	0.22	275.59	271.13	279.74	292.00	275.43	283.80	-8.36
10	M	R	0.28	196.97	208.47	187.22	204.45	197.84	200.71	-2.87
11	M	R	0.34	214.35	212.34	238.00	220.87	225.17	217.61	7.56
12	M	R	-0.06	274.16	257.44	256.26	246.22	256.85	260.19	-3.34
13	M	R	0.07	294.03	286.19	264.39	293.46	275.29	293.75	-18.46
14	M	R	0.35	253.56	246.28	254.03	253.28	250.16	253.42	-3.27
15	M	R	0.22	254.13	258.58	247.81	263.75	253.19	258.94	-5.74
16	M	R	0.22	239.66	250.66	252.69	263.81	251.67	251.73	-0.06
17	M	R	0.22	214.28	222.13	230.25	212.72	226.19	213.50	12.69
18	M	R	0.26	236.84	241.06	247.91	252.63	244.48	244.73	-0.25
19	F	L	0.15	358.37	373.48	361.14	375.63	367.31	367.00	0.32
20	F	L	-0.09	251.34	254.88	269.56	263.94	262.22	257.64	4.58
21	F	L	0.04	371.17	423.05	367.47	413.13	395.26	392.15	3.11
22	F	L	0.35	289.68	285.55	293.09	280.91	289.32	285.29	4.03
23	F	L	0.25	233.84	244.28	234.66	246.44	239.47	240.14	-0.67
24	F	L	0.17	265.31	263.06	245.47	251.66	254.27	258.48	-4.22
25	F	L	0.38	277.00	286.91	277.69	262.42	282.30	269.71	12.59
26	F	L	0.15	253.48	259.13	295.78	266.42	277.45	259.95	17.50
27	F	L	0.09	236.94	232.25	252.13	266.96	242.19	251.95	-9.76
28	F	L	0.13	287.41	280.28	265.59	263.47	272.94	275.44	-2.50
29	F	R	0.06	242.28	258.00	225.72	233.56	241.86	237.92	3.94
30	F	R	0.33	278.32	289.19	256.68	280.63	272.93	279.47	-6.54
31	F	R	0.06	243.06	248.25	237.48	252.78	242.87	247.92	-5.05
32	F	R	0.24	275.64	280.59	276.75	281.23	278.67	278.43	0.24
33	F	R	0.34	281.41	274.41	260.03	257.13	267.22	269.27	-2.05
34	F	R	0.07	213.75	210.00	224.06	224.57	217.03	219.16	-2.13
35	F	R	0.15	274.75	266.87	307.06	282.21	286.97	278.48	8.49
36	F	R	0.04	287.90	269.83	277.71	287.57	273.77	287.73	-13.96
37	F	R	0.41	330.07	353.48	317.03	314.58	335.26	322.33	12.93
38	F	R	0.40	240.94	239.75	243.34	251.16	241.55	246.05	-4.50
	overall means		0.21	263.44	268.50	267.77	269.87	268.13	266.65	1.48

Appendix N: Experiment 3: Individual Participant Data for Reaction Time to Auditory Stimuli

					Auditory					
				left hand response		right hand response				
ID	Sex	Hand	FDWT	left ear	right ear	left ear	right ear	A-crossed	A-uncross	Difference
1	M	L	0.33	157.65	160.00	161.42	142.03	160.71	149.84	10.87
2	M	L	0.36	219.31	207.33	227.87	189.29	217.60	204.30	13.30
3	M	L	0.26	218.25	231.03	212.63	192.50	221.83	205.38	16.45
4	M	L	0.34	145.35	142.20	166.52	152.88	154.36	149.11	5.24
5	M	L	0.17	196.03	183.72	196.00	179.00	189.86	187.52	2.34
6	M	L	0.32	370.37	354.86	377.44	388.30	366.15	379.34	-13.18
7	M	L	0.09	275.42	292.17	282.83	275.03	287.50	275.23	12.27
8	M	L	0.16	168.31	159.84	179.63	160.16	169.73	164.24	5.50
9	M	R	0.22	231.84	222.29	270.81	260.59	246.55	246.22	0.33
10	M	R	0.28	163.00	144.50	152.14	132.23	148.32	147.62	0.71
11	M	R	0.34	121.04	125.38	159.20	143.90	142.29	132.47	9.82
12	M	R	-0.06	128.73	138.00	144.00	165.38	141.00	147.05	-6.05
13	M	R	0.07	198.40	201.94	191.61	195.07	196.77	196.73	0.04
14	M	R	0.35	160.52	182.56	162.50	151.81	172.53	156.16	16.37
15	M	R	0.22	170.66	165.23	179.16	183.23	172.19	176.94	-4.75
16	M	R	0.22	200.34	195.03	200.97	176.47	198.00	188.41	9.59
17	M	R	0.22	120.75	128.47	116.70	126.43	122.58	123.59	-1.01
18	M	R	0.26	218.25	231.03	212.63	192.50	221.83	205.38	16.45
19	F	L	0.15	284.83	319.62	281.93	307.74	300.78	296.29	4.49
20	F	L	-0.09	142.77	134.56	143.29	150.19	138.93	146.48	-7.55
21	F	L	0.04	334.89	392.19	336.50	381.18	364.35	358.04	6.31
22	F	L	0.35	174.63	169.84	162.53	160.65	166.19	167.64	-1.45
23	F	L	0.25	219.19	223.78	205.57	218.66	214.67	218.92	-4.25
24	F	L	0.17	186.71	165.31	156.44	160.97	160.88	173.84	-12.96
25	F	L	0.38	192.90	198.66	173.06	171.82	185.86	182.36	3.50
26	F	L	0.15	176.17	183.37	183.13	180.77	183.25	178.47	4.78
27	F	L	0.09	182.10	176.35	145.14	152.43	160.75	167.26	-6.52
28	F	L	0.13	168.31	159.84	179.63	160.16	169.73	164.24	5.50
29	F	R	0.06	188.44	203.06	198.00	208.23	200.53	198.33	2.20
30	F	R	0.33	153.00	161.29	153.72	184.23	157.50	168.62	-11.11
31	F	R	0.06	193.19	167.72	170.59	147.41	169.16	170.30	-1.14
32	F	R	0.24	254.48	222.69	227.81	208.93	225.25	231.71	-6.46
33	F	R	0.34	164.48	153.72	172.97	154.16	163.34	159.32	4.02
34	F	R	0.07	166.97	154.32	162.26	161.04	158.29	164.00	-5.71
35	F	R	0.15	205.14	211.52	226.94	229.06	219.23	217.10	2.12
36	F	R	0.04	194.16	203.10	189.31	185.14	196.20	189.65	6.55
37	F	R	0.41	251.94	234.75	255.56	245.13	245.16	248.53	-3.38
38	F	R	0.40	188.10	187.55	175.23	174.10	181.39	181.10	0.29
		overall means	0.21	197.02	197.07	197.20	193.39	197.14	195.20	1.93

Appendix O: Experiment 3: ANOVA Table for Reaction Time

Tests of Within-Subjects Effects

Measure: Reaction Time

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
M (modality)	371940.6	1	371940.621	159.180	.000
M * HAND	687.174	1	687.174	.294	.591
M * SEX	4533.474	1	4533.474	1.940	.173
M * HAND * SEX	3748.528	1	3748.528	1.604	.214
Error(M)	79444.546	34	2336.604		
H (response hand)	53.377	1	53.377	.239	.628
H * HAND	20.127	1	20.127	.090	.766
H * SEX	1149.026	1	1149.026	5.137	.030
H * HAND * SEX	100.641	1	100.641	.450	.507
Error(H)	7604.350	34	223.657		
S (Side of Presentation)	33.907	1	33.907	.134	.716
S * HAND	80.444	1	80.444	.318	.576
S * SEX	293.683	1	293.683	1.162	.289
S * HAND * SEX	450.910	1	450.910	1.784	.191
Error(S)	8595.519	34	252.809		
M * H	470.532	1	470.532	1.816	.187
M * H * HAND	753.937	1	753.937	2.910	.097
M * H * SEX	16.121	1	16.121	.062	.805
M * H * HAND * SEX	2.754	1	2.754	.011	.918
Error(M*H)	8809.571	34	259.105		
M * S	635.984	1	635.984	6.083	.019
M * S * HAND	1.478	1	1.478	.014	.906
M * S * SEX	135.390	1	135.390	1.295	.263
M * S * HAND * SEX	370.177	1	370.177	3.540	.068
Error(M*S)	3555.001	34	104.559		
H * S	295.182	1	295.182	4.696	.037
H * S * HAND	309.227	1	309.227	4.919	.033
H * S * SEX	329.242	1	329.242	5.238	.028
H * S * HAND * SEX	96.071	1	96.071	1.384	.248

Appendix O: Experiment 3: ANOVA Table for Reaction Time - Continued

Tests of Between-Subjects Effects

Measure: MEASURE_1

Transformed Variable: Average

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Intercept	16264694	1	16264694	936.110	.000	936.110	1.000
HAND	47443.725	1	47443.725	2.731	.108	2.731	.362
SEX	8222.028	1	8222.028	.473	.496	.473	.103
HAND * SEX	5259.395	1	5259.395	.303	.586	.303	.083
Error	590742.3	34	17374.774				

[a] Computed using alpha = .05

Appendix P: Experiment 2: ANOVA Table for FDWT data

Tests of Between-Subjects Effects

Dependent Variable: FDWT

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power[a]
Corrected Model	3.580E-02[b]	3	1.193E-02	.696	.561	2.088	.181
Intercept	1.637	1	1.637	95.487	.000	95.487	1.000
HAND	6.485E-05	1	6.485E-05	.004	.951	.004	.050
SEX	1.929E-02	1	1.929E-02	1.125	.296	1.125	.178
HAND * SEX	1.804E-02	1	1.804E-02	1.052	.312	1.052	.169
Error	.583	34	1.715E-02				
Total	2.235	38					
Corrected Total	.619	37					

[a] Computed using alpha = .05

[b] R Squared = .058 (Adjusted R Squared = -.025)

Appendix Q: Experiment 3: Correlation Matrix for CUD and FDWT Data

Correlations

		FDWT	VL-RCUD	VR-LCUD	AL-RCUD	AR-LCUD
FDWT	Pearson Correlation	1.000	.168	.195	-.183	.354
	Sig. (1-tailed)	.	.157	.120	.136	.015
	N	38	38	38	38	38
VL-RCUD	Pearson Correlation	.168	1.000	-.297	.266	-.287
	Sig. (1-tailed)	.157	.	.035	.053	.041
	N	38	38	38	38	38
VR-LCUD	Pearson Correlation	.195	-.297	1.000	-.248	.367
	Sig. (1-tailed)	.120	.035	.	.067	.012
	N	38	38	38	38	38
AL-RCUD	Pearson Correlation	-.183	.266	-.248	1.000	-.568
	Sig. (1-tailed)	.136	.053	.067	.	.000
	N	38	38	38	38	38
AL-RCUD	Pearson Correlation	.354	-.287	.367	-.568	1.000
	Sig. (1-tailed)	.015	.041	.012	.000	.
	N	38	38	38	38	38

* Correlation is significant at the 0.05 level (1-tailed).

** Correlation is significant at the 0.01 level (1-tailed).

Appendix R: Experiment 4: Individual Participant Data for the FDWT and EWT

					Emotional Words Test							
ID	Write	Throw	Kick	Eye	Sex	L-Corr	R-Corr	fal alarm	L-%cor	R-%cor	EWT lambda	FDWT
1	L	L	L	R	M	33.00	26.00	0.00	91.67	72.22	-1.34	0.10
2	L	L	L	L	M	31.00	28.00	5.00	86.11	77.78	-0.54	0.05
3	L	L	L	R	M	29.00	26.00	3.00	80.56	72.22	-0.45	0.04
4	L	L	L	R	M	29.00	25.00	0.00	80.56	69.44	-0.58	-0.09
5	L	L	L	L	M	35.00	31.00	2.00	97.22	86.11	-1.42	0.04
6	L	L	L	L	F	34.00	26.00	7.00	94.44	72.22	-1.70	-0.04
7	L	L	L	L	F	33.00	27.00	2.00	91.67	75.00	-1.20	0.12
8	L	L	L	R	F	21.00	20.00	1.00	58.33	55.56	-0.11	0.01
9	L	L	L	R	F	26.00	29.00	2.00	72.22	80.56	0.45	0.04
10	L	L	L	L	F	34.00	29.00	5.00	94.44	80.56	-1.26	0.21
11	L	L	L	L	F	29.00	9.00	0.00	80.56	25.00	-2.47	0.07
12	L	L	L	L	F	19.00	10.00	2.00	52.78	27.78	-1.06	0.04
13	L	L	L	L	F	35.00	33.00	7.00	97.22	91.67	-0.91	-0.01
14	L	L	R	R	M	35.00	24.00	0.00	97.22	66.67	-2.50	0.05
15	L	L	R	L	M	16.00	13.00	18.00	44.44	36.11	-0.34	0.18
16	L	L	R	L	M	36.00	35.00	0.00	100.00	97.22	-1.13	0.11
17	L	L	R	R	M	35.00	18.00	0.00	97.22	50.00	-3.18	-0.03
18	L	L	R	L	M	28.00	23.00	21.00	77.78	63.89	-0.66	0.07
19	L	L	R	L	F	33.00	20.00	3.00	91.67	55.56	-2.05	-0.11
20	L	R	R	R	M	28.00	23.00	3.00	77.78	63.89	-0.66	0.13
21	L	R	R	R	M	34.00	27.00	0.00	94.44	75.00	-1.57	0.00
22	L	R	R	L	M	35.00	12.00	0.00	97.22	33.33	-3.86	-0.04
23	L	R	R	R	M	23.00	21.00	3.00	63.89	58.33	-0.23	0.16
24	L	R	R	L	M	24.00	13.00	4.00	66.67	36.11	-1.24	0.05
25	L	R	R	R	F	25.00	19.00	29.00	69.44	52.78	-0.69	0.03
26	L	R	R	L	F	28.00	19.00	0.00	77.78	52.78	-1.11	0.09
27	L	R	R	R	F	20.00	14.00	0.00	55.56	38.89	-0.67	0.04
28	R	L	L	R	M	23.00	12.00	4.00	63.89	33.33	-1.25	0.03
29	R	L	L	L	F	32.00	27.00	0.00	88.89	75.00	-0.92	-0.03
30	R	L	R	R	M	30.00	13.00	3.00	83.33	36.11	-2.12	-0.02
31	R	L	R	L	M	35.00	30.00	2.00	97.22	83.33	-1.62	0.02
32	R	L	R	R	F	33.00	34.00	0.00	91.67	94.44	0.37	0.16
33	R	R	L	R	M	30.00	20.00	0.00	83.33	55.56	-1.34	0.14
34	R	R	L	R	M	31.00	32.00	1.00	86.11	88.89	0.23	0.06
35	R	R	L	L	M	29.00	25.00	1.00	80.56	69.44	-0.58	0.02
36	R	R	L	L	M	34.00	34.00	2.00	94.44	94.44	0.00	0.15
37	R	R	L	R	F	31.00	31.00	1.00	86.11	86.11	0.00	0.23
38	R	R	R	L	M	35.00	20.00	0.00	97.22	55.56	-2.96	0.19
39	R	R	R	R	M	30.00	20.00	0.00	83.33	55.56	-1.34	0.02
40	R	R	R	R	F	35.00	36.00	1.00	97.22	100.00	1.13	0.14
41	R	R	R	R	F	32.00	29.00	12.00	88.89	80.56	-0.61	0.08
42	R	R	R	R	F	36.00	32.00	4.00	100.00	88.89	-2.32	0.17
43	R	R	R	L	F	33.00	28.00	2.00	91.67	77.78	-1.05	0.10
44	R	R	R	R	F	20.00	22.00	5.00	55.56	61.11	0.22	0.11
45	R	R	R	R	F	34.00	29.00	5.00	94.44	80.56	-1.26	0.02
46	R	R	R	L	F	28.00	14.00	1.00	77.78	38.89	-1.67	0.01
47	R	R	L	L	F	35.00	15.00	2.00	97.22	41.67	-3.51	0.02
48	R	R	0.00	R	M	30.00	19.00	1.00	83.33	52.78	-1.45	0.23

Appendix S: Experiment 4: Multiple Regression Analyses for the FDWT and EWT

Coefficients[a]

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.	Collinearity Statistics	
		B	Std. Error	Beta			Tolerance	VIF
1	(Constant)	3.423E-02	.051		.677	.502		
	XWXT	4.413E-02	.019	.325	2.353	.023	1.000	1.000

[illegible]

Model Summary[a,b]

Model	Variables Entered	Variables Removed	R	R Square	Adjusted R Square	Std. Error of the Estimate
	XWXT	.	.325	.105	.086	.1692

[a] Dependent Variable: CFWDT

[b] Method: Stepwise (Criteria: Probability-of-F-to-enter <= .050, Probability-of-F-to-remove >= .100).

EWT Regressions

Coefficients[a]

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.	Collinearity Statistics	
		B	Std. Error	Beta			Tolerance	VIF
1	(Constant)	-1.898	.360		-5.276	.000		
	XEXS	.305	.132	.322	2.311	.025	1.000	1.000

[a] Dependent Variable: LAMBDA

Model Summary[a,b]

Model	Variables Entered	Variables Removed	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	XEXS	.	.322	.104	.085	.9886

[a] Dependent Variable: LAMBDA

[b] Method: Stepwise (Criteria: Probability-of-F-to-enter <= .050, Probability-of-F-to-remove >= .100).

Appendix T: Rationale and Procedure for Calculating λ and λ^*

When employing the dichotic-listening paradigm, one must use a numerical index of ear advantage which transforms the raw data (usually the number of correct responses or percentage of correct responses for each ear) into a single index of lateralization. Initially, investigators simply calculated the difference between the proportions of correct responses for the two ears:

$$d = P_r - P_l$$

Where d = difference between proportions of correct responses
P_r = probability of a correct response for stimuli presented to the right ear
P_l = probability of a correct response for stimuli presented to the left ear

This formula is still widely used, but it is very problematic when one compares dichotic listening performance between different groups of people. Some groups of subjects may be very good at the task, hardly ever making an error (correctly identifying the stimuli presented to each ear) making it almost impossible for any ear advantage to appear. Therefore, the value of each subject's d is correlated with (and confounded by) overall performance.

Bryden and Sprott (1981) proposed the λ index which is the natural log-odds ratio of right-ear responses to left-ear responses:

$$\lambda = \log P_r / (1 - P_r) - \log P_l / (1 - P_l)$$

Where λ = An index of ear advantage
P_r = Probability of a correct response for stimuli presented to the right ear
P_l = Probability of a correct response for stimuli presented to the left ear

The λ index is advantageous for a number of reasons. It is unbounded, approximately normally distributed, and it is unconstrained by accuracy. Perhaps most importantly, it has a standard error associated with it, allowing statistical testing of individual subjects to determine whether each subject demonstrates a significant ear advantage, not just the group as a whole. Unfortunately, the λ index is not immune to confounding.

When two very similar stimuli are presented dichotically, they often 'fuse' into a single percept. For example, when the word "pit" is presented to the left ear and the word "kit" is presented to the right ear, these two words may be (and usually are) perceived as only one word, **either** 'pit' **or** 'kit'. This phenomenon is referred to as *dichotic fusion* (see Grimshaw et al, 1994).

Dichotic fusion itself is not statistically problematic. However, dichotic fusion can give rise to *stimulus dominance*. If the words "pit" and "kit" are presented simultaneously, presenting each word to each ear an equal number of times and the subject's response is **always** "kit", then "kit" is considered to be a dominant stimulus. Any trial response vulnerable to the effects of stimulus dominance is completely uninformative about ear advantage. Therefore, "because any laterality index for an individual subject is a combination of ear dominance and stimulus dominance, interpretation of the laterality index is extremely difficult so long as the two variables are confounded..." (Grimshaw, McManus, & Bryden, 1994, pg. 279).

For the purposes of dichotic listening studies, one can represent the data in three terms: the word pair (ex. pit-kit), the stimulus arrangement (which word is presented to which ear), and the subject's response (the word reported). When using log-linear analysis, main effects can reflect any imbalances in these three terms. If stimuli are presented an equal number of times to each ear and there is a significant main effect for 'response', this would indicate *stimulus dominance*; that the subject systematically reported one word more often than another word, regardless of the ear to which the word was presented. Further, interactions in these log-linear models can indicate whether these terms are statistically dependant. For example, an interaction between 'subject response' and 'stimulus arrangement' would indicate that subject response is dependant on the ear to which the word is presented. This interaction would represent an 'ear-advantage' effect.

To test this interaction (which is usually the effect of interest), one must first fit a model including every relevant effect except the 'response' × 'stimulus arrangement' interaction (one would include main effects of 'stimulus pair', 'response', 'stimulus arrangement', and the 'stimulus pair' × 'stimulus arrangement' interaction) and note the likelihood ratio chi-square test statistic. Next, one must fit a second model which includes every effect in the first model in addition to the 'response' × 'stimulus arrangement' interaction. If the second model provides a significantly better fit of the data than the first, (tested with the change in likelihood ratios of the chi-square values at the change in *df* between the two models) the interaction is significant.

Parameter estimates (λs) are produced for each effect, and the parameter estimate for the 'response' × 'arrangement' interaction (referred to as λ^*) is analogous to the λ index proposed by Bryden and Sprott (1981). It is the log-odds ratio of the responses to stimuli presented to each ear after stimulus dominance has been controlled statistically. By definition, positive values are indicative of REAs.

Appendix U: Waterloo Handedness Questionnaire - Revised

Name: ______________________________ Age: ______ Sex **M** **F**

Instructions: Please indicate your hand preference for the following activities by circling the appropriate response. If you **always** (i.e. 95% or more of the time) use one hand to perform the described activity, circle **Ra** or **La** (for **right always** or **left always**). If you **usually** (i.e. about 75% of the time) use one hand circle **Ru** or **Lu** as appropriate. If you use both hands **equally often** (i.e. you use each hand about 50% of the time),circle **Eq**

1. Which hand would you use to adjust the volume knob on a radio?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
2. With which hand would you use a paintbrush to paint a wall?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
3. With which hand would you use a spoon to eat soup?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
4. Which hand would you use to point to something in the distance?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
5. Which hand would you use to throw a dart?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
6. With which hand would you use the eraser on the end of a pencil?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
7. I which hand would you hold a walking stick?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
8. With which hand would you use an iron to iron a shirt?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
9. Which hand would you use to draw a picture?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
10. In which hand would you hold a mug full of coffee?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
11. Which hand would you use to hammer a nail?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
12. With which hand would you use the remote control for a TV?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
13. With which hand would you use a knife to cut bread?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
14. Which hand would you use to turn the pages of a book?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
15. With which hand would you use a pair of scissors to cut paper?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
16. Which hand would you use to erase a blackboard?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
17. With which hand would you use a pair of tweezers?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
18. Which hand would you use to pick up a book?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
19. Which hand would you use to carry a suitcase?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
20. Which hand would you use to pour a cup of coffee?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
21. With which hand would you use a computer mouse?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
22. Which hand would you use to insert a plug into an outlet?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
23. Which hand would you use to flip a coin?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
24. With which hand would you use a toothbrush to brush your teeth?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
25. Which hand would you use to throw a baseball?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
26. Which hand would you use to turn a doorknob?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
27. Which hand do you use for writing?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
28. Which hand would you use to pick up a piece of paper?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
29. Which hand would you use a hand saw?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
30. Which hand would you use to stir a liquid with a spoon?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
31. In which hand would you hold an open umbrella?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
32. In which hand would you hold a needle while sewing?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
33. Which hand would you use to strike a match?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
34. Which hand would you use to turn on a light switch?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
35. Which hand would you use to open a drawer?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
36. Which hand would you use to press buttons on a calculator?	**La**	**Lu**	**Eq**	**Ru**	**Ra**

37. Is there any reason (i.e. injury) why you have changed your hand preference for any of the above activities?
YES/NO (circle one)

38. Have you been given special training or encouragement to use a particular hand for certain activities?
YES/NO (circle one)

39. If you have answered YES for either Questions 37 or 38, please explain:

Appendix V: Waterloo Footedness Questionnaire - Revised

Name: ______________________________ Age: _____ Sex **M** **F**

Instructions: Answer each of the following questions as best you can. If you always use one foot to perform the described activity, circle **Ra** or **La** (for **right always** or **left always**). If you **usually** use one foot circle **Ru** or **Lu**, as appropriate. If you use **both** feet **equally often**, circle **Eq**. Please do not simply circle one answer for all questions, but imagine yourself performing each activity in turn, and then mark the appropriate answer. If necessary, stop and pantomime the activity.

1.	Which foot would you use to kick a stationary ball at a target straight in front of you?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
2.	If you had to stand on one foot, which foot would it be?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
3.	Which foot would you use to smooth sand at the beach?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
4.	If you had to step up onto a chair, which foot would you place on the chair first?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
5.	Which foot would you use to stomp on a fast-moving bug?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
6.	If you were to balance on one foot on a railway track, which foot would you use?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
7.	If you wanted to pick up a marble with your toes, which foot would you use?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
8.	If you had to hop on one foot, which foot would you use?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
9.	Which foot would you use to help push a shovel into the ground?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
10.	During relaxed standing, people initially put most of their weight on one foot, leaving the other leg slightly bent. Which foot do you put most of your weight on first?	**La**	**Lu**	**Eq**	**Ru**	**Ra**

11. Is there any reason (i.e. injury) why you have changed your foot preference for any of the above activities? **YES** **NO** (circle one)

12. Have you ever been given special training or encouragement to use a particular foot for certain activities? **YES** **NO** (circle one)

13. If you have answered **YES** for either question 11 or 12, please explain:

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