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Estimation of Interhemispheric Dynamics from Simple Unimanual Reaction Time to Extrafoveal Stimuli

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This essay reviews research on interhemispheric transfer time derived from simple unimanual reaction time to hemitachistoscopically presented visual stimuli. Part 1 reviews major theoretical themes including (a) the significance of the eccentricity effect on interhemispheric transfer time in the context of proposed underlying neurohistological constraints; (b) the significance of gender differences in interhemispheric transfer time and findings in dyslexics and left-handers in the context of a fetal brain testosterone model; and (c) the significance of complexity effects on interhemispheric transfer time in a context of "dynamic" vs. "hard-wired" concepts of the underlying interhemispheric communication systems. Part 2 consists of a meta-analysis of 49 published behavioral experiments, in view of drawing a portrait of the best set of experimental conditions apt to produce salient, reliable, and statistically significant measures of interhemispheric transfer time, namely (a) index rather than thumb response, (b) low rather than high target luminance, (c) short rather than prolonged target display, and (d) very eccentric rather than near-foveal stimulus location. Part 3 proposes a theoretical model of interhemispheric transfer time, postulating the measurable existence of fast and slow interhemispheric channels. The proposed mechanism's evolutionary adaptive value, the neurophysiological evidence in its support, and favorable functional evidence from studies of callosotomized patients are then presented followed by proposals for critical experimental tests of the model.

KEY WORDS: interhemispheric; corpus callosum; simple reaction time; commissure; normal human

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INTRODUCTION

This essay answers to three distinct objectives. The first objective, dealt with in Part 1, consists of reviewing the present state of advancement of theoretical models of interhemispheric relay effects in the normal human subject using simple reaction time. A major review article published by Bashore in the *Psychological Bulletin* (1981) is now 12 years old. Because a large number of studies driven by new themes, generating interesting theoretical models, have since been published, it is judged that the time has come for a new review. This will establish that this field of research has matured into a theoretically driven domain and therefore that carrying out further research is worthwhile. Part 2 of this essay will comprise a review of the major methodological issues that have been of concern. A large number of studies have now been published varying only in minute aspects of their methodology. Nevertheless, to this day, experimenters are still having difficulty obtaining salient, reliable, and statistically significant visual-field/responding-hand interactions. Since the latter are a basic methodological prerequisite for model building in this domain, it seems important that the issue be dealt with in detail. To this end, Part 2 consists of a meta-analysis of the numerous relevant methodological details of published studies. The objective of Part 2 is to provide the basis for a proposal for a set of guidelines designed to maximally ensure obtention of salient, reliable, and statistically significant field/hand interactions in future experimental studies. The third objective of this essay, dealt with in Part 3, is an attempt at a theoretical contribution in and of itself. A general dynamic model of interhemispheric transfer time is drawn from the reviewed literature. The model is then articulated in terms of relevant data, namely evolutionary adaptiveness of the proposed mechanism, recent critical findings in callosal neurophysiology, and certain functional findings in callosotomized patients. Finally, critical experimental tests of the model are proposed.

PART 1. THE STATUS OF THE SIMPLE REACTION TIME PARADIGM IN MODELS OF INTERHEMISPHERIC RELAY

The idea of inferring the time it takes for a neural message to cross the corpus callosum using reaction time dates back to Poffenberger (1912). The basic inference is as follows. Since the visual and distal motor projections are both contralateral, responses of the hand ipsilateral to the stimulated visual field (the uncrossed pathway) ought to be faster than responses of the hand contralateral to the stimulated visual field (the crossed pathway), and this *crossed-uncrossed differential* (subtraction of reaction time in the uncrossed condition from reaction time in the crossed condition) ought to correspond to the time it takes for the neural message to cross the corpus callosum. Nearly a hundred investigations have now addressed the issue of whether this basic inference is sound. Though it has become apparent that crossed-uncrossed differentials cannot be assimilated to interhemispheric transfer time in any simple or uniform manner, there is general agreement that paradigms involving presentation of brief laterally emplaced unpatterned visual stimuli and unimanual finger response to detection represent the most appropriate behavioral approach to the interhemispheric transfer time inference (see Milner, 1986).

Response-choice reaction time paradigms make the interhemispheric transfer time inference more tenuous than do simple reaction time paradigms because they are complicated by numerous powerful effects that may mask or distort crossed-uncrossed differentials. For example, contrary to simple reaction time paradigms, crossed-uncrossed differentials derived from complex reaction time paradigms are subject to highly significant effects of the type of cognitive categorization required (Filbey and Gazzaniga, 1969; McKeever *et al.,* 1975), or of the type of motor response required (Hedge and Marsh, 1975; Simon *et al.,* 1981). Contrary to simple reaction time paradigms, they also manifest significant effects of responding hand emplacement to the right or left of body midline, i.e., spatial compatibility effects (Wallace, 1971). Finally, crossed-uncrossed differentials obtained in response-choice paradigms appear to be extremely variable. They range from significantly negative (Green, 1984) to positively prolonged beyond any reasonable account of synaptic and axonal relay time in the interhemispheric commissures (Amadeo *et al.,* 1977; Filbey and Gazzaniga, 1969; McKeever *et al.,* 1975). Simple reaction time paradigms have never yielded a significantly negative crossed-uncrossed differential (as measured by the Visual Field × Responding Hand interaction in analysis of variance). The majority of the crossed-uncrossed differentials reported from simple reaction time experiments have been statistically significant and positive (2–5 msec). See Tables I–III.

That the interhemispheric transfer time inference has withstood the test of time (and of large-scale experimentation) in the domain of *simple* reaction time is extremely important. Indeed, this inference is one of very few, if not the only one, which affords a paradigm whereby brain dynamics can be modeled and tested in anatomically localized subcircuits of the brain in something approximating real space and real time. In other words, the interhemispheric transfer time inference is a major tool of present day behavioral modeling of neurodynamic information processing. However, consideration of the entire set of published experiments (or close to it) using

Table I.

Authors and date of publication	General reaction time (msec)	Finger used to respond	Stimulus luminance	Hand emplacement
Distefano *et al.* (1980)	198	Thumb	1000 μ cd	Lateral
	223	"Hand"	1000 μ cd	Lateral
McKeever and Hoff (1983)	251	Index	29.12 cd/m^2	Lateral
	255	Index	29.12 cd/m^2	Lateral
	241	Index	29.12 cd/m^2	Lateral
Tassinari *et al.* (1983)	193	Thumb	1000 μ cd	Lateral
McKeever and Hoff (1979)	253	Thumb	49.67 cd/m^2	Center
	273	Thumb	49.67 cd/m^2	Center
Jeeves and Dixon (1970)	237	?	?	Lateral
	220	?	?	Lateral
Berlucchi *et al.* (1977)	187	Thumb	?	Lateral (uncrossed)
	189	Thumb	?	Lateral (uncrossed)
	194	Thumb	?	Lateral (uncrossed)
	186	Thumb	?	Lateral (crossed)
	188	Thumb	?	Lateral (crossed)
	193	Thumb	?	Lateral (crossed)
Anzola *et al.* (1977)	206	Thumb	?	Lateral (uncrossed)
	206	Thumb	?	Lateral (crossed)
Berlucchi *et al.* (1971)	239	Index	?	Lateral
	246	Index	?	Lateral
	253	Index	?	Lateral
Milner *et al.* (1982)	293	Index	5.1×10^{-2} μ W/deg^2	Central
	247	Index	2.3×10^{-3} μ W/deg^2	Central (?)
	210	Index	9.4×10^{-5} μ W/deg^2	Central (?)
Milner and Lines (1982)	212	Thumb	.05 μ W/deg^2	Central
	555	Thumb	.05 μ W/deg^2	Central
	261	Thumb	.05 μ W/deg^2	Central
	443	Thumb	.05 μ W/deg^2	Central
Lines and Milner (1983)	276	Index	9.4×10^{-5} μ W/deg^2	Central
	284	Index	9.4×10^{-5} μ W/deg^2	Central
	292	Index	9.4×10^{-5} μ W/deg^2	Central
	301	Index	9.4×10^{-5} μ W/deg^2	Central
Jeeves (1969)	228	?	?	Central
Rizzolatti (1979)	210	Thumb	28 cd/m^2	Lateral
	269	Thumb	28 cd/m^2	Lateral
	208	Thumb	28 cd/m^2	Lateral

Table I. Continued

Authors and date of publication	General reaction time (msec)	Finger used to respond	Stimulus luminance	Hand emplacement
St.-John *et al.* (1987)	248	Index	30 cd/m^2	Central
	254	Index	30 cd/m^2	Central
	270	Index	30 cd/m^2	Central
Lines *et al.* (1984)	252	Index	140 cd/m^2	Central
	265	Index	7 cd/m^2	Central
Saron and Davidson (1989)	256	Index	19.7 cd/m^2	Lateral
Clarke and Zaidel (1989)	326	Index	.63 cd/m^2	Central
	296	Index	54.5 cd/m^2	Central
	300	Index	3.9 cd/m^2	Central
	316	Index	3.9 cd/m^2	Central
Levy and Wagner (1984)	214	Thumb	?	Lateral
	213	Thumb	?	Lateral
	217	Thumb	?	Lateral

simple unimanual reaction time to extrafoveal stimuli reveals a number of substantial challenges to the now antiquated and untenable inference that the crossed-uncrossed differential *is* interhemispheric transfer time in any uniform manner, or that there is nothing new or important left to discover in this field: First, though these behaviorally measured crossed-uncrossed differentials are much more uniform than those obtained from complex reaction time experiments, they are not uniform enough to be considered to reliably reflect a pathway-length difference, as currently interpreted. Nonsignificant, and even negative crossed-uncrossed differentials have often been reported in groups of normal subjects despite large numbers of stimulations (see Table I); the range of magnitudes of these crossed-uncrossed differentials is from −.05 msec to 15.1 msec (see Table III). Second, evoked potential latencies to visual stimulation in humans consistently reveal statistically significant crossed-uncrossed differentials over the occipital lobes, but these have always been substantially longer (11–15 msec) than those typically observed in the behavioral data (typically 2-5 msec). The crossed-uncrossed differentials obtained over central electrode emplacements have generally fallen short of statistical significance but have corresponded to the general range of duration of behavioral crossed-uncrossed differentials (Lines *et al.*, 1984; Rugg, Lines, and Milner, 1984; 1985; Rugg, Milner, and Lines, 1985). Saron and Davidson (1989) were the first to determine the extent to which evoked potential latency crossed-uncrossed differentials and reaction time latency crossed-uncrossed differentials are correlated. They found no correlation at occipital leads despite the fact that the behavioral and evoked potential latency crossed-uncrossed differentials were both statistically significant. Third, the anatomical inference generally proposed, to date, to explain the crossed-uncrossed differential in simple visual reaction time (i.e., callosal relay time) may have been precipitous. It is now known that there are extracallosal visual interneurons between the two lateral geniculate bodies, between the two superior colliculi, between the two pretectal nuclei, and between the temporal lobes (see Fig. 1 and subsequent sections for details of this issue).

Table II.

Authors and date of publication	Stimulus duration (msec)	Stimulus eccentricity (arc degrees)	Finger lift or press	Blocked or random stimulus hemilocation
Distefano *et al.* (1980)	5	15	Press	Random
	5	15	Lift	Random
McKeever and Hoff (1983)	100	6.5	Press	Random
	100	6.5	Press	Random
	100	6.5	Press	Random
Tassinari *et al.* (1983)	5	5	Press	Random
McKeever and Hoff (1979)	150	2.4	Press	Random
	150	2.4	Press	Random
Jeeves and Dixon (1970)	2	70	Lift	Blocked (?)
	2	70	Lift	Blocked (?)
Berlucchi *et al.* (1977)	5	5	Press	Blocked
	5	20	Press	Blocked
	5	5	Press	Blocked
	5	5	Press	Blocked
	5	20	Press	Blocked
	5	35	Press	Blocked
Anzola *et al.* (1977)	100	5	Press	Random
	100	5	Press	Random
Berlucchi *et al.* (1971)	32	5	Press	Blocked
	32	20	Press	Blocked
	32	35	Press	Blocked
Milner et al. (1982)	2	4	Lift	Random
	2	4	Lift	Random
	2	4	Lift	Random

Table II. Continued

Authors and date of publication	Stimulus duration (msec)	Stimulus eccentricity (arc degrees)	Finger lift or press	Blocked or random stimulus hemilocation
Milner and Lines (1982)	2	16	Press	Random
	2	16	Press	Random
	2	16	Press	Random
	2	16	Press	Random
Lines and Milner (1983)	2	5	Lift	Random
	2	1	Lift	Random
	2	2	Lift	Random
	2	4	Lift	Random
Jeeves (1969)	2	70	Press	Blocked
Rizzolatti (1979)	50	5	Press	Random
	50	5	Press	Random
	50	5	Press	Random
St.-John *et al.* (1987)	32	2	Press	Random
	32	5	Press	Random
	32	15	Press	Random
Lines *et al.* (1984)	5	4	Press	Random
	5	4	Press	Random
Saron and Davidson (1989)	10	2.8	Lift	Blocked
Clarke and Zaidel (1989)				
	35	4	Press	Random
	35	4	Press	Random
	35	4	Press	Random
	35	10	Press	Random
Levy and Wagner (1984)	250	8	Press	Blocked
	250	8	Press	Blocked
	250	8	Press	Blocked

Any one of these circuits could, in principle, be responsible for the crossed-uncrossed differential instead of the corpus callosum, and perhaps even to the exclusion of the striate cortex. The superior colliculus, for example, is known to contain much of the circuitry necessary for the orienting response at least in subhuman species. Simple visual reaction time is indeed not much more than an orienting response. Fourth, simple vocal reaction time and simple unimanual reaction time to unpatterned light stimuli produce crossed-uncrossed differentials that are uncorrelated (Kleinman *et al.*, 1976), suggesting again that it has been naive to think that there is a single inter-

Table III.

Authors and date of publication	Number of stimuli	Target size in arc degrees	Handedness of subjects	Crossed-uncrossed difference	Probability that field × hand interaction due to chance[a]
Distefano *et al.* (1980)	1440	.66 × .66	Right	2.8	.04 (?)
	1440	.66 × .66	Right	2.5	.07 (?)
McKeever and Hoff (1983)	312	4.5 × 20	Right	2.5	.05
	312	4.5 × 20	Left (ni)	4.2	.03
	312	4.5 × 20	Left (i)	0.6	NS
Tassinari et al. (1983)	160	.66 × .66	Right	2.9	.05
McKeever and Hoff (1979)	324	.3 × .3	Left (ni)	2.6	.007
	324	.3 × .3	Left (i)	−0.6	NS
Jeeves and Dixon (1970)	300	?	Right	3.6	NR
	300	?	Right	3.0	NR
Berlucchi *et al.* (1977)	160	3 × 3	Right	4.5	NR
	160	3 × 3	Right	13.5	NR
	160	3 × 3	Right	15.1	NR ↑
	160	3 × 3	Right	7.0	NR .005
	160	3 × 3	Right	10.0	NR ↓
	160	3 × 3	Right	11.5	NR
Anzola *et al.* (1977)	1600	.4 × .4	Right	11.0	.03 (?)
	1600	.4 × .4	Right	7.5	.03 (?)
Berlucchi *et al.* (1971)	120	1 × 1	Right (?)	3.0	NR ↑
	120	1 × 1	Right (?)	2.1	NR .01
	120	1 × 1	Right (?)	4.5	NR ↓
Milner *et al.* (1982a)	600	.03 × .03	Right	1.9	NR ↑
	600	.03 × .03	Right	1.4	NR .01
	600	.03 × .03	Right	1.7	NR ↓
Milner and Lines (1982)	480	.03 × .03	Right	−0.6	NR
	480	.03 × .03	Right	13.5	.01
	480	.03 × .03	Right	3.9	NS
	480	.03 × .03	Right	11.0	.01
Lines and Milner (1983)	600	.03 × .03	Right (?)	2.4	NR ↑
	600	.03 × .03	Right (?)	1.3	NR .0005
	600	.03 × .03	Right (?)	2.0	NR ↓
	600	.03 × .03	Right (?)	3.4	NR
Jeeves (1969)	600	?	Right	2.8	.005 (?)
Rizzolatti (1979)	800	.67 × .67	Right	−0.5	NS
	800	.67 × .67	Right	2.5	NS
	800	.67 × .67	Right	2.5	NS

Table III. Continued

Authors and date of publication	Number of stimuli	Target size in arc degrees	Handedness of subjects	Crossed-uncrossed difference	Probability that field × hand interaction due to chance[a]
St.-John *et al.* (1987)	1920	1 × 1	Right	4.6	NR
	1920	1 × 1	Right	5.1	NR
	1920	1 × 1	Right	5.4	NR
Lines *et al.* (1984)	420	.03 × .03	Right	−0.1	NR .05
	420	.03 × .03	Right	3.6	NR ↓
Saron and Davidson (1989)	400	3.66 × 2.93	Right	10.3	NS
Clarke and Zaidel (1989)	400	03 × .03	Right	−.05	NS
	400	03 × .03	Right	2.1	NS (?)
	400	03 × .03	Most right	2.1	.01 (?)
	400	03 × .03	Most right	3.5	.01 (?)
Levy and Wagner (1984)	480	?	Right	2.0	$< .05$
	480	?	Left (ni)	2.3	$< .05$
	480	?	Left (i)	1.7	$= .05$

[a] NS: not significant; NR: not reported; ni: non-inverted; i: inverted.

hemispheric relay mechanism that should be reflected as a uniform time interval, or in other words as an invariant crossed-uncrossed differential.

The leading figures in crossed-uncrossed differential research have been aware of several of these problems, as well as many others, and have designed experiments to manipulate or isolate parameters that might reliably influence crossed-uncrossed differentials derived from simple reaction time, and that could then somehow explain why results have been so inconsistent in the past. In all, at least 49 such experiments have been published based on unimanual responses to simple detection of extrafoveal targets using reasonably large groups of well-defined normal subjects (see Tables I–III). Certain subsets of these studies can be viewed as forming the basis for theoretical models of interhemispheric transfer of information, and the following pages will present the three themes that appear to the author to hold the most promise.

Toward a Neurohistological Model of Interhemispheric Transfer

The eccentricity of stimuli relative to the central fixation point addresses a key theoretical issue in the interpretation of the anatomical sig-

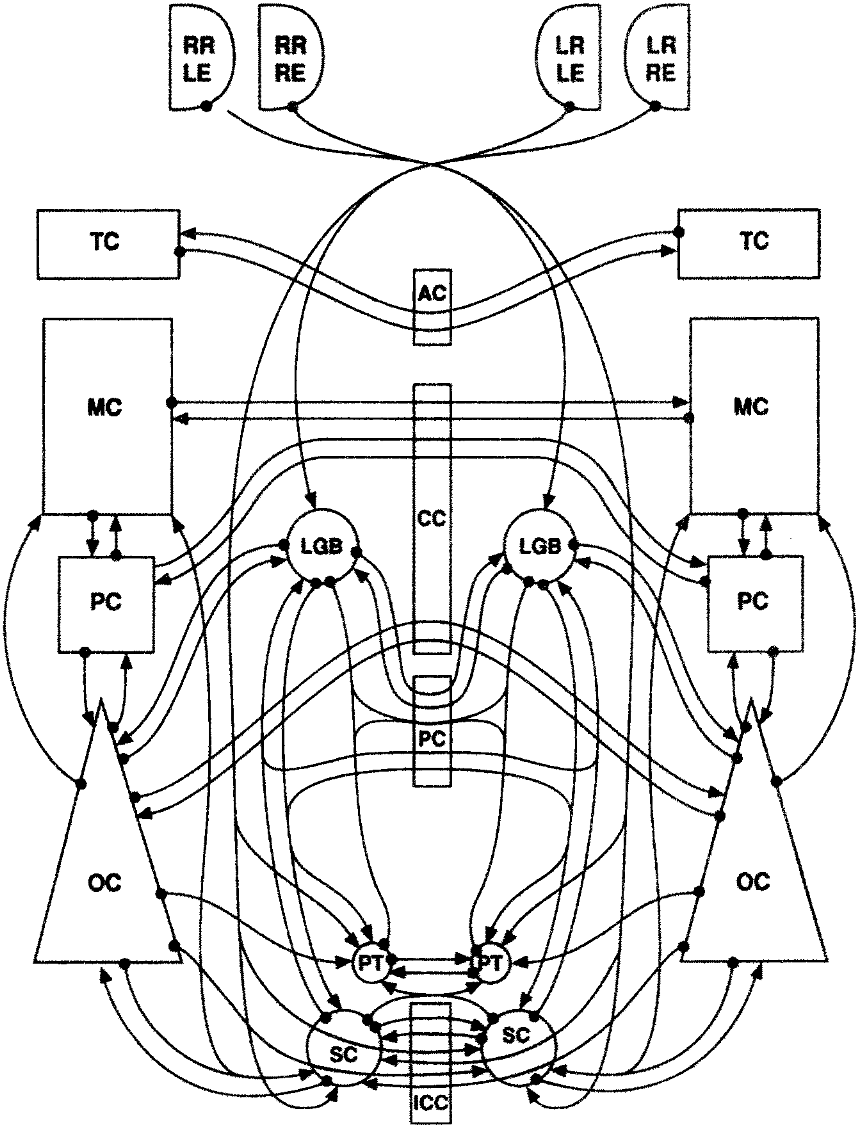

Fig. 1. Wiring diagram of known connections in mammalian brain that could most plausibly contribute to crossed-uncrossed differential effects in normal, callosal agenesic and callosotomized humans (RR, LR: right or left retina; RE, LE: right or left eye; TC: temporal cortex, MC: motor cortex; PC: parietal cortex; OC: occipital cortex; LGB: lateral geniculate body; PT: pretectum; SC: superior colliculus; AC: anterior commissure; CC: corpus callosum; PC: posterior commissure, ICC: intercollicular commissure).

nificance of crossed-uncrossed differentials. The splenium of the corpus callosum contains an overrepresentation of cortical afferants whose receptive fields are in or around the vertical meridian. It has therefore been argued that if the visual decussation is an important component of the crossed-uncrossed differential, then increasing eccentricity of targets ought to result in prolonged crossed-uncrossed differentials (Berlucchi *et al.*, 1971). Five studies have experimentally manipulated eccentricity in simple reaction time paradigms in normal subjects. All of these reported massively *increased* crossed-uncrossed differentials as a function of stimulus eccentricity (see Table I). Only the study by St.-John and colleagues (1987), however, obtained this effect beyond the usual .05 alpha level of significance. Absence of a *significant* effect of eccentricity has been interpreted (prior to the paper by St.-John and colleagues) to mean that a motor component, rather than a visual component, is the critical one underlying the crossed-uncrossed differential. However, the effect of increasing eccentricity on the crossed-uncrossed differential, though usually nonsignificant, was always proportionately greater (20–30%) than the effect on general reaction time (5–10%), which was usually found to be statistically significant. This is a typical example of researchers, in this field, having been prevented from supporting their own predictions, and even of having been misled to incorrect alternative interpretations, because of high variability of the crossed-uncrossed differential. Aglioti and colleagues (1991) recently investigated a wider range of eccentricity, from 1° to 70°. They did not obtain a significant field/hand/eccentricity interaction, and unfortunately did not report the crossed-uncrossed differentials in each eccentricity condition.

Toward a Fetal Brain Testosterone Model of Interhemispheric Transfer

Most studies have used only male subjects or a large majority of male subjects. Only two studies were designed to test sex differences in relation to crossed-uncrossed differentials derived from simple reaction time. St.-John *et al.* (1987) found that women had significantly longer positive crossed-uncrossed differentials (5.9 msec) than men (4.1 msec; $p <$ .01). They also found that the crossed-uncrossed differentials of women were much more variable than those of men. These effects were not replicated by Clarke and Zaidel (1989), however, who found no significant effect of gender on the crossed-uncrossed differential. Unfortunately, the direction of trends was not reported. Aglioti and colleagues (1991) compared 12 men and 12 women and did not obtain a significant field/hand/sex interaction nor did they report the crossed-uncrossed differentials for each sex. We (Dufresne *et al.*, 1992) looked at sex differences in a simple visual reaction time paradigm and found that the crossed-uncrossed differential was indeed prolonged in 21 women (2.6 msec) relative to 21 men (.8 msec; $p < .03$). The issue of a basic sex difference of the crossed-uncrossed differential is important for neuropsychology. Indeed, the most commonly replicated finding with regard to sex differences in callosal dimensions is that men's callosi are significantly larger, overall, than women's, even when measured proportionally to total brain size (Witelson, 1990). This predicts the finding of St.-John and colleagues reviewed above. Witelson argues that the sex difference in callosal anatomy is probably determined by fetal brain testosterone infusion. It is interesting in such a context to consider that dyslexia, interpreted in an extended context of the Geschwind–Galaburda model of fetal brain testosterone dynamics (Geschwind and Galaburda, 1985), could be predicted to be associated with excessively brief crossed-uncrossed differentials. This is precisely what has been reported by Davidson *et al.* (1990). They found that degree of dyslexia in boys was significantly negatively correlated to the crossed-uncrossed differential in a simple visual reaction time task. This finding is coherent with the magnetic resonance imaging (MRI) findings of Duara and colleagues (1991) to the effect that dyslexics have larger callosal spleniae than nondyslexics. The Geschwind–Galaburda model also relates fetal brain testosterone to increased risk for left-handedness. This may be germane to the fact that inverted left-handers (left-handers who write with a flexed hand) consistently manifest shorter crossed-uncrossed differentials than do right-handers (Levy and Wagner, 1984; McKeever and Hoff, 1979, 1983). Recent large scale MRI findings are accruing in support of the notion that left-handers have larger callosi than right handers (Habib *et al.*, 1991). The direction of these findings can be explained by a notion whereby increased fetal brain testosterone would favor increased callosal size, faster interhemispheric relay, dyslexia, and inverted left-handedness. To consolidate what might be emerging as a testosterone model of interhemispheric transfer time, one could test predictions of brief interhemispheric transfer times in male stutterers, in individuals who had high fetal testosterone, or in people with large callosi.

This whole issue is further complicated by the very recent finding (Aboitiz *et al.*, 1992) of no histological differences between the sexes in the human corpus callosum. It is possible that prenatally fixed testosterone effects on the crossed-uncrossed differential result from differences in circuits *adjacent* to callosal neurons.

Toward a Dynamic Model of Interhemispheric Transfer

The effects of task complexity within simple (or relatively simple) reaction time experiments are of critical theoretical importance. Indeed, two clearly articulated and mutually incompatible positions have been taken on this issue. Rizzolatti (1979) stated that the crossed-uncrossed differential derived from simple reaction time ought to be invariant, or in other words, impervious to experimental manipulation. He believed, at least at the time, that the crossed-uncrossed differential is nothing other than a pathway-length difference. Other authors have assumed that interhemispheric relay is essentially dynamic, comprising fast and slow channels, inhibitory and excitatory channels, etc., and have not precluded such modulation from being expected to occur even in simple reaction time experiments (Clarke and Zaidel, 1989). Furthermore, it has often been noted that more complex reaction time paradigms tend to yield markedly prolonged crossed-uncrossed differentials. Several authors have speculated from this that increased task complexity reflects itself in the interhemispheric communication system, thereby causing prolonged crossed-uncrossed differentials (Bashore, 1981; Zaidel, 1983). Moscovitch (1986) has even proposed that it is the late parts of information processing that are more responsible for crossed-uncrossed differential effects, and he also implied that task complexity ought to, in principle, prolong the crossed-uncrossed differential. However, though many experiments have been carried out, looking at crossed-uncrossed differentials in complex reaction time experiments comprising varying degrees of complexity, surprisingly few have dealt with the issue using simple reaction time.

Simple detection of targets is so easy that subjects can be asked to carry out concurrent mental operations without inordinate error rates occurring. The use of tasks concurrent to simple reaction time represents an interesting approximation to a test of a complexity effect because the contamination of the "test" by stimulus-response coding artefacts is precluded. In the study carried out by Milner *et al.* (1982), concurrent mental tasks more than doubled general simple reaction time and more than tripled the crossed-uncrossed differential. Unfortunately, though the Visual Field × Responding Hand interaction was significant, the authors did not carry out, or did not report, a test of the significance of the Visual Field × Responding Hand × "Complexity" interaction. It is assumed that had the interaction been significant, the authors would probably have reported it. In a study by Rizzolatti *et al.* (1982), general reaction time was not remarkably prolonged by a concurrent task, the crossed-uncrossed differentials were small and nonsignificant, and the Visual Field × Responding Hand × "Complexity" interaction was also nonsignificant. Unfortunately, in this report, the data were not presented in such a manner as to determine whether crossed-uncrossed differentials were actually prolonged or shortened as a function of "complexity."

Though go/no-go paradigms are more complex than the ideal (which is the simple reaction time paradigm) for testing hypotheses about interhemispheric transfer time, the absence of stimulus-response relation contaminants in such paradigms justifies their review in this section. In a study reported by Umilta and colleagues (1985), subjects had to respond, or abstain from responding, to concrete or abstract words, or imageable or nonimageable words, with or without a concurrent motor task. The Visual Field × Responding Hand × "Complexity" interactions did not reach significance, or were not reported, and the data were not presented in a manner permitting determination of whether the crossed-uncrossed differential was prolonged or shortened as a function of "complexity." However, in another study reported by Umilta and colleagues (1972), these relevant data were presented. In experiment one, a go/no-go task required the subject to respond (or not) to, and discriminate, one letter, two-letter, and three-letter displays. The crossed-uncrossed differentials in each of these conditions were 2.6, 2.4 and 0.1 msec, respectively. These were all nonsignificant, however, and the test of a Visual Field × Responding Hand × "Complexity" interaction was not reported. Mean reaction times in these three conditions steadily increased (as has been reported many times) as a function of "complexity." Reaction times were 474, 627, and 654 msec, respectively.

Finally, there is another very indirect means by which to judge whether "complexity" influences the duration of the crossed-uncrossed differential. If one accepts the assumption that within simple reaction time paradigms, more complex tasks will prolong overall reaction time, then one will feel safe to meta-analyze the literature in view of making the determination of interest. A meta-analysis was carried out on all 49 of the published studies found (see Table I), which investigated interhemispheric transfer time using simple reaction time. It revealed that general reaction time, which varied considerably from one experiment to another, was only mildly positively related to the crossed-uncrossed differential ($r = .13$, ns).

In short, the direction of the effects on the crossed-uncrossed differential suggests little basis for believing that crossed-uncrossed differentials are prolonged as a function of increasing complexity. The evidence for and against the "cable" and "dynamic systems" models of interhemispheric transfer is very incomplete and inconclusive at this stage. A critical test of the hypothesis of a complexity effect on interhemispheric transfer time must comprise (a) a highly significant effect of complexity on general reaction time, (b) significant field–hand interactions at each level of complexity, or at least experimentwise, and (c) then and only then, the critical presence or absence of a field–hand–complexity interaction.

PART 2: METHODOLOGICAL ISSUES IN THE INVESTIGATION OF INTERHEMISPHERIC TRANSFER TIME

The next pages comprise a systematic review of 49 published experiments, all of which derived a crossed-uncrossed differential from simple unimanual reaction time to hemitachistoscopic stimuli. The focus of this review is methodological. Its purpose is to outline the experimental conditions that are most apt to yield salient, reliable, and statistically significant crossed-uncrossed differentials, in view of orienting future research in the field. This is judged necessary because researchers in the field are still having difficulty obtaining robust crossed-uncrossed differentials. To this end, a simple meta-analytical procedure will be applied: whenever possible, a product-moment correlation between the crossed-uncrossed differential and any given experimental parameter will be reported, and in some instances commented. The methodological options that are unambiguously promising will be reviewed in decreasing order of importance, as determined post hoc by the correlation coefficients. Subsequently, special issues that cannot be reduced to such a simplistic constraint will be discussed in more detail. Because none of the parameters reviewed can be considered "independent," or in other words, because intervening variables are probably operating beneath any such correlation coefficient, Tables I–III provide the actual data from which coefficients are drawn. This will enable the reader to carry out his or her own analyses answering to special needs in each case.

Which Finger Should be Used for Responding?

Of the 49 experiments reviewed, 22 used a *thumb* response, 23 used an *index* finger response, and 4 did not specify. The use of the index finger, rather than the *thumb*, substantially prolonged the crossed-uncrossed differential ($r = .35$; see Table I).

Which Stimulus Intensity Should Be Used?

It is now well known that increased stimulus luminance generally shortens simple reaction time. Three studies were designed to manipulate stimulus intensity in simple reaction time paradigms (Clarke and Zaidel, 1989; Lines *et al.*, 1984; Milner and Lines, 1982). Though a significant decreases in reaction time resulted from increasing stimulus intensity, there was no trend whatsoever for the crossed-uncrossed differential to be correspondingly shortened. Meta-analysis of the published studies reporting stimulus luminance (rather than illumination, which is less relevant) revealed that increased luminance was mildly related to shorter crossed-uncrossed differentials ($r = -.29$; see Table I). For this meta-analysis, all reported luminances were converted to the candelas per square meter scale of measurement (Pokorny *et al.*, 1979). This relation could be due to uncontrolled reflection or diffusion of light to the unintended hemifield, effects that are more likely to occur with bright than dim stimuli.

Where Should the Responding Hand be Emplaced?

In choice reaction time experiments, responding hand emplacement lateral to body midline significantly shortens choice reaction time when stimuli are presented in the hemifield corresponding to (compatible with) the responding hand, and significantly prolongs it when stimuli and responses are in noncorresponding (incompatible) relation. This effect holds even when the hands are crossed (Wallace, 1971). However, in two simple reaction time experiments this effect was tested and did not occur (Anzola *et al.*, 1977; Berlucchi *et al.*, 1977). Furthermore, contrary to what occurred in Wallace's experiment, general reaction time was not significantly affected by crossing or uncrossing the hands nor was the crossed-uncrossed differential (see Table I). Meta-analysis revealed that *lateral* vs. *central* emplacement of the responding hand was, in fact, mildly related to the magnitude of the crossed-uncrossed differential ($r = .25$). Emplacement of the responding hand was blocked (i.e., fixed for large sets of trials) in all of these experiments. Central hand emplacement (which was always in front of body midline) produced slightly larger crossed-uncrossed differentials than lateral hand emplacement (see Table I). Central hand emplacement is all the more advisable to the extent that were spatial compatibility to operate, central hand emplacement would preclude it a priori.

Which Stimulus Duration is Advisable?

Stimulus duration has a nonlinear effect on reaction time within the testable range. Simple reaction times are shortest to stimuli of approximately 50–90 msec, and become increasingly prolonged as a function of shortening or lengthening of stimulus durations (Kaswan and Young, 1965; Raab *et al.*, 1961). No published investigation has yet comprised experimental manipulation of stimulus duration in view of understanding its impact on the crossed-uncrossed differential. Meta-analysis of these experiments, which comprised a wide range of stimulus durations (see Table II), revealed a mild negative correlation ($r = -.22$) between stimulus duration and the crossed-uncrossed differential. Another meta-analysis was done to determine whether this relation could, within the range of stimulus durations used in this particular literature, be due to a negative relation between stimulus duration and overall reaction time. The relation ($r = -.15$) was too mild to support such a notion.

How Eccentric Should Targets Be?

It was shown in Part 1 that experimental manipulation of target eccentricity (horizontal distance from fixation point in arc degrees) reveals a relation of increasing eccentricity with increasing duration of the crossed-uncrossed differential. Meta-analysis (see Table II) revealed that stimulus eccentricity has in fact been mildly related ($r = .2$) to the crossed-uncrossed differential.

Which Type of Finger Movement Should be Selected?

There are two dimension of the finger response that have been used independently of each other across experiments, and these are finger lift and finger press. The effect of these two types of finger response was manipulated experimentally by DiStefano and colleagues (1980), producing no differential effect. Of the 49 experiments reviewed, 38 used a finger *press* as the response and 11 used a finger *lift* (or "release"). Meta-analysis (see Table II) suggests that the finger lift tended, mildly, to prolong the crossed-uncrossed differential ($r = .16$).

Should Hemilocation of Targets be Blocked or Randomized?

The issue of whether the subject can expect the stimulus to occur in a hemifield is of critical importance for two reasons. First, in principle, blocking of target locations in one hemifield could make central fixation difficult for certain subjects and could then possibly weaken experimental effects by increasing reaction time variance generally. Second, one hemisphere could be selectively and increasingly aroused by being the first to receive initial input from each stimulus. This in turn could affect intrahemispheric and interhemispheric dynamics in a number of ways. Of the

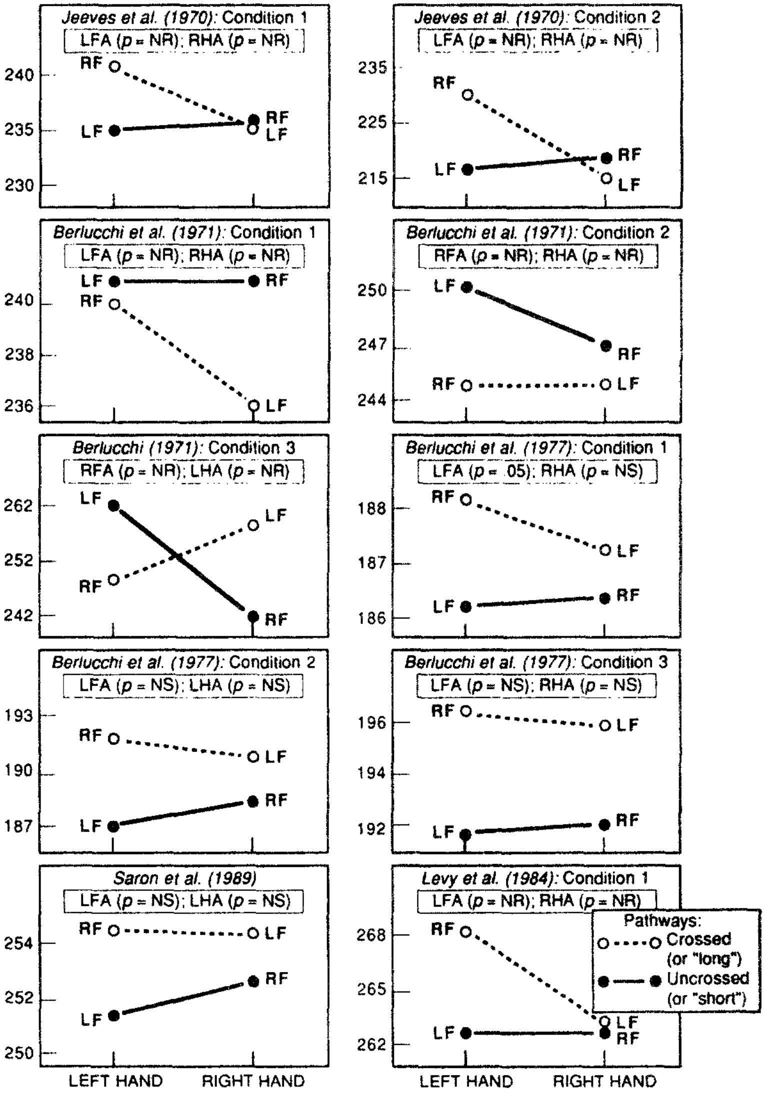

Fig. 2. Mean simple reaction times of groups of normal subjects to extrafoveal stimuli with unimanual response. These experiments comprised large blocks of stimulations within one hemifield rather than the usual random alternation of target hemilocation. (NS: nonsignificant; NR: not reported; LFA; RFA: left or right field advantage, LHA; RHA: left- or right-hand advantage).

49 published experiments reviewed here, 16 used a blocking design, 33 used a randomized design, and 2 did not specify. The relationship between this particular dimension and the crossed-uncrossed differential was impressive

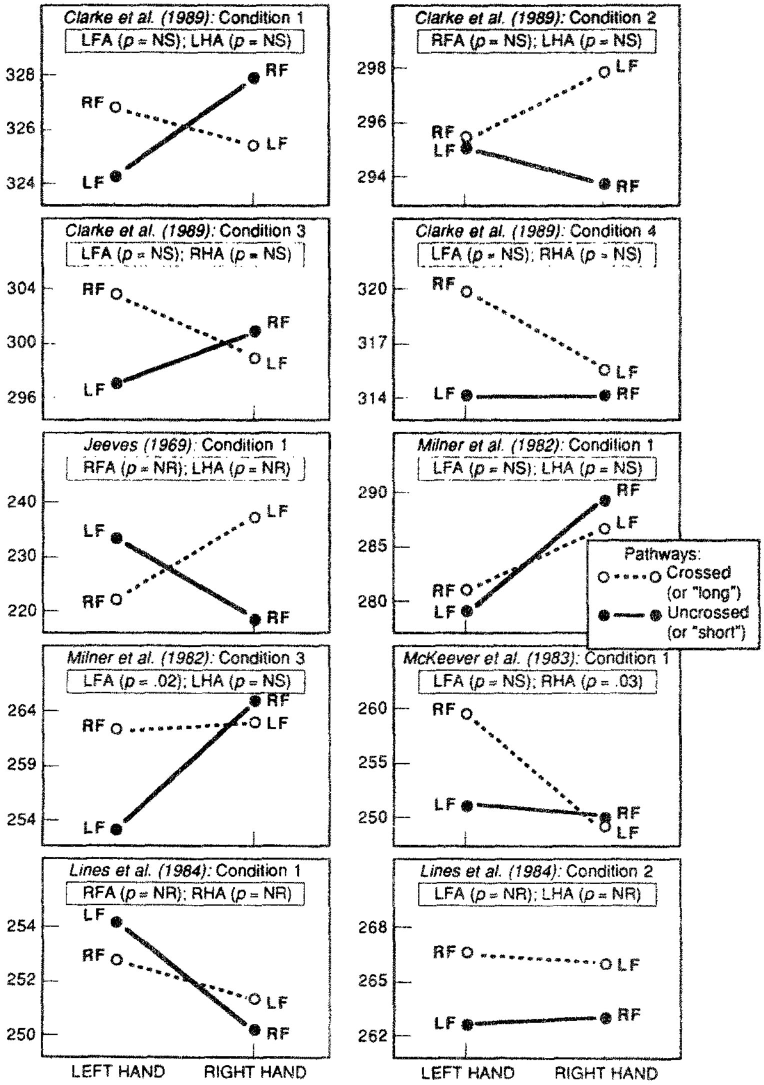

Fig. 3. Mean simple reaction times of groups of normal subjects to extrafoveal stimuli with unimanual centrally emplaced finger and randomly distributed (unpredictable) stimulus hemilocation (NS: nonsignificant; NR: not reported, LFA, RFA: left or right field advantage, LHA, RHA: left- or right-hand advantage).

($r = .29$). Blocking of stimulus location in a field tended to result in greater crossed-uncrossed differentials (see Table II).

If the effect of blocking were to introduce an advantage of one hemisphere over the other, this could conceivably result in Visual Field or Responding Hand effects, which could in turn affect crossed-uncrossed differentials. However, inspection of the relevant data points of six studies (eight experiments) having blocked stimulus location (see Fig. 2) reveals that Visual Field and Responding Hand advantages tended not to be significant and were not much different from patterns observed in experiments comprising randomized stimulus location (see Fig. 3). In short, even though blocking of targets in the hemifields appears inelegant, a priori, it seems effective a posteriori, in producing salient crossed-uncrossed differentials. It seems plausible that blocking stimulus location might reduce overall variance of reaction time because subjects are attentionally focused on a very small segment of space. This in turn could play a role in favoring significant emergence of the crossed-uncrossed differential.

This has now been tested experimentally. Aglioti and colleagues (1991) administered a blocked design to 12 subjects, and a random design to 12 other subjects. Reaction times in the blocked design were briefer, as expected ($p = .01$) but the magnitudes of the crossed-uncrossed differentials did not differ significantly from one condition to the other. The reliability of each crossed-uncrossed differential was unfortunately not reported.

How Many Trials Are Required?

It can be expected that increasing numbers of trials would, of course, increase significance levels of experimental effects. Aside from this obvious though nevertheless important consideration, it is also possible that practice effects, fatigue, or other motivational effects could alter the crossed-uncrossed differential over time, defining, in combination with the logistic difficulty of repeated testing, the limit of advisability of extending numbers of trials. This issue has been addressed experimentally by St.-John *et al.* (1987). They found no effect of numerous repeated sessions over different days. Meta-analysis (see Table II) gives an indication of whether or not number of trials, within a session, affects the crossed-uncrossed differential. There was in fact no relationship between number of trials and the crossed-uncrossed differential ($r = -.03$). Similarly, there was no relation between number of trials and significance level of the visual Field × Responding Hand interaction ($r = -.07$). Despite this, one should probably not conclude that large numbers of trials are entirely futile in this type of research. For example, whereas other studies failed to obtain significant eccentricity effects and sex differences on the crossed-uncrossed differential, St.-John and colleagues (1987), whose study comprised by far the largest number of trials, succeeded.

What Is an Appropriate Target Size in Retinal Coordinates?

Target size means very little in the absolute, though it could, in principle, relate to perceived luminance. To estimate whether size of the stimulus at the retina has any effect, the stimulus dimension in square arc degrees is probably the most relevant index. This dimension has never been manipulated experimentally in studies designed to investigate the crossed-uncrossed differential. One would expect that retinal image size should relate to reaction time in a manner similar to stimulus luminance. Meta-analysis (see Table III) revealed, however, that retinal size was not at all related to general reaction time ($r = 0.04$) or to the crossed-uncrossed differential ($r = -.07$).

Should Left-Handers Be Excluded?

It was mentioned in Part 1 that inverted left-handers consistently produce much smaller crossed-uncrossed differentials than noninverted left-handed or right-handed subjects (Levy and Wagner, 1984; McKeever and Hoff, 1979, 1983). It has become customary in all fields of neuropsychological research to screen out left-handers. However, in this particular field, such screening may be imperative.

PART 3: A NEW MODEL OF INTERHEMISPHERIC TRANSFER—DIFFERENTIALLY SPEEDED (EXCITATORY) CHANNELS

Visual Field and Responding-Hand Advantages and Their Effects on the Crossed-Uncrossed Differential: The State of the Literature

It seems commonly believed that Visual Field and especially Responding Hand effects (other than crossed-uncrossed differentials) are rare in simple reaction time experiments, and that when they do occur, they are of little significance in the interpretation of brain dynamics (Sergent, 1982). Researchers interested in the crossed-uncrossed differential, who have used simple unimanual reaction time to extrafoveal stimuli, have perforce used Visual Field and Responding Hand advantages to estimate what they have considered the best measure of interhemispheric transfer time, namely, the crossed-uncrossed differential. It has generally been accepted that the best statistical test of the existence of a crossed-uncrossed differential is a significant Visual Field × Responding Hand interaction in analysis of variance. It is also generally assumed that a Visual Field effect at one hand cannot be considered, in and of itself, to reflect interhemispheric transfer time because such an effect cannot be distinguished from a Visual Field effect pure and simple. In other words, such an effect could be a hemispheric dominance effect, which has nothing to do with interhemispheric relay. While this is undoubtedly true, the analysis of Visual Field effects at each hand can be interpreted, beyond the limited notion of pure Visual Field effects, if and when they are analyzed in relation to each other as well as to additional parameters such as experimentwise Visual Field effects (i.e., main effects) and Responding Hand main effects. Unfortunately, not all experiments reviewed included reports of the mean reaction times at each hand and for each field. Many studies did not test the main effects of field or hand. Only *a very few* reports included *post hoc* tests of crossed-uncrossed differentials occurring at each hand. Finally, and most importantly, no author has looked at the relationship between field main effects or hand main effects and crossed-uncrossed differentials at each hand. Because all of the authors reviewed have not focused on, or have neglected, detailed aspects of field and hand effects on crossed-uncrossed differentials, the fact that massive *negative* crossed-uncrossed differentials (briefer reaction times along the "long" pathway than along the "short" pathway) frequently occur at one hand but not the other has been entirely overlooked.

The following sections will establish the hitherto unreported fact that strong universally observable predictions can be made concerning crossed-uncrossed differentials on the basis of Visual Field main effects. In subsequent sections, a functional-anatomic explanation of how and why the valence of crossed-uncrossed differentials, occurring at each hand, can be predicted from Visual Field main effects, will be provided. In addition, it will be shown that Responding Hand main effects play a non-negligible role in the magnitude of the experimentwise crossed-uncrossed differential, and a functional-anatomic explanation of this will also be provided.

Meta-Analysis of Main Effects of Field and Their Relation to Crossed-Uncrossed Differentials at Each Hand

A useful way to understand field and hand effects in any experiment is to graph all the means in a standard format representing the body in terms of hands (the left hand on the left side of the figure and the right hand on the right side). Thus the viewer-reader can represent to him- or herself the subject's body during the experiment. It is also useful to connect crossed (or long) pathways together and uncrossed (or short) pathways together in a manner different for each of the two (say, a dotted line for crossed pathways vs. a continuous line for uncrossed pathways). This helps the reader-viewer visualize crossed-uncrossed differentials, and even immediately spot a negative crossed-uncrossed differential (i.e., a faster response in the uncrossed condition than in the crossed condition), to determine relative magnitude of crossed-uncrossed differentials at each hand, and to estimate the extent of field and hand main effects (see Figs. 2 and 3).

Figure 3 illustrates, in this manner, the results obtained from experiments representing the basic (purest) paradigm involving unimanual detection reaction time to extrafoveal stimuli in right-handed normal subjects. In these experiments there were no concurrent tasks. The responding hand was placed in front of the subject at body midline and the stimulus hemilocation was unpredictable (random).

The main empirical points that are worth drawing from these data are the following: (1) One of ten experiments yielded a significant (left) experimentwise Visual Field advantage, and another, a significant (right) experimentwise Responding Hand advantage. (2) Seven of 10 experiments obtained a negative crossed-uncrossed differential at one or the other hand. (3) One experiment even produced a negative crossed-uncrossed differential that was larger at one hand than the positive crossed-uncrossed differential obtained at the other hand.

Two postulates, with apparently universal application, emerge from these data:

Postulate 1

The crossed-uncrossed differential is always larger (or more positive) at the hand ipsilateral to the field advantaged, whether the field advantage (main effect) is significant or not, and whether it is left or right.

Postulate 2

When there is a significant main effect of field ($p < .02$) there is always a negative crossed-uncrossed differential at the hand contralateral to the field advantaged.

Of course these statements seem preposterous in the context of the "classical" interhemispheric transfer time/crossed-uncrossed differential inference where crossed-uncrossed differentials would be expected to be positive and of same magnitude at each hand. The above 10 experiments should perhaps not be considered sufficient to revise the classical interhemispheric transfer time/crossed-uncrossed differential inference in favor of Postulate 1 and 2. Consequently, we shall review results of 4 experiments similar to the above except for the fact that the responding hand was emplaced laterally to body midline—a condition that is not supposed to affect the crossed-uncrossed differential in simple reaction time experiments (Anzola and colleagues, 1977, Experiment 1; DiStefano and colleagues, 1980, Experiments 1 and 2, and Tassinari and colleagues, 1983). Again one experiment produced a significant left Visual Field advantage and another a significant right Responding Hand advantage. However, another experiment produced a highly significant left Responding Hand advantage. Postulates 1 and 2 are further upheld by these data.

Fourteen experiments are still insufficient to support Postulates 1 and 2 in their general, or even universal, pretention. We shall therefore review the data of ten experiments similar to the previous sets except for the fact that hemilocation of stimuli was blocked, that is, known to the subject (Berlucchi and colleagues, 1971, Experiments 1–3, and 1977, Experiments 1–3; Jeeves, 1969; Jeeves and Dixon, 1970; Levy and Wagner, 1984; Saron and Davidson, 1989). There was only one report of a significant (left) Visual Field advantage ($p < .02$) and none of a significant Responding Hand advantage. Postulates 1 and 2 are further supported on the basis of these data.

Because crossing of the responding hands so markedly affects field and hand effects in choice-reaction time experiments, 4 such experiments carried out in conditions of simple stimulus detection are reviewed next (Anzola and colleagues, 1977, Experiment 2; Berlucchi and colleagues 1977, Experiments 4–6). Only one significant (left) Visual Field advantage is reported. Postulates 1 and 2 are both further supported by these data.

It is conceivable that by means of a concurrent task strategy, Visual Field and/or Responding Hand advantages may be enhanced, or perhaps even reversed, by using verbal or visuospatial concurrent tasks, or vice versa. Five such experiments were reviewed (Milner and colleagues, 1982, Experiments 2 and 4; Rizzolatti and colleagues, 1982, Experiments 1–3). All of these experiments, except condition 3 of the study by Rizzolatti and colleagues (1982), were designed to enhance the left Visual Field advantage. It seems that (left) Visual Field advantages may indeed have been enhanced since 3 of 5 experiments yielded highly significant ($p < .02$) such effects. In addition, however, one left and one right Responding Hand advantage reached significance. Postulates 1 and 2 are again further strongly supported by these data.

Since left-handers, particularly those who write with an inverted (i.e., flexed) hand, are known to manifest patterns of lateralized behavior that are different from right handers, 3 experiments using "inverted" and 3 experiments using "noninverted" left-handed subjects were reviewed (Levy and Wagner, 1984, Experiments 2 and 3; McKeever and colleagues, 1979, Experiments 1 and 2, and 1983, Experiments 2 and 3). Two experiments, both using "noninverted" left-handers, yielded a highly significant (left) Visual Field advantage ($p < .02$). One experiment produced a significant (left) Responding Hand advantage. Postulates 1 and 2 receive further support from these data.

It is now established that patients with callosal agenesis are usually capable of interhemispheric transfer, albeit in many cases somewhat slowed in simple reaction time experiments. Several commissures have been postulated to contribute to the observed crossed-uncrossed differentials in these subjects. The group data of Ettlinger and colleagues (1972) and cases B. F., M. M., S. F., and K. C., published in separate reports (Clarke and Zaidel, 1989; Kinsbourne and Fisher, 1971; Lines, 1984; Milner *et al.*, 1985), also basically support Postulates 1 and 2. Negative crossed-uncrossed differentials occurred at the hand contralateral to the Visual Field advantage, on three occasions, and the crossed-uncrossed differential at the hand ipsilateral to the Visual Field advantage was more positive in all cases. Even surgically callosotomized patients manifest relatively well-preserved ability to produce a unimanual response to a lateralized light flash. The overall crossed-uncrossed differential of these patients is greatly prolonged, however, relative to the normal range (Smith, 1947; Sergent and Myers, 1985). It is interesting that even the cases reported by these authors, all of whom manifested right Visual Field advantages, produced the greatest crossed-uncrossed differential at the hand ipsilateral to the crossed-uncrossed differential. The study by Smith presented group data of 5 cases of "complete callosotomy," one of which also received a section of the anterior commissure. The study by Sergent and Myers presented individual data from 2 patients both of whom received "complete forebrain commissurotomy." It is presumed that in addition to the corpus callosum, the anterior and posterior commissures were sectioned as well.

In short, Postulates 1 and 2 have been supported by all the experiments reviewed. Postulate 2 states that negative crossed-uncrossed differentials "produced by" significant Visual Field advantages can result from "right" as well as "left" field advantages. The trends certainly support this idea. Unfortunately, no *significant* experimentwise *right* Visual Field advantage has yet been reported in the crossed-uncrossed differential studies. However, a study by Braun and Daigneault (1993) does report a highly significant experimentwise right Visual Field advantage in normal subjects in a simple visual reaction time experiment. The crossed-uncrossed differentials were significantly negative at the left hand and significantly positive at the right hand, as predicted from Postulates 1 and 2. This double dissociation is, as of yet, the strongest single experimental demonstration of the importance of Postulates 1 and 2.

It is worthy of note that significant Responding Hand main effects occurred sufficiently frequently in the 49 experiments reviewed to determine whether such effects can be used to predict at which hand positive and negative crossed-uncrossed differentials will occur. It is very clear that they cannot. This suggests that the modulation of valences of the crossed-uncrossed differentials, at each hand, is caused by hemispheric specialization at the receptive (i.e., visual) level, reflected in Visual Field main effects.

This suggestion has to be tempered, however, by an extraordinary finding that emanated from another meta-analysis of the same 49 studies. The correlation between the magnitude of the experimentwise crossed-uncrossed differential and the magnitude of the experimentwise Visual Field advantage was unremarkable ($r = .1$). However, the correlation between the magnitude of the experimentwise crossed-uncrossed differential and the magnitude of the experimentwise Responding Hand advantage was highly significant ($r = .6$). This is all the more impressive in light of the fact that the experimentwise Visual Field advantage was completely unrelated to the experimentwise Responding Hand advantage ($r = .0$). This suggests that whereas the valence of crossed-uncrossed differentials at each hand is strongly determined by hemispheric specialization for receptive aspects of the task (reflected in Visual Field effects), the magnitude of the overall crossed-uncrossed differential is more strongly determined by hemispheric specialization for the executive aspects of the task (reflected in Responding Hand effects).

Toward a Dynamic Model of Interhemispheric Transfer Time: Differentially Speeded (Excitatory) Channels

The simplest interpretation of the ensemble of these results, and of the evoked potential studies as well, is the following. There are fast and slow channels from each side of the brain to the other. When neither hemisphere is specialized for reception of the stimuli, the slow channel is selected by each hemisphere. When one hemisphere is highly specialized for reception, it strongly funnels its own processing through the fast channel. As the task proceeds, the other hemisphere funnels its own processing through its slow channel, to varying degrees. The degree to which neurons

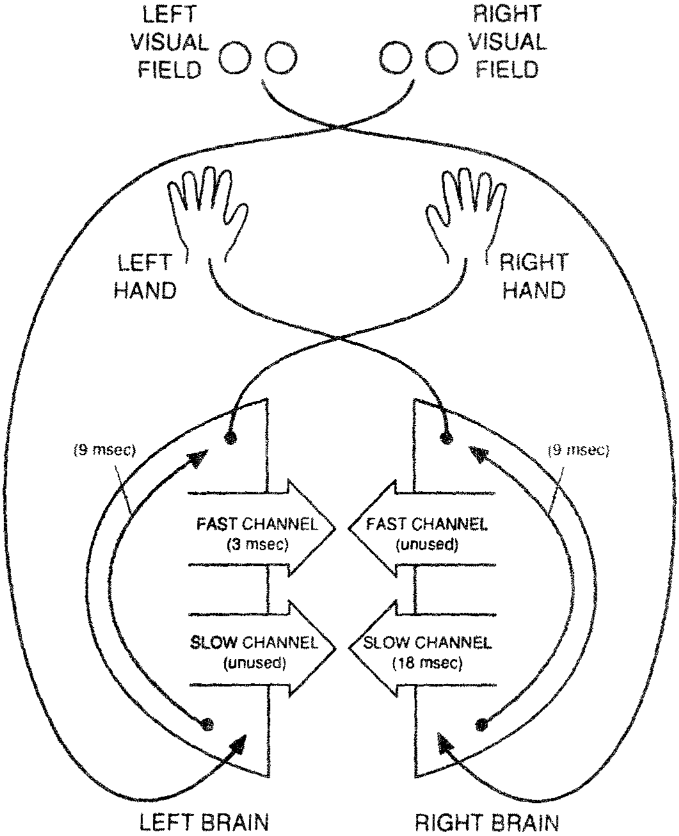

Fig. 4. Schematic representation of the differentially speeded channel model proposed in the present investigation, comprising fast and slow interhemispheric relay channels—including a simulation of lags that could account for the results of condition 1 of the Clarke and Zaidel (1989) study (see Fig. 3) that clearly manifest presence of a positive crossed-uncrossed differential at one hand, and of a negative crossed-uncrossed differential at the other hand.

from the slow channel are selectively exploited by the "nonspecialized" hemisphere is weaker and more variable than the selection of fast channel neurons by the "specialized" hemisphere. This is so because the selection of these fast and slow neurons in the nonspecialized hemisphere is ultimately under the control of the specialized hemisphere. This selection occurring in the nonspecialized hemisphere is therefore controlled by a more complex and remote circuit than the selection occurring in the specialized hemisphere. This selection process, modulating relay from the nondominant to the dominant hemisphere, probably takes time to "build up" as the experiment progresses and this in turn probably makes the corresponding crossed-uncrossed differential more variable (sometimes negative, sometimes positive). To explain *negative* crossed-uncrossed differentials with this model, it is necessary to postulate that the *fast* callosal channel can be *faster* than the connections between the relevant visual and motor processors *within* the dominant hemisphere (or brain side). To illustrate how this model would apply to empirical results, Fig. 4 simulates schematically how these callosal channel lags could be represented, relative to intrahemispheric lags, to depict the result obtained in the study by Clarke and Zaidel (1989), the data of which are also presented in Fig. 3.

The Functional and Adaptive Significance of Differentially Speeded Channels

Primates in general and humans in particular are required to engage in rapid synchronized bimanual responding under visual guidance (grabbing, placing, catching, etc.). In such circumstances, it is obviously adaptive for the two hands to respond synchronously, so that they will arrive on target at the same time. However, initial components of the visuomotor response can be (and often are, at least in humans) specialized (i.e., processed more quickly) in one hemisphere. It would be adaptive for the brain to slow down the hand controlled by the dominant (faster) hemisphere, and/or speedup the hand contralateral to the dominant hemisphere—if a synchronized bimanual response is required. It seems likely that such a mechanism is quite automatic and relatively rigid (hard-wired). Indeed, a bimanual coordination impairment seems one of the most, if not *the* most, salient and permanent deficit resulting from callosotomy and even from callosal agenesis. Long-term studies of the former (Zaidel and Sperry, 1977) and of the latter (Jeeves, 1979) suggest as much. These studies as well as many others (Chiarello, 1980; Dennis, 1976; Ferris and Dorsen, 1975; Field *et al.*, 1978; Gordon *et al.*, 1971; Mark and Sperry, 1968; Jeeves *et al.*, 1988; Preilowsky, 1972, 1975; Reynolds and Jeeves, 1974) strongly suggest that of the numerous interhemispheric commissures, the corpus callosum may be the critical one for this particular mechanism. These studies also suggest that the corpus callosum is most heavily involved in bimanual responses that are (a) under a heavy time pressure in the sense that they must be executed very rapidly, (b) under visual guidance, and (c) are not heavily overlearned.

On the other hand, we have seen that studies of agenesic and callosotomized humans show that negative crossed-uncrossed differentials can and do occur at one hand in a manner similar to normals. This suggests that the anatomical-functional circuitry subtending the modulation of unimanual reaction time by differentially speeded channels might be more plastic than that subtending bimanual coordination.

An Alternative Explanation of Differentially Speeded Channels in Terms of Interhemispheric Inhibition

A negative crossed-uncrossed differential at one hand could be explained, in principle, as an inhibitory interhemispheric influence of the nondominant hemisphere on the motor output of the dominant hemisphere. Several authors have expressed a belief in the plausibility of callosal inhibition (Dennis, 1976; Gazzaniga and Hillyard, 1973; Jeeves, 1983; Zaidel, 1986). Preilowski (1972, 1975), investigating bimanual coordination in anterior callosotomy cases, even came to the conclusion that "the predominant flow of inhibitory impulses through the intact commissures is from the right *(non-dominant)* to the left *(dominant)* hemisphere" (1945, p. 125, our italics). Several authors have interpreted slow simple reaction times at the dominant hand as an effect of intrahemispheric inhibition of visual processing within the dominant hemisphere upon motor output of the same hemisphere. However, their subjects were commissurotomized and they did not fully consider the other commissures, carrying differentially speeded channels, which may have been responsible for the effect (Gazzaniga and Hillyard, 1973, Murofushi, 1975). The differentially speeded channel model appears, however, more promising than accounts based on inhibition in three respects: (1) It is more parsimonious because interplay of excitatory and inhibitory callosal or intrahemispheric relay would require more complex circuitry than differentially speeded excitatory channels (2) if one hemisphere is specialized for a task, then it should also dominate for interhemispheric channel selection required by the task; the differentially speeded channel model is compatible with this notion whereas a system of inhibition from the nondominant hemisphere suggests dominance of that hemisphere for selection of inhibitory callosal relay (3) none of the cited authors provide any anatomical evidence of the existence of direct callosal inhibition per se; a subsequent section will show that there is evidence of total or near complete absence of direct inhibitory action of callosal neurons.

Implications of Human Evoked Potential Findings in the Context of the Differentially Speeded Channel Model

This differentially speeded channel model also accounts for the main findings of the evoked potential investigations of the crossed-uncrossed differential. One of these studies is particularly relevant to the present discussion. Lines *et al.* (1984) submitted normal subjects to a simple reaction time task and used bright stimuli (140 cd/m^2) in one of the conditions. They recorded negative peaks at approximately 160 msec (N160 wave) at lateral-central and lateral-occipital sites. Mean latency of N160 at the central electrode sites was 140.9 msec, and was 163.5 msec (delta = 22.6 msec) at the occipital sites. The crossed-uncrossed differential for the same wave at the central sites was 2.8 msec, and was 11 msec at the occipital sites. These general effects have been roughly replicated in conditions of dim targets (Lines *et al.*, 1984), and also using go/no-go tasks (Lines *et al.*, 1984; Rugg *et al.*, 1984; Rugg *et al.*, 1985). The occipital findings have been roughly replicated by Andreassi *et al.* (1975) and Saron and Davidson (1989), and have been extended to the P1 wave (positive wave at approximately 125 msec). These findings are in agreement with the model proposed above. More specifically, they are compatible with the idea that "fast" callosal channel activity is picked up at lateral central electrode sites, and that "slow" callosal channel activity is picked up at the lateral occipital electrode sites. Viewed in this manner, the results of the ensemble become compatible with the ensemble of the behavioral literature based on simple reaction time. They also illustrate that a "fast" interhemispheric channel (as indexed by delays between central lateral sites) can be much faster than an intrahemispheric pathway of equal length (i.e., activity picked up at central vs. occipital electrode sites). These findings provide a heuristic basis for thinking about how apparently absurd negative crossed-uncrossed differentials (according to classical models) may in fact be quite meaningful.

The value of the evoked potential findings must, however, be regarded, with much caution, as no more than heuristic. Evoked potentials recorded at the scalp provide very ambiguous indexes of brain dynamics. They probably require synchronized recurrent firing of thousands of neurons. The sources of evoked potential waves can be very remote from the scalp location at which they are first seen or have highest amplitude. The P1 and N160 waves of the visual evoked potential are a prime example of such. The information required for transferring a preplanned stereotyped reaction time could conceivably be relayed through the brain by a few hundred neurons, the activity of which might never be picked up by scalp recordings.

Anatomical Evidence in Support of the Differentially Speeded Channel Model

The differentially speeded channel model proposed above is supported by findings from animal and human research on commissural neuron and circuit anatomy and function. The human corpus callosum contains large diameter myelinated neurons and small diameter unmyelinated neurons (Swadlow *et al.*, 1979; see also recent quantitative findings in the rhesus monkey by Lamantia and Rakic, 1990). Swadlow and Waxman (1979) found that the range of diameters of rabbit callosal neurons was 20 to 1, indicating a range of total volume of 400 to 1. Presence of qualitatively differing neurons in the corpus callosum would also support a notion of differing functional channels. Indeed, the corpus callosum contains pyramidal and stellate cells (Naporn *et al.*, 1984). Electron microscopy of stained and/or degenerated callosal neurons and of the attenuant input and output synapses has revealed that both synapses are exclusively (or nearly exclusively) of the excitatory rather than inhibitory anatomical type (Cipolloni and Peters, 1983; Swadlow and Waxman, 1979). There are also cortical axonal collaterals, in small numbers that project homotopically and heterotopically to the contralateral hemisphere as well as projecting ipsilaterally within the hemisphere of origin. Heterotopic decussation includes projection from visual cortex to contralateral motor cortex (O'Leary *et al.*, 1981; Schwartz and Goldman-Rakic, 1982).

Physiological Evidence in Support of the Differentially Speeded Excitatory-Channel Model

Physiological investigations suggest that callosal potentials are exclusively excitatory. Furthermore, recordings of potentials subsequent to callosal relay suggest absence of direct inhibitory postsynaptic action. Though inhibitory influences are commonly observed beyond the first synapse, these are always of less amplitude and greater latency than excitatory influences (Ajmone-Marsan and Morillo, 1963; Hossman, 1975; Tomaya *et al.*, 1974). It has been concluded therefore that inhibitory postsynaptic potentials occur only beyond the first postcallosal synapse (Asanuma and Okamoto, 1959; Matsunami and Hamada, 1984; Swadlow, 1979). An immunocytochemical survey failed to find any GABAergic neurons in the corpus callosum of the cat (Voigt *et al.*, 1988) leading the investigators to conclude that there are probably very few inhibitory neurons in the corpus callosum. Another recent investigation found that 50–74% of callosal neurons are glutamatergic in the cat, leading the investigators to the same conclusion (Conti *et al.*, 1988). A predominantly excitatory role of the corpus callosum has been proposed by Lassonde (1986). Her main argument is the callosal "amplification" effect of epileptic discharge. A fast channel subtending negative crossed-uncrossed differentials in simple reaction time should contain neurons manifesting a relay time (callosal stimulation to postsynaptic discharge) of 2 msec or less. Such neurons exist in the corpus callosum of the monkey (Matsunami and Hamada, 1984). Interestingly, these authors did not find relay times of more than 8 msec in over 242 callosal neurons. Shorter relay times (.7–1 msec) have been observed in the cat (Clare *et al.,* 1961). Another study reported even more relevant relay times, from striate stimulation to contralateral striate depolarization, in monkeys (Tomaya *et al.,* 1974). Mean relay time was a mere 2.03 msec. Swadlow and Waxman (1979) found that the range of variation of rabbit callosal neuron velocity was 40 to 1, supporting the idea that differentially speeded channels could certainly exist in the corpus callosum. All of these findings are compatible with the model proposed here, which limits its schematic to excitatory channels (without denying that interhemispheric inhibition most certainly exists in other conditions and situations including callosal excitation of inhibitory circuits).

Which Commissure(s) Might Most Likely Carry the Differentially Speeded Channels Observed in Simple Reaction Time?

Though most of the writing on behavioral crossed-uncrossed differentials in normal humans has emphasized, nearly exclusively, the corpus callosum as the inferred commissure, it remains fully pertinent to ask the following question: "What is the evidence for contribution(s) from each of the commissures to the crossed-uncrossed differential?"

The functional repertoire of neurons in the diencephalic commissures is not well known. It remains possible that visual and/or motor information may be relayed across the fornix, which connects mostly the hippocampi; Ganser's or Meynert's commissures, which connect the basal ganglia; Guddens's commissure, which connects the medial geniculate bodies; Forel's commissure, which connects the subthalamic nuclei; and the interhabenular commissure, which connects the habenular, septal, preoptic, and supraoptic nuclei.

The visuomotor role of neurons of the posterior commissure is well established and is very important in the present context. This commissure connects the lateral geniculate bodies and the superior colliculi, as well as visual neurons of the pulvinar (Nakamura and Kawamura, 1988). Despite its obvious relevance in the field of interhemispheric transfer of visual information, this commissure has been completely neglected. Reciprocal innervation of the pretectal nuclei has recently been demonstrated in the rat using a retrograde transport technique. The locus of the commissure remains unknown (Foster *et al.,* 1989). Visual neurons traverse the anterior commissure, which connects the anterotemporal cortex, uncus, and amygdala (Carpenter, 1972; Gross *et al.*, 1977). The basal telencephalic commissure connects basal regions of the telencephalon possibly including the pyriform and entorhinal cortices (Lamantia and Rakic, 1990).

Pretectal and/or collicular processing and relay of extrafoveal stimulation in the simple reaction time paradigm appears, however, to be the most plausible alternative to the callosal model usually proposed. There is reciprocal visual and motor innervation of the superior colliculi via the intercollicular commissure (Yamasaki *et al.*, 1984). Afferants from visual cortex to the contralateral superior colliculus also course through the intercollicular commissure (Bayleydier *et al.*, 1983). Each hemiretina projects to both superior colliculi (Antonini *et al.*, 1979). Receptive fields of collicular neurons are extrafoveal (Antonini *et al.*, 1979). There is clearly a strong contribution of the tectum to visual orienting responses, and other visual responses to brief flashes of light in subhuman mammals—including primates (Pasik and Pasik, 1982). The collicular system is activated preferentially by intense light stimuli, a property consistent with its pupillary role (Dean and Redgrave, 1984). Patients with postgeniculate lesions, including hemidecortication, can under forced-choice conditions localize extrafoveal stimuli. However, they are never aware of having seen these stimuli (Perenin and Jeannerod, 1975; Zihl and Werth, 1984). On the basis of near normal crossed-uncrossed differentials in human callosal agenesics (Ettlinger *et al.*, 1972; Kinsbourne and Fisher, 1971) or of only moderately prolonged crossed-uncrossed differentials (Clarke and Zaidel, 1989; Lines, 1984; Milner *et al.*, 1985; Reynolds and Jeeves, 1974), it has been proposed that an intertemporal relay via the sometimes hypertrophied anterior commissure, or an "intercollicular relay via the intercollicular commissure," could be invoked in such cases to explain the presence of crossed-uncrossed differentials. Further evidence for a collicular mechanism in these agenesic cases is the finding of a marked shortening of crossed-uncrossed differentials as a function of increasing stimulus intensity (Clarke and Zaidel, 1989; Milner *et al.*, 1985). The issue of the relative extent of callosal contribution (as opposed to midbrain contribution) to the crossed-uncrossed differential is addressed more directly by studies of surgically callosotomized patients. Callosal agenesis may result in a number of compensatory rewirings developed pre- or postnatally. If the crossed-uncrossed differential were entirely dependent on the corpus callosum in normals, then surgical callosotomy ought to abolish interhemispheric transfer altogether, at least in the short term after surgery. However, though the crossed-uncrossed differentials of callosotomized patients are markedly prolonged, even relatively to agenesics, these patients are nevertheless capable of detecting and responding to extrafoveal stimuli with the hand contralateral to the stimulus (the experiments were carried out, it must be noted, long after surgery however).

This competence is observed even in cases with surgical section of the anterior and posterior commissures in addition to the callosotomy (Clarke and Zaidel, 1989; Risse *et al.*, 1978; Sergent and Myers, 1985; Smith, 1947). Monkeys are also capable of responding with the paw contralateral to an eccentric stimulus even after section of the chiasm as well as the corpus callosum, though very slowly (Murofushi, 1975).

Where in the Brain Might the Processing Responsible for Differentially Speeded Channels in Simple Reaction Time Take Place?

Several lines of evidence reveal that a midbrain mechanism cannot suffice to support simple reaction time, and even less the crossed-uncrossed differential derived from it, especially in humans. Since Visual Field effects seem to play a critical role in modulation of the valence of the crossed-uncrossed differential at each hand, as demonstrated meta-analytically and experimentally in the preceding pages, and since Visual Field effects are generally believed to result from cortical activity, it would seem unlikely that the crossed-uncrossed differential could be *entirely* subcortically determined. Furthermore, collicular function has been shown to depend heavily on integrity of the corpus callosum. Antonini and colleagues (1979) sectioned the posterior two-thirds of the corpus callosum of split-chiasm cats and observed near complete elimination of activity of visual collicular neurons. Despite attempts to shape reaction time responses to light flashes, cortically blind patients are never able to produce a button press to a visual stimulus (Marzi *et al.*, 1986). Thus, visual cortex is indispensable for any visual reaction time. Furthermore, this cortical contribution to visual reaction time may depend heavily on modulation via the corpus callosum. As an indication of this possibility, visual cortical neurons ipsilateral to extrafoveal stimuli seem to remain silent after callosotomy in rats (Silveira *et al.*, 1989) and in cats (Dow and Dubner, 1971). Evoked potentials are massively dampened in human agenesics ipsilaterally to the stimulated field (Rugg *et al.*, 1985).

Sergent and Myers (1985) have proposed that some of the processing underlying the crossed-uncrossed differential may be subcortical, and some may be cortical. The normal brain probably responds indeed as a distributed network of multiple cortical and subcortical nodes diversely connected via several cortical and subcortical intrahemispheric pathways and interhemispheric commissures, the net result of which produces the Visual Field, Responding Hand, and Visual Field × Responding Hand effects observed to date in the behavioral investigations. During the 160–300 msec interval between a visual stimulus and a button press in normals, several million depolarizations have occurred, most of which are unrelated to the task. There are probably a number of (bidirectional) depolarizations of commissural fibers throughout the interval. Moscovitch (1983) and Marzi (1986) have proposed that relatively late commissural relay has the most impact on the crossed-uncrossed differential, and that this relay carries preprocessed visual information. Modulation of the crossed-uncrossed differential as a function of field advantages, as suggested by the present review, supports this argument.

Are Crossed-Uncrossed Differentials Determined by Sensory or Motor Processing?

Past arguments for the hypothesis of "motor" relay underlying crossed-uncrossed differentials have been centered on the absence of an effect of experimental manipulation of target eccentricity. However, it is now clear that this argument is unfounded. Anatomical studies indicate that there is no callosal connection for cortical motor neurons innervating the hand, only more axial musculature. Physiological studies, however, suggest that there may be such relay (Matsunami and Hamada, 1984). Simple reaction time experiments designed to investigate crossed-uncrossed differentials have always involved *distal* rather than *axial* responses. Results of evoked potential investigations showing shorter crossed-uncrossed differentials at central leads than occipital leads have been construed to suggest motor rather than visual transfer. However, given that the latencies of visual evoked potentials at central leads is much shorter than at occipital leads, the results should perhaps rather be construed to suggest *visual* transfer. On the other hand, were crossed-uncrossed differentials to be primarily "motor," then Responding Hand advantages could be expected, more than Visual Field advantages, to modulate them. This is indeed what seems to occur, at least at the level of the magnitude of the experimentwise crossed-uncrossed differential. It is therefore concluded that even though it may well be primarily the "motor" message that dominates in interhemispheric relay, the "visual" systems seem more specifically involved in selecting fast and slow interhemispheric channels than are "motor" systems.

Evidence of Motor Relay Through the Anterior Part of the Corpus Callosum

It has been proposed occasionally that interhemispheric relay underlying the overall crossed-uncrossed differential in simple reaction time consists of pre-processed motor commands traveling through the anterior part of the corpus callosum (Berlucci *et al.,* 1971; Milner and Lines, 1982). Though this may certainly be true, it has been argued above that the differential pattern of crossed-uncrossed differentials observed at each hand results from relay of *visual* information. There are now well-established demonstrations of the existence of tasks that clearly involve motor relay through the anterior corpus callosum. Tasks requiring rapid bimanual coordination of *different* movements at each hand, and that are minimally under visual control (i.e., which could in principle be carried out with eyes closed), have been demonstrated to depend heavily upon the supplementary motor area and to require relay via the anterior corpus callosum (Brinkman, 1984; Chan and Ross, 1988; Freund, 1987; McNabb *et al.,* 1988; Passingham, 1987; Porter, 1990; Tanji, 1987; Wiesendanger *et al.,* 1987). This does not remotely mean, however, that a unimanual detection response to an extrafoveal stimulus operates entirely through the same system. In fact, it appears more likely that it should not, at least as far as concerns its more dynamic aspects. However, there must be some motor processing involved in balancing out the speeds at which each hand responds to a visual stimulus, whether the response is unilateral or not, and this processing could indeed occur in the supplementary motor area or in other areas of motor cortex that also receive visual input. The cortical circuits subtending these effects are less well known than those subtending the bimanual coordination tasks. Furthermore, this particular effect (i.e., modulation of crossed-uncrossed differentials at each hand) is unlikely to lend itself well to animal research since it seems to depend upon hemispheric specialization—which is rarely encountered in animals.

Which Part of the Corpus Callosum Most Likely Carries Differentially Speeded Channel Effects Observed in Human Simple Reaction Time?

Marzi (1986) wrote an essay on the topic of interhemispheric relay in the context of simple reaction time and concluded that the midportion of the corpus callosum, connecting parietal cortex, is probably the most involved in visual transfer responsible for the (overall) crossed-uncrossed differential. If this issue is addressed in the context of modulation of crossed-uncrossed differentials at each hand by posterior cortex, relaying impulses via fast and/or slow commissural channels, the problem can be viewed with more nuance. Lamantia and Rakic (1990) have clearly demonstrated, in the monkey, that large caliber myelinated callosal axons are much more present in sensory areas, such as the splenium than associative areas such as the isthmus that contain a higher proportion of small caliber unmyelinated axons. Tomasch (1954) studied 3 human brains and found large axons (up to 6 microns) mostly in the splenium and just anterior to the splenium. The proportion of small axons (as small as 1.5 microns) was highest in the genu and rostrum. He also found that the proportion of myelinated fibers was consistently highest in the splenium. Microelectrode investigations suggest that motor relay across the corpus callosum seems slower than visual relay (Matsunami and Hamada, 1984; Tomaya *et al.*, 1974). It is therefore proposed that when there is no hemispheric specialization for a simple reaction time task, the normal brain is forced to use slow commissural channels located in the anterior corpus callosum, because the attentional task load requires frontal and parietal monitoring of extrafoveal space and distal motor activity. When the task gives a Visual Field advantage, the specialized hemisphere shuttles rapidly pre-processed information through fast channels that cross the splenium but project to contralateral motor cortex. Finally, it is proposed that since crossed-uncrossed differentials of callosal agenesics and callosotomized patients are modulated in the same way as normals as a function of Visual Field advantages, selection of fast and slow channels through the anterior commissure or collicular commissure must take place similarly to what occurs in normals' corpus callosi. This suggests that crossed-uncrossed differentials obtained from simple reaction time paradigms represent a net effect of functional neuronal-net activity that is quite plastic, probably because the function involved is important for the organism's adaptation to the environment. These functions might include stereopsis, i.e., vergence movements of the eyes, and other aspects of fine bilateral coordination of the two sides of the body.

Proposed Tests of the Differentially Speeded Channel Model

The most promising test of the validity of the model proposed here could consist of manipulation of stimulus intensity producing a double dissociation of intensity by field advantage accompanied by the predicted double dissociation of negative and positive crossed-uncrossed differentials. Two studies in particular (Clarke and Zaidel, 1989; Lines *et al.*, 1984) provide relevant data suggesting that intense luminance may produce right field advantages. Very dim (.63 and 7 cd/m^2, respectively) and very bright stimuli (54.8 and 140 cd/m^2, respectively) were presented in blocks of trials to a same cohort (see Tables I–III for further details). A right field advantage in the "bright" condition and a left field advantage in the "dim" condition were obtained in both studies (see Fig. 1: Clarke & Zaidel, 1989, conditions 1 [dim] and 2 [bright] and Lines *et al.*, 1984, conditions 1 [bright] and 2 [dim]). Unfortunately, probability levels of these particular effects were not reported in these studies. No other report including simple reaction times at each field as a function of stimulus luminance was found. However, Sergent (1982b) manipulated luminance in a face categorization task and also found that "bright" stimuli (38.20 cd/m^2) resulted in a *right* visual field advantage, and that "dim" stimuli (2.55 cd/m^2) resulted in a *left* visual field advantage (the Field × Luminance interaction was significant at $p = .05$). She concluded that "the left hemisphere was found to benefit more than the right hemisphere from an increase in luminance-dependent energy" (p. 222). Why would high and low luminance of targets in a simple reaction time paradigm favor the left and right hemispheres, respectively? A plausible answer to this question comes from the literature on right hemisphere attentional dominance in simple reaction time experiments. Heilman and Van Den Abell (1979) found that lateralized warning stimuli produced a right hemisphere (left hand) advantage of simple reaction time to a central stimulus when the warning stimuli were projected to the left visual field but did not produce a left hemisphere (right hand) advantage when projected to the right visual field. Activation of the normal right hemisphere was greater than of the left hemisphere in a sustained attention task as indexed by positron emission tomography scanning (Pardo *et al.*, 1991). Other studies using a slightly more complicated paradigm comprising valid and invalid lateralized warning cues have not obtained any field effect of cueing in normal subjects (Petersen *et al.*, 1989; Posner *et al.*, 1988). However, the target stimulus luminance in these latter two studies were unreported, and were probably greater than the extremely low target luminance (.1 cd/m^2) of the Heilman and Van Den Abell study. Though probabilistic cueing of hemitargets has not shown any effect of field when applied in the classical manner proposed by Posner and Cohen (1980), if the subjects are asked to maintain attention to one hemifield through blocks of trials, a left hemifield (right hemisphere) modulation of cueing effects emerges significantly more strongly than the modulation in the right hemifield (left hemisphere) (Proverbio and Bisiacchi, 1992). Finally, numerous studies have now shown that right hemisphere lesions, more than left hemisphere lesions, impair simple reaction time (Dee and Van Allen, 1971; Howes and Boller, 1975; Tartaglione *et al.*, 1986; Tartaglione *et al.*, 1987), and compromise attentional effects of cueing on simple reaction time even more than they do simple reaction time itself (Baynes *et al.*, 1986; Ladavas *et al.*, 1989). Taken together, these findings suggest that the right hemisphere dominates for at least some aspects of attentional control inherent to simple reaction time task requirements, particularly when targets are extrameridianal. Furthermore, it appears that in normal subjects, this particular contribution of the right hemisphere can be made evident (i.e., experimentally demonstrated) when target intensity is low enough to maximally tax the subject's attentional monitoring of the two peripheral visual fields. Other tests of the model proposed here could consist of artificial induction of field advantages (by cueing in one field in a block of trials, by increasing stimulus intensity in one field in a block of trials, etc.) accompanied by the predicted crossed-uncrossed differential effects, or induction of right and left field advantages by means of nonverbal and verbal concurrent tasks, accompanied by the predicted crossed-uncrossed differential effects. Finally, lateralized cortical lesions, according to the proposed differentially speeded channels model, ought to yield ipsilesional Visual Field advantages, as well as a pattern of positive contralesional and negative ipsilesional crossed-uncrossed differentials.

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