

SIMPLE REACTION TIMES OF IPSILATERAL AND CONTRALATERAL HAND TO LATERALIZED VISUAL STIMULI

BY

G. BERLUCCHI, W. HERON,¹ R. HYMAN,² G. RIZZOLATTI AND C. UMILTÀ

(From the Istituto di Fisiologia dell'Università di Pisa e Laboratorio di Neurofisiologia del CNR, Pisa, Istituto di Fisiologia Umana dell'Università di Parma, Istituto di Psicologia dell'Università di Bologna)

INTRODUCTION

THE central neural pathways involved in the mediation of even the crudest forms of motor reaction to a visual stimulus are practically unknown. Traditional neurological theories of visually guided behaviour have generally assumed that, at least in man, the great majority of visuomotor reactions are crucially dependent on a pathway joining the visual cortex to the motor cortex. Poffenberger (1912) was the first to attempt to deal experimentally with the analysis of the neural circuits underlying a simple visuomotor task, by measuring the reaction time of each hand when restricted visual stimuli were presented on one side of the fixation point or the other. Since the central connexions of the retinae are such that each half of the visual field is projected on to the cortex of the contralateral hemisphere, and since the movements of each hand are to a major extent controlled by the contralateral motor cortex, the reactions of the hand to visual stimuli presented in the ipsilateral hemifield (uncrossed reactions) should be integrated within one hemisphere, whereas the reactions to visual stimuli presented in the contralateral hemifield (crossed reactions) should require the co-ordinated activity of the visual cortex in one hemisphere and the motor cortex in the other. As the interhemispheric cortical connexions through the corpus callosum are predominantly between homonymous areas, and no direct pathway between the visual cortex of one side and the motor cortex of the other is known to exist, the neural pathway serving crossed reactions should contain at least one more synaptic link than the pathway mediating uncrossed reactions. Hence, crossed reactions should be longer than uncrossed ones: the right hand should react faster to stimuli presented in the right visual field and the left hand should react faster to stimuli presented in the left visual field.

¹Senior Research Fellow NRC of Canada, 1967-8.

²Fullbright-Hays Senior Research Scholar, 1967-9.

This is precisely what was found by Poffenberger (1912), who showed that crossed reactions were on the average about 6 msec. longer than uncrossed ones; but Poffenberger's results were not confirmed by a later study of Smith (1938), who found that in only about a half of the cases were the uncrossed reactions faster than the crossed ones, while in the remaining cases the reverse was true. A further challenge to the schema proposed by Poffenberger came from the observation that, in patients who had undergone a surgical section of the corpus callosum, post-operative differences in the reaction time of the two hands to lateralized visual stimuli were not appreciably different from those found before the operation (Smith, 1947). More recently, however, Jeeves (1965) has confirmed Poffenberger's finding that there is a shorter reaction time for uncrossed than crossed reactions in normal subjects; further, he has shown that the time lag between crossed and uncrossed reactions was strikingly longer in two subjects with agenesis of the corpus callosum. In view of these discrepancies, and of the renewed interest in problems of interhemispheric relationships stemming from the work of Sperry (1968), we have reinvestigated the problem. We have been interested in studying not only the times of crossed and uncrossed reactions, but also in finding out the precise relationship between the time of interhemispheric transmission and the lateral position of the stimulus pattern in the visual field. Recent animal studies show that both the origin and the termination of callosal fibres joining the visual cortices are restricted to those areas connected with the parts of the visual field bordering the central vertical meridian (Choudhury, Whitteridge and Wilson, 1965; Whitteridge, 1965; Berlucchi, Gazzaniga and Rizzolatti, 1967; Hubel and Wiesel, 1967; Heimer, Ebner and Nauta, 1967; Berlucchi and Rizzolatti, 1968; Garey, Jones and Powell, 1968; Wilson, 1968; Hughes and Wilson, 1969; Zeki, 1969; Cragg and Ainsworth, 1969). If the callosal connexions of the visual cortex play a major role in the interhemispheric mediation of crossed reactions, then one would expect that the difference between crossed and uncrossed reactions should be definitely greater when the stimulus is presented at some distance from the vertical meridian and thus is projected to points in the visual cortex devoid of direct callosal connexions.

MATERIAL AND METHOD

The present study used the authors and nine male students of the University of Bologna as subjects. The authors and one of the students had practised for a considerable time in the experimental situation before the actual testing so as to eliminate practice effects, whereas the remainder of the students had no prior experience in reaction time work. All the students were ignorant of the purpose of the experiments.

During the experimental session the subject sat in a soundproof room in front of a translucent hemispheric dome, one metre in diameter, and fixated a small patch glued to the pole of the hemisphere. The position of the head was held constant by means of a head and chin rest, adjusted so that the right eye was positioned in the centre of the hemisphere. Thus, the distance between the right eye and any point on the hemisphere was 50 cm. The left eye was completely occluded with a special mask. The hemispheric screen was diffusely illuminated by an overhead light source whose

intensity, measured at the screen, was 20 lux. The stimulus was a square patch of light one square degree in area, flashed on different points of the screen from the rear by means of a remotely operated projector. The duration of the flash was 32 msec., its intensity was 0.12 log units brighter than the background, and its rise and fall times were shorter than one msec. A warning "ready" signal, delivered to the subject via an intercommunication system, preceded the stimulus. The duration of the fore-period was randomly varied with a range of 2 to 3 sec.

The subject responded as fast as he could by pressing with his fore-finger one of two switches beside him. The right hand and the right hand switch or the left hand and the left hand switch were used depending on the particular experimental condition. Reaction times were recorded to the nearest millisecond by an electronic counter in the adjoining room.

Three experimental sessions were carried out with each subject, the inter-session period being about a week. In each session the stimulus pattern was presented in succession to six retinal points all lying on the horizontal meridian: 5 degrees, 20 degrees and 35 degrees nasal; 5 degrees, 20 degrees and 35 degrees temporal. A session was divided into three parts and in each part, four blocks of 15 trials were run with the stimulus on one side of the fixation point, then another four blocks were run with the stimulus at the same visual angle on the other side (for example, 5 degrees temporal, then 5 degrees nasal). The first and fourth blocks of 15 trials were done with one hand, the second and third blocks with the other. Whether the stimulus would appear in the right or left field and whether the right or left hand would be used first, was decided on a random basis for each part of the session. The order in which the three parts of each session would follow each other was also randomly selected for each subject, with the restriction that over the three sessions the three positions of the stimulus pattern (i.e. 5 degrees, 20 degrees and 35 degrees) would constitute a Latin square. In this way the patch of light would appear once in any given position in the first, second, and third part of each session.

Thus, any given session involved 360 trials altogether, consisting of 60 trials with each of the six retinal points tested. Half of these trials were with the right hand, half with the left hand. Before these experimental trials there were another five practice trials with both hands with the stimulus in each position.

One further point should be made about the method. If a subject made an anticipatory response or did not respond within a certain period, this response was discarded and the subject was given another trial. Anticipatory responses were defined as any reaction time less than 180, 190 and 200 msec. for the retinal positions of 5, 20 and 35 degrees respectively, while the limits of delay of response for the same stimulus positions were 320, 350 and 380 msec. These cut-off points were arrived at by examining the distribution of the reaction times of the training trials of the six subjects who had undergone intensive training. It may also be pointed out here that analysis of the present data shows that the number of anticipatory reactions and reactions that were too late was similar for each position of the stimulus, and that the ratios of anticipatory and delayed responses was essentially the same.

Within each session the average reaction time for each hand, for each position of the stimulus pattern, was obtained by finding the median of each consecutive run of five reaction times, then by computing the mean of the (six) medians. Four groups of reaction time measures were thus obtained for any given position of the visual stimulus: right hand and right field, left hand and left field (uncrossed reactions); right hand and left field, left hand and right field (crossed reactions). An analysis of variance was carried out to find the influence of four variables: stimulus position, side of stimulation, hand, and the practice effect. The data from the two groups of subjects were analysed separately, so as to assess the possible effects of previous practice and/or knowledge of the problem.

RESULTS

The averages of the reaction times of each hand for each subject across the three sessions are presented in Tables I and II. In 9 subjects out of 14 the left hand was on the average faster than the right hand, but in neither group did this difference reach the level of significance. The most obvious finding is that, regardless of the hand used, reaction time increases progressively as the stimulus is moved out toward the periphery. If the two visual fields and the two hands are considered together, there is in the first group of subjects an overall 7 msec. increase in reaction time when the stimulus is moved from 5 to 20 degrees, and an additional 6 msec. increase when the stimulus is further moved to 35 degrees (Table III). Corresponding figures for the second group are 7 and 8 msec. respectively (Table III). Thus the overall difference in reaction time between 5 and 35 degrees is 13 msec. in the first group and 15 msec. in the second group. As shown by the analysis of variance using "degree" as a source, the results are significant at the 0.001 level in both groups (Tables IV and V). When the combined reaction times of the two hands are examined separately for the two fields, the increment in reaction time with the increase in eccentricity of

TABLE I

	<i>Temporal field</i>		<i>Nasal field</i>	
	<i>Right hand</i>	<i>Left hand</i>	<i>Right hand</i>	<i>Left hand</i>
5°	219	219	211	219
20°	223	232	218	221
35°	229	233	229	236
5°	243	240	239	243
20°	254	253	250	253
35°	254	250	252	261
5°	250	253	257	255
20°	247	253	255	263
35°	245	254	275	281
5°	245	240	245	241
20°	249	250	245	251
35°	255	250	262	260
5°	225	224	217	224
20°	228	231	228	233
35°	233	235	238	246
5°	226	233	231	236
20°	247	244	241	248
35°	240	242	248	255

The averages of the three sets of mean reaction times of each hand to stimuli at 5 degrees, 20 degrees and 35 degrees from the fovea in each half-field in group I. Each figure is a measure in msec. obtained from 90 reaction times (*see Method*).

TABLE II

<i>Temporal field</i>		<i>Nasal field</i>		<i>Temporal field</i>		<i>Nasal field</i>	
<i>Right hand</i>	<i>Left hand</i>	<i>Left hand</i>	<i>Right hand</i>	<i>Right hand</i>	<i>Left hand</i>	<i>Left hand</i>	<i>Right hand</i>
5°	264	261	238	246	5°	247	245
20°	266	253	271	269	20°	247	246
35°	259	261	266	271	35°	257	260
5°	228	221	223	230	5°	237	235
20°	231	223	229	243	20°	242	243
35°	241	251	245	248	35°	239	241
5°	256	250	243	256	5°	261	260
20°	257	259	258	261	20°	274	260
35°	269	254	269	289	35°	274	271
5°	248	251	246	246	5°	223	233
20°	254	262	257	256	20°	232	231
35°	245	263	265	259	35°	234	235

Average of the three sets of mean reaction times of each hand to stimuli at 5 degrees, 20 degrees and 35 degrees from the fovea in each half-field in group II. Each figure is a measure in msec. obtained from 90 reaction times (*see Method*).

the stimulus is still clearly present in both fields, but is much less evident with the stimulus in the temporal field than with the stimulus in the nasal field (fig. 1). This is due to the fact that while reaction times to stimuli at 5 and 20 degrees are not significantly different in the two fields, at 35 degrees the reaction is much faster when the stimulus pattern is in the temporal field (fig. 1 and also degree/hemifield interaction in Tables IV and V).

At first sight this indication of a systematic difference in responses to the stimulus pattern at the same angular distance in the two halves of the retina would seem to pose a serious difficulty for obtaining separate measurements of the central delays of crossed and uncrossed reactions. In fact, a difference in reaction time between the two hands when the stimulus is presented to the same retinal locus could depend upon a difference in the motor mechanisms controlling the two hands just as well as upon different intrinsic delays of central crossed and uncrossed association pathways; similarly, a difference between the reaction time of one hand to stimulus patterns

TABLE III

	5°	20°	35°
Group I	235	242	248
Group II	243	250	258

Average values of reaction times for both hands and both half-field as a function of eccentricity of stimulus.

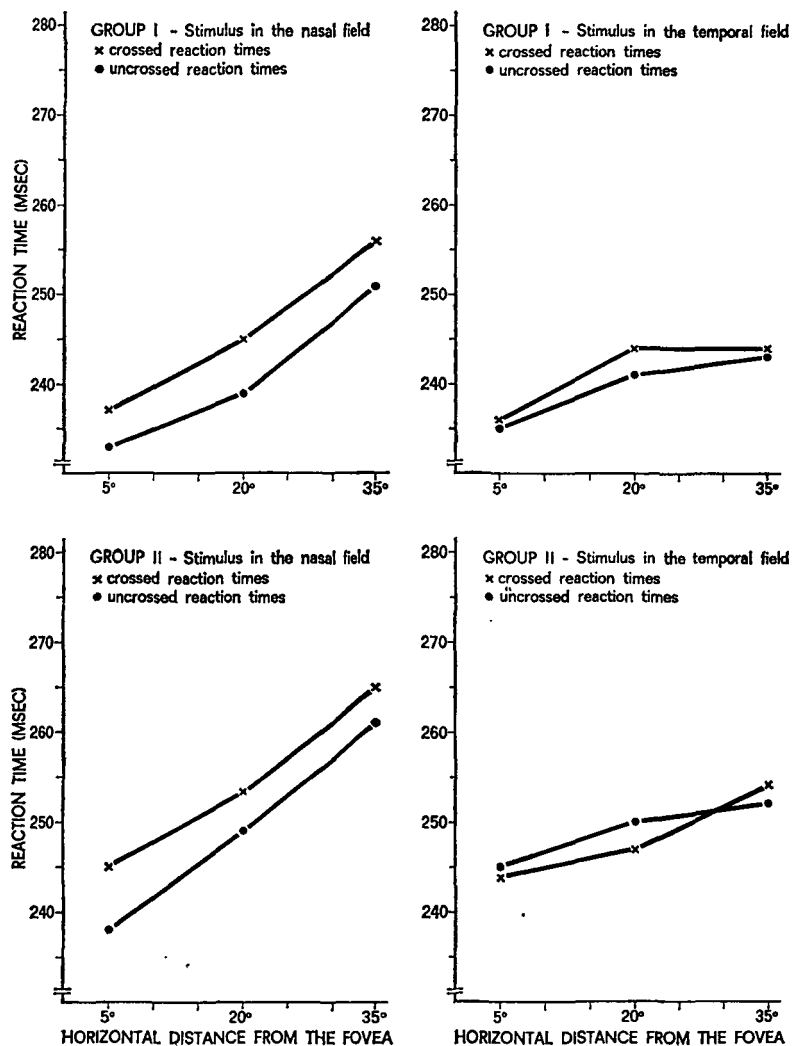


FIG. 1.—Reaction time of ipsilateral and contralateral hand as a function of stimulus eccentricity in nasal and temporal hemifields. When the stimulus is either at 5 or at 20 degrees from the vertical meridian there are no differences between the two hemifields. When the stimulus is at 35 degrees from the mid-line, reaction times to stimuli in the temporal hemifield are significantly shorter than times of reaction to stimuli in the nasal field. In the nasal (left) hemifield the superiority of the ipsilateral (left) hand is evident in both groups. In the temporal (right) hemifield the ipsilateral (right) hand is slightly faster in group 1, whereas in group 2 the left hand is somewhat superior with the stimulus at 5 and 20 degrees from the mid-line. The lack of a clear predominance of the right hand in the ipsilateral hemifield is due to a systematic superiority of the left hand in most subjects.

TABLE IV

SV	SS	df	MS	F
D	6,342	2	3,171.00	41.08†
F	716	1	716.00	2.88
H	170	1	170.00	4.75
E	1,717	2	858.50	5.58*
S	30,044	5	6,008.80	
DF	1,228	2	614.00	14.52
DH	28	2	14.00	0.57
DE	189	4	47.25	0.68
SD	772	10	77.20	
FH	628	1	628.00	19.75†
FE	82	2	41.00	0.76
SF	1,241	5	248.20	
HE	42	2	21.00	0.38
SH	179	5	35.80	
SE	1,542	10	154.20	
DFH	11	2	5.50	0.32
DHE	70	4	17.50	0.60
SDF	423	10	42.30	
DHE	64	4	16.00	0.86
SDH	246	10	24.60	
SDE	1,380	20	69.00	
FHE	81	2	40.50	1.08
SFH	159	5	31.80	
SFE	536	10	53.60	
SHE	556	10	55.60	
DFHE	100	4	25.00	0.58
SDFH	170	10	17.00	
SDHE	372	20	18.60	
SFHE	373	10	37.30	
SDFE	585	20	29.25	
SDFHE	868	20	43.40	
Total	50,914	215		

Analysis of variance for group I; experimental design: SxDxFxHxE. S: subjects, $n = 6$; D: degrees, $d = 3$; F: fields, $f = 2$; H: hands, $h = 2$; E: sessions, $e = 3$. * $P < .05$. † $P < .01$. ‡ $P < .001$.

TABLE V

SV	SS	df	MS	F
D	10,572	2	5,286.00	25.15‡
F	578	1	578.00	6.88*
H	601	1	601.00	2.31
E	6,112	2	3,056.00	5.89*
S	39,679	7	5,668.43	
DF	1,916	2	958.00	6.61*
DH	136	2	68.00	0.89
DE	904	4	226.00	1.42
SD	2,943	14	210.21	
FH	460	1	460.00	460.00‡
FE	97	2	48.50	0.73
SF	588	7	84.00	
HE	419	2	209.50	4.12*
SH	1,820	7	260.00	
SE	7,261	14	518.64	
DFH	83	2	41.50	1.22
DHE	242	4	60.50	0.91
SDF	2,028	14	144.86	
DHE	11	4	2.75	0.08
SDH	1,066	14	76.14	
SDE	4,452	28	159.00	
FHE	25	2	12.50	0.28
SFH	7	7	1.00	
SFE	924	14	66.00	
SHE	712	14	50.86	
DFHE	211	4	52.75	2.19
SDFH	478	14	34.14	
SDHE	1,004	28	35.86	
SFHE	633	14	45.21	
SDFE	1,859	28	66.39	
SDFHE	675	28	24.11	
Total	88,496	287		

Analysis of variance for group II; experimental design: SxDxFxHxE. S: subjects, $n = 8$; D: degrees, $d = 3$; F: fields, $f = 2$; H: hands, $h = 2$; E: sessions, $e = 3$. * $P < .05$. † $P < .01$. ‡ $P < .001$.

in the left field and right field could reflect differences in the two halves of the retina. Yet, these difficulties can be overcome if the average of the two possible ipsilateral hand-field combinations is assumed as an index of uncrossed reactions, and the average of the two possible contralateral hand-hemifield combinations is taken as an index of crossed reactions. A comparison between these two indices will provide a measure of the delay between crossed and uncrossed reactions which is free from any systematic differences in favour of one hand and/or one half of the retina, for such differences will appear in both indices and will therefore counterbalance each other. By carrying out this analysis separately for each of the three angular positions of the stimulus pattern, it is possible to establish the function relating the magnitude of the delay between crossed and uncrossed reactions and the distance of the stimulus pattern from the vertical meridian of the visual field.

Fig. 2 plots the reaction time of the contralateral and ipsilateral hand as a function of the angular distance of the stimulus pattern from the fixation point. Both curves show the typical increase of reaction time as the angular distance increases. Further, in both groups all the points of the curve of the contralateral hand lie above the corresponding points of the curve of the ipsilateral hand, thus showing that crossed reactions do indeed take longer than uncrossed ones. The delay between contralateral and ipsilateral hand appears to be approximately the same at the three positions

of the stimulus: in the first group it is 2.5 msec. at 5 degrees, 4.5 msec. at 20 degrees, 3 msec. at 35 degrees; in the second group it amounts to 3 msec. at 5 degrees, to 0.5 msec. at 20 degrees, to 3 msec. at 35 degrees. That the magnitude of the delay is indeed independent of the distance of the stimulus from the fixation point is shown by the low F value for the hand/field/degree interaction in both groups of

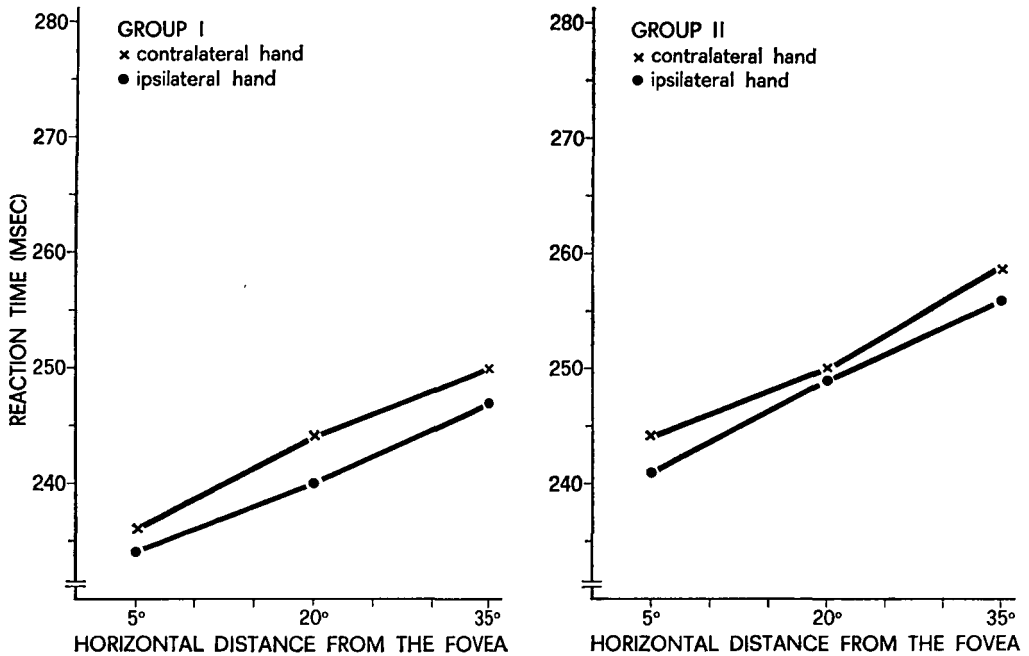


FIG. 2.—Reaction time of ipsilateral and contralateral hand as a function of stimulus eccentricity. By combining the data concerning the reaction times to stimuli in both hemifields it is possible to eliminate the systematic bias in favour of the left hand and to demonstrate a constant superiority of the ipsilateral hand for all the stimulus positions.

subjects (see Tables IV and V). We are therefore justified if we average the delays at the three positions of the stimulus in order to obtain an overall measure of the lag between crossed and uncrossed reactions. The average delay is 3.3 msec. in the first group of subjects and 2.1 msec. in the second group: the differences between crossed and uncrossed reactions are highly significant (see hand/field interaction in Tables IV and V).

In both groups of subjects, reaction times decreased significantly with practice (see source sessions (E), Tables IV and V), but this is not related to angular position of the stimulus pattern or field (see source degree/sessions and hemifield/sessions in Tables IV and V).

DISCUSSION

The results indicate that for the six retinal points investigated, reaction time increases progressively with the angular position of the visual stimulus, and that this trend is more obvious in the temporal than in the nasal half of the retina. They are thus in good agreement with previous classical and modern experiments on visual reaction time (Hall and Kries, 1879; Poffenberger, 1912; Lichtenstein and White, 1961; Rains, 1963; Payne, 1966; Eason, Oden and White, 1967). They are also in accord with sensitivity maps of the visual field obtained by testing differential perceptual thresholds (Sloan, 1961; Marks, 1968). It is now well established that the common factor underlying these various results is a positive correlation between visual sensitivity, as determined by reaction time or perceptual threshold, and density of receptors in the stimulated retinal area (Østerberg, 1935).

The basic purpose of the present study was to find out whether there is a measurable delay between reactions involving ipsilateral hand-visual hemifield combinations and reactions involving contralateral hand-visual hemifield combinations. Further, we were interested in finding if the magnitude of any delay present would depend upon the distance of the visual stimulus from the vertical meridian of the visual field. The results give an affirmative answer to the first question and a negative one to the second. Like Poffenberger (1912), we have found that crossed reaction times are significantly longer than uncrossed reaction times, the overall average difference being 3.3 msec. in one group of subjects and 2.1 msec. in the other group. These values are different from those reported by Poffenberger, who obtained a delay of 6 msec. in one subject and 5.6 msec. in another subject. This discrepancy may be due to differences in method. In any case, the present confirmation of Poffenberger's results under more stringent conditions leaves no doubt that he was correct in concluding that stimulus patterns in one visual field elicit faster reactions from the ipsilateral than from the contralateral hand.

The recent experiments of Gazzaniga, Bogen and Sperry (1965, 1967) on "split-brain" patients, have shown the importance of the fore-brain commissures for the performance of visuomotor tasks involving a visual input restricted to one hemisphere and a motor response governed by the other hemisphere. On these grounds, it seems reasonable to assume that the delay between crossed and uncrossed reactions, as measured in the present study, corresponds to the conduction time of the callosal fibres, very likely of the largest, fast conducting ones (*see* Tomasch, 1954). This assumption is not necessarily in conflict with the data of Smith (1947), showing that section of the corpus callosum does not modify the time relationships between crossed and uncrossed simple visuomotor reactions. His results are based on a small number of tests; further, it is possible that, because of early cerebral lesions, each hemisphere had established unusually strong motor control of the ipsilateral hand before surgical section of the callosum. This point of view is supported by the fact that Smith's subjects showed no statistically significant difference between crossed and uncrossed reactions before surgery. Moreover, Gazzaniga, Bogen and

Sperry (1967) have reported that it is possible for each hemisphere to control the ipsilateral hand efficiently in the performance of very simple visuomotor reactions after section of the fore-brain commissures.

If one accepts the conclusion that the delay between crossed and uncrossed reactions is due to transmission of information by the corpus callosum, we may ask whether this transmission takes place at the level of the callosal connexions of the visual cortex, of the motor cortex, or of both. Anatomical and electrophysiological studies of the callosal connexions of the visual cortex in several subhuman mammalian species have shown that only the cortical areas related to the vertical meridian of the visual field give origin to and receive commissural fibres (*see* Introduction). There is indirect evidence which suggests that this peculiar pattern of interhemispheric connexions of the visual cortex occurs also in man (Whitteridge, 1965). The data from the cat indicate that the width of the central vertical strip of the visual field projected into visual cortical areas interconnected via the callosum is about 20 degrees on each side of the vertical meridian (Berlucchi, Gazzaniga and Rizzolatti, 1967; Berlucchi and Rizzolatti, 1968). If the callosal connexions of the visual cortex were crucially involved in the interhemispheric exchange of information necessary for crossed visuomotor reactions, one could predict that the delay between crossed and uncrossed reactions would increase dramatically when the stimulus is moved out of the region of the visual field connected with the corpus callosum. Our results showing that the delay between crossed and uncrossed reactions is constant, independent of the degree of eccentricity of the stimulus, clearly fails to support such a prediction. Instead, they suggest that the callosal connexions of the visual cortex are not a major component of the neural substrate underlying this type of interhemispheric sensorimotor co-ordination. This conclusion is in accord with recent experiments on monkeys, showing that portions of the corpus callosum not originating in the occipital lobe play an important role in the interhemispheric integration of simple responses requiring the activity of the visual cortex in one hemisphere and the motor cortex in the other (Lehman, 1968).

SUMMARY

Simple reaction times to lateralized visual stimuli were studied in 14 normal subjects. Visual stimuli presented on one side of the fixation point elicit faster reactions from the ipsilateral than from the contralateral hand. The delay between the crossed and uncrossed responses remains constant regardless of the degree of eccentricity of the visual stimuli. It is concluded that the interhemispheric integration of simple visuomotor tasks is not crucially dependent upon the callosal connexions of the visual cortex.

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