

## Hemispheric Control of Unilateral and Bilateral Movements of Proximal and Distal Parts of the Arm as Inferred from Simple Reaction Time to Lateralized Light Stimuli in Man

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**Summary.** In 12 normal, right-handed male subjects simple reaction time of key-pressing and lever-pulling responses to light flashes presented in the right or left visual fields was faster with the arm ipsilateral to the visual stimulus, provided the responses were made unilaterally. Key-pressing responses involved a movement of a single finger, whereas lever-pulling responses involved an integrated movement of the proximal parts of the arm. The mean difference in reaction time between reactions ipsilateral to the stimulus and reactions contralateral to the stimulus was about 2 ms for both key-pressing and lever-pulling responses. When key-pressing and lever-pulling responses to a single lateralized light stimulus were made bilaterally, the advantage in favor of the ipsilateral responses was still present, although it was mainly limited to the right hand, on key-pressing, whereas it was completely absent on lever pulling.

The difference between ipsilateral and contralateral reactions on unilateral responding, whether proximal or distal, is attributed to the consistent initiation of the response by the contralateral hemisphere. Given that a lateralized visual stimulus is projected to the opposite hemisphere, ipsilateral responses can be integrated within a single hemisphere, whereas contralateral responses are integrated interhemispherically and therefore require additional time. The reduction or lack of the ipsilateral advantage on bilateral responding is attributed to the engagement of a bilaterally distributed motor control that is preferentially directed to the proximal musculature.

**Key words:** Man – Cerebral hemispheres – Simple reaction time – Visuomotor control

The notion that the motor cortical areas of each hemisphere control the motility of the contralateral extremities is classical in clinical neurology (Penfield and Jasper, 1954), and has been amply confirmed by recent analyses of the effects of local excisions in these areas (Laplaine et al., 1977a and b). However, uncrossed motor pathways are also known to exist, and their functional role has been considerably elucidated by studies of motor behavior in subjects with a surgical section of the forebrain commissures (Gazzaniga et al., 1967; Zaidel and Sperry, 1977) as well as in brain-damaged patients with apraxic disturbances (Geschwind, 1975).

Ipsilateral motor control appears to be most effective for the guidance of axial and proximal limb musculature, and least effective in governing distal limb musculature, particularly in relation to individual movements of the hand and fingers. Similarly, in the monkey bilaterally distributed cortical and subcortical pathways can guide integrated limb-body movements and synergistic movements of the limbs involving chiefly the proximal joints. In contrast to such bilaterally distributed motor systems, predominantly or exclusively crossed cortico-spinal and cortico-subcortico-spinal systems are especially concerned with movements of the individual limbs, notably of their distal parts (Kuypers, 1973, 1978).

Reaction time studies of simple visuomotor responses in normal man can contribute to the analysis of the respective roles of ipsilateral and contralateral descending pathways in the organization of motor output. Simple key-pressing or key-releasing responses to a flash of light appearing in the right or left visual fields are faster when performed with the hand ipsilateral to the visual stimulus (Poffenberger, 1912; Jeeves, 1969, 1972; Jeeves and Dixon, 1970; Bradshaw and Perriment, 1970; Berlucchi et al., 1971; Anzola et al., 1977; Berlucchi et al., 1977). This finding has commonly been attributed to

a crossed motor control of the responding hand, combined with the projection of the lateralized light stimulus to the opposite hemisphere. When the light stimulus is ipsilateral to the responding hand, the response can be integrated within a single hemisphere, i.e., the hemisphere contralateral to both stimulus and responding hand. On the contrary, when the light stimulus is contralateral to the responding hand, the performance of the response is likely to require an interhemispheric interaction which takes additional time. This explanation is strengthened by the fact that in subjects with an agenesis of the main interhemispheric pathway, the corpus callosum, the ipsilateral advantage is several times greater than that of normal controls (Jeeves, 1969; Reynolds and Jeeves, 1974). Further, other possible interpretations of these findings, such as those based on effects of spatial compatibility between stimulus and response, have been ruled out by direct experimental checks (Anzola et al., 1977; Berlucchi et al., 1977).

All these previous experiments have employed as responses discrete hand or finger movements, i.e., movements which are chiefly, if not exclusively, guided by the contralateral hemisphere. A different outcome might be expected from comparable experiments on reaction time of movements performed by muscles which act at proximal, rather than distal, joints of the upper limb. Since each hemisphere can efficiently control these movements on either side of the body, the difference in speed between ipsilateral and contralateral responses to a right or left flash of light may be largely diminished or even abolished. In addition, the time difference between unilateral and contralateral responses may conceivably be eliminated if subjects were required to perform associated bilateral responses, instead of a single unilateral response, to the lateralized light flash. Mechanisms of right-left synchronization of motor output, possibly based on the bilaterally distributed motor pathways, may become selectively operant under these conditions, thereby suppressing the ipsilateral advantage. A reduction of the ipsilateral advantage for bilateral reactions predominantly employing distal muscles has indeed been reported (Jeeves and Dixon, 1970; Jeeves, 1972; Reynolds and Jeeves, 1974).

The present study is an analysis of the influence of the two factors, nature of the movement (proximal vs. distal) and laterality of the response (unilateral vs. bilateral), on simple reaction time to flashes of light presented in the right and left visual fields. Subjects were examined under four response conditions:

(1) unimanual key-pressing response, basically

consisting of a single finger movement; (2) unimanual lever-pulling response, involving an integrated movement of shoulder, elbow, and hand; (3) bimanual key-pressing response; (4) bimanual lever-pulling response.

## Methods

Twelve male subjects, ranging in age from 21 to 43 years and including two of the authors (C.A.M. and G.B.), participated in the experiments. All of them proved to be strongly right-handed on a modified version of the 12-item questionnaire test of Biggs and Nebes (1975), and had normal or corrected vision. The right eye was dominant for sighting in 10 subjects and the left in the remaining two. All subjects had considerable experience with visuomotor reaction time tasks.

Each subject sat alone in a sound-proof room and faced an horizontal arc perimeter, 57 cm in radius, mounted on a white tangential screen. His head was positioned in a head-and chin-rest with the midpoint between the eyes in the center of curvature of the perimeter. The screen and the perimeter received indirect illumination from above, their luminance being 0.15 cd/m<sup>2</sup>. A fixation mark was provided on the perimeter exactly in front of the eyes. Two solid state miniature bulbs (TIL 222) were fastened to the perimeter, one on the right and the other on the left of the fixation mark, at a distance of 15 cm from it, subtending 15° of visual angle at the subject's eyes. Each bulb could be lighted individually by a 15 mA square pulse of current 5 ms long which produced a gallium phosphide green flash of light with an intensity of 1,000  $\mu$  cd. Each bulb was mounted on its support so that its round tip, 5 mm in diameter, faced the subject. When the subject fixated the central mark, the flash stimulus was projected to the blind spot of the ipsilateral eye and to the temporal hemiretina of the contralateral eye, so that visual stimulation was limited to the latter hemiretina in spite of both eyes being open. Two response devices were provided on each side of the subject: a button-key, mounted on the top of a vertical brass cylinder, which could be operated by pressing with the tip of the thumb, and a lever acting on a spring, which could be operated by the subject's pulling the brass cylinder toward himself. The brass cylinder was 3 cm large and 10 cm long, and its upper base, holding the button-key, was positioned 29 cm from the midsagittal plane of the subject, 16 cm below and 22 cm in front of the fixation point. Pressing the key and pulling the lever closed two separate electrical contacts, the forces necessary for this being respectively 60 g and 3.5 kg. The total excursion of the lever was 2 cm, but the electrical contact was closed as soon as the lever was displaced from the rest position. The subject rested his elbow and part of the forearm on a support which restrained the position of the forearm. The button-key was operated by flexing the thumb, the other fingers encircling the brass cylinder. The spring-lever was operated by clutching the brass cylinder with the whole hand and by pulling on it by a flexion of the elbow and an abduction of the shoulder. The movement required was a full excursion of the lever, and during it the forearm could slide on its restraining support which was covered with rubber foam. The task consisted in pressing one or both keys, or pulling one or both levers as soon as possible following the appearance of a light flash. The time elapsing between the onset of the stimulus and the closing of the contact(s) by the key(s) or the lever(s) was electronically measured to the nearest millisecond. Each stimulus was preceded by an auditory tone peep, 50 ms in duration, delivered via an earphone set. The interval between the auditory signal and the light stimulus varied randomly from 1 to 3 s. Subjects were instructed to fixate on the central mark after hearing the warning stimulus and to maintain fixation until after

performing the response. Eye position and maintenance of fixation were monitored by television.

Each subject completed 12 sessions on separate days. Each half session consisted of six blocks of 20 trials, corresponding to the six following combinations: unilateral key-pressing with right hand; unilateral key-pressing with left hand; bilateral key-pressing; unilateral lever-pulling with right arm; unilateral lever-pulling with left arm; bilateral lever-pulling. The order of alternation of the six conditions within each half session varied from session to session, and was counterbalanced across subjects and across sessions according to a Latin square design. Within each block the light flash was presented 10 times on the right and 10 times on the left, in a random sequence. Responses shorter than 150 ms were considered premature and the trial was repeated later in the sequence. Each subject provided altogether 480 reaction times for each hand for each condition. The basic data used for analysis were eight median reaction times for each visual field for each subject, corresponding to the six experimental conditions, each of the two bilateral conditions providing two median reaction times, one for each limb. Statistical assessment of the results was obtained by analysis of variance and two-tailed *t*-tests.

**Results**

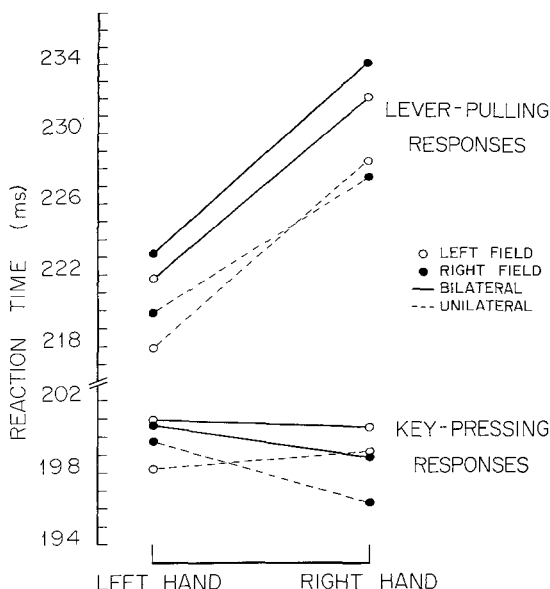
An analysis of variance using field, hand, and response condition as the main factors showed that

(1) neither field nor the field/response condition interaction were significant sources of variance; (2) the hand factor was highly significant ( $p < 0.005$ ) because of a systematic advantage of the left hand, which, however, was present only for lever-pulling responses, resulting in a significant hand/response condition interaction ( $p < 0.001$ ). There was no difference between the hands on key-pressing responses; (3) response condition was also a significant source of variance ( $p < 0.001$ ) due to a longer reaction time for lever-pulling as compared to key-pressing, and a longer reaction time for bilateral responses as compared to unilateral responses; (4) a significant hand/field interaction ( $p < 0.001$ ) resulted from the fact that responses made with the limb ipsilateral to the stimulus were faster than responses made with the limb contralateral to the stimulus. However this interaction depended on the response condition, as shown by a significant three-factor interaction ( $p < 0.005$ ), since there was no advantage for the ipsilateral limb over the contralateral limb on bilateral lever pulling.

**Table 1**

		Left field		Right field	
	Unilateral key-pressing responses	Left hand	198.97±3.45	$p < 0.08$	199.7±3.63
		n.s.	n.s.		$p < 0.01$
		Right hand	197.83±3.35	$p < 0.01$	196.31±3.39
		Field $\bar{x}$	198.8±3.27		n.s.
$p < 0.05$	Unilateral lever-pulling responses	Left hand	218.87±3.58	$p < 0.09$	219.83±3.56
		$p < 0.001$	$p < 0.001$		$p < 0.01$
		Right hand	227.59±3.45	$p < 0.05$	226.59±3.35
		Field $\bar{x}$	223.25±3.45		n.s.
$p < 0.01$	Bilateral key-pressing responses	Left hand	200.72±3.21	n.s.	200.6±3.22
		n.s.	n.s.		n.s.
		Right hand	199.7±3.13	n.s.	198.87±3.09
		Field $\bar{x}$	200.68±3.2		n.s.
	Bilateral lever-pulling responses	Left hand	222.5±3.5	n.s.	223.2±3.42
		$p < 0.001$	$p < 0.001$		$p < 0.001$
		Right hand	232.87±3.44	n.s.	233.35±3.38
		Field $\bar{x}$	227.11±3.53		n.s.

Reaction time in ms (mean ± standard error)



**Fig. 1.** Reaction time (ms) as a function of field of stimulation and responding hand for unilateral and bilateral key-pressing and lever-pulling reactions

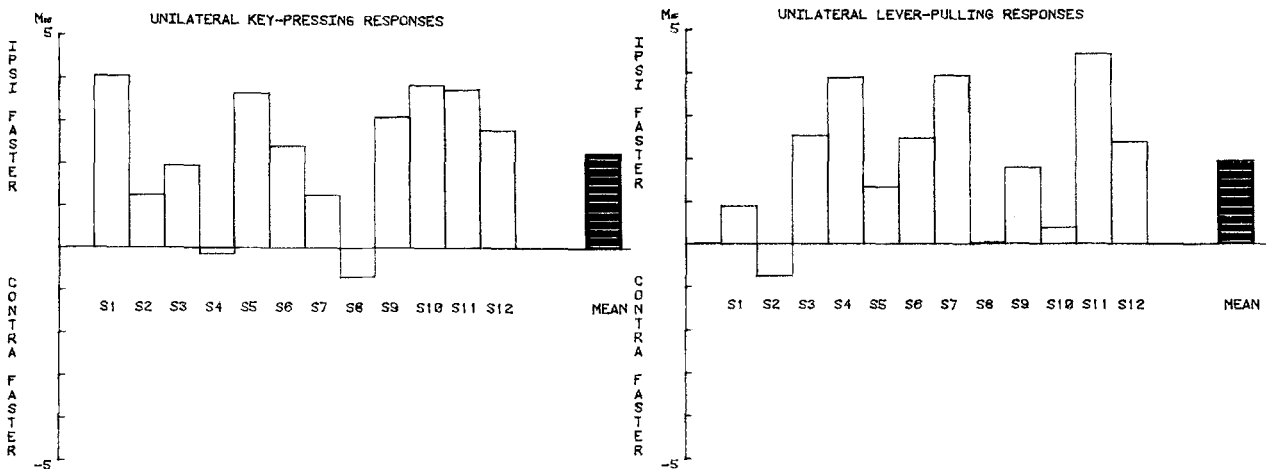
The results are presented in diagrammatic form in Fig. 1. Table 1 shows mean reaction time as a function of the experimental variables and their interactions, and indicates the statistical significance of specific comparisons. A more detailed inspection of the trends brought out by the analysis of variance leads to the following conclusions.

Mean reaction time was significantly shorter for key-pressing responses than for lever-pulling

responses, and with both types of responses there was a small but highly significant advantage of unilateral reactions over bilateral reactions. With unilateral responses there was a left field superiority for both key-pressing and lever-pulling responses with the left hand, and a similar superiority of the right field for both key-pressing and lever-pulling responses with the right hand. As a result ipsilateral responses were significantly faster than contralateral responses, and the difference between the two sets of responses was about the same (approximately 2 ms) for both key-pressing and lever-pulling. The systematic advantage for ipsilateral responses in the unilateral responding condition is shown for individual subjects in Fig. 2 (key-pressing, left; lever-pulling, right).

In the bilateral responding condition, the right field was favored for key-pressing responses on the right, although the difference was not significant; but there was no difference in mean reaction time between the two hands upon left field stimulation. With lever-pulling responses, there was no difference in reaction time between the right and left fields as a function of the responding arm.

Ipsilateral responses were significantly faster than contralateral responses in the key-pressing condition ( $p < 0.01$ ) mainly due to the advantage of the right hand over the left upon right field stimulation; but in the lever-pulling condition, mean reaction time was virtually identical for ipsilateral and contralateral responses. This finding is illustrated for individual subjects in Fig. 3 (key pressing, left; lever pulling, right). With both unilateral and bilateral key-



**Fig. 2.** Individual differences in reaction time between ipsilateral and contralateral responses on unilateral key-pressing and lever-pulling reactions. The time of ipsilateral reactions is the mean between the time of reactions with the right hand to right field stimuli and the time of reactions with the left hand to left field stimuli. The time of contralateral reactions is the mean between the time of reactions with the right hand to left field stimuli and the time of reactions with the left hand to right field stimuli. Bars extending above the 0 line indicate an advantage for the speed of ipsilateral reactions, while bars extending below the 0 line indicate an advantage for contralateral reactions. Note similarity of advantage for ipsilateral reactions with both key-pressing and lever-pulling

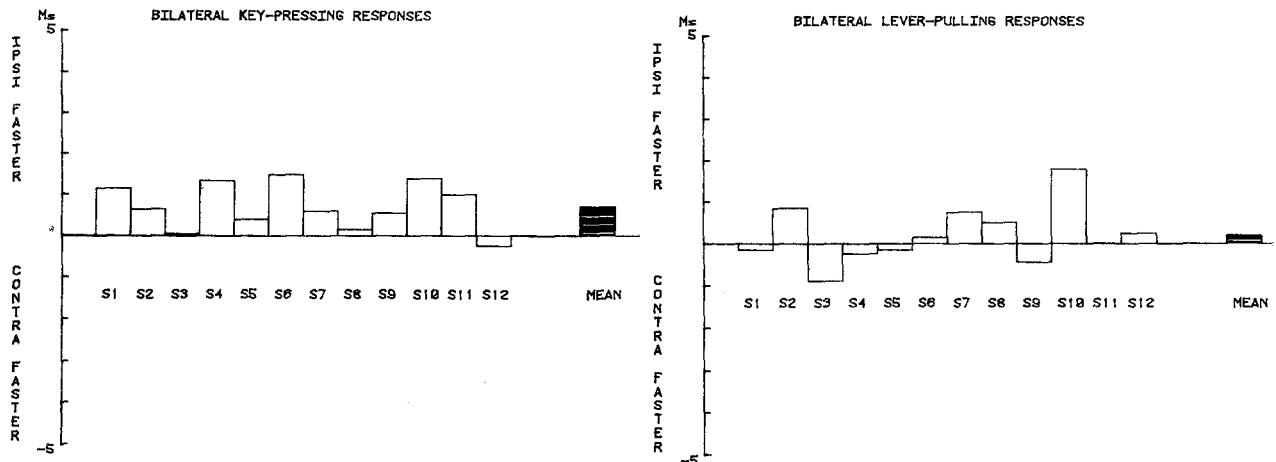


Fig. 3. Individual differences in reaction time between ipsilateral and contralateral responses on bilateral key-pressing and lever-pulling reactions. Conventions as in Fig. 2. Note presence of an advantage for ipsilateral reactions on key-pressing, though reduced in comparison with unilateral reactions (Fig. 2), and absence of such an advantage on lever-pulling

pressing responses there was no significant difference in speed of reaction between the right and left visual fields or between the right and left hands. Similarly, overall speed of reaction was not affected by the side of stimulation with both unilateral and bilateral lever-pulling responses. However, there was a large superiority of the left hand over the right in both unilateral and bilateral lever-pulling responses, irrespective of the field of stimulation. A detailed regression analysis of the bilateral responses showed that right and left lever-pulling reactions were linearly related, with the left arm leading the right on 90.8% of the trials on the average, regardless of the side of the visual stimulus. Correlation coefficients between the two arms varied from 0.95 to 0.98 across subjects, with a mean of 0.97. With key-pressing bilateral responses there was also a linear relation between right and left hand, but this was less strong than with lever-pulling responses. Individual correlation coefficients varied from 0.73 to 0.96 with a mean of 0.91. In 10 subjects the right hand tended to lead the left upon right field stimulation, but this trend disappeared or reversed upon left field stimulation. In all subjects the right-left correlation coefficient for bilateral lever-pulling responses was greater than the right-left correlation coefficient for key-pressing responses ( $p < 0.01$ ). Figure 4 shows the scattergrams and the regression lines for the reaction times of the right and left hands of a single subject on bilateral key-pressing and lever-pulling responses for each visual field.

### Discussion

According to the basic postulate of the experiment, a difference in speed of response favoring the hand

ipsilateral to the visual stimulus implies that the movement ultimately depends on motor pathways originating from the hemisphere opposite to the responding limb. Since on both key-pressing and lever-pulling, unilateral reactions made with the hand ipsilateral to the light stimulus were consistently faster than contralateral reactions, it follows that key-pressing and lever-pulling movements, at least when performed unilaterally, are both actuated by a motor command coming from the contralateral hemisphere. Interhemispheric transmission time, measured as the time lag between ipsilateral and contralateral reactions, was identical for unilateral key-pressing and lever-pulling responses. This suggests that both types of movements, when performed with the limb contralateral to the light stimulus, utilize a common mechanism of interhemispheric transmission with constant temporal characteristics (Berlucchi et al., 1977). In monkeys, the motor pathways subserving fast reactive movements of the fingers may at least in part differ from those subserving fast reactive movements of the whole upper limb, since simple reaction time of the former movements is considerably increased by a transection of the pyramidal tract (Hepp-Reymond et al., 1974) while that of the latter movements is not (Beck and Chambers, 1970). If this differential motor organization is also present in man, the conclusion from our results is that the motor pathways ultimately producing unilateral key-pressing and lever-pulling reactions, whether pyramidal or non-pyramidal, originate from the hemisphere contralateral to the responding limb, and are both accessible to the same interhemispheric control.

For both key-pressing and lever-pulling, bilateral responses were slightly but systematically slower than

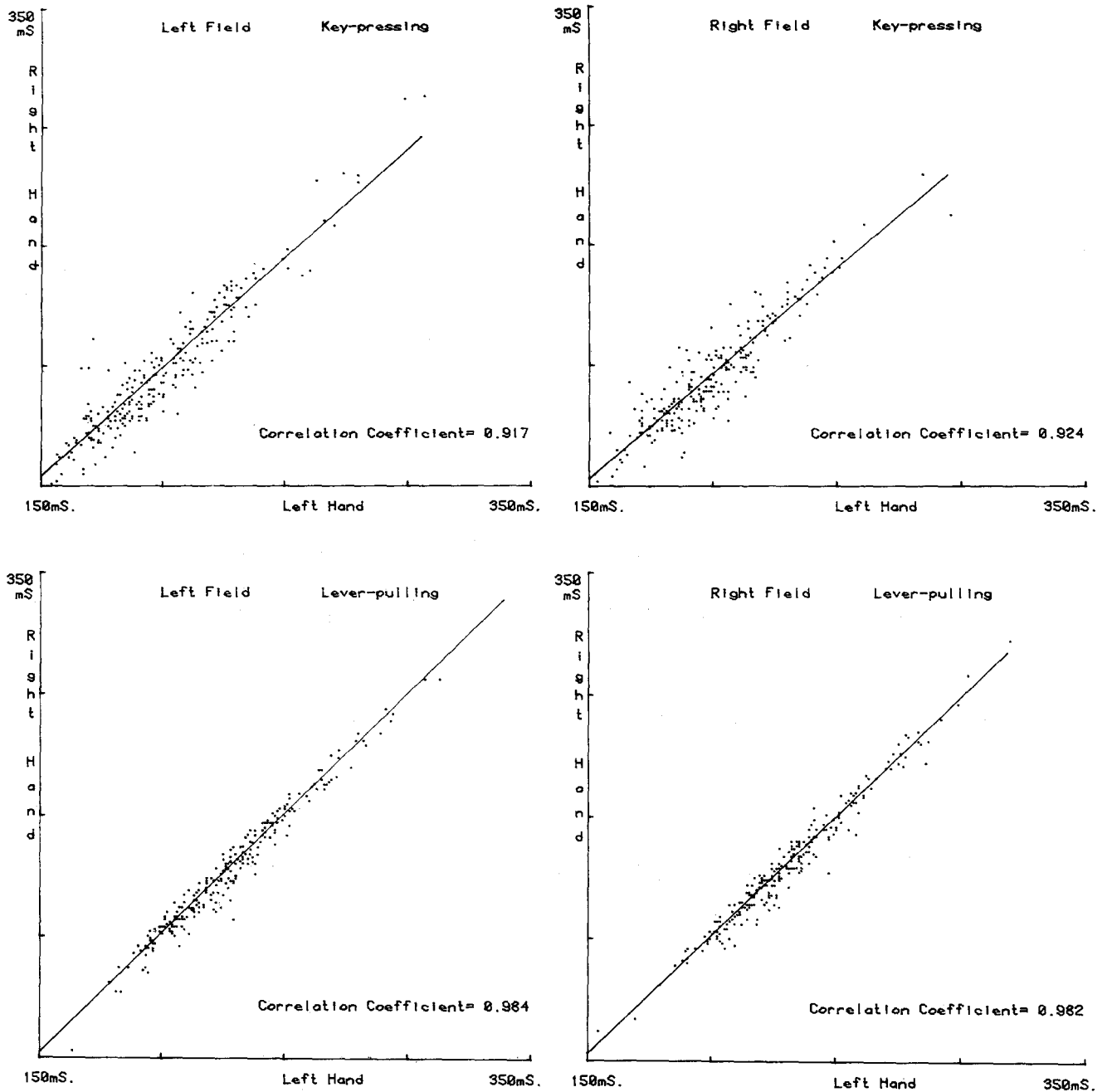


Fig. 4. Scattergrams and regression lines for bilateral key-pressing and lever-pulling responses upon left and right visual field stimulation in a single subject. Each diagram is based on 240 reaction times

corresponding unilateral responses, in agreement with several previous observations (Salow, 1913; Jeeves, 1969; Jeeves and Dixon, 1970; Nakamura and Saito, 1974). This difference can perhaps be attributed to the same mechanisms of central interference which have been postulated to underlie interlimb competition effects in more complex types of motor performance (Cohn, 1951; Wyke, 1967,

1968, 1969, 1971; Cohen, 1970, 1971; Kelso et al., 1979).

The finding that the ipsilateral-contralateral time difference was largely reduced with bilateral key-pressing responses, and abolished with bilateral lever-pulling responses cannot be ascribed to the longer reaction time of the latter reactions, since ipsilateral advantage seen under conditions of uni-

lateral responding is largely unaffected by various factors which increase overall reaction time (Berlucchi et al., 1977).

One is thus led to attribute to differences in organization of motor outflow the different patterns of relations between ipsilateral and contralateral responses observed under conditions of unilateral and bilateral responding. Bilateral lever-pulling responses showed a very tight temporal coupling between the two sides, and unlike the unilateral reactions, there was no relation between the side of the light stimulus and the side of the faster response. Bimanual key-pressing responses were also bilaterally correlated, but the side-to-side correlation was not as strong as with lever-pulling responses, suggesting the operation of a different coupling mechanism. In addition, ipsilateral responses were significantly faster than contralateral responses, an effect largely limited, however, to the right hand.

These results can be accounted for tentatively by assuming that while motion of the active limb on unilateral responding is produced by a motor pathway, specific for that limb (possibly the crossed cortico-spinal and lateral brainstem systems of Kuypers, 1973), bilateral responses are instead at least in part dependent on a bilateral motor system which ensures a yoked movement of both limbs (presumably the bilaterally distributed ventromedial brainstem system of Kuypers, 1973). An additional assumption is that the motor system controlling bilateral lever-pulling (proximal) movements can be activated equally by visual stimuli channeled into either hemisphere, whereas for key-pressing (distal) movements the left hemisphere can exert a more efficient bilateral control than the right.

These assumptions are indirectly supported by a number of previous observations. Jung and Dietz (1975) have reported that in patients with unilateral central motor lesions the reaction time of the affected limb is considerably longer than that of the corresponding contralateral limb, provided the reactions are made unilaterally. If the reactions are performed with both the affected and the normal limb concurrently, the difference in reaction time between the two sides tends to disappear. This suggests the recruitment of an ipsilateral control by the intact hemisphere on the affected limb during bilateral responding, in agreement with our hypothesis. An asymmetry of ipsilateral motor control on the distal parts of the extremities, such as that postulated here, has been found in right-handed split-brain subjects, where left-hand control by the left hemisphere is more efficient than right-hand control by the right hemisphere (Gazzaniga et al., 1967; Zaidel and Sperry, 1977). In addition, left-hemisphere lesions in

dextrals appear to impair the speed of reaction of both hands, whereas right-hemisphere lesions affect the reaction time of the left hand only (Wyke, 1967, 1971).

The systematic superiority of the left hand in both unilateral and bilateral lever-pulling responses is in accord with many previous experiments on simple reaction time, especially where synchronous bilateral responses were examined (Buytendyk, 1912; Salow, 1913; Metfessel and Warren, 1934; Paillard, 1947; Nakamura and Saito, 1974; Nakamura et al., 1975). On the other hand, there was no significant difference between the hands in reaction time of key-pressing responses, in agreement with other comparable studies of simple reaction time (Berlucchi et al., 1977). These findings can be related to recent analyses showing that manual dominance in reaction time may vary as a function of posture and type of movement (Nakamura and Saito, 1974; Hongo et al., 1976) as well as of the nature of decision preceding the reaction (Kerr et al., 1963; Flowers, 1975; Anzola et al., 1977; Rabbit, 1978).

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