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HEMISPHERIC ASYMMETRY AND INTERHEMISPHERIC TRANSFER IN POINTING DEPEND ON THE SPATIAL COMPONENTS OF THE MOVEMENT

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ABSTRACT

The purpose of the present study was to compare the asymmetry and transfer in 3 pointing movements with increasing spatial requirements. The triggering signal was one of four visual targets appearing on the right or left of a central fixation point (FP). The first task consisted in simply removing the arm from the starting platform; the second was a pointing movement towards the FP, and the third was a classical pointing task towards one of the four lateral targets. 20 right-handers (Rhrs) and 20 left-handers (Lhrs) participated in this experiment. In the classical pointing task (task 3), the reaction times were shorter in the Rhrs using their left hand. No such hand-related difference was observed in the Lhrs. No hand asymmetry was observed in the other tasks. In addition, the responses were faster in the uncrossed than in the crossed conditions, in task 3 only. It was concluded that in pointing tasks, both the hemispheric asymmetry and the interhemispheric transfer depend on the spatial requirements of the movement.

Key words: reaching, handedness, reaction time, interhemispheric transfer, asymmetry, humans

INTRODUCTION

The experimental task which consists in very quickly pressing or releasing a key in response to lateralized visual stimuli has been widely used to investigate interhemispheric communication and hemispheric asymmetry. As far as hemispheric asymmetry is concerned, a systematic advantage for one hand or visual field can be taken to reflect an advantage of the contralateral hemisphere for motor or visual processing, respectively. In fact, in key-pressing or releasing, no hemispheric asymmetry has been consistently found to exist (Marzi, Bisiacchi and Nicoletti, 1991). In hemispheric communications, when the stimulus is on the side of the responding hand (uncrossed or intrahemispheric condition), all the processes between the visual input and the motor output are thought to occur in the contralateral hemisphere, whereas when the stimulus and the hand used are not on the same side (crossed or interhemispheric condition), some information has to be transferred from the hemisphere receiving the visual input to the hemisphere that generates the motor commands. The crossed-uncrossed difference (CUD) between the reaction times has been taken to reflect the interhemispheric transfer time. With this simple key-pressing response, the grand mean CUD has been found to be around 3-4 ms in healthy subjects, but it could

increase greatly in patients with callosal agenesis as well as in split-brain patients (Bashore, 1981; Marzi et al., 1991).

In reaching tasks, hemispheric asymmetry and interhemispheric transfer can be approached using similar experimental conditions to those described above. However, unlike key-pressing, which is a digital response involving distal muscles, reaching mainly involves the elbow and shoulder, and hence proximal and axial muscles. These muscles can be theoretically activated by both contralateral and ipsilateral motor commands. Anatomical data on animals (Brinkman and Kuypers, 1972) and pathological and functional data on humans (Gazzaniga, 1970; Colebatch, Deiber, Passingham et al., 1991; Aglioti, Berlucchi, Pallini et al., 1993) have in fact shown that axial and proximal muscles can be activated via bilateral motor pathways. The occurrence of a transfer is therefore not strictly necessary in pointing, and no significant CUD will necessarily be found in this task. Now paradoxically, the CUD recorded in the pointing task was often around 10-15 ms in healthy subjects, which was a greater value than in key-pressing (Bradshaw, Bradshaw and Nettleton, 1990; Carson, Chua, Elliott et al., 1990; Carson, Chua, Goodman et al., 1995; Elliott, Roy, Goodman et al., 1993; Fisk and Goodale, 1985, 1988; Van der Staak, 1975). Furthermore, the CUD was much higher (nearly 100 ms) in a patient with a callosal lesion (Velay and Benoit-Dubrocard, 1999), which supports the assumption that an interhemispheric transfer may actually occur via a callosal pathway in reaching. Lastly, contrary to the key-pressing response, a left-hand advantage of around 10 to 15 ms has often been observed in reaching reaction times (Bradshaw et al., 1990; Carson et al., 1990; Carson, Goodman and Elliott, 1992; Carson et al., 1995; Chua, Carson, Goodman et al., 1992; Elliott et al., 1993; Haaland and Harrington, 1989; Helsen, Starkes, Elliott et al., 1998; Hodges, Lyons, Cockell et al., 1997; Roy and Elliott, 1989). This asymmetry seems to be specific to right-handers (Rhrs), however, since it has not been observed in left-handers (Lhrs) (Velay and Benoit-Dubrocard, 1999).

The fact that these two visually triggered hand responses yield discrepant results under similar conditions therefore suggests that the underlying neural processes involved may differ. In fact, the two responses are not only different with regard to the muscles they involve, but they also differ in their spatial components. Key-pressing or releasing requires a movement in response to a visual stimulus and reaching, a movement directed towards this stimulus. This difference between the spatial components of the two tasks might explain why asymmetry was observed in reaching and not in key-pressing: the left-hand advantage reflected in the reaction times has been attributed to a right hemisphere superiority in solving the spatial problems required to plan the pointing movement. Since very little movement planning is required in key-pressing, the right hemisphere is not likely to have an advantage in this task. The interhemispheric transfer time might depend on the nature of the information exchanged. It has been observed in key-pressing that the CUD varied with the complexity of the motor response (Iacoboni and Zaidel, 1995). The fact that the signals exchanged in pointing tasks are more complex might account for the paradoxically long CUD recorded in comparison with key-pressing. If this explanation is correct, a movement mobilizing the shoulder and

elbow, that is, one equivalent to pointing from the motor point of view, but requiring a weaker spatial component, as does key-pressing, should give rise to no manual asymmetry and no significant CUD.

To test this hypothesis, we compared three responses to the same visual stimuli, which differed in their level of visuomotor difficulty (Figure 1). In the first task, the participants had only to remove their hand from the starting platform, using their shoulder and elbow, exactly as if they were about to point towards the target, but without actually performing the movement. This task was similar to the classic keyrelease task, except that it involved proximal joints and muscles. Like the keyrelease task, it was a response to targets appearing in the visual field and not a movement directed towards these targets, and hence, its spatial component was relatively small or even absent. In the second task, the participants always had to reach towards the central fixation point, whichever lateral target was switched on. They therefore produced a pointing response, but since the movement was always the same, it could be programmed in advance, before the onset of the target, and the target only served here as trigger signal. In the third task, the participants had to perform the classical pointing movement toward the lateral target. This task involved the complete visuomotor processes required in pointing movements. The spatial and temporal variables of these movements were recorded, but since the present study focused on movement programming, the reaction times (RTs) were the variables of greatest interest.

MATERIALS AND METHODS

Subjects

The study was approved by the University Ethics committee. The participants were 40 men (20 to 43 years of age). Twenty of them were right-handed and 20 left-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). They were all volunteers and had all given their verbal consent. They all had normal or corrected to normal visual acuity in both eyes. Some of them were members of the Laboratory staff, and the others were students at the University. The latter were paid for participating.

Apparatus and Procedure

Each participant was seated with his head in a chin and forehead restraint, facing a vertical panel situated 47 cm from his eyes, which was fitted at the bottom with a small starting platform. He was asked to gaze at the fixation point (FP), which was a green light-emitting diode (5 mm in diameter) at the center of the panel, exactly straight-ahead at eye level. By contacting the starting platform with his hand, the participant triggered the foreperiod onset. After this unpredictable delay, the visual target was one out of four red LEDs, which were symmetrically arranged 6 and 12 deg to the right and left of the FP. It was switched on very briefly (50 ms), and the participant was instructed to keep fixating the FP, which remained lit until the end of the trial. The fixation was checked by means of a video system. Fifty ms exposure is well below the time necessary for stimulus foveation, and after some training, all the participants were able to refrain from making eye saccades during the presentation of the target. They were then required to lift their hand from the starting point (task 1), or point either towards the FP (task 2) or to the place where the red target had just appeared (task 3). In task 1, they were asked not to lift their hand alone, but their whole arm as if they actually wanted to reach the target. In task 2, they had to point to the central FP, whichever target was switched on, and in task 3, they had to actually reach the lateral target. In all 3 tasks, they were required to respond as rapidly and accurately as possible. The small plate used as the

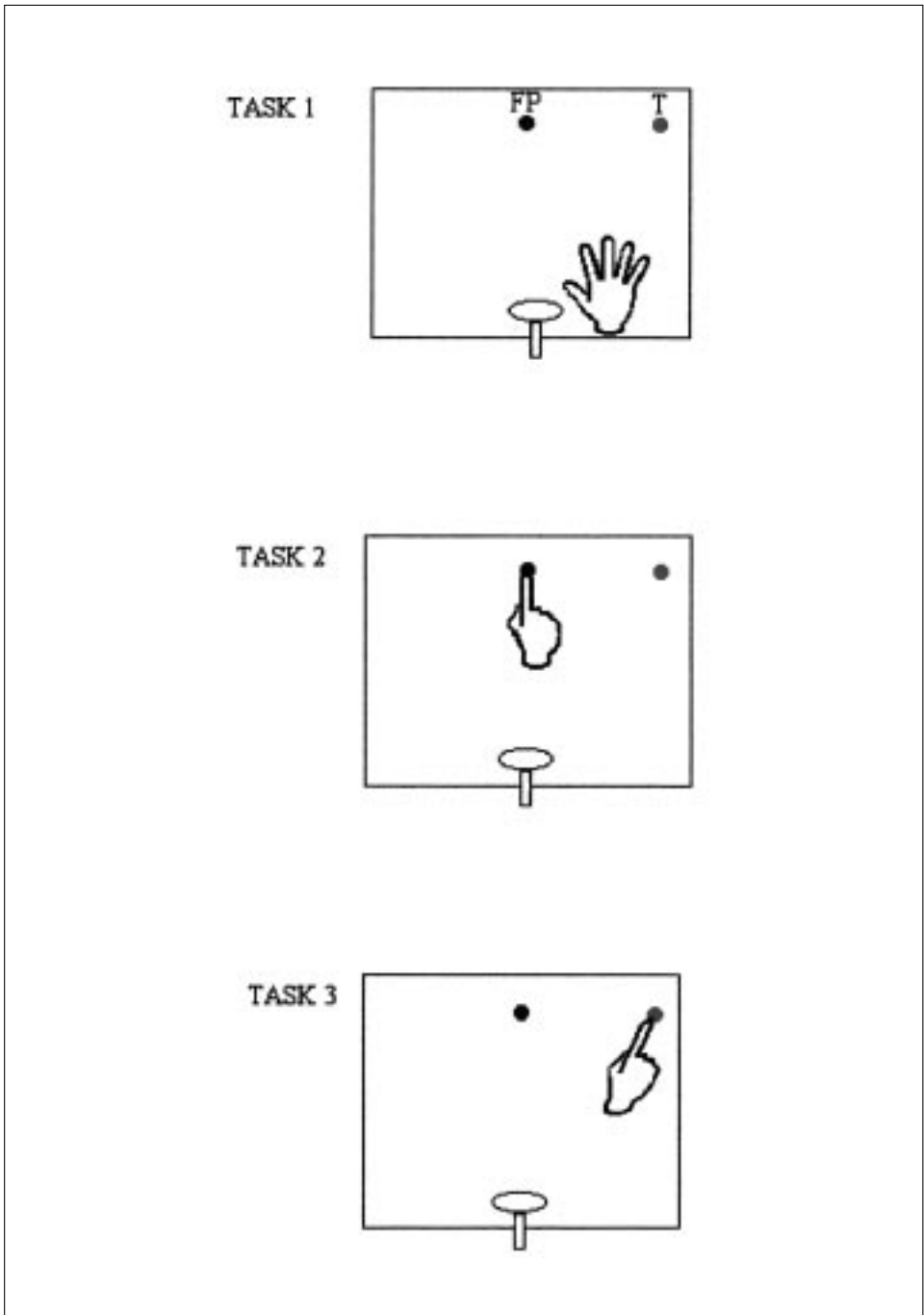


Fig. 1 – Diagram of the 3 tasks. FP: fixation point, T: target. In all 3 tasks, the participants had to react to the onset of one the 4 lateral targets. Task 1 consisted in simply removing the arm from the starting platform; task 2 consisted in pointing towards the central fixation point, and task 3 consisted in pointing towards the lateral target, as in the classical pointing tasks.

starting point of the movement was located 45 cm beneath the grid-center. It was in the mid-sagittal plane and at the same location for both right- and left-hand responses. The pointing (tasks 2 and 3) thus consisted in a vertical movement, from bottom to top, involving mainly the shoulder and elbow. Its amplitude was 45.3 cm and 46.1 cm with the 6 and 12 deg targets, respectively. The panel consisted of a grid-patterned printed circuit (32 × 32 cm), and as soon as the participant's finger contacted it, the pointing coordinates were recorded on a computer and a tone was emitted signaling that the participant could begin the next trial. He then had to place his hand again on the starting platform, thus triggering the onset of the target for the subsequent trial, and so on up to the end of the series. The pseudo-random order in which the targets were illuminated could not be predicted. The whole series of reaches was run in total darkness, so that the participants were unable to see their hands, and they were given no information about the accuracy of their movements. Experiments were run in six blocks, one with each hand in each of the three different tasks. The order of the 6 blocks varied across participants. Half of the Rhrs and the Lhrs began with their right hands (Rh) and half with their left hands (Lh). In all 3 tasks, two foreperiods with an unpredictable duration (0.5 or 1 s) were used, so that one set of 64 measurements (2 foreperiods × 4 targets × 8 repetitions) was recorded with each hand.

In tasks 2 and 3, each participant's spatial accuracy was determined with each target by calculating the centroid of the 16 pointing shots. Two variables were then computed: (1) the mean radial error (in cm), i.e. the distance between the centroid and the target, and (2) the pointing area (in cm²), i.e. the dispersion of the 16 pointing spots with respect to the centroid.

The RTs (in ms), i.e. the time elapsing between the onset of the target and the release of the starting platform, were measured during all the responses. In tasks 2 and 3, we also measured the movement time (MT, in ms), i.e., the time elapsing between the movement onset and the finger contact with the grid. The RTs and MTs were recorded with a sampling rate of 1000 Hz. Before the experiments began, one series of 64 trials in each of the 3 tasks was run with each hand to make the participants familiar with the pointing task requirements. During this training session, the participants were informed about the accuracy of their performances. The spatial and temporal variables were recorded and analyzed in separate 2 groups (Rh, Lh) × 2 hands (Rh, Lh) × 2 visual fields (RVF, LVF) × 2 eccentricities (6°, 12°) ANOVAs.

RESULTS

Task 1: Releasing the Starting Platform

RTs were the only variables recorded in task 1, and they are summarized in Table I. A 2 groups (Rh, Lh) × 2 hands (Rh, Lh) × 2 visual fields (RVF, LVF)

TABLE I
Mean Reaction Times in Task 1

| | Left hand | | | | Right hand | | | |
|------|-----------|--------|-------|--------|------------|--------|-------|-------|
| | LVF | | RVF | | LVF | | RVF | |
| | 6 deg | 12 deg | 6 deg | 12 deg | 6 deg | 12 deg | 6 deg | 12deg |
| Rhrs | | | | | | | | |
| Mean | 216 | 217 | 216 | 215 | 218 | 218 | 221 | 222 |
| S.D. | 26 | 29 | 29 | 27 | 26 | 24 | 27 | 28 |
| Lhrs | | | | | | | | |
| Mean | 218 | 222 | 219 | 221 | 218 | 222 | 225 | 224 |
| S.D. | 24 | 25 | 28 | 26 | 27 | 23 | 28 | 26 |

LVF: left visual field; RVF: right visual field; Rhrs: Right-handers; Lhrs: Left-handers. S.D.: between subjects standard deviations.

× 2 eccentricities (6°, 12°) ANOVA yielded no main effect of group, visual field or eccentricity. A significant main effect of hand was observed [$F(1, 38) = 4.43$, $p < .05$]. The participants were faster with their Lh (218 ms) than with their Rh (221 ms). The Lh advantage was of the same magnitude in both Rhrs (3.8 ms) and Lhrs (2.3 ms) but was not significant in each group separately [$F(1, 19) = 2.69$, n.s., and $F(1, 19) = 1.74$, n.s., in Rhrs and Lhrs, respectively]. The hand by visual field interaction was the only interaction to reach significance level [$F(1, 38) = 5.74$, $p < .025$], which shows that paradoxically, the crossed responses (218 ms) were faster than the uncrossed ones (221 ms).

Task 2: Pointing to the Central FP

Spatial Variables

The mean radial error was equal to 2.99 cm (S.D. 2.9). The mean pointing area was 5.38 cm². With both spatial variables, none of the main factors or interactions reached the significance level.

Movement Time

The mean MT recorded in task 2 was equal to 195 ms. None of the main factors or interactions yielded significant comparisons.

Reaction Time

The RTs are summarized in Table II. The ANOVA revealed no main effect of group, hand, visual field, or eccentricity. None of the interactions reached significance level. In particular, the absence of any hand by visual field interactions showed that crossed (237.4 ms) and uncrossed responses (237.0 ms) were not statistically different. In addition, the absence of any hand by group interactions indicated that there was no hand asymmetry in either Rhrs or Lhrs.

TABLE II
Mean Reaction Times in Task 2

| | Left hand | | | | Right hand | | | |
|------|-----------|--------|-------|--------|------------|--------|-------|-------|
| | LVF | | RVF | | LVF | | RVF | |
| | 6 deg | 12 deg | 6 deg | 12 deg | 6 deg | 12 deg | 6 deg | 12deg |
| Rhrs | | | | | | | | |
| Mean | 237 | 237 | 237 | 236 | 241 | 240 | 238 | 240 |
| S.D. | 25 | 24 | 27 | 24 | 23 | 25 | 26 | 26 |
| Lhrs | | | | | | | | |
| Mean | 237 | 241 | 236 | 242 | 233 | 234 | 232 | 233 |
| S.D. | 23 | 23 | 25 | 28 | 21 | 16 | 24 | 19 |

LVF: left visual field; RVF: right visual field; Rhrs: Right-handers; Lhrs: Left-handers. S.D.: between subjects standard deviations.

Task 3: Pointing to the Lateral Target

Spatial Variables

The mean radial error was very similar between Rhrs (3.0 cm, S.D. 0.9) and Lhrs (3.6 cm, S.D. 2.2). Only the main effect of eccentricity yielded a significant comparison: the 12° target was associated with greater errors than the 6° target [3.6 cm vs 3.0 cm, $F(1, 38) = 32.8, p < .0001$]. The mean pointing areas did not differ statistically between the Rhrs (7.50 cm², S.D. 3.1) and the Lhrs (7.32 cm², S.D. 3.5). Again, the main effect of eccentricity yielded a significant comparison: the 12° target gave rise to a significantly greater dispersion than the 6° target [7.75 cm² vs 7.07 cm², $F(1, 38) = 7.15, p < .02$].

Movement Time

The mean MT in task 3 was 196 ms. Only the main effect of eccentricity was found to be significant [$F(1, 38) = 16.9, p < .0005$]: the MTs were smaller with the 6 deg targets (193 ms) than with the 12 deg targets (198 ms). In addition, the group by hand interaction was significant [$F(1, 38) = 15.6, p < .0005$]: the Rhrs tended to be faster with their right hand [190 ms vs 202 ms, $F(1, 19) = 3.2, ns$] whereas the Lhrs were clearly faster with their left hand [186 ms vs 205 ms, $F(1, 19) = 21.9, p < .0005$]. The hand by visual field interaction was also significant [$F(1, 38) = 128.3, p < .0005$]: in both groups, although the distances to the right and left targets were identical, ipsilateral responses were completed more quickly than contralateral responses (187 ms vs 205 ms). This difference was similar between Rhrs [17.6 ms, $F(1, 19) = 91.0, p < .0005$] and Lhrs [18.2 ms, $F(1, 19) = 50.0, p < .0005$].

Reaction Time

The RTs are summarized in Table III. The ANOVA showed no existence of main effect of group, hand or visual field. The main effect of eccentricity was significant: the RTs were faster with 6 deg (239 ms) than with 12 deg targets (241 ms) [$F(1, 38) = 5.16, p < .05$]. The hand by group interaction was

TABLE III
Mean Reaction Times in Task 3

| | Left hand | | | | Right hand | | | |
|------|-----------|--------|-------|--------|------------|--------|-------|-------|
| | LVF | | RVF | | LVF | | RVF | |
| | 6 deg | 12 deg | 6 deg | 12 deg | 6 deg | 12 deg | 6 deg | 12deg |
| Rhrs | | | | | | | | |
| Mean | 232 | 231 | 239 | 246 | 253 | 257 | 240 | 241 |
| S.D. | 24 | 21 | 25 | 21 | 23 | 24 | 25 | 23 |
| Lhrs | | | | | | | | |
| Mean | 234 | 235 | 239 | 246 | 241 | 242 | 232 | 231 |
| S.D. | 25 | 27 | 28 | 28 | 21 | 19 | 23 | 24 |

LVF: left visual field; RVF: right visual field; Rhrs: Right-handers; Lhrs: Left-handers. S.D.: between subjects standard deviations.

significant [$F(1, 38) = 6.61, p < .025$]: the Rhrs were faster with their Lh (Lh: 237 ms, Rh: 248 ms), the Lhrs were not faster with either hand (Lh: 238 ms, Rh: 237 ms). The hand by visual field interaction was significant [$F(1, 38) = 138.8, p < .0005$]: the responses were faster when the target appeared in the visual field homolateral (235 ms) to the pointing hand than in the contralateral visual field (245 ms). The mean CUD was 11 ms (12.6 with Rhrs and 9.4 with Lhrs). Lastly, the hand by visual field by eccentricity interaction was significant [$F(1, 38) = 17.0, p < .001$], which indicates that the CUD differed between the 2 targets. The CUD was equal to 7.6 ms with the 6 deg target and 11.1 ms with the 12 deg target. Since an interaction was found to occur between group and hand, we analyzed the effect of hand taking each group separately. A Lh advantage was present in the Rhrs [10.6 ms, $F(1, 19) = 16.0, p < .001$] but no such manual difference was observed in the Lhrs (1.7 ms, $F < 1$).

Comparisons between the Responses Recorded in the 3 Tasks

In the second step, we performed an overall 2 groups \times 3 tasks \times 2 hands \times 2 visual fields \times 2 eccentricities ANOVA comparing the RTs in the 3 tasks. The ANOVA yielded no main effects of group, hand, or visual field. It showed the main effects of task [$F(2, 76) = 35.9, p < .0001$], since the RTs decreased from task 3 to task 1, and eccentricity [$F(1, 38) = 6.2, p < .025$], since the responses to the 6 deg targets were initiated faster (231 ms) than the responses to the 12 deg targets (233 ms).

The analysis of the task effect showed that the mean RT did not differ between tasks 2 and 3 [237 ms vs 240 ms respectively, $F(1, 38) = 1.99, ns$]. However, it was significantly shorter in task 1 (220 ms) than in task 3 [$F(1, 38) = 46.2, p < .0001$] or task 2 [$F(1, 38) = 40.2, p < .0001$]. The hand by group interaction was significant [$F(1, 38) = 5.1, p < .05$], which means that the same hand was not the faster one in both groups. A post-hoc analysis showed an advantage for the non preferred hand only significant in the Rhrs [Lh 230 ms, Rh 236 ms, $F(1, 19) = 9.07, p < .01$].

The hand by visual field interaction was significant [$F(1, 38) = 26.9, p < .0005$]. Specifically, the responses were faster when the target appeared in the homolateral (231 ms) than in the contralateral visual field (234 ms) with respect to the pointing hand. Lastly, the task by hand by visual field interaction reached the significance level [$F(2, 76) = 57.85, p < .0001$]; this means that the CUD varied with the task. To further study this effect, we computed the CUD for each hand, in all the conditions and participants and subjected the data to a 2 groups \times 3 tasks \times 2 hands \times 2 eccentricities ANOVA. The results of the ANOVA confirmed the main effect of the task [$F(2, 76) = 57.9, p < .001$]. The mean CUD in all the tasks combined was 3.1 ms, but it varied between the 3 tasks. It was greater in task 3 than in task 2 [11 ms vs 0.4 ms, $F(1, 38) = 62.5, p < .001$] and greater in task 3 than in task 1 [11 ms vs 2.3 ms, $F(1, 38) = 92.6, p < .001$], as well as being greater in task 2 than in task 1 [$F(1, 38) = 4.55, p < .05$].

DISCUSSION

The RT was the dependent variable in which we were mainly interested, and it was the only variable recorded in task 1. Furthermore, the experimental conditions we used (short period of target illumination, very fast movements and total darkness) did not favor either ongoing corrections or spatial accuracy in tasks 2 and 3. It was important to check, however, whether the participants actually performed the task correctly. In fact, despite these severe constraints, the pointing error and dispersion were not very large. These parameters did not vary between the experimental situations, except in task 3, where greater values were recorded in both cases with the more eccentric targets.

Movement Time

The MTs were recorded in tasks 2 and 3. The significant effect of eccentricity which was observed in task 3 resulted from the greater amplitude of the movement required to reach the more eccentric targets. This effect did not operate in task 2, where all the movements were directed toward the PF and therefore had the same amplitude. In task 3, the MT was shorter with the dominant hand in both groups. In other words, the participants executed the required movement with the same accuracy but more quickly with their dominant hand. This advantage for the Rh in motor execution has previously been observed in Rhrs (Helsen et al., 1998; Hodges et al., 1997; Velay and Benoit-Dubrocard, 1999; see Elliott and Chua, 1996, for a review), and it was assumed to reflect a left hemisphere (LH) superiority in defining the temporal parameters of the motor commands, or in the use of feedback, or both (Elliott et al., 1993; Elliott and Chua, 1996). As previously observed under the same conditions (Velay and Benoit-Dubrocard, 1999), a symmetrical advantage for the left dominant hand was observed in Lhrs in the present experiment. If the same explanation holds in both sinistrals and dextrals, this left hand advantage can be said to reflect a right hemisphere (RH) advantage for the movement execution in Lhrs. As mentioned above, very few relevant sensory signals were available under our experimental conditions, and few ongoing movement corrections could probably be made. This might seem to suggest that the advantage for the dominant hand was due to a greater impulse being sent to the dominant arm. However, this interpretation does not explain why the hand difference was not present in task 2, both in dextrals and sinistrals.

Both groups performed the movements in task 3 more slowly in the crossed than in the uncrossed situations, although the mean distances from the starting platform to the targets were identical. Similar findings have often been made in reaching tasks (Carson et al., 1990; Carson et al., 1995; Chua et al., 1992; Fisk and Goodale, 1985; Hodges et al., 1997; Velay and Benoit-Dubrocard, 1999), but they are not easy to explain. They might simply have resulted here from the differential biomechanical constraints imposed by the two movement directions. The fact that no such difference was observed in task 2, where the movements did not cross the midline, argues in favor of this explanation. However, the fact that this difference has been reported to be greater in acallosal patients than in

intact participants (Jakobson, Servos, Goodale et al., 1994) suggests that it might also somehow result from interhemispheric differences.

Reaction Time

The aim of this study was to compare hemispheric asymmetry and interhemispheric transfer in 3 tasks which were similar to each other from the motor point of view, but involved different spatial components. The main RT results can be summarized as follows: in task 3, the classical reaching task, a hand asymmetry was found to exist in the Rhrs in favor of the Lh. A significant positive CUD was also observed in this task, in both Lhrs and Rhrs. In the other two tasks, neither asymmetry nor CUD was clearly detected.

Hand Asymmetry

In the classical pointing task (task 3), the Rhrs exhibited shorter RTs with their Lh (– 11 ms). This Lh advantage is consistent with the results of previous studies in which asymmetries of the same order of magnitude were observed (Bradschaw et al., 1990; Carson et al., 1990; Chua et al. 1992; Elliott et al., 1993; Haaland and Harrington, 1989; Roy and Elliott, 1986; Velay and Benoit-Dubrocard, 1999). This asymmetry was not due to the transfer, since it was found to be present when the two uncrossed conditions were compared. In addition, it did not occur in the Lhrs, who had similar CUDs to those of the Rhrs. In the Rhrs, some time was therefore gained in the RH (or lost in the LH), in one of the neural processes involved in the pointing movement planning (Carson, 1996). With a view to identifying the process possibly involved, one can distinguish very schematically between 3 successive steps, namely the visual, visuomotor and motor steps in the programming of a pointing movement. At least one of these steps might be faster in the RH than in the LH (or correspondingly slower in the LH). On the one hand, the visual processing might have been faster in the RH because this hemisphere may be specifically involved in visual attention. However, no visual field effect in favor of the left visual field was observed here, and in addition, the visual inputs present in task 3 were strictly identical to those available in tasks 1 and 2, where no asymmetry was observed. Early visual processing is therefore not the best candidate for explaining the RH advantage. On the other hand, the time gained might result from the motor output being faster in the case of the left arm. It is possible that since the right arm is heavier in Rhrs, a greater force will be required to overcome the inertia, and it will therefore take longer to initiate the motor command. However, if this had been the case, we would not only have observed a symmetrical effect in Lhrs, but the same asymmetry would have been present in tasks 1 and 2. In fact, a small Lh advantage was observed in task 1: the starting platform was released slightly faster with the Lh than with the Rh. This Lh advantage was of the same magnitude (3 ms) in both groups, but was not significant in either group alone, and was weaker than in task 3. There is no obvious explanation available so far for this Lh advantage, which has sometimes been observed in distal key-pressing tasks (Annett and Annett, 1979; Di Stefano,

Morelli, Marzi et al., 1980). Since no hand asymmetry was observed in task 2 in either Rhrs or Lhrs, a purely motor explanation for the hemispheric asymmetry is hardly likely to suffice. It seems more likely that the reason why a faster step occurred in the RH may have had something to do with the visuomotor processes involved in the pointing movement. Reaching towards a target requires forming a spatial relationship between a point located in extra-personal space and the limb extremity. Building this relationship involves making spatial coordinate transformations, in which the endpoint of the movement is computed from the retinal coordinates of the target. Once the endpoint has been specified, the trajectory of the index from its initial position to this endpoint has to be planned. One of these two visuomotor processes might be responsible for the asymmetry observed. It has been previously suggested that it may have been due to a RH superiority in solving the target location problems (Guiard, Diaz and Beaubaton, 1983). This hypothesis was tested further by increasing the complexity of the spatial processing required to establish the position of the target without making use of changes in the response movement (Carson et al., 1992; Chua et al., 1992; Elliott et al., 1993). Chua et al. (1992), for instance, asked their subjects to make aiming movements either directly towards the target or towards its mirror image with respect to the FP. These authors observed that increasing the spatial complexity did not increase the magnitude of the Lh advantage. The authors of all these studies concluded that the RH superiority was not due to the localization processes.

Attempts have also been made to manipulate the second visuomotor process, i.e. the specification of the spatial parameters of the movement. Here the idea was to modify the difficulty of the movement programming without interfering with the spatial localization processes. Carson et al. (1995) used the precuing technique and gave the participants advance information about the spatial position of the target so that they could partly plan their movement before the target onset. The authors compared this situation with a control situation in which no precuing was available, and where the movement could be completely planned during the RT. They observed that the Lh advantage reflected in the RTs decreased when advance information was provided, and could even be abolished when the participants knew the exact position of the target. These data were ambiguous, however, because giving the subjects advance information about the position of the target may both affect their visual attention and enable them to partly process the spatial coordinates. In task 2 in the present study, the movement to be performed was completely precued, but there was as much uncertainty about the target location as in task 3, and the motor component was very similar in both cases. The two responses differed only in terms of the movement planning: the movement trajectory was defined before the target onset in task 2, whereas it had to be completely defined after the target onset in task 3. Since the Lh advantage disappeared in task 2, our conclusions concord with those of Carson and coll. (1995), who suggested that the specification of the movement parameters may have be responsible for the hemispheric asymmetry in favor of the RH observed in pointing tasks. This explains why no hemispheric asymmetry is observed when the spatial requirements of the task are too weak, as in the task 1, or when the spatial parameters of the movement can be partly

specified in advance, as in the task 2. In Rhrs, the LH may be less efficient, or at least slower, than the right at performing these spatial operations. Interestingly, as previously observed (Velay and Benoit-Dubrocard, 1999), this hand asymmetry was not observed in the present study in Lhrs, who seem to have a less pronounced hemispheric lateralization than Rhrs (Bryden, 1982; Marzi, Grabowska, Tressoldi et al., 1988).

Interhemispheric Transfer

In the usual pointing movement (task 3), the RTs were shorter in uncrossed than in crossed situations. The mean CUD was 11 ms: this value is greater than that recorded in the key-pressing task (about 4 ms, see Marzi et al., 1991), but similar to that obtained in other pointing movement studies. It was found to be greater with the most eccentric target. This was not in agreement with the previous keypress data, which showed that retinal eccentricity does not affect the CUD to any significant extent (e.g. Aglioti, Dall'Agnola, Girelli et al., 1991). As previously observed (Bashore, 1981), the CUD was not found to differ between Rhrs and Lhrs. As in the case of hand asymmetry, the CUD seems to depend on the spatial complexity of the movement, since no significant positive CUDs were recorded in either tasks 1 or 2. Assuming that the CUD reflects the interhemispheric transfer time, a null CUD means that no net transfer has taken place. In turn, this suggests that the hemisphere that received the visual input, that is the hemisphere ipsilateral to the arm used, is the one which sent the motor commands to the arm muscles. This is theoretically possible, because ipsilateral motor pathways can activate proximal muscles: ipsilateral corticospinal projections from the motor cortex to the trunk and proximal upper limb muscles have been found to exist in monkeys (Brinkman and Kuypers, 1972). They have also been found to exist in humans, but they are probably weaker than the contralateral projections, and their role still remains to be elucidated (Chen, Cohen and Hallet, 1997). In this context, the weak negative CUD recorded in task 1 (– 3 ms) suggests that the ipsilateral command might be faster than the contralateral one. The movement involved in task 2 was a pointing movement, the trajectory of which did not depend on the position of the stimulus. Its spatial component was presumably planned in advance, before the stimulus onset. From this point of view, it was more like the keyrelease response 1 and required no interhemispheric transfer. If we assume that in tasks 1 and 2, the motor command was sent from the hemisphere which received the visual input whichever hand was used, it remains to be explained why in response 1 the motor commands may have been generated in the contralateral hemisphere although the same proximal muscles were involved. It seems likely that some process must certainly occur in the contralateral hemisphere, and that this lateralized process had something to do with the specification of the arm trajectory. In other words, each hemisphere might represent the movement of the contralateral but not that of the ipsilateral hand (Parsons, Gabrieli, Phelps et al., 1998). Some information therefore has to be transferred between the two hemispheres in the crossed situations, in both Rhrs and Lhrs. The fact that the transfer usually took longer in pointing than in digital key-pressing tasks

suggests that the nature of the information exchanged differed between the two tasks. In pointing, some visuomotor information relating to either the location of the target in space or the arm motor program, or some combination of both, might be transferred.

The RT data recorded in task 3 have been summarized in Figure 2 in a very schematic model. The RTs in each situation are on the side of each line. For the sake of clarity, the asymmetry has been modelled as time lost in the left hemisphere, and for the reasons mentioned above, these extra 11 ms have been included in the visuomotor (VM) step. In Rhrs, if the CUD were computed in each visual field, it would be 23 ms (255 – 232) in the case of the LVF and only 2 ms (243 – 241) in that of the RVF. This would reflect a substantial right/left asymmetry in the transfer time. However, this asymmetry might be only apparent if one assumes that the transfer may occur before the 11 ms longer step in the left hemisphere. In this case, the transfer times computed in both directions are not very different (Figure 2). If the transfer occurs after the longer step, however, the transfer times would be very asymmetric. We are in

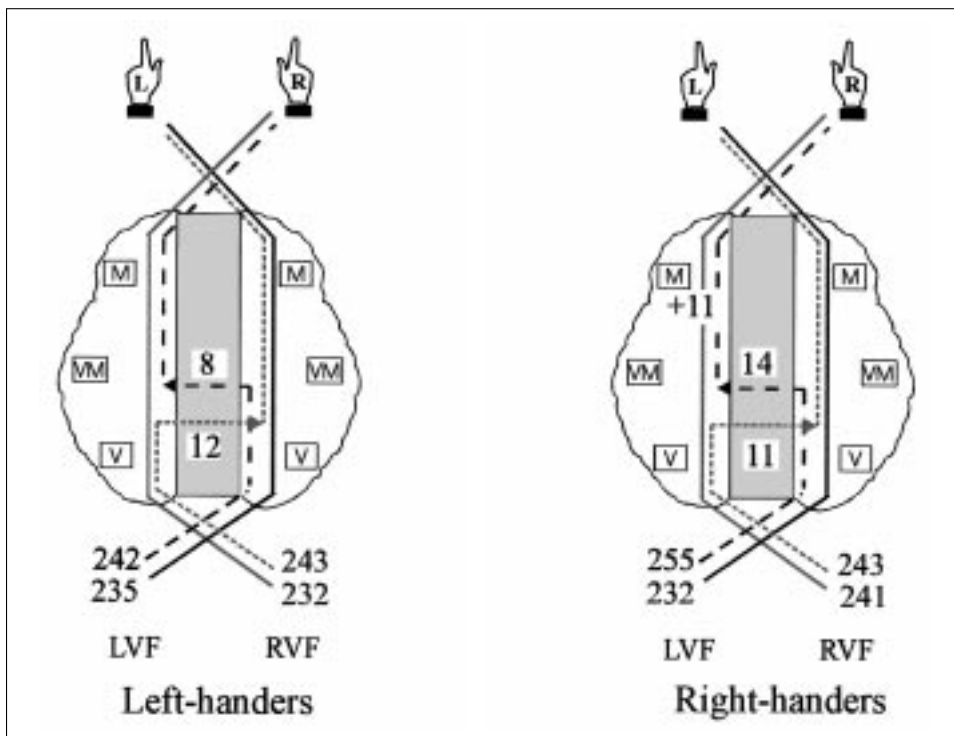


Fig. 2 – RVF: right visual field; LVF: left visual field. Diagram of the experimental data recorded during task 3: three distinct processes were taken to occur from the visual input to the motor output: the visual process (V), the visuomotor transformation process (VM), and the motor process per se (M). The gray area between the hemispheres denotes the CC. The intrahemispheric and interhemispheric pathways are drawn in solid and dashed lines, respectively. The RTs in each situation are given beside each line. The values in the CC under or above the dashed lines are the CUDs measured, and reflect the transfer times. Note the extra 11 ms taken by the LH of Rhrs.

favor of the first hypothesis, but it still needs to be checked experimentally. Of course, this model does not fit the data obtained in tasks 1 and 2, where no transfer time was measured. Another model not involving a transfer therefore had to be used in this case. Here the structure responsible for the VM step, which is liable to be the crucial step, might be the parietal cortex which, among the numerous structures involved in pointing programming, seems to have a special role to play: the sensorimotor transformations required by complex hand movements are likely to be performed in the parietal cortex (Sakata and Taira, 1994; Andersen, Snyder, Bradley et al., 1997). In humans, the activity of the superior parietal cortex has been found to increase in diverse motor tasks, all of which require visuomotor transformation in extra-personal space (Grafton, Fagg, Woods et al., 1996). Lastly, a study by Rushworth, Nixon and Passingham (1997) relates directly to the results presented here. The latter authors performed bilateral lesions on parietal areas 5/7b/MIP in monkeys trained to reach towards visual targets in the dark. They compared two reaching conditions: (1) a control situation where the reaching was always carried out from the same starting position to the same target position and (2) another condition involving a single target but any of four different starting positions. The control condition resembled our task 2 and the other condition, our task 3. Upon the removal of the parietal areas, only a very mild impairment was observed in the control condition, but a severe impairment in the other condition. The authors concluded that these parietal areas were involved when a spatial representation of the limb was needed and not in the control condition, because the latter task could be performed by repeating the same pattern of joint positions and muscle activation.

CONCLUSION

The results of this study confirm previous data indicating that in Rhrs, the programming of goal-directed movements is faster in the RH, and that no such hemispheric asymmetry exists in Lhrs. The results also confirm that some information is exchanged between the two hemispheres during the programming of pointing movements, although proximal muscles are involved. These two points depend strongly on the spatial requirements of the movement, however. If little spatial processing is required, each hemisphere alone may be able to command both arms without any need for the interhemispheric transfer of information. The apparently paradoxical long transfer time which elapses in pointing in comparison with key-pressing may therefore be due to the processing of the spatial component of pointing. For some reasons, the sensorimotor processes underlying the specification of the movement trajectory might be carried out in the contralateral hemisphere. Since real-life targets can be located anywhere in the visual field, the neural networks involved in the programming of reaching movements can be said to involve not just one but both hemispheres.

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REFERENCES

- AGLIOTI, S., BERLUCCHI, G., PALLINI, R., ROSSI, G.F., and TASSINARI, G. Hemispheric control of unilateral and bilateral responses to lateralized light stimuli after callosotomy and in callosal agenesis. *Experimental Brain Research*, 95: 151-165, 1993.
- AGLIOTI, S., DALL'AGNOLA, R., GIRELLI, M., and MARZI, C.A. Bilateral hemispheric control of foot distal movements: Evidence from normal subjects. *Cortex*, 27: 571-581, 1991.
- ANDERSEN, R.A., SNYDER, L.H., BRADLEY, D.C., and XING, J. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neurosciences*, 20: 303-330, 1997.
- ANNETT, M., and ANNETT, J. Individual differences in right and left reaction time. *British Journal of Psychology*, 70: 393-404, 1979.
- BASHORE, T.R. Vocal and manual reaction time estimates of interhemispheric transmission time. *Psychological Bulletin*, 89: 352-368, 1981.
- BRADSHAW, J.L., BRADSHAW, J.A., and NETTLETON, N.C. Abduction, adduction and hand differences in simple and serial movements. *Neuropsychologia*, 28: 917-931, 1990.
- BRINKMAN, J., and KUYPERS, H.G.J.M. Splitbrain monkeys: Cerebral control of ipsilateral and contralateral arm, hand, and finger movements. *Science*, 176: 536-539, 1972.
- BRYDEN, M.P. *Laterality*. New York: Academic Press, 1982.
- CARSON, R.G. Putative right hemisphere contributions to the preparation of reaching and aiming movements. In D. Elliott and E.A. Roy (Eds.), *Manual Asymmetries in Motor Performance*. Boca Raton, FL: CRC Press, 1996, Ch 8, pp. 159-172.
- CARSON, R.G., CHUA, R., ELLIOTT, D., and GOODMAN, D. The contribution of vision to asymmetries in manual aiming. *Neuropsychologia*, 28: 1215-1220, 1990.
- CARSON, R.G., CHUA, R., GOODMAN, D., and BYBLOW, W.D. The preparation of aiming movements. *Brain and Cognition*, 28: 133-154, 1995.
- CARSON, R.G., GOODMAN, D., and ELLIOTT, D. Asymmetries in the discrete and pseudocontinuous regulation of visually guided reaching. *Brain and Cognition*, 18: 169-191, 1992.
- CHEN, R., COHEN, L.G., and HALLET, M. Role of the ipsilateral motor cortex in voluntary movement. *Canadian Journal of Neurological Sciences*, 24: 284-291, 1997.
- CHUA, R., CARSON, R.G., GOODMAN, D., and ELLIOTT, D. Asymmetries in the spatial localization of transferred targets. *Brain and Cognition*, 20: 227-235, 1992.
- COLEBATCH, J.G., DEIBER, M.P., PASSINGHAM, R.E., FRISTON, K.J., and FRACKOWIAK, R.S.J. Regional cerebral blood flow during voluntary arm and hand movements in human subjects. *Journal of Neurophysiology*, 65: 1392-1401, 1991.
- DI STEFANO, M., MORELLI, M., MARZI, C.A., and BERLUCCHI, G. 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. *Experimental Brain Research*, 38: 197-204, 1980.
- ELLIOTT, D., and CHUA, R. Manual asymmetries in goal-directed movement. In D. Elliott and E.A. Roy (Eds.), *Manual Asymmetries in Motor Performance*. Boca Raton, FL: CRC Press, 1996, Ch 7, pp. 143-158.
- ELLIOTT, D., ROY, E.A., GOODMAN, D., CARSON, R.G., CHUA, R., and MARAJ, B.K.V. Asymmetries in the preparation and control of manual aiming movements. *Canadian Journal of Experimental Psychology*, 47: 570-589, 1993.
- FISK, J.D., and GOODALE, M.A. The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research*, 60: 159-178, 1985.
- FISK, J.D., and GOODALE, M.A. The effects of unilateral brain damage on visually guided reaching: Hemispheric differences in the nature of the deficit. *Experimental Brain Research*, 72: 425-435, 1988.
- GAZZANIGA, M.S. *The Bisected Brain*. New York: Appleton-Century-Crofts, 1970.
- GRAFTON, S.T., FAGG, A.H., WOODS, R.P., and ARBIB, M.A. Functional anatomy of pointing and grasping in humans. *Cerebral Cortex*, 6: 226-237, 1996.
- GUIARD, Y., DIAZ, G., and BEAUBATON, D. Left-hand advantage in right-handers for spatial constant error: Preliminary evidence in a unimanual ballistic aimed movement. *Neuropsychologia*, 21: 111-115, 1983.
- HAALAND, K.Y., and HARRINGTON, D.L. The role of the hemispheres in closed loop movements. *Brain and Cognition*, 9: 158-180, 1989.
- HELSEN, W.F., STARKES, J.L., ELLIOTT, D., and BUEKERS, M.J. Manual asymmetries and saccadic eye movements in right-handers during single and reciprocal aiming movements. *Cortex*, 34: 513-529, 1998.
- HODGES, N.J., LYONS, J., COCKELL, D., REED, A., and ELLIOTT, D. Hand, space and attentional asymmetries in goal-directed manual aiming. *Cortex*, 33: 251-269, 1997.
- ILCOBONI, M., and ZAIDEL, E. Channels of the corpus callosum: Evidence from simple reaction times to

- lateralized flashes in the normal and the split brain. *Brain*, 118: 779-788, 1995.
- JAKOBSON, L.S., SERVOS, P., GOODALE, M.A., and LASSONDE, M. Control of proximal and distal components of prehension in callosal agenesis. *Brain*, 117: 1107-1113, 1994.
- MARZI, C.A., BISIACCHI, P., and NICOLETTI, R. Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*, 29: 1163-1177, 1991.
- MARZI, C.A., GRABOWSKA, A., TRESSOLDI, P., and BISIACCHI, P.S. Left hemisphere superiority for visuospatial functions in left-handers. *Behavioral and Brain Research*, 30: 183-192, 1988.
- OLDFIELD, R.C. The assessment and analysis of handedness. The Edinburgh Inventory. *Neuropsychologia*, 9: 97-113, 1971.
- PARSONS, L.M., GABRIELI, J.D.E., PHELPS, E.A., and GAZZANIGA, M.S. Cerebrally lateralized mental representations of hand shape and movement. *The Journal of Neuroscience*, 18: 6539-6548, 1998.
- ROY, E.A., and ELLIOTT, D. Manual asymmetries in aimed movements. *Quarterly Journal of Experimental Psychology*, 41A: 501-516, 1989.
- RUSHWORTH, M.F.S., NIXON, P.D., and PASSINGHAM, R.E. Parietal cortex and movement. II. Spatial representation. *Experimental Brain Research*, 117: 311-323, 1997.
- SAKATA, H., and TAIRA, M. Parietal control of hand action. *Current Opinion in Neurobiology*, 4: 847-856, 1994.
- VAN DER STAAK, C. Intra- and interhemispheric visual-motor control of human arm movements. *Neuropsychologia*, 13: 439-448, 1975.
- VELAY, J.L., and BENOIT-DUBROCARD, S. Hemispheric asymmetry and interhemispheric transfer in reaching programming. *Neuropsychologia*, 37: 895-903, 1999.

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