

HEMISPHERIC PROCESSING OF TEMPORAL INFORMATION

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ABSTRACT: The capacity of the two cerebral hemispheres for temporal processing was investigated in two experiments concerned with sensory and motor processing, respectively. The temporal processing of sensory information was examined in a task requiring simultaneity judgement of pairs of tactile stimuli delivered unimanually or bimanually. Unimanual stimulation permitted presentation of both events to the same hemisphere while bimanual stimulation involved both hemispheres and necessarily required interhemispheric communication to compare stimulus onset asynchrony (SOA). The order of presentation of asynchronous pairs determined which cerebral hemisphere was activated first. Pairs of stimuli were judged as simultaneous at longer SOAs in the bimanual than the unimanual conditions whilst unimanual left and right simultaneity thresholds did not differ. These results suggest that the two hemispheres are equally capable of temporally resolving a pair of simple tactile stimuli. A structural model proposing that temporal comparisons are carried out in the hemisphere receiving the second stimulus provides the best account of the results.

The temporal processing of motor information was examined in a task requiring the planning and execution of sequences of finger movements. A predetermined number of double-tap responses with the index and middle fingers of a given hand were required in response to a visual cue in the ipsilateral visual field. The restriction of the performance cue in each trial to the hemisphere controlling the response permitted assessment of the contribution of each cerebral hemisphere to differences in hand skill. Movement time increased linearly for both hands with increasing length of tap sequence and did not differentiate hand performance. Response preparation time, however, increased linearly with increasing task load for the preferred hand but varied quadratically for the non-preferred hand. These results indicate that differences in hand skill may be determined by the mode of response preparation within the contralateral hemisphere. They also suggest that studies of hand differences involving fixed levels of motor demand would not properly differentiate hand performance.

Together, these studies indicate that both cerebral hemispheres are capable of the temporal processing of sensory and motor information but that the hemisphere primarily involved is determined by side of stimulus or response, respectively.

Hemispheric specialisation for the processing of information has commonly been studied with techniques and tests which demonstrate sensory field advantages (see Zaidel, 1983). Many studies have con-

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centrated on hemispheric differences in the processing of verbal as opposed to visuospatial material. In this regard, the left hemisphere appears to be preferentially specialised for the processing of verbal information (see Geffen & Quinn, 1984) whilst the right hemisphere appears to play a major role in many nonverbal cognitive functions such as pattern or spatial analysis (see Milner, 1971; Bradshaw & Nettleton, 1981). Few studies have addressed the issue of hemispheric contribution to the processing of temporal as opposed to spatial information (see Mills & Rollman, 1980) though some have suggested that temporal processing takes place in the hemisphere dominant for speech since speech may be regarded as one form of this type of processing (e.g. Efron, 1963; Schwartz & Tallal, 1980). However, in assessing this matter, it would seem prudent to distinguish between the temporal processing of sensory as opposed to motor information since speech is predominantly a motor skill. This paper reports two independent experiments carried out to assess hemispheric contributions to the temporal processing of information in sensory and motor modalities, respectively. The first experiment investigated hemispheric differences in the sensory discrimination of temporal order whilst the second was concerned with the hemispheric basis of handedness in fine motor skills.

EXPERIMENT 1: THE TEMPORAL PROCESSING OF SENSORY INFORMATION

The few studies that have investigated hemispheric differences in the sensory discrimination of temporal order have tended to support the view that there is left hemisphere specialisation or superiority for this sort of judgement (Efron, 1963; Mills & Rollman, 1980). The experimental approach taken by these studies has required a judgement of whether or not pairs of bilateral stimuli are delivered simultaneously. Laterality for temporal judgement has been inferred on the basis that the stimulus onset asynchrony threshold for simultaneity judgement was smaller when the right-sided stimulus preceded the left-sided stimulus than when vice-versa. This explanation assumes that lateralised signals are initially directed to the contralateral hemisphere via contralateral sensory pathways (Corkin, 1978; Darian-Smith, 1982; Desmedt & Bourguet, 1985), that the comparison of lateralised signals requires the passage of at least one of the signals across the corpus callosum and that there is some intra-hemispheric timing mechanism which ultimately compares the signals as a basis for judgement. The modelled relationship (see Mills & Rollman, 1980) between psychophysical temporal order thresholds and neural events for left hemisphere specialisation is shown in Fig-

ure 1a. The psychophysical data cited above fit both this model (Left specialisation) and one in which judgement is always performed in the hemisphere receiving the first stimulus but more efficiently in the left hemisphere (Left asymmetry).

The purpose of the present experiment was to investigate hemispheric differences in the tactile discrimination of temporal order under conditions of both bilateral and unilateral finger stimulation, since a comparison between these conditions should discriminate between the specialisation and asymmetry models described above. In the case of left specialisation, there should be no difference between unilateral left and unilateral right hand thresholds and these should themselves be intermediate to the two bilateral condition thresholds (see Figure 1). In the case of left asymmetry, unilateral right hand judgements should simply be smaller than unilateral left hand judgements. Thus, in the terms of Figure 1a, the value of T which reflects the resolution of the hypothetical, intrahemispheric timing process associated with temporal judgement would be greater for the right compared to the left hemisphere. The use of discrete tactile stimulation to the distal portion of the limbs was chosen in this experiment since it has now been shown that the transmission of sensorimotor information between these locations and the cerebral cortex is exclusively cross-lateralized (Darian-Smith, 1982).

METHOD

Subjects

Subjects were 4 male and 8 female adult volunteers between the ages of 17 and 37 years. All subjects were classified as right-handed using the six primary questions of Annett's handedness questionnaire (Annett, 1970a) and as left hemisphere language dominant according to discriminant function analysis of measures obtained during dichotic monitoring of word lists (Geffen & Caudrey, 1981). Normal hearing was assessed using pure tone audiometry with the maximum acceptable hearing loss on each ear being 25 decibels (ISD) between 250 and 8000 Hz.

Task

The task required subjects to complete series of trials in which they judged whether two point stimuli presented to separate fingers were delivered simultaneously (YES response) or not (NO response). The stimulus onset asynchrony (SOA) for each consecutive trial of a series was determined according to a variation of the PEST (parame-

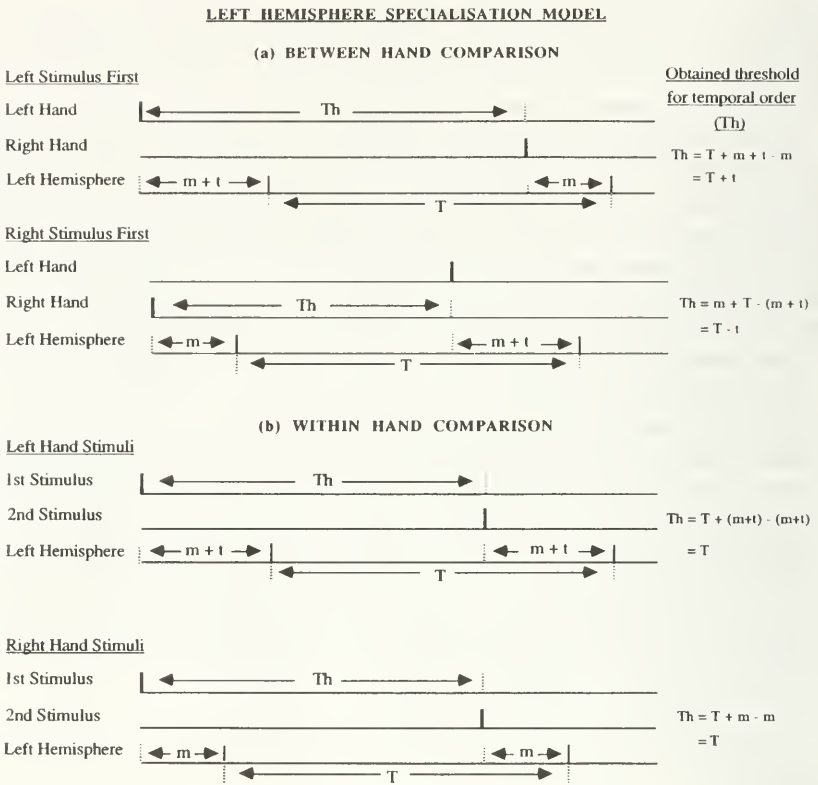


FIGURE 1. Temporal processing model based on the hypothesis of left hemisphere specialisation for the temporal resolution of consecutive pairs of tactile events. A right hand stimulus takes m ms to be transmitted to the left hemisphere via the exclusive contralateral pathway for digital touch information. The left hand stimulus takes $m+t$ ms to reach the left hemisphere since it must additionally cross the corpus callosum (t ms) after contralateral transmission to the right hemisphere (m ms). The respective arrival of two neural events in the left hemisphere must be separated by at least T ms for the perceptual discrimination of the stimulus events they represent. (a) *Between-hand comparisons*: the psychophysical threshold for perceptual discrimination (Th) differs according to whether the left hand stimulus precedes the right hand stimulus ($T+t$ ms) or the right hand stimulus precedes the left ($T-t$ ms) (adapted from Mills and Rollman 1980) (b) *Within-hand comparisons*: the psychophysical threshold for perceptual discrimination ($\text{Th} = T$ ms) is not affected by hand of stimulation. This model predicts that the threshold for within-hand comparisons will be intermediate to the two between-hand thresholds.

ter estimation by sequential testing) algorithmic technique (see Taylor & Creelman, 1967; Findlay, 1978) for psychophysical threshold determination. Each series of trials continued under the control of the PEST algorithm until the threshold SOA for simultaneity judgement in that series was determined or the series abandoned. The stimuli were of fixed duration (10 ms) and constant amplitude (1 mm of skin depression) and were presented mechanically with timed onset under computer control (PDP-11/34). Auditory cues from the mechanical operation were masked by binaural pink noise presented continuously through headphones during each series of trials. Pink noise levels were adjusted according to the hearing levels of the subject.

Each trial commenced with the presentation of two stimuli separated by an SOA appropriate to that trial (as determined by the PEST algorithm). A judgement was required after each trial. If no response was received within 3 s following presentation of a stimulus pair, a warning tone was presented through headphones instructing the subject to respond immediately. The tone was then repeated every 3 s until either response was received or the series abandoned.

Parameter Estimation by Sequential Testing (PEST)

This technique allows threshold parameter estimation in as few trials as possible for a given level of precision. In contrast to classical psychophysical techniques where the test values of the parameter are determined in advance, PEST uses an adaptive method in which the value adopted for any trial is determined by rules (see Findlay, 1978) which operate upon trial history. By applying PEST rules to the present task, an initial SOA is gradually reduced by steps. When the rules indicate that the threshold sought has been passed, the step direction is reversed and the SOA gradually increased by steps until a second reversal in step direction is required. Following each such reversal, the step size is reduced. The process continues until the step size falls below a predetermined value chosen to provide the required degree of precision in threshold estimation. The SOA at the termination of a series provides the series estimate of threshold.

Design

Subjects completed six test blocks of trials in each of two testing sessions no more than a week apart. In one session subjects were required to indicate their judgements verbally and in the other by bipedal depression of a two-way footswitch. The order of these sessions was counterbalanced over subjects. Verbal and non-verbal response modes were tested due to the suggestion (Efron, 1963) that verbal expression of temporal judgements may 'prime' the left hemisphere in

left dominant subjects and thereby prejudice threshold determination. It was assumed that the use of a bipedal footswitch ensured both non-verbal response and activation of both hemispheres during response. Each session commenced with practice on the task during which the smallest SOA at which a NO response could be confidently expected was estimated. This estimate was used to determine the lower limit of a 15 ms range of initial SOA values for the six test blocks. The initial SOA for these blocks was varied randomly within this range.

In each of two blocks of each session, stimulus pairs were presented to the index and middle finger of the left hand (Within Left condition), the index and middle finger of the right hand (Within Right condition) and the index fingers of both hands (Between Hands condition). The order of finger stimulation during asynchronous trials ($SOA > 0$) was counterbalanced over the two blocks for each condition within each session. Thus, in half the sequences for each within-hands condition the index finger was stimulated first and in the other half the middle finger was stimulated first. Similarly, in half the sequences for the between-hands condition the index finger of the left hand was stimulated first and in the other half the index finger of the right hand was stimulated first. The mapping of finger to stimulator was counterbalanced over subjects within condition.

Each trial block consisted of four randomly interwoven sequences of trials with each sequence controlled independently by a governing PEST algorithm. The initial and termination step sizes for each block were 8 and 1 ms, respectively. If a sequence was not terminated by 50 trials then it was abandoned. The simultaneity threshold estimate for a block was the mean termination SOA from completed sequences within that block.

Procedure

At the beginning of each block subjects were instructed about the task and asked to rest their fingers lightly on the stimulator housings throughout each block, to avoid pressing down and to keep all fingers still since finger movement has been found to interfere with tactile perception (Angel, Weinrich & Rodnizky, 1986). They were asked to focus their attention on a midline point about 90 cm in front of them at eye level. In the session requiring verbal response, subjects were asked to respond 'Yes' when they judged that stimuli were simultaneous and 'No' when they judged that they were not. In the foot response condition, they were instructed to press forward with the toes of both feet for a 'Yes' response and with both heels for a 'No' response. There was a 5 min rest between each block of trials.

Apparatus

Two mechanical tactile stimulators were placed in a line extending forward at 90 degrees to the vertical of the body midline. They were secured in metal housings 1.5 cm in diameter and 0.75 cm apart. Each stimulator consisted of a thin rod attached at its base to a driving solenoid. When charged, the solenoid thrust the rod vertically upwards through the central core of a cylindrical metal reel. At the height of the thrust, the rod projects vertically upwards from the concave surface of the cylinder on which rests the palmar surface of the fingertip to be stimulated. Stimulus delivery was under control of a PDP-11/34 computer programmed with the PEST algorithm. Foot responses were registered on a bipedal, heel-toe rocker switch which was also connected to the computer and provided automatic feedback to the PEST algorithm for computation of the stimulus values for the following trial. Verbal responses were entered directly by the experimenter on the computer keyboard.

RESULTS AND DISCUSSION

The mean simultaneity threshold values obtained from each block were analysed by planned comparisons with repeated measures analysis of variance (SPSS-X MANOVA) on the factors of Response mode (Footswitch, Voice), Hand Condition (Between, Within-Left, Within-Right), Stimulus order (Left hand vs Right hand first for the between-hand condition; Index finger vs Middle finger first for the within-hand conditions). The mean and individual threshold scores for these factors are shown in Table 1.

The reliability of the PEST technique employed for threshold measurement was assessed by confirming that there was no significant effect of stimulus order on threshold values in either of the within-hand stimulus conditions (see Table 1). Further analysis of the scores from the within-hand conditions found no significant main effect or interactions involving response mode or hand, indicating that simultaneity judgement was not affected by either hand of stimulus or manner of reporting. Analysis of between-hand scores also revealed no main significant effects or interactions involving mode of response or stimulus order although the latter approached significance ($F(1,11) = 3.312, p = 0.096$). A comparison of the mean threshold scores from each of the two between-hand conditions (left hand stimulation preceding right, right hand stimulation preceding left) with the mean of those from the within-hand conditions yielded a highly significant main effect of condition ($F(1,11) = 11.914, p < 0.001$).

TABLE 1
Stimulus Onset Asynchrony (SOA) Scores for Simultaneity
Judgement of Pairs of Tactile Stimuli.

	<i>(i)</i> <i>Between</i> <i>Hands</i>		<i>(ii)</i> <i>Within</i> <i>Left</i>		<i>(iii)</i> <i>Within</i> <i>Right</i>		<i>(iv)</i> <i>IHTT</i> <i>Estimate</i>
Subject	left index before right	right index before left	index before middle	middle before index	index before middle	middle before index	
1	98	76	56	61	61	53	29
2	79	75	64	62	72	63	12
3	47	39	30	39	35	34	9
4	33	34	18	18	7	12	20
5	47	34	34	34	15	21	14
6	36	17	13	20	27	35	3
7	42	48	35	35	38	32	10
8	4	14	6	3	13	16	-1
9	18	12	18	17	12	12	0
10	13	10	6	3	6	5	6
11	79	72	56	45	58	55	22
12	24	26	12	12	15	13	12
MEAN	43	38	29	29	30	29	11
SD	29	25	20	20	23	19	9

Individual and mean scores (\pm s.d.) from twelve right-handed, left-hemisphere dominant subjects are combined over response condition for the two possible stimulus presentation orders within each hand condition in Experiment 1. Estimates of inter-hemispheric transmission time (IHTT) shown are calculated by subtracting mean within-hand from mean between-hand thresholds.

Post hoc testing indicated that both between-hand thresholds were significantly larger than the within-hand thresholds (see Figure 2). Examination of individual scores revealed that 10 out of the 12 subjects demonstrated this relationship. This was significant by sign test (2,12; $p = 0.019$).

Support for the view that there is exclusive left hemisphere processing of temporal information required a particular pattern of results in the present study. The processing model outlined in Figure 1 predicts firstly that threshold SOA will be largest in the between-hands condition when left hand stimulation precedes the right, smallest in the between-hands condition when right hand stimulation precedes the left and intermediate in the judgement of within-hand stimulation. None of these conditions were met. The alternative view that the left hemisphere is simply more able than the right at mediating

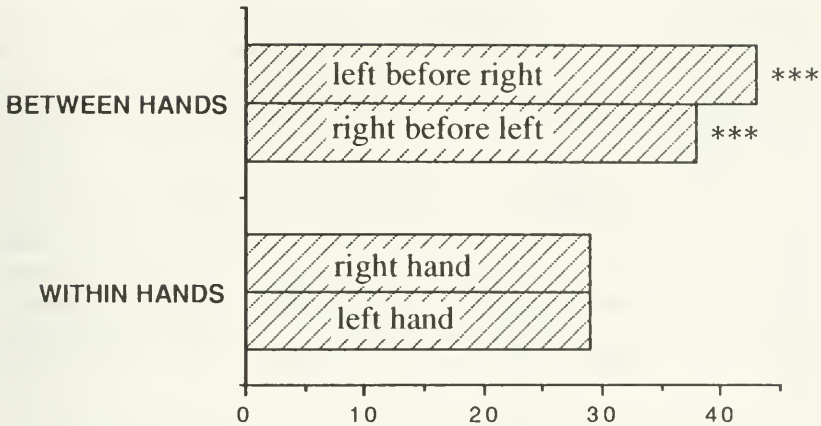


FIGURE 2. Experiment 1: Mean stimulus onset asynchrony (SOA, ms) from 12 right handed, left dominant subjects for simultaneity judgement of consecutive pairs of tactile stimuli delivered to the index fingers for between-hand judgements and to the index and middle fingers for within-hand judgements. SOA values for between-hand judgements were obtained under conditions of left-before-right hand stimulation and right-before-left hand stimulation. Within-hand judgements are the average of those obtained from index-before-middle finger and middle-before-index finger stimulation. Values have been averaged across bipedal and verbal response conditions. Individual threshold estimates were derived from four randomly interwoven PEST sequences. * $p < 0.05$.

temporal judgement was not supported either: the requirement that the within-right hand simultaneity threshold be smaller than the within-left hand threshold was not satisfied. Finally, the view (Efron, 1963) that verbal expression of temporal judgement may prejudice threshold determination in favour of the left hemisphere was not supported.

The results demonstrated that the threshold for simultaneity judgement of asynchronous tactile stimuli was higher when stimuli were presented between-hands than within-hands and that the order in which hands in the between-hands condition or fingers in the within-hand conditions were stimulated did not differ significantly. In relation to between hand stimulation, these findings are not in agreement with earlier work (Efron, 1963; Mills & Rollman, 1980) which found lower thresholds when right side stimuli preceded left side stimuli compared to the opposite order of presentation.

The failure to replicate earlier work in the tactile modality (Efron, 1963) may be due to controls employed in the present study on the effects of body hemispace on performance. It has recently been

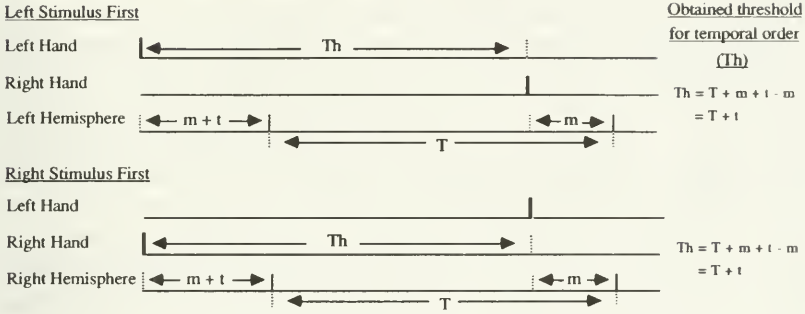
demonstrated (see Bradshaw, Nathan, Nettleton, Pierson & Wilson, 1983) that locating the hands in right hemispace reduces reaction time to right-handed stimuli. The advantage so gained by attention to the right half of space may also apply to temporal judgements in which attention is first directed to the right, as in right before left hand stimulus judgements, compared to when it is initially directed to the left (i.e. left before right). Similar arguments may apply to those earlier studies involving auditory or visual stimulation (Efron, 1963; Mills & Rollman, 1980) which necessarily confounded stimulus condition with body hemispace. In the present study, hands were always located on the body midline during stimulation, thereby neutralising any effect of hemispace. Other factors which may be crucial to the results of the present study may include the use of a more sensitive step size (Pentland, 1980) to determine thresholds (1 ms vs 5 ms), the use of a technique with greater specificity for determining the language dominant hemisphere (Geffen & Caudrey, 1981) and the use of within-hand threshold estimates for assessing the significance of between-hand threshold values.

The results of this experiment suggest that both hemispheres have equivalent capacity for simultaneity judgements. The explanatory model shown in Figure 3 assumes as before that lateralised signals are initially directed to the contralateral hemisphere via contralateral sensory pathways, that the comparison of lateralised signals requires the passage of at least one of the signals across the corpus callosum and that there is some intra-hemispheric timing mechanism which ultimately compares the signals as a basis for judgement. The additional assumption that judgement is performed in the hemisphere receiving the second of the two bilateral stimuli permits an interpretation of the data. This account holds that lateralised stimuli are transmitted to both hemispheres as a matter of course: initially to the contralateral hemisphere then to the ipsilateral hemisphere by passage across the corpus callosum. In this way both hemispheres are prepared to compare subsequent stimuli irrespective of their side of origin with the initial stimulus. In the present experiment, 11 out of 12 subjects (92%) showed lower within-hand than between-hand thresholds as predicted by this model. Only 8 out of the 12 (67%) showed lower right-before-left than left-before-right between-hand thresholds as predicted by the left hemisphere specialisation or superiority models (see Figure 3).

Physiological data supporting the hypothesis that lateralised stimuli are transmitted to both hemispheres is available from somatosensory evoked potential (SEP) studies involving stimulation of the median nerve (Tamura, 1972; Salmay, 1978). In addition to the traditional SEPs obtained over the hemisphere contralateral to the stimulated nerve, these studies report ipsilateral responses delayed

HEMISPHERIC SYMMETRY MODEL

(a) BETWEEN HAND COMPARISON



(b) WITHIN HAND COMPARISON

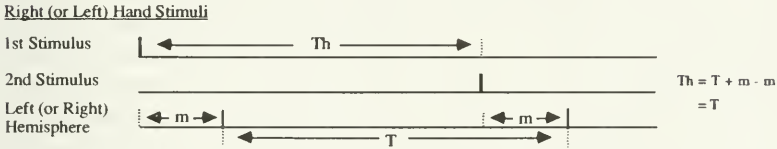


FIGURE 3. Temporal processing model based on the hypotheses that there is hemispheric equivalence for the temporal resolution of a consecutive pair of tactile events and that resolution engages the hemisphere contralateral to the second stimulus event. A stimulus takes m ms to be transmitted to the contralateral hemisphere and $m + t$ ms to reach the ipsilateral hemisphere after crossing the corpus callosum. The arrival of neural events in the hemisphere contralateral to the second stimulus must be separated by at least T ms for perceptual discrimination to take place. The recognition threshold for perceptual discrimination (Th) is larger for (a) between-hand ($T = t$ ms) than for (b) within-hand (T ms) stimuli.

between 4 and 8 ms compared to the contralateral wave. It was suggested that the latency difference may be due to interhemispheric transmission time via the corpus callosum though there has been a recent suggestion that interhemispheric transmission may be by volume conduction (Kakigi, 1986). Similar electrophysiological evidence has also been obtained from a visual evoked potential study involving lateralised light flashes (Rugg, Lines & Milner, 1984) which demonstrated a smaller and delayed (14 ms) N160 component over contralateral compared to ipsilateral occipital sites. As for the somatosensory studies, the delay in the ipsilateral waveform strongly suggests indirect transcallosal rather than direct transmission to the ipsilateral hemisphere.

The symmetry model of temporal judgement described in Figure

3 indicates that interhemispheric transmission time (IHTT) can be computed as the difference between the between- and within-hand simultaneity thresholds since interhemispheric transmission takes place only during between-hand stimulation. Individual estimates of IHTT ranged up to 29 ms (mean IHTT of 11 m, see Table 1). This estimate for tactile stimulation is of the same order as those from evoked potential studies such as those above, from other temporal order judgement studies (e.g. Efron, 1963) and from reaction time studies (e.g. Muram & Carmon, 1972; Moscovitch & Smith, 1979).

This experiment highlights an important distinction between corporeal hemifields (i.e. left and right hand receptor fields) and extracorporeal hemispaces (the spaces to the left and right of body midline) and the possible consequences of confounding them not only in tactile but also in visual and auditory laterality studies (see also Bradshaw, Nathan, Nettleton, Pierson & Wilson, 1983). It has been suggested above that previous experimental support for hemispheric asymmetry in temporal judgement may be an artifact of attentional biases to right hemispace. This issue can be resolved by experimental manipulation of hemispace and hemifield and a comparison of their relative effects on temporal judgement thresholds using the tactile modality.

EXPERIMENT 2: THE TEMPORAL PROCESSING OF MOTOR INFORMATION

'Handedness' or the preferential and superior use of one hand (the right in 90% of the population) to perform complex fine motor tasks has been documented historically and cross-culturally (Annett, 1985). Hand differences have a powerful genetic component (Newman, 1928; Rife, 1948), remain essentially unchanged during growth (Annett, 1970b) and persist in the face of extensive practice by the nonpreferred hand, particularly in tasks that involve temporal sequencing of movements (Annett, Annett, Hudson & Turner, 1979; Annett, Hudson & Turner, 1974; Peters, 1976, 1981). They have been shown not to be related to differences in peripheral nerve conduction (Tan, 1985). It would appear, therefore, that handedness arises from central processing differences that are permanent in nature. Further, since the distal musculature is discretely contralaterally controlled (Ghez, 1981) the asymmetry appears to be related to differences between the cerebral hemispheres. A cerebral asymmetry basis for hand differences is consistent with other left-right performance differences such as those related to language and spatial functions, and is particularly relevant to asymmetries in the perception of temporal order and the production of rapidly changing sequential information

(Bradshaw & Nettleton, 1983). More recently, it was reported that performance of a concurrent verbal task impairs sequential tapping performance of both hands but the single finger tapping of only the right hand in right handed subjects (van Strien & Bouma, 1988), suggesting that the sequential ordering of a response sequence is performed by the left hemisphere.

Consistent with the above findings, handedness is particularly evident in tasks involving the complex serial organization of muscle activity (Provins, 1967). Most studies have examined movement time (as opposed to reaction time) in a variety of continuous performance tasks including finger tapping (Peters, 1976, 1980, 1981), peg placing (Annett, 1976) and tracking (Ammons & Ammons, 1970). In general, differences in movement time increase with task complexity and are often not found in simple tasks (Provins, 1967; Steingruber, 1975). However, whilst the nonpreferred hand can be trained to move as quickly as the preferred hand, the delay between successive movements remains more variable (Peters, 1981). This implies that differences in skill between the hands are related to the preparatory phase before movement onset as well as to task complexity. This view is consistent with a recent proposal that hemispheric differences in motor planning but not motor execution underlie differences between the hands for skilled tasks (Annett, 1985). In support of this Schmidt (1975) and Annett (1985) have pointed out that many skilled movements are characterized by the rapid production of movement sequences which preclude the use of feedback cues during movement.

Previous research on motor programming (Sternberg, Monsell, Knoll & Wright, 1980) has shown that reaction time increases linearly with the number of consecutive units in the response to be made on a task (typing of letter bigrams). A modified version of the task used by Sternberg was used in the present study to examine hand differences in reaction time over a range of task difficulties. The more traditional measures (movement time, accuracy and consistency) associated with subsequent movement time were also obtained. Tachistoscopic visual cues presented to either the left or right visual field signalled the contralateral hemisphere that a response sequence was to commence. Highly trained subjects were informed in advance of the number of response units required in the sequence and the hand to be used. This design permitted a precise mapping of hand and hemisphere at different levels of response complexity since finger movements are contralaterally controlled (Ghez, 1981). The specific assumptions are that, left visual field cueing and left hand response exclusively engage the right hemisphere whilst right visual field cueing and right hand response exclusively engage the left hemisphere. It was predicted that reaction time but not movement time would differentiate left and right hand performance in our highly trained

subjects but that both measures would increase with difficulty level. Eight levels of difficulty were used in the present design.

This experiment combined techniques used in neuropsychological and skill learning paradigms, and is particularly unique in that (a) the pattern of performance was assessed over a systematically increased range of response loads, and (b) motor complexity was varied independently of perceptual uncertainty which was fully controlled and maintained constant.

METHOD

Subjects

Fourteen male university undergraduates between 18 and 30 years participated in the experiment as paid volunteers. All subjects were right handed according to a 12-item questionnaire (Annett, 1970a), had normal or corrected normal vision in both eyes, no deficits in fine motor control and no history of central or peripheral neurological damage/abnormality.

Task

Subjects completed a number of trials in which they were required to focus on a central fixation stimulus and respond to a simple visual cue presented in either the left or right visual field by tapping two keys with the index and middle fingers respectively. A midline dot at eye level was the fixation point. The visual cue was a closed square (0.5cm^2) presented for 140 ms at 2° to the left or right of central fixation. The stimulus preceded the cue by one second and remained on until the response was initiated (see Figure 4). The re-

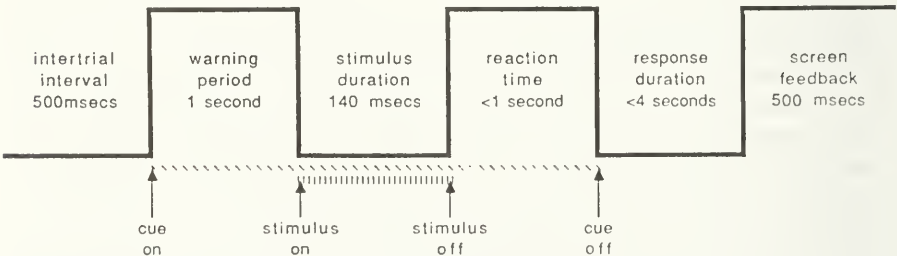


FIGURE 4. The sequence of events (from the appearance of the fixation cue to presentation of post response performance feedback) associated with a single experimental trial of the tapping task used in this experiment.

sponse consisted of a predefined number (1,2,4 or 8) of index-to-middle finger tap (response) units. Blocks of trials were given. Within each block, the response hand, visual field stimulated and number or response units was kept constant. Eye movements were monitored and trials were rejected if an eye movement occurred between the onset of the fixation cue and the first response tap.

Design

Each subject completed a required number of blocks of 20 trials in each of two experimental sessions conducted weekly at approximately the same time of day. Prior to each session subjects were advised to respond as quickly, accurately, and consistently as possible, and told that trials upon which responses were too slow, too fast, or involved eye movement would be rejected and have to be repeated. In one session, responses were made with the left hand (lh) and in the other with the right hand (rh). In half of the blocks in each session, the stimulus was presented to the left visual field (LVF), and in the other half, to the right visual field (RVF). Eight levels of response difficulty (one, two, three, four, five, six, seven, and eight response unit sequences) were completed for each visual field/hand combination within each session. Blocks were randomly ordered within sessions and the order of response hand counterbalanced over sessions. To prevent stimulus anticipation, four additional 'catch trials' occurred at random intervals within each block. In these trials no stimulus occurred following presentation of the fixation cue and the inter-trial interval extended for one second. Within each session blocks were randomly ordered. The order of response hand was counterbalanced between sessions.

Procedure

Each subject completed one practice session which contained a block of ten satisfactory trials for each test condition (visual field x hand x number of response units). For a trial to be deemed satisfactory, the first tap of the trial had to occur between 150 and 1000 ms following stimulus presentation, and the correct number of taps completed in correct sequence within four seconds. A trial in any given block was rejected if response duration or latency was two standard deviations or more beyond the ongoing mean of responses so far for that block. At the beginning of each session subjects completed a warm-up block of five satisfactory trials for each experimental condition to be tested in that session. This was followed by the first block of trials. At the beginning of each block the subject was informed by screen display of the visual field in which the stimulus would occur

and the number of response units required for that block. Following each response, subjects were given visual feedback on its acceptability. Trials in a block continued until 20 satisfactory trials had been obtained.

Apparatus

Stimuli were presented on a high resolution monitor (Apple green composite) under the control of a specially programmed micro-computer (Vision AT PC compatible) which collected and timed the response sequences and related them to visual cue onset. Monitor height was adjusted so that the fixation point was at eye level on the body midline. Response sequences were mediated by a pair of micro-switches attached to a response panel located on a desktop secured over the subject's lap. To minimize head movement, a velcro strap was secured across the forehead and attached to a headrest. The subject's arm and hand were restrained by weights and velcro straps respectively, so that only the distal musculature was effective. Pink noise was presented through earphones to obscure auditory cues. The microswitches were positioned on the body midline so that the index finger was located on the switch closest to the body. This was done to avoid a left-right component in the response.

Eye movements were measured electrooculographically using two cross-referenced AgAgCl electrodes located on the outer canthus and nasion, respectively, of one eye. The eye measured was counter-balanced with response hand.

Data Collection and Analysis

The dependent measures derived from each block of trials were: (1) reaction time: median of the time elapsed between visual cue presentation and initiation of the first tap in the response; (2) movement time: median of the time elapsed between initiation of the first and last tap in each response sequence; (3) movement consistency: the mean of the intertap intervals between successive index-middle finger taps was obtained, and the standard deviation of this mean was used to measure intraresponse unit consistency; and (4) rejections: the total number of trials rejected due to (a) incorrect number of response units, (b) incorrect finger sequencing, (c) being too fast or too slow, or (d) eye movement, and analyzed separately. Regression analyses (using GLIM) were also conducted.

Data were analysed using repeated measures factorial analyses of variance (SPSS-X MANOVA) on (a) number of Response Units (1,2,4,8), and (b) Visual Field/Hand condition (LVF/lh, RVF/rh) using polynomial trend analyses on the number of response units factor.

Data were also obtained from two crossed stimulus-response conditions (LVF/rh and RVF/lh) but will not be presented in this paper.

RESULTS AND DISCUSSION

Mean scores on all variables for the LVF/lh and RVF/rh conditions collapsed across number of response units are shown in Table 2. Reaction time, movement time, movement consistency and rejections for the two conditions as a function of number of response units are shown in Figure 5.

There was no main effect of VF/h on reaction time ($F < 1$) but both linear and quadratic trend components were obtained for reaction time as a function of number of Response Units [linear $F(1,13) = 5.6, p < .04$; quadratic $F(1,13) = 7.5, p < .02$]. A significant quadratic trend was found for the Response Units by VF/h interaction [$F(1,13) = 6.7, p < .03$]. Separate polynomial analyses over number of Response Units were then conducted for the LVF/lh and RVF/rh conditions. Reaction time in the RVF/rh condition was found to increase linearly with increasing number of Response Units [$F(1,13) = 5.5, p < .04$], whilst reaction time in the LVF/lh condition varied quadratically [$F(1,13) = 9.4, p < .01$ —see Figure 5]. Regression analyses were then conducted to generate the appropriate regression equations and determine the amount of variance accounted for by the fitted trends (Fig-

TABLE 2
Mean and Standard Deviation Scores from the Left Visual Field Stimulus/Left Hand Response (LVF/LH) and Right Visual Field Stimulus/Right Hand Response (RVF/RH) Conditions Collapsed across Number of Response Units for Reaction Time, Duration, Consistency and Number of Rejections.

<i>Variables</i>	<i>Left Visual Field/ Left Hand</i>		<i>Right Visual Field/ Right Hand</i>	
	<i>Mean</i>	<i>SD</i>	<i>Mean</i>	<i>SD</i>
Reaction time (ms)	304	91	307	75
Duration (ms)	1562	313	1509	244
Consistency (sds)	21.2	7.6	19.2	7.3
Total rejection (number)	5.7	1.1	5.8	1.2
Wrong sequence	2.6	2.8	2.9	2.9
Wrong number	1.0	1.5	0.9	1.2
Too fast/slow	0.8	0.09	0.7	0.1
Eye movements	1.4	0.6	1.3	0.5

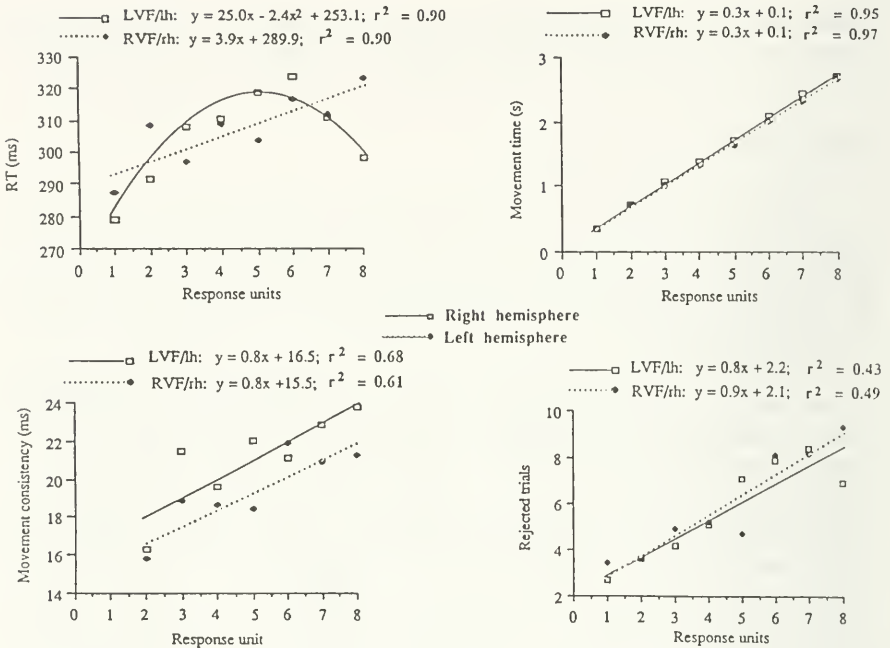


FIGURE 5. Reaction time, movement time, movement consistency and number of rejections with increasing number of Response Units for the left visual field stimulus/left hand response (LVF/LH) and right visual field stimulus/right hand response (RVF/RH) conditions ($n = 14$).

ure 5). In this and subsequent regression analyses, the percentage variance accounted for by the fitted trend also reflects the effect of the absolute level of each subject's performance. The linear trend in the RVF/rh condition accounted for 90.3% of the variance, and the quadratic trend in the LVF/lh condition accounted for 90.4% of the variance. Regression analyses were then conducted on the points from one to six response units to compare the linear component of LVF/lh with RVF/rh. The results indicate that preparation time in the LVF/lh condition increased over twice as steeply as the RVF/rh condition (LVF/lh:8.9; RVF/rh:4.1). The intercept with LVF/lh condition was 15 ms less than in the RVF/rh condition (274.3 vs 289.3).

There was no main effect of VF/h on either movement time, movement consistency or total number of rejections ($F < 1$). Each of these measures increased linearly with number of Response Units [movement time $F(1,13) = 1351.8$, $p < .001$; consistency $F(1,13) = 9.9$, $p < .01$; total number of rejections $F(1,13) = 28.5$, $p < .001$ —see Figure 3 or 4]. There was no interaction of Response Unit and VF/h for these measures ($F < 1$). Analysis of the individual error measures revealed

that the linear trend over number of Response Units resulted from trials rejected due to incorrect number of response units [$F(1,13) = 24.38, p < .04$] and incorrect finger sequencing [$F(1,13) = 14.8, p < .01$]. The number of trials rejected for being too fast, too slow or those rejected for eye movement were not effected by number of Response Units or VF/h ($F < 1$).

In summary, this experiment examined differences in fine motor skill between the left and right hand under increasing levels of performance demand. Performance involved the cued production of sequences of double taps with the index and middle fingers of one hand. The specific contribution of the left and right cerebral hemispheres to differences in hand skill was assessed by restricting performance cues to the hemisphere controlling motor preparation and movement. It was assumed that performance conditions involving left hand response to left visual field cues exclusively engaged the right cerebral hemisphere whilst right hand response to right visual field cues only engaged the left hemisphere. The pattern of results obtained indicates that the left and right hemispheres differ in the manner of preparation for the production of finely controlled motor sequences, but not in the production of the sequence itself. It suggests that the time required for motor preparation increases with increasing motor demand when the task at hand is under left hemisphere control but only to a limited extent when under right hemisphere control. Preparation time increased linearly up to six response units when the task was under right hemisphere control. Regression analyses showed that when absolute level of performance was taken into account, the fitted trends accounted for over 90% of the variance.

Whilst the effect of load on response time has been well established, very few studies have distinguished between the effect on the preparation and execution components of response. Sternberg et al. (1980) found a linear increase with load on both measures in cued verbal and bimanual typing tasks. They proposed that response to a simple cue involved not only the completion of each response unit but also the time required to organize ('unpack') each unit. Since reaction time to the cue increased linearly with the number of response units required, they concluded that unit organization prior to response must involve a serial process. The finding of a linear as opposed to a log linear relationship between preparation time and number of response units indicated that the information was not being dealt with in 'bit' form as Hick's law would predict (Hick, 1952).

Studies which have examined preparation time have generally included a stimulus choice component in the performance cue (e.g. Barnsley & Rabinovitch, 1970) which precludes an easy separation of stimulus evaluation from response organization components. The task involved in this experiment provided simple, consistent cueing

for both left and right hand performance. The critical difference obtained between left and right hand/visual field performance was reflected in the pattern of reaction times for each hand with increasing task load. The linear increase in preparation time obtained for the preferred right hand (left hemisphere control) is consistent with the serial process proposed by Sternberg et al. (1980). In this regard, the linear relationship between load and reaction time obtained by Sternberg et al. (1980) can be attributed to left hemisphere function, since both skilled typing and the rapid articulation of words may be considered to be predominantly controlled by the left hemisphere. However, the quadratic trend obtained in the present experiment for the left hand (right hemisphere control) indicates that unit organization prior to response by the nonpreferred hand may not necessarily involve serial processing. A possible explanation is that at low load levels right hemisphere preparation engages limited serial processing capacities, but takes considerably longer (over twice according to this experiment) to prepare for each additional unit than the left hemisphere, but converts to parallel processing as serial capacities are exhausted. Data supporting differential hemispheric processing strategies is provided by Oghishi (1978, cited in Bradshaw & Nettleton, 1981) who found that right but not left hand reaction times increased with the number of units of information that had to be dealt with in a choice reaction time task. No other studies examining the differential effect of response load on left versus right hand motor preparation time have been located.

GENERAL SUMMARY AND CONCLUSIONS

The data from the two experiments reported in this paper indicate that both cerebral hemispheres have the capacity for the processing of temporal information. Experiment 1 indicated that the two hemispheres have equivalent capacity for simple temporal order judgements of pairs of tactile stimuli and suggested that judgements were carried out in the hemisphere contralateral to the second stimulus. Experiment 2 examined the hemispheric processing associated with sequences of finger movements. The results of this experiment indicated that the two hemispheres differ in the manner of preparation for the production of finely controlled motor sequences, but not in the production of the sequence itself. Response preparation time by the left hemisphere of right hand (usually the preferred) movement sequences increases linearly with length of sequence, suggesting that preparation involves a serial process. Preparation time by the right hemisphere of left hand (non-preferred) movement sequences varies

quadratically with length of sequence; the particular pattern of results obtained suggests that right hemisphere response preparation converts from a limited capacity, serial process for short movement sequences to a larger capacity, order-insensitive parallel process for longer movement sequences.

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