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TEMPORAL UNCERTAINTY AND MOVEMENT REPLICATION: EFFECTS OF RANDOMIZED INTERVAL, ARM, SEX, END POSITION AND EXCURSION LENGTH

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TEMPORAL UNCERTAINTY AND MOVEMENT REPLICATION: EFFECTS OF RANDOMIZED INTERVAL, ARM, SEX, END POSITION AND EXCURSION LENGTH

by

JOYCE COCHRAN

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1986

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

TEMPORAL UNCERTAINTY AND MOVEMENT REPLICATION: EFFECTS OF RANDOMIZED INTERVAL, ARM, END POSITION AND EXCURSION LENGTH

by

Joyce Cochran

Adviser: Professor Doreen Berman

In arm position replication tasks, the retention intervals between model (criterion) and replication movements are often manipulated to examine the effect of forgetting on performance. Because a left arm advantage has been found in such a task with retention intervals randomized (Nadler, 1983), it was suspected that one factor which might influence asymmetry of performance is temporal uncertainty. This can occur when retention intervals are randomized over the session rather than blocked.

Therefore, in this study, the effects of temporal uncertainty on performance in an arm positioning task were examined. Five variables, each with two levels, were investigated in Experiment 1: likelihood of occurence of a short retention interval (temporal uncertainty), arm, end position, replication excursion length, and sex.

Results showed that at the medial position, AE was lower for the left than for the right arm, but greater at the lateral position, regardless of other variables.

The 5-way interaction was significant for CE. Difference score analysis showed that temporal uncertainty affected the lateral position of the left arm for males, the medial position of the left arm and, to a lesser degree, the lateral position of the right arm for females. The finding that temporal uncertainty had a lateralized influence on performance led to the suggestion that sequential ordering of trials would also influence lateralization of performance, since both are known to alter expectancy. This prediction was confirmed in Experiment 2, in which sequential ordering was reversed, by the absence of a significant 5-way interaction for CE.

For females, the more rightward the target position, the less the VE in Experiment 2. Also, AE was smaller for short than for long target excursion lengths. These effects may have been obscured in Experiment 1 due to the greater influence of temporal uncertainty.

The data of Experiments 1 and 2 were combined and sequential ordering effects for retention interval were examined directly. The CE was shifted positively for the left, but not for the right arm, when preceded by a long prior retention interval.

Results are discussed with reference to the right-brain arousal and left-brain activation systems. This study suggests a need to reanalyze studies of motor performance with regard to unintended arousal effects.

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Dr. Ramsey gave direction to the statistical analyses which conferred a clarity of interpretation upon otherwise complex interactions. Dr. Ramsey's influence extended, as well, to substantive matters and grammatical details.

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CHAPTER I

INTRODUCTION

The ability to produce accurate movements by utilizing position sense is believed to involve both peripheral and central mechanisms. The existence of peripheral mechanisms of position sense has been confirmed by electrophysiological (Mountcastle, Poggio, & Werner, 1963; Mountcastle & Powell, 1959) and behavioral studies (Goodwin, McCloskey, & Matthews, 1972; Larish, Volp, & Wallace, 1984; Matthews & Simmonds, 1974). Central mechanisms have been inferred on the basis of motor performance in the absence of peripheral feedback (Lashley, 1917; Knapp, Taub, & Berman, 1958).

Positioning ability has been examined extensively in a task that requires a model (criterion) movement to an end position, a retention interval, and a replication movement to the same target end position (Adams & Dijkstra, 1966; Adams, Marshall, & Goetz, 1972; Marteniuk & Roy, 1972). Many variables are known to affect performance accuracy on a task of this nature. For example, performance with an active model movement differs from that of a passive model movement (Craske & Crawshaw, 1975), presumably due to the presence or absence of an efferent command, a deceleration phase, gamma-activation of muscle spindles, and to the inferred presence or absence of preknowledge of movement parmeters or goal.

Some task variables may bias the subject toward greater reliance on kinesthetic information to replicate a target position of the limb or toward greater reliance on a theorized egocentric spatial coordinate system to replicate a target spatial location (Larish & Stelmack, 1982; Stevens, 1978). The thesis will be developed that the arm-positioning (peripheral) and spatial location (central) components of the task are inextricably intertwined in normal subjects. Spatial abilities pertinent to accuracy in reproducing spatial location are discussed, as well as purported sex differences in these spatial abilities.

Performance on an arm positioning task has shown a left side advantage in some studies (Christina, 1967; Nadler, 1983; Phillips & Summers, 1954), but not others (Lloyd & Caldwell, 1965; Wallace, 1977). One task variable which may have differed between these studies and which might in itself have contributed to asymmetry in motor performance is temporal uncertainty. Temporal uncertainty about the length of the retention interval or onset of the signal to replicate may alter performance by influencing organismic variables such as arousal level. The purpose of this study was investigate the role of temporal uncertainty in a movement replication task.

Sense of Position and Spatial Location

Peripheral Regulation

Peripheral regulation of positioning ability is subserved by kinesthetic information. The muscle spindles have been most directly implicated in kinesthesia (Grigg, Finerman, & Riley, 1973; Kelso, Holt, & Flatt, 1980) and a 'muscle sense' apparently even reaches consciousness (Matthews & Simmonds, 1974). However, there is no evidence for asymmetry in kinesthetic information.

Central Regulation

MacNeilage (1970) proposed in his "target hypothesis" that a target location, specified as a point within the space coordinate system, is the only information necessary for the motor system to produce a movement to that location. This hypothesis is supported by clinical reports of ability to position anaesthetic limbs (Lashley, 1917; Volpe, LeDoux, & Gazzaniga, 1979) and from experiments on deafferented animals (Knapp, Taub, & Berman, 1958).

Feedforward signals. With every active movement, it is believed that a number of internal feedforward signals are produced, signals which subserve different functions (Kelso, 1982). One such signal is "efference copy" (von Holst & Mittelstaedt, 1950, in Hinde, 1966, p. 98), the copy of the motor command, which is stored for comparison to the reafference from the movement in order to detect and correct error. For example, in a yoked-control experiment, two kittens had similar visual experiences but one was allowed active movement while the other was forced to remain passive. Only the active kitten developed visuomotor coordination, presumably due to efference copy (Held & Hein, 1963). As a second example, if the eye muscles are paralyzed and the subject attempts to produce an eye movement, the perception is that the visual field has jumped in the same direction (Helmholtz, 1866; Stevens, 1978). The illusion is believed to be due to the inconsistency between the efference copy and its associated feedback. The efference copy monitors whether the movement was executed accurately but not whether the goal was obtained.

A second hypothesized feedforward signal is "corollary discharge" (Teuber, 1974, p. 551), which signals that sensory feedback is expected from the movement. Corollary discharge allows an individual to distinguish between volitional and passive movements. It is an afferent signal sent from motor to sensory systems to prepare them for the sensory consequences of the movement. It is predictive; the expected sensory consequences are anticipated in planned, active movement because the sensory receiving areas are 'tuned' (Kelso, 1982). Stevens (1978) distinguishes between a sense of limb position based on sensory feedback and perception of egocentric space which is interpreted through corollary discharge. Corollary discharge allows effective movement to be produced without visual guidance, if the environment is familiar. As Smyth (1984) explains, corollary discharge refers to advance knowledge of sensory input whereas efference copy is information about the movement production itself.

A third feedforward signal is thought to be "central monitoring of efference" (Jones, 1972, p. 95), the use of the motor command copy to monitor outgoing efferent signals for error detection and correction without comparison to peripheral feedback. The existence of this proposed central signal is supported by the above mentioned deafferentation experiment in animals (Knapp, Taub, & Berman, 1958), wherein accurate positioning movements could be learned in the absence of peripheral feedback, and by the demonstration that actively produced movements are better replicated than are passively induced movements (Craske & Crawshaw, 1975; Marteniuk, 1973).

Thus, efference copy is hypothesized to explain the interactions between active movement and perception; corollary discharge, to explain accurate goal-directed movement in the absence of exteroceptive (visual) or external feedback; and central monitoring of efference, to explain improvement in motor performance when knowledge of results, but not sensory feedback, is available.

In the intact state, four major types of information are stored from a movement: the initial conditions such as the position of an individual's limbs and orientation in space; knowledge of results or outcome of the movement;

sensory consequences; and response specifications (Schmidt, 1976). Schmidt (1976) postulated two separate states of memory: recall and recognition. The former generates muscular impulses for movements, including movement correction. The latter evaluates movement-produced feedback for errors. When a movement is to be produced, response specifications are extrapolated from the recall schema. The expected sensory consequences from the recognition schema are compared to the response-produced feedback to detect error. Taking into account the initial conditions, the recall schema reflects the relationship between response specifications and actual outcomes which have evolved from past movements. The recall schema can provide the response specifications for novel movements by interpolation between two familiar movements if the desired outcome and initial conditions are given. According to Schmidt (1976), the recall schema also explains the ability of animals to achieve positioning accuracy with a deafferented limb.

The recognition schema is built up by comparing sensory consequences with actual outcomes, taking into account initial conditions. If the desired outcome is specified, the recognition schema allows a prediction to be made about the expected sensory consequences. With no knowledge of results, the recognition schema can signal error, which updates the recall schema to improve performance. For ballistic movements, correction occurs over trials, but for slow, ramp-generated movements, this correction is ongoing during the movement. A movement is terminated when error detection is cancelled and, without knowledge of results, no further learning occurs.

Preselection. Just as reliance on central mechanisms can be forced by interrupting somatosensory input (Lashley, 1917; Knapp, Taub, & Berman, 1968), reliance on kinesthetic information may be forced, or at least emphasized, by task demands. One task used for this purpose is a linear positioning task wherein the arm and hand are stabilized and a movement of the arm is made in a straight or curved line. In the model movement, which is the criterion or standard, a particular extent or end position is produced. The subject attempts, after a specified retention interval, to replicate the target distance or end position (Smyth, 1984). A passive movement, made by an external force with the subject's arm muscles relaxed, or a constrained movement, which is volitional but terminated by an external force, are experimenter defined and lack a movement plan on the part of the subject. An active movement, in which a volitional excursion is voluntarily terminated, or a subject defined movement, in which the terminal location of a passive or constrained movement is selected by the subject (movement plan) or known to the subject (preknowledge), do have a movement plan. Because active movements generally lead to more accurate replication than do constrained or passive movements, the question arises as to what aspect of the active movement (preselection) is responsible for the superior performance. Preselection may confer an advantage due to the availability of central motor signals (efferent copy, corollary discharge, central monitoring of efference). On the other hand, preselection may improve performance by allowing a cognitive strategy, such as a plan of action (Miller, Galanter, & Pribram, 1960) or an image (Posner, 1967), to develop.

Jones (1972) hypothesized that because efferent signals could be preset for active movements, these would be replicated more accurately than either constrained or passive movements, even though afferent feedback should be similar for active and constrained movements. Actually, some difference might occur in afferent feedback under these conditions because the active, but not the constrained, movement has a final deceleration phase (Hall & Wilberg, 1978). Jones (1972) found that active model movements lead to superior performance, compared to passive movements, lending support to the hypothesis that efferent copies are used to match efferent commands to stored copies. Jones and Hulme (1976) concluded that sensory receiving areas were preset (corollary discharge) for better encoding in an active movement. However, since subjects chose their end positions in the active movement condition (preselection), improved performance may have been due to a preknowledge (prior knowlege, movement plan or planning) rather than due to a central efferent signal, since other cognitive factors, such as ordering the lengths or positions of movements across trials during testing (Nacson, 1973) or only during practice (Diewert & Stelmach, 1978), are known to improve performance. Roy and Diewert (1975, 1978) and Runnings and Diewert (1982) found that when subjects were told the extent of the constrained movement in advance (preknowledge), the advantage of the active over the constrained movement disappeared. But, it is possible that an efferent command for the termination of the 'constrained' movement was produced due to preknowledge, making the movement, in fact, active. Thus, more definitive support is needed for the idea that a cognitive component of preselection exists independent of efferent command of the active movement.

Both Kelso (1977) and Roy (1978) monitored muscle activity to assure that movements of the passive-preselection condition were indeed passive and both came to different conclusions concerning the relative importance of the cognitive and efferent components of preselection. Kelso (1977) had subjects perform, in a distance-location task, under four different model/replication movement conditions: active/active, constrained/active, passive-preselected/active or passive-preselected/passive. The active/active condition led to better performance than all other conditions. It is unlikely that in the passive-preselected/active condition an incompatibility of model/reproduction modes diminished performance since performance in the passive-preselected/active condition was better than the passive-preselected/passive condition. Thus, Kelso concluded that efferent signals and preselection are independently beneficial to performance.

Roy (1978) tested groups of subjects in a distance replication task with different model movement conditions: active, constrained, passive-preselected, or passive. For the active and passive-preselection groups, each trial was preceded by a pretrial orientation movement (of the same type as the model movement of the trial), and subjects were told that the model movement was to be half the distance of the orientation movement. Start positions were varied between the model and replication movements of the trial. The retention intervals for each of these conditions were, immediate, 20 sec (unfilled), and 20 sec with an interpolated mental task. When the model movement was preselected (active or passive-preselected), performance was no different for volitional or externally produced model movements and both were better than the passive condition, unless the interval was filled. However, when the movement was not accompanied by a movement plan (constrained or passive), then the volitional model movement led to better performance than that produced by an external force. Roy concluded that an efferent command was important only when preselection was not permitted; the amount of clues available for reproduction could interact with the availability of an efferent signal.

Summers, Levey, and Wrigley (1981) examined the components of preselection as a function of movement cue (distance or location). Preselection was manipulated by an interpolated rehearsal task with four conditions: active, passive, mental, or no rehearsal. Results showed that active and passive rehearsal produced the best performance in the location task (i.e., efferent command and planning benefit location replication), whereas performance was more improved due to active, than to passive, rehearsal when distance was replicated. Thus, Summers et al. (1981) agreed with Kelso (1977) that efferent signals and planning are equally important aspects of the active mode of movement reproduction, but only for location. Along with Roy (1978), Summers et al. (1981) also agreed that the relative contribution of the preselection components depends on the form of the movement cue to be replicated. Summers et al. believe that the disparity between the results of Roy (1978) and of Kelso (1977) are due to methodological differences. In the Roy study, replication movements approximated half the range of the orientation movement and although start position was varied between model and replication movement the change was only 5 or 10 cm. The range of the movements was very restricted: the model start position was, apparently, held constant and replication start position was ± 5 cm. These factors could allow a limb position encoding strategy to be employed, rather than distance cues. In the Kelso study either distance or position cues were intended to be reliable, and because a wide range of positions was used distance cues may have had a stronger influence than position cues.

Thus, performance in distance and location tasks may be subserved by different mechanisms. Location tasks may use peripheral information about limb position, which is more accurate with prior knowledge. Extent cues may be encoded by velocity x time or force x time characteristics of efferent commands.

Measures of Error

In order to understand how distance and position estimation may be differentially affected by task variables, it is helpful to examine the three most commonly used performance measures for movement tasks: absolute error (AE), constant error (CE), and variable error (VE). The AE is the unsigned error or difference between the criterion and replication movement, averaged over trials. The CE is the signed error (arithmetic or algebraic), between criterion and replication movement, averaged over trials. The VE is the standard deviation or variance of CE.

Schutz (Schutz, 1974; Schutz & Roy, 1973) believes that VE, the measure of reliability, and CE, the measure of directional bias, are independent measures but that AE is a function of both CE and VE. He bases this view on two arguments: if CE equals zero (i.e., undershoots and overshoots are essentially equivalent), then AE and VE give the same information, reflecting the spread of scores around zero; if CE is derived from all overshoots or all undershoots, AE is equivalent to CE. If CE is very different from zero, but contains overshoots and undershoots, AE reflects a combination of CE and VE information. If the variability of AE is small, AE approximates the square root of the sum of CE squared plus VE squared. Since AE is sensitive to the change in CE or VE, an increase in one measure can compensate for a decrease in the other, leading to the false conclusion that no change has occurred. Thus, when AE is the only dependent variable, performance is not adequately measured.

The CE is considered to be a measure of response bias because only the first trial is uncontaminated by previous trials. However, this first trial, itself, may be effected by prior knowledge of the overall range of movements (Smyth, 1984). The CE is sensitive to a frame of reference which is the combined influences of all previous movements (Summers, Sommer, Sharp, Levey, & Murray, 1982).

When a series of stimuli along a given dimension are to be estimated in the same task, small stimulus intensities tend to be overestimated and large stimulus intensities tend to be underestimated. This is also true for movement amplitudes in positioning tasks (Fitts, 1947). For example, short movements lead to a positve CE; long movements lead to a negative CE (Marteniuk, Shields, & Campbell, 1972; Pepper & Herman, 1970). Because of this central tendency or range effect, only the first trial is uncontaminated by other trials (Poulton, 1981) but if subjects have prior knowledge of the overall range of movements, even this first movement is biased (Smyth, 1984).

The central tendency effect can obscure another phenomenon. According to Pepper and Herman (1970), CE is shifted in a negative direction with an increase in the unfilled retention interval and shifted in a positive direction with mental activity during the retention interval. Laabs (1971) does not agree that increasing duration of an unfilled interval produces a negative shift. He used two retention intervals, one somewhat longer than 3 sec (wich he called immediate) and another one of 12 sec. His results showed a positive shift over time for the position replication; for the distance replication, short movements became more positive, long movements more negative. However, in this study, subjects turned away and flipped a switch after the model movement, then turned back for the replication movement. This interpolated task, although not 'mental', may have increased arousal, leading to a positive shift in CE and adding a constant to all trials. For the distance task, however, this positive constant might have been obscured by the greater negativity of the longer length trials but not by the small negative shift of the short length trials. There is some support for this view. Firstly, Pepper and Herman (1970) found that interpolated mental activity produced a positive shift in CE. Secondly, Marshall, Jones, and Sheehan (1977) found that CE shifted in a positive direction when subjects were either told to pay close attention or that their grades would be posted. The manipulations in these two studies may have led to the positive shift in CE by increasing the level of arousal.

The VE is used to measure reliability and, by inference, memory; VE is not necessarily related to accuracy (Smyth, 1984). For instance, Seashore and Bavelas (1941) found that performance in the absence of knowledge of results became more consistent, though less accurate, over several reproduction trials.

Thus, AE, CE and VE reflect different aspects of performance and may be differently affected by distance and position variables.

Distance Versus Location

As mentioned above, distance and location replication are movement tasks differentially affected by preselection variables. Although some authors have examined performance on distance or location tasks separately (Blick & Bilodeau, 1963; Keele & Ells, 1972; Posner, 1967; Posner & Konick, 1966; Shagan, 1970; Williams, Beaver, Spence, & Rundell, 1969), it was Laabs (1971; 1973) who first emphasized the importance of maintaining an independence between distance and location variables by employing different start positions for the model and replication movements of a trial.

There is disagreement concerning whether distance cues can be stored centrally and whether distance and location cues have a "dual storage" in memory. Laabs (1971, 1973) used a constrained model/active replication movement paradigm to examine the differences in retention of distance and position cues. He found that VE, after an unfilled retention interval, was greater for distance than for location replication and interpreted this to mean that distance, but not location information, decays over time. If the retention interval was filled with an intervening task, location information was more disturbed than distance information. He concluded from these findings that position cues are stored centrally for rehearsal in memory whereas distance cues are stored as a kinesthetic trace which fades over time but is relatively impervious to disruption by distractors.

This postulation of separate storage modes for distance and position cues has been challenged by Marteniuk (1973) who found that performance based on distance cues was equivalent, in its retention characteristics, to that based on position cues. Interference or rehearsal affected distance and position replication, similarly. Both Laabs (1973) and Marteniuk (1973) calculated VE and CE. For Marteniuk, VE did not differentiate between performance based on distance or location cues. A resolution of this discrepancy has not yet been achieved.

That movement is an important part of distance judgments under normal circumstances, i.e., that distance is not simply extrapolated from position cues, is supported by a study by Stelmach and McCracken (1978). Subjects performed more poorly if their arms were positioned first at the start position and then at the end position rather than moving between the two locations. However, this experiment suffered the flaw that kinesthetic feedback was not equated across conditions; movement trials were constrained-active whereas positioning trials were passive.

Kelso (1977) suggested that whether distance cues can be retained over an interval is determined by procedural variables. Those studies that found distance cues to decay over an interval employed a constrained model movement; those that found distance cues to be resistant to decay employed an active model movement. Thus, retention of distance information appears to require an efferent command whereas retention of position information may be based on peripheral position sensation, perhaps related to a central coordinate system. This view is quite opposite to that of Laabs (1971, 1973) who stated that distance cues, but not position cues, depend on kinesthetic storage. One difficulty with the Laabs' conclusion is his assumption that VE can, as a measure of reliability, adequately measure performance. In Laabs' study, the only significant finding for CE was that the CE for long movements was more negative than for short movements, and AE was not calculated. As discussed earlier, it is possible for performance to become more consistent even as it becomes less accurate. The Laabs finding of greater VE for distance than for position with an unfilled interval, and greater VE for position than for distance with a filled interval, cannot be interpreted as necessarily representing poorer performance. It is a faulty assumption that VE, by itself, is an indicator of discrimination, as Laabs infers. The CE and AE measures must also be considered. Still, it does seem to be the case that location is better replicated than distance when the model movement is constrained and there is an unfilled interval, when the model movement is preselected or subject defined, or when peripheral feedback is removed (Sheridan, 1979).

Keele (1968), Stelmach, Kelso, & Wallace (1975), Gundry (1975), and Roy and Kelso (1977) concluded that when subjects are not instructed as to the cue to use in replicating a movement, they tend to rely on distance cues for a short excursion to target and on position cues for a long excursion to target. However, Hagman and Williams (1977) found that, if needed, both distance and position cues can be used, regardless of excursion length. Subjects performed a distance/location replication task. In the retention interval, subjects performed an interpolated movement, which varied either position, distance or both. Performance was impaired only if the interpolated task varied both position and distance cues. They concluded that since interfering with distance and location cues jointly, but not singly, disrupts performance, each type of cue provides sufficient kinesthetic information to perform the task.

It appears that for interference produced by an interpolated task, either position or distance cues are as effective as both combined to sustain performance, but this is not the case when the cues are altered by changing the start position of the replication movement. Walsh, Russell, Imanaka and James (1979) varied the replication start position to the left and right of the criterion start position and had subjects demonstrate recall of either distance, location, or both. The results showed that each cue was contaminated by the other; both distance and location replications erred in the direction of the other, irrelevant cue. They concluded that neither location nor distance are coded independently of the other but rather interact. This is true whether the model movement is active or passive (Walsh et al., 1979); the unfilled retention interval is short (5 sec) or long (30 sec) (Walsh & Russell, 1979); or subjects have a high or low mental imagery score (Walsh, Russell, & Imanaka, 1980).

Can this interaction between distance and location cues be found over an unlimited range of excursion lengths? Walsh et al. (1979) did not report the excursion lengths used in their task but from the tabled lengths of the active condition, it appears that, for the constrained conditions, short and long lengths were 15 cm and 30 cm. They did note that in the experiment of Stelmach, Kelso, and Wallace (1975), location cues were reported to be more accurate than distance cues, yet location and distance cues led to equally accurate performance for excursions up to 24.9 cm. The implication is that distance cues are as accurate as location cues, but only for movements less than some unspecified length.

Wrisberg and Winter (1985) extended the range of excursion lengths. Model movements (constrained) were 20, 50, or 80 cm and replication movements (active) were ±5 cm of the model movement lengths. CE shifted in the direction of the replication start position for the 20 and 50 cm, but not for the 80 cm trials. Wrisberg and Winter concluded that shifting the start position biased the short excursions most, the medium excursions less, and the long excursions not at all.

According to Smyth (1984), large excursions in a spatial location task are much less affected than small excursions by a change in the start position. Perhaps this is because, with large displacements between the start and end position, location is fitted into a spatial framework, whereas with small displacements, location discrimination is more difficult, forcing reliance on distance cues.

The transfer from reliance on distance cues with short excursions to reliance on position cues with long excursions is attributed by Wallace (1977) to increasing use, with increasing excursion length, of a spatial reference system like that postulated by Lashley (1917) and Russell (1976). Howard and Templeton (1966) and Pick (1970) believe that, for positioning tasks, the system is egocentric, involving body-related reference points to encode location. Larish and Stelmach (1982) suggested that this egocentric system is limited to use of body reference points near the spatial target; the target location needs to be in near extrapersonal space and in front of the subject. Wrisberg and Winter (1985) believe that their results fit this model: short movements were eccentric to the body-based reference points, so that a distance cue strategy was probably employed. For the long excursion trials, subjects made use of a sensed limb position when the position was eccentric but employed the egocentric reference system for those positions near the body reference points.

Another point, not raised by Smyth (1984), is that the variablility of the replication start position from the model start position was held constant, rather than made proportionate to each excursion length in the Wrisberg and Winter (1985) study. The difference between the model and reproduction excursion lengths was .25 and .10 of the model movement for short and medium excursions, respectively; for the long excursion, the difference was only .06 of the model movement. Perhaps, some minimal proportionate difference must be exceeded to be perceived, a just noticable difference in distance.

Other factors, not yet examined, may be relevant to the interpretation of the effect of excursion length on shift in CE. Wrisberg & Winter (1985) conducted two different experiments with somewhat different results. The

CE for short excursions were more positive in the first than in the second experiment. Only the first experiment included randomized retention intervals (5 and 45 sec) and it is possible that this condition was responsible for the positive shift in CE for short excursions.

One problem with the Wrisberg & Winter study is that subjects reported calculating the distance between the start and end positions for short movements, even though they were told that distance would be an unreliable cue. Apparently, the instructions did not sufficiently emphasize that using distance cues would lead to error.

With some reservations, the Wrisberg and Winter (1985) study may be interpreted to support the existence of an egocentric reference system, just as Russell (1976) postulated. Kinesthetic information is believed to be converted by a perceptual process into an abstract form to be represented as a point within a three dimensional coordinate system and built up by the relationship between various body parts and experience. Stelmach and Larish (1980) also found that performance of same-limb and switched-limb positioning did not differ unless the target end position was outside of near extrapersonal space, 30 cm from the midline. Thus, when kinesthetic information is not readily available, as in the switched limb procedure, the egocentric reference system allows accurate target localization unless the target is too far from body referents.

Another qualification must be made concerning the egocentric reference system. In an experiment comparing switched-limb to same-limb positioning, Wallace (1977) found performance to be equally accurate under either condition as long as direction was constant. If direction was reversed between model and reproduction movements, then same-limb performance showed less error than switched limb performance. Thus, when kinesthetic matching is not possible, the efficient use of the egocentric coordinate system requires that the target end position be near a body referent and that both model and reproduction movements be in the same direction.

Housner and Hoffman (1981) postulated that end position cues, but not distance cues, can be incorporated into a visuo-spatial map for retrieval. This ability to imagine location information confers a quality of concreteness which is not available for distance information. Imagining ability may account for the differences between distance and location retention for constrained movements. To test this hypothesis, subjects with high or low visual imagery scores were tested on a switched-limb positioning task. A comparison of high and low imagery groups showed no differences in performance, confirming the results reported by Walsh et al. (1980). However, those of the high imagery group who actually reported using an imagery strategy had lower error scores for position replication with a 30 sec retention interval (rest or mental rehearsal) than low imagery subjects, who reported not using such a strategy.

There was, however, no difference in performance for distance replication between the two groups. Housner and Hoffman concluded that when subjects use an imagery strategy, visual imagery ability is an important factor in retaining location, but not distance, information.

If visual imagery is indeed important in developing an egocentric reference system and in localizing ability, then congenitally blind and sighted subjects should perform differently. Hermelin and O'Conner (1975) did not find this to be so. Congenitally blind children, who could not have stored a visual image, performed as well as blindfolded normals (not tested for imagery ability) in a switched-limb location replication task, suggesting that kinesthetic cues may be stored centrally for later use.

However, the finding of Hermelin and O'Conner is not in agreement with the findings of others. Millar (1975) found that sighted children with vision excluded, but not blind children, could repeat a series of movements backwards. Evidently, blind children could not manipulate the kinesthetic information in memory, but sighted children could "scan" the mental image in either direction. Also, Colley and Colley (1981) tested early blinded and late blinded subjects, aged 24-64 yr, on an active model/active replication movement task for replication of distance and location. Performance of both groups was more accurate for location than for distance replication, consistent with the performance of the sighted (Marteniuk & Roy, 1972).

However, the early blinded were less accurate in both tasks than the late blinded, reflecting the absence of a contribution from visual experience. Colley and Colley speculated that the difference between their results and those of Hermelin and O'Conner (1975) was that the latter used a constrained model movement but they used a preselected model movement, which makes better use of central processes. A particular problem with the Hermelin and O'Conner study, which makes comparison with other studies questionable, is that the movements were vertical. Thus, both groups may have produced similar results because they matched muscular force or resistance to gravity to replicate position.

Colley and Colley (1981) suggested that memory strategies for the early blinded rely more on kinesthesic memory, such as remembering the angle of the arm. The late-blinded may have relied on imagining how the unseen equipment, positions, etc. could be visualized. Other possibilities are that the late blinded were able to develop an accurate perception of body space to act as a reference for kinesthetic input or that the late-blinded had developed a more fully encoded kinesthetic system as a result of greater early mobility.

Dodds and Carter (1983) tested congenitally blind, late-blinded (blindness onset not reported), and sighted children, 8-15 yr of age, on a triangle retracing task. Overshoots in judging the length of the sides of the triangles (CE) were equivalent across groups, but orientation of the triangles (AE) was poorer for the congenitally blinded than for the other two groups. It is of interest that Hermelin and O'Conner (1982) reported that sighted children perform better than congenitally blind children on a kinesthetic switched-limb task with direction reversal, if the excursions are long. Thus, there is concurrence across investigators for the finding that early visual experience aids nonvisual positioning ability.

The comparative studies of the blind and sighted suggest that, for the sighted, space is represented mainly in a visual mode. For that reason, information from movement is partially recoded in visual terms. A close association exists between movement and visually-derived spatial representations (Attneave & Benson, 1969) and this visual-kinesthetic linkage seems to be innate, but requires experience to be maintained. For example, congenitally blind infants produce eye tracking movements to follow their hands between 16 and 18 weeks of age, but not after this time (Freedman, 1964).

The linkage or association between the visual and kinesthetic systems may obtain for higher order functions, also. Information which is addressed to a particular perceptual system, but is not readily available for processing, is believed to be encoded, through supramodal feature extraction, into a schema of a more appropriate modality (Hermelin & O'Conner, 1982). Kinesthesia has salient spatial and temporal features, while vision is predominantly a spatial sense. Therefore, kinesthetic information about space can only be partially recoded in visual terms for storage and that only if early visual experience has occurred.

To summarize, evidence indicates that a movement replication task may emphasize kinesthetic cues for limb positioning, or an egocentric spatial coordinate system for spatial location, but under natural circumstances, both strategies are used. The movement replication task necessarily involves a spatial ability, and this spatial ability most likely includes some degree of feature extraction and transfer from the kinesthetic to the visual modality.

Spatial Orientation

Spatial abilities can be divided into two distinct categories (McGee, 1979). One type is spatial visualization, the ability to rotate, twist, or invert a pictured object mentally. Either a pictured object is mentally manipulated in three-dimensional space, the movement among its internal parts is envisaged, or the folding or unfolding of a flat pattern is imagined. The other type of spatial ability is spatial orientation, which includes the ability to comprehend the arrangement of elements in a visual stimulus pattern, remaining unconfused by various perspectives and to accurately perceive one's physical spatial relation to the environment and to monitor changing relations during movement. (Sedgwick, 1982). Thus, spatial orientation often includes spatial relations with reference to body orientation. It would appear to be this spatial ability, spatial orientation with a body referent that is incorporated into the arm positioning spatial location task since stabilized posture is a requisite for performing the task.

Sex differences. Sex differences in spatial orientation are reported by some to be present at puberty and to lead secondarily to sex differences in field dependency, sense of direction, and maze tasks (Keogh & Ryan, 1971; McGee, 1979; Silverman, Buchsbaum, & Stierlin, 1973). The rod-and-frame test, which supposedly has a spatial component, measures field dependence-field independence by testing a person's ability to adjust a rod to the vertical position with only the square frame as an external orientation cue. Women appear to be more dependent on field than men in determining the vertical position of the rod (McGee, 1979; Witkin, 1950; Witkin, Dyk, Faterson, Goodenough, & Karp, 1962). The embedded figures test, which also is said to have a spatial orientation component, requires a subject to hold a simple geometric form in memory and then to identify it in a more complex figure. Adult or adolescent males perform better than age-matched females. Similar tests with no spatial component which measure field dependence/independence, such as the brightness constancy matching or body steadiness task, show no sex differences. However, attributing the sex differences in performance on the rod-and-frame test to reputed sex differences in spatial ability has been challenged by Naditch (1976). When the standard rod was replaced with a human figure and subjects were told that the test was one of empathy, women performed better than men. Thus, at least some suggested sex differences in specific tests of spatial orientation may be attibuted to nonspatial cognitive variables and may be much less generalizable to other spatial tasks than was once believed.

Both right and left hemispheres are required to perform complex spatial tasks, such as synthesizing components into a whole configuration or identifying superordinate categories. For individuals with non-anomolous dominance, though, only the right hemisphere is required for elementary spatial abilities (Bradshaw & Nettleton, 1983). However, one source of variation, superimposed on this general schema of right hemisphere specialization for elementary spatial abilities, is attributed to sex differences in spatial abilities. Much of the variation between the sexes on spatial abilities might be due to sex differences in maturation, since females, on the average, mature earlier than males (Newcombe, 1982). Waber (1976, 1977) found that, regardless of sex, those with a history of early maturation performed more poorly on spatial tasks than those who matured late. Furthermore, dextral, teen-aged females, with a history of precocious puberty, showed decreased averaged performance on the Block Design and Object Assembly tests as compared to age-matched controls, as well as a suggestive, but nonsignificant, decrease in left-ear (right hemisphere) performance on the Staggered Spondaic Word Test, a test of central auditory dysfunction (Meyer-Bahlburg, Bruder, Feldman, Ehrhardt, & Healey, 1985).

Buffery and Gray (1972) proposed a bilateral representation of elementary spatial skills for males but a unilateral representation for females. The data of Lansdell (1968) support this view. Both men and women scored lower on nonverbal test items with right than with left hemisphere lesions. But a left hemisphere lesion produced poorer performance in males as compared to females. Yet, most studies reporting sex differences in spatial abilities conclude that males are superior to, or more lateralized than, females for right hemisphere mediated spatial abilities (McGlone, 1980).

A relationship exists between hemispheric activity as determined by physiological measures and lateralized cognitive functions as measured by performance (Gur & Reivich, 1980). Hemispheric activity as measured by cerebral blood flow (Gur, Gur, Obrist, Hungerbuhler, Younkin, Rosen, Skolnick, & Reivich, 1982) or by electroencephalography (Ray, Newcombe, Semon, & Cole, 1981) appears to interact with sex. Males with a high spatial ability showed a positive correlation between performance on spatial tasks and hemispheric activity (Gur et al., 1982). The best performance of males with low spatial ability was correlated with greater left than right hemisphere activity. However, females, regardless of whether their scores were high or low, showed no correlation of hemispheric activation with performance (Ray et al., 1981). Although this result showed a physiological correlate of the spatial ability which interacts with sex, the argument might still be made that different non-spatial cognitive strategies led to differences in the physiological recordings.

Fairweather (1976) and Caplan, MacPherson, & Tobin (1985) have summarized the vast body of literature on sex differences in spatial abilities. They concur that while many studies purport to find a superior spatial ability in males, these claims are not supported strongly by experimental evidence. Appropriate statistical tests and significance levels tend to be disregarded, as are proper experimental controls.

In short, the evidence for nontrivial sex differences in spatial abilities is sparse. What would lend support to the hypothesis that sex differences in lateralization of spatial abilities are due to an underlying biological asymmetry which differs in male and female would be a spatial task which reflects a change in performance asymmetry between the sexes over conditions not likely to alter cognitive strategy. The arm positioning task may be such a task.

Lateral differences. A small number of studies have addressed the question of lateralization of performance in the positioning task. For example, Phillips and Summers (1954) examined the ability of subjects to replicate spatial location using kinesthetic cues in vertically aligned side and front arm movements. A significant asymmetry was found in two of the several arcs and movements tested. The left arm performed significantly better in the 180° to 75° side arm movement, whereas the right arm performed better in the 90° to 40° forward arm movement. Whether right or left arm performance is better, Phillips and Summers concluded, depends on whether the movements are familiar or unfamiliar, although these terms were not defined.

Christina (1967) tested subjects in a similar side arm task and reported a left arm advantage. However, Christina tested the right arm on each series of trials and then the left arm, both in the preliminary procedure and in the experiments proper. Thus, one could argue that the left arm superior performance was a learning effect.

Nadler (1983), on the other hand, found a left arm advantage for dextrals under much improved control conditions. Arm movements were horizontal, to equalize gravitational effects amongst the different positions; a chinrest stabilized posture, equal numbers of right and left arm trials were presented in a random order; and most importantly, since asymmetry would be more likely in dextrals than in sinistrals, a strict criterion for determining handedness was employed.

Rationale

The rationale for the present experiment is to extend information concerning the arm positioning task and to relate this to the body of literature already in existence.

Replication Movement Target Excursion Length

The errors in a kinesthetic, spatial replication task systematically increase in negativity as the target movement extent increases for a bidirectional model plus replication movement task (Adams & Dijkstra, 1966) or for a lever displacement task (Stelmach, 1970; Stelmach & Bassin, 1971). The Nadler (1983) study has suggested that this outcome holds, as well, for the medially-directed, lateral arm movement task and for both the right and left arm. However, since excursion lengths were not equated for end positions in the Nadler study, the present study determines the independence of this phenomenon from the previously mentioned effect of spatial location on replication excursion length. One short (20°) and one long (50°) excursion length were chosen with the constraint that the long excursion length must not be so long as to negate the restrictions imposed for the end positions. These lengths were comparable to those used already to measure range effects of length (e.g., Wrisberg & Winter, 1985). It was decided to hold the model movement excursion length constant at a length midway between the two replication excursion lengths (35°) because, although some range effects will be produced regardless of the length selected, the purpose of this study was not to examine the effects of model movement on performance. Therefore, model movement extent was not manipulated across trials.

Proportionality between Absolute Error and Excursion Length

It is possible that AE may reflect a proportionate error, based on a percentage of the replication movement length. Therefore, if a main effect for Length is found, AE should be evaluated with regard to replication excursion length.

Spatial Location of Target End Position

Nadler (1983) found that movements to the more lateral positions were associated with more overshooting than movements to more medial positions, contrary to the prediction of Laabs (1973). However, the target excursion lengths for the replication movements were longer for the medial end positions and could have been responsible for the effect. End positions in the present study were chosen to be repesentative of a lateral and a medial position in order to test the generalizability of this position effect for both sexes with excursion lengths equated.

The final selection of end positions was influenced by the restrictions listed below. The requirements for the end positions were: 1) to be mirror image positions for right and left arm in order to allow comparison of performance between the two arms, 2) for each arm to be confined to each ipsilateral hemispace, to prevent confounding of hemisphere-hemispace and hemisphere-anatomical limb effects, 3) to be sufficiently far from the midline to avoid crossing the midline if an overshoot in the replication movement occurred, and 4) to be representative of a lateral and a medial position in order to examine the "position effect" suggested by the Nadler study (1983). The choice of end positions also involved their effect on other parameters. For, example, the excursion lengths of the movements (see below) constrained the choice of the lateral-most end position: the end position must be medial enough to allow a comfortable resting angle of the shoulder joint at the start position to avoid undue activation of skin-stretch and joint receptors. The two end positions chosen were comparable to the most medial and most lateral end positions of the Nadler study, met all of the above criteria and were separated by an adequate distance: the medial end position was 75° and the lateral end position was 50°.

Right Versus Left Arm Performance

The present study was designed, in part, to adress the question of whether left arm performance is more accurate than right arm performance in a horizontal movement replication task, as was the case in Nadler's (1983) study.

The randomized schedule of trials included an equal number of trials, equated for start and end positions, excursion length, and retention intervals for each arm.

Temporal Uncertainty

Nadler (1983) randomized short (5 sec) and long (20 sec) retention intervals over the trials of each session, in an arm positioning task. The intent was to examine the effects of the passage of time on memory of the target location. However, this design could also be viewed as a paradigm which introduces temporal uncertainty. Therefore, one goal of the present experiment was to examine the effects of temporal uncertainty on performance in an arm positioning task.

Temporal uncertainty is the inability to predict the timing of stimulus occurrence, and it may be generated from within or imposed from without. Internal uncertainty about time of stimulus occurrence is the result of an imperfect ability to measure time subjectively and is positively correlated with the length of the interval (Niemi & Naatanen, 1981). External uncertainty about time of stimulus occurrence is the result of unpredictable, randomized interstimulus intervals, foreperiods (FPs) or retention intervals. External uncertainty about time involves conditional probability: the probability of one event occurring is conditional on another event having occurred (McNicol, 1972). With different time intervals presented in random order, the nonoccurence of a stimulus earlier in the interval leads to an increase in probability of occurrence with the passage of time. For example, consider the situation wherein intervals of two different lengths, each with an objective probability of occurrence of .50, are randomized and no catch trials are included. Since, at the start of a trial, the conditional probability equals the objective probability, a short interval stimulus has a conditional probability of .50. If the interval continues with no stimulus after the short interval, then the trial interval must be long and the stimulus must have a conditional probability of 1.00. The most uncertainty is resolved or the most information delivered with the short interval stimulus. The long interval stimulus has no information to deliver; the information was delivered at the time of the non-occurrence of the short interval stimulus.

Put another way, when intervals are randomized, the long interval stimuli would be associated with maximal expectancy and short interval stimuli, with minimal expectancy. Low expectancy, as compared to high expectancy, would then lead to more surprise, in addition to information delivery, and result in a higher arousal state.

Another aspect of the temporal uncertainty paradigm is that random intervals or irregular FPs lead to a change in preparatory set and thereby alter the amount of effort employed in tasks which require vigilance. If the subject cannot accurately predict stimulus occurrence, he must attempt to maintain a state of readiness over the interval preceding the stimulus.

There are two areas of psychological research which typically employ temporal uncertainty designs: event-related potential research into the P3 waveform and simple reaction time (RT) studies. These are discussed below.

P3. Sutton, Braren, Zubin, and John (1965) discovered that uncertainty about the sensory modality of a stimulus elicited a long-latency (approximately 300 ms), positive potential, the P300 or P3 waveform. This P3 waveform, which is elicited by a task-relevant or surprising stimulus has been designated by Squires, Squires, & Hillyard (1975) as P3b but will be referred to here as simply P3. Sutton, Tueting, Zubin, and John (1967) found that P3 is also elicited by a temporally uncertain stimulus: subjects were required to guess whether randomized interclick intervals would be short, medium or long and P3 was elicited approximately 300 ms after presentation of the second click. The largest P3's were elicited by those clicks which resolved the most uncertainty: the second clicks of short or medium interval stimuli. The one exception was a "short interval" guess on a medium interval trial since enough information was delivered by the absence of the short interval stimulus to evaluate the guess before occurrence of the medium interval stimulus.

Friedman, Hakerem, Sutton, and Fleiss (1973), Sutton, Braren, Zubin, and John (1965), and Sutton, Tueting, Zubin, and John (1967) concluded that P3 is related to resolution of uncertainty (information delivery), since a task-relevant stimulus elicits the P3. It is said to reflect stimulus evaluation time (Kutas, McCarthy, & Donchin, 1977).

However, Tueting, Sutton, and Zubin (1971) report that information delivery is not the only source of P3. Even when subjects are informed in advance about the identity of a stimulus, P3 is elicited from the stimulus if it has a low *a priori* probability. They noted that outcome probabilities for P3 are reminiscent of the arousal concept of Pribram (1967). Amplitude of an arousal response (or P3) is greater the more unexpected or rare the stimulus.

Sutton and Ruchkin (1984) proposed that P3 is related to the affective value or importance of a stimulus, a view which is consistent with P3's origin in the limbic system. Surprising events and events that reduce uncertainty have greater affective value. This interpretation would also support the Pribram and McGuinness (1975) type of arousal which is thought to originate in the amygdala and to be integrated in the hippocampus into effort. Thus, the P3 response to low probability signal stimuli in the conditional probability paradigm suggests the involvement of arousal. As Tueting (1968) stated, introducing uncertainty into a task enhances involvement, and, therefore, arousal.

Reaction time. Reaction time (RT) is the measure of time between two events, the first of which is a stimulus, and the second, the motor response to that stimulus, under the condition that the subject perform as rapidly as possible (Posner, 1978; Teichner, 1954). The most important determinant of performance in a simple RT task is preparation to respond (Niemi & Naatanen, 1981). If subjects are able to estimate the foreperiod length--the time between the warning signal and the signal to respond--they will be accurate in timing their readiness to respond. As the foreperiod increases in duration, increasing subjective temporal uncertainty diminishes expectancy so that, for regular (blocked) foreperiod designs, RT is lengthened as the foreperiod is lengthened. The irregular (variable) foreperiod design, on the other hand, generally produces longer RTs than the blocked foreperiod design, because timing cues are reduced. In particular, RT is increased for the short foreperiod trials due to the objective temporal uncertainty which accompanies the irregular design (Woodrow, 1914).

Yet, the temporal manipulation can be considered as a stimulus variable which leads to changes in preparatory set. A subject tends to increase effort when sensory adequacy is decreased below some critical value and to decrease effort when above this value. Therefore, a stimulus is not necessarily optimal for both motor preparation and sensitivity (Johnson, 1923; Thrane, 1960a, b, 1961a, b, 1962). If a subject assumes a 'prior attitude', then the expected monotonic relationship between stimulus intensity and latency is obscured (Sutton, Note 1).

Thus, temporal uncertainty may affect P3 or RT performance by inducing arousal and/or shifting preparatory set. The likelihood exists that temporal uncertainty also has an effect on performance in the arm positioning task. A major difference between the P3 and RT versus the movement replication research, though, is that, heretofore, the temporal uncertainty manipulations in the latter have been unintended.

There are indications in the literature that increased level of arousal, either by "threat" (e.g., Marshall, Jones, & Sheehan, 1977), or through effort (Pepper & Herman, 1970), or by unintended temporal uncertainty manipulations (Wrisberg & Winter, 1985) leads to a positive shift in CE. Since the effect of temporal uncertainty on performance in the arm positioning task has not yet been systematically examined, the present experiment was intended to serve this purpose and to further examine performance with regard to end position, excursion length, sex differences and asymmetry.

Design

A repeated measures design (with the grouping factor of sex) was chosen due to its increased sensitivity: such a design is associated with a smaller likelihood of a Type 2 error than is a between group design, allowing for greater degrees of freedom and, thus, more accuracy. Robustness was increased by selecting two, rather than three, levels of each repeated measures variable. However, testing all variables, simultaneously, as is the case with a repeated measures design, inflates the overall alpha level, due to the large number of F-tests performed. Therefore, a strict confidence level ($p \leq .01$) was adopted.

Statement of Hypotheses

The present study investigated the following hypotheses based on performance of dextrals:

1. Replication movements requiring a long excursion to the target end position produce greater undershoots (or smaller overshoots) than replication movements requiring a short excursion to the target end position.

2. A proportionate relationship exists between AE and intended replication excursion length.

3. With model movement excursion length held constant and end positions equated for replication excursion lengths, replication movements to a lateral target end position are longer than replication movements to a medial target end position.

4. Replication movement is more accurate for the left than for the right arm, as measured by AE.

5. Introducing temporal uncertainty via randomized short and long retention intervals improves left arm performance as measured by AE.

6. Introducing temporal uncertainty differentially affects right and left arm performance as measured by CE.

7. The asymmetry of performance introduced by temporal uncertainty is greater for males than for females (see Appendix K).

CHAPTER II

EXPERIMENT 1

Method

Subjects

Twelve male and 12 female subjects, 18-40 years of age, and all dextrals, were chosen from a group of graduate and undergraduate psychology student volunteers. An individual was considered dextral if a) the response "right" was given on the Marian Annett Inventory, Questionnaire 3, to at least five of the six primary questions and to at least nine questions in total, b) no more than one sinistral member of the nuclear family was reported and c) the subject answered "no" to the question asking if writing hand had been switched from left to right in school. (see Appendix A for the inventory and a discussion concerning its selection.)

Subjects understood the purpose of the experiment in part: they knew that they were to perform a spatial motor task which relied on kinesthetic information and some guessed that lateral differences or sex differences might emerge. However, subjects had no information about the manipulation of expectancy as a factor.

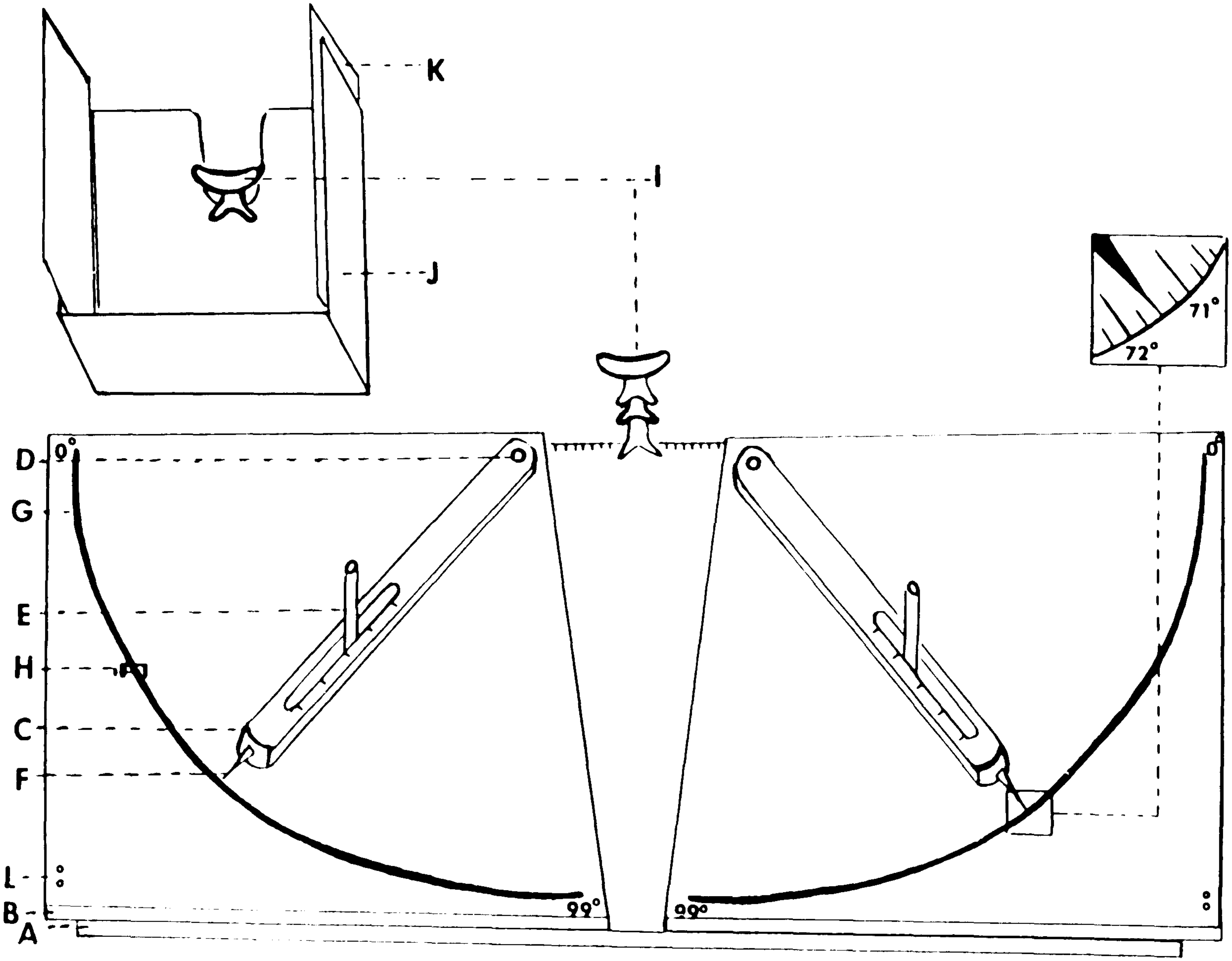
Apparatus

The apparatus (see Fig. 1) consisted of a 72" x 31" base (A) with two 36" x 31" boards (B), one atop each side of the base. The boards could be moved laterally to adjust the distance between them from 5.25" to 16". Two wooden beams (C), 28" in length, served as the armpieces. The proximal end of each armpiece was attached to the medial edge of its respective board by a ball-bearing pivot (D). These allowed free rotation of the arms in the horizontal plane. At the distal end of each armpiece, there was a vertical, cylindrical swivel handgrip (E), 1" in diameter. The distance of each handgrip from the proximal end of its armpiece was adjustable from 16.75" to 25.50". The adjustable boards and handgrips allowed the equipment to accommodate subjects of different sizes.

The arc of rotation of each armpiece was mapped on its respective board in .25° from the most lateral (0°) to the most medial (99°) position. At the distal end of each armpiece was a centrally aligned pointer (F) which indicated the position of the armpiece on the mapped arc. A curved metal band (G) secured to each board followed the arc of rotation of the armpiece just distal to the pointer. Metal clamps (H), placed along the two bands, were used as stops to define the start and end positions of movements of the armpieces.

When either armpiece contacted its end position stop,

Figure 1: Arm movement apparatus. The components are labelled: A. base; B. board; C. armpiece; D. pivot; E. handgrip; F. pointer; G. metal band; H. metal clamp; I. switches; J. chinrest; K. box; L. shield. See text for description.


K
I
J
71°
72°
0°
0°
D
G
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H
C
F
L
B
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99°
99°

a magnet, mounted on the armpiece, triggered a magnetic switch to produce two consecutive signals. The choice of interval between the two signals could be selected via a switch (I) mounted on each board.

Signals (70 dB, 115K Hz, 750 ms) and continuous white noise (62 dB) were delivered binaurally to the subject through earphones.

An adjustable chinrest (J) mounted at the midpoint of the base, between the two boards, was used to stabilize the subject's head position. At the same time, the subject's chin depressed the lever of a microswitch. Raising the chin slightly released the lever, producing an immediate auditory signal.

A 12 x 12 x 10 ", four-sided box (K), mounted around the chinrest was used to occlude the subject's vision. Adjustable shields (L) extended the sides and bottom of the box to insure that all visual cues were eliminated. A stopwatch was used to time movements during practice trials.

Procedure

Each subject was tested individually during two sessions. Before the beginning of the first session, the subject read and signed a form stating that participation was voluntary, and then read these instructions:

> The task you are about to perform was designed to assess how accurately you can replicate the end position of movements made with either

> your right or left arm.
>
> On each trial there will be two movements made; the first movement will define the end position to be replicated, while the second movement will be your attempt at replicating the end position. The arm being tested and the end position will vary from trial to trial and I will inform you before each trial which arm is to be tested.
>
> Place your chin in the chinrest. I will then indicate the arm being tested and you should place that arm on the corresponding armpiece (right or left). Begin moving your arm in a smooth, continuous manner until the armpiece contacts the metal stop defining the end position to be replicated. Maintain your arm at the end position until you hear a 'beep', at which time you can remove your arm from the armpiece and place it in your lap.
>
> There will be a time delay which may vary from trial to trial. During this delay, do not move your arms or remove your chin from the chinrest. Following the appropriate time delay, you will hear a second 'beep'. You should then reposition the arm being tested on the armpiece and attempt to return to the end position defined by the initial movement. Once again, move your arm in a continuous manner and in one direction only. Once you are satisfied that you have returned to the desired end position, indicate this by raising your chin slightly from the chinrest. However, do not remove your arm from the armpiece until I say "Done", which will signal the end of the trial. Do you have any questions?

The subject was then seated centrally behind the apparatus on a stool adjusted to a comfortable height. While the subject sat with chin in the chinrest and arms extended laterally, the boards of the base were adjusted so that the pivots of the armpieces could be placed underneath, but not touching, the axillae. With chin still in the chinrest and vision occluded, the subject adjusted the handgrips by grasping both grips and pushing them outward simultaneously. When the arms felt comfortable and equally extended over the range of positions to be used in the task, but not touching the armpieces, the handgrips were tightened in that position.

Next, the subject received verbal instructions from the experimenter who stood on the right or the left side of the subject according to a counterbalanced design, determined by whether the subject was to receive Form A or Form B of the practice trials. The verbal instructions were as follows:

> I will just briefly go over the instructions that you read and add a few things. Firstly, your arms should be resting in your lap. You will know that a trial is to begin and also which arm you should use because I will say 'right' or 'left'. You should bring your right (left) arm up and grasp the handgrip or handle. However, you will not be able to see the handgrip so you might find yourself groping around to find it. There is an easy way to locate it, though. No matter what position the mechanical arm is in, the proximal portion will always be in the same place. You can locate this easily and then just tap or slide your hand out to the handgrip. It's okay to touch the arm to do this. Once you've found it, no part of your arm should be touching the mechanical arm--only your fingers and thumb which should be wrapped around the handgrip. It may seem natural for you to want to place your thumb on top of the grip to help support your hand, but it is important that you remember to keep your thumb down and wrapped around the handgrip. This is to prevent different tactile information from being produced by different positions of the arm. Before beginning your movement, just tap the back stop to make sure that your movement is beginning from the correct position. Your movement should be smooth and continuous until you reach the second stop. Hold that position until you hear a 'beep'. Then release the handle and place your arm in your lap. When you hear a second 'beep', again, find the handle and again make a smooth, continuous movement. This time, though, stop at that place where, to the best of your ability, you believe you were stopped on the previous

> movement. Signal me that you have made your decision by slightly raising your chin from the chinrest. You will find that just a slight chin-lift will be enough. It is important to keep your arm still during this time so that I can record your position accurately. Do not remove your hand from the grip until I say 'Done'. When I say 'Done', we will both know that the trial is over; you don't need to answer me. You should remove your hand and place it in your lap.
>
> It is important also, during the running, that you keep your chin in the chinrest except during a break. If you do need to bring your head out for any reason, please tell me first.
>
> One other thing. Some of us may have a tendency to use a type of internal clock in a task of this sort. That is, we may count to give ourselves a sense of time and then by trying to move at the same speed for the same amount of time, get back to the same position. But that won't work in this task and may even increase error because the start position will always be different for the first and second movements of a trial. In other words, this task is designed not to have you try to replicate distance. But, rather, this task is designed to have you ask 'How does it feel to be in a certain position? Does it feel like I'm back in that position again?'
>
> Now, we'll go through the practise trials and then I'll ask you if you have any questions before we begin. The session will contain three short breaks. Are you ready?

After the verbal instructions, the subject was fitted with earphones. Continuous white noise, channeled through the earphones, prevented localization of sound within the experimental cubicle and blocked out irrelevant noises. The tones used as signals were superimposed over the white noise and were clearly audible. The subject was also able to hear simple verbal commands such as "Right", "Left", "Done" or "Break" with the earphones in place.

There were eight practice trials in a pattern of RRLLLLRR (Form A) or LLRRRRLL (Form B). The two patterns were counterbalanced over subjects in an ABBA fashion.

Each trial consisted of a model movement and a replication movement. The model movement was cued by the verbal command of "Right" or "Left". The subject then raised his right (left) arm from his lap and grasped the appropriate handgrip. The subject brought the armpiece back to the stop, to insure that the movement would begin from the specified start position, and then made a smooth, continuous, medially directed movement until halted by a second stop. The subject held this position for 2 sec until a tone signaled that it was time to release the grip and place his arm again in his lap. At the end of a 10 sec retention interval, the subject heard a second tone which was the signal to relocate the handgrip and move the armpiece from the start position a second time in a smooth, continuous, medially directed movement. This was the reproduction movement, and was terminated by the subject at the point which he estimated to best represent the target end position. While carefully holding this position, the subject raised his chin slightly, producing a tone to indicate that his decision had been made. The position of the armpiece was recorded manually, accurate to at least $.5^{\circ}$. Lastly, a verbal signal, "Done", told the subject to release the handgrip and place his arm back in his lap.

The movement duration of the practice trials was timed by stopwatch. A t-test was used to determine whether there was a significant difference in movement durations for the right and left arms.

The retention interval was manipulated on each trial by pressing the switch ipsilateral to the performing arm, in order to keep any auditory cues constant across trials. The subject remained with chin in the chinrest throughout the session so that at no time was the placement of the armpiece visible. Verification that the chin was in place was provided by monitoring the reflection of the subject's profile.

Experimental sessions directly followed the practice trials. Each session was divided into four blocks of twelve trials with a brief rest period of about five minutes after each block. Before each rest period, the armpieces were placed in the extreme lateral position (-10°) to prevent visual cues of test positions. At least one day but no more than 14 days separated the first and second sessions. If the first session was a mixed interval session, then the second was a fixed interval session and *vice versa*, in accordance with a counterbalanced design.

Design

Each subject participated in two sessions, one mixed interval and one fixed interval. The mixed interval session was comprised of 48 trials; 24 right-arm and 24 left-arm trials. Within each group of 24 trials for a single arm, 12 had a long (20 sec) retention interval and 12 had a short (5 sec) retention interval. Each group of 12 trials with a particular retention interval was comprised of six trials with a lateral (50°) end position and six trials with a medial (75°) end position. Although the model movement excursion length was 35° to each end position, three trials had a short replication excursion length (20° to the target end position) and three had a long replication excursion length (50° to the target end position). The two excursion lengths were equated across the two end positions and the two retention intervals were equated across excursion lengths and end positions for both arms. This yielded eight distinct types of trials matched for the right and left arm, each of which occurred three times in one session (see Appendix B for a sample data collection sheet).

The 48 trials were ordered in a random fashion with some constraints. The first four trials were long interval trials, to allow a 'set' to develop, after which no more than three trials in succession with the same retention interval or arm were allowed.

The fixed interval session was identical to the mixed interval session except that the retention interval was 5 sec for all trials.

Response Measures

The raw data were the actual end positions of the replication movements, in degrees. Three different response measures, discussed earlier, were derived from this data: absolute or unsigned error (AE) (the difference between the target and the actual end position without regard to direction), constant or algebraic error (CE) (the directional or signed difference between the target and actual end position), and variable error (VE), (the standard deviation of CE).

Data Analysis

Trials from the mixed interval session which had a 5 sec retention interval were matched with similar trials from the fixed interval session. The unmatched long interval trials of the mixed interval session and the unmatched short interval trials from the fixed interval session were used to provide a 'set' and did not enter into the analysis. Thus, for analysis, there were 2 Sexes, 2 Arms, 2 (end) Positions, 2 (excursion) Lengths and 2 Session Types (Mixed and Fixed). This resulted in a 2 x 2 x 2 x 2 x 2 design. The data were subjected to an analysis of variance with one 2-level grouping factor (Sex) and four 2-level repeated measures factors (Winer, 1967).

Because three different response measures (AE, CE, and VE) were obtained from each trial, a separate analysis of variance was calculated for each type of measure. Although studies in this area generally accept a $p \leq .05$ level of confidence as significant, a $p \leq .01$ level of confidence was adopted due to the many F-tests included in each analysis of variance.

Results

Absolute Error

The analysis of variance of AE (see Appendix C) showed no significant main effects. One 2-way interaction, Arm x Position was significant ($p \leq .0001$). Mean AE for the right arm was smaller at the lateral position than at the medial position; for the left arm, mean AE was smaller at the medial position than at the lateral position (see Table 1).

Constant Error

The analysis of variance of CE (see Appendix D) showed two significant main effects, Position ($p < .0001$) and Length ($p < .0001$); two significant 2-way interactions, Session Type x Length ($p \leq .004$) and Position x Length ($p \leq .0007$); and one significant 5-way interaction, Session Type x Arm x Position x Length x Sex ($p \leq .005$).

For the main effect of Position, mean CE was more negative at the medial position (-4.72°) than at the lateral position (-1.29°). For the main effect of Length, mean CE was significantly more negative for a trial requiring the long target excursion length (-5.74°) than the short excursion length ($-.27^\circ$). Put another way, on long target excursion trials, replication excursion length was likely to undershoot the target by a greater amount, or overshoot

Table 1

Mean Absolute Error in Degrees:
Arm x Position Interaction

	Right	Left
Medial	7.75	6.65
Lateral	6.43	7.75

the target by a lesser amount, than on short target excursion trials.

The Session Type x Length interaction showed that the main effect of Length was greater in the Fixed than in the Mixed Session (see Table 2) and the Position x Length interaction showed that the main effect of Length was greater at the lateral (50°) position than at the medial (75°) position (see Table 3).

To determine the proportion of variance explained due to the 5-way interaction, an η^2 test was performed: sum of squares of the 5-way interaction was divided by the total sum of squares. The η^2 was found to be low (.02) but significant. This Session Type x Arm x Position x Length x Sex interaction is shown in Figure 2. Difference scores are tabulated in Appendix F.

First order difference scores for Length reflect the main effect: mean CE was more positive for short target excursion trials than for long target excursion trials. Second order difference scores reflect the 2-way interaction of Position x Length: the main effect of Length was greater at the lateral (50°) than at the medial (75°) end position. Third order difference scores show that the difference between the Mixed and the Fixed Sessions, for the 2-way interaction, was greater in magnitude for the left than for the right arm. Fourth order difference scores showed that direction of the third order difference was opposite for the two sexes.

Table 2

Mean Constant Error in Degrees:
Session Type x Length Interaction

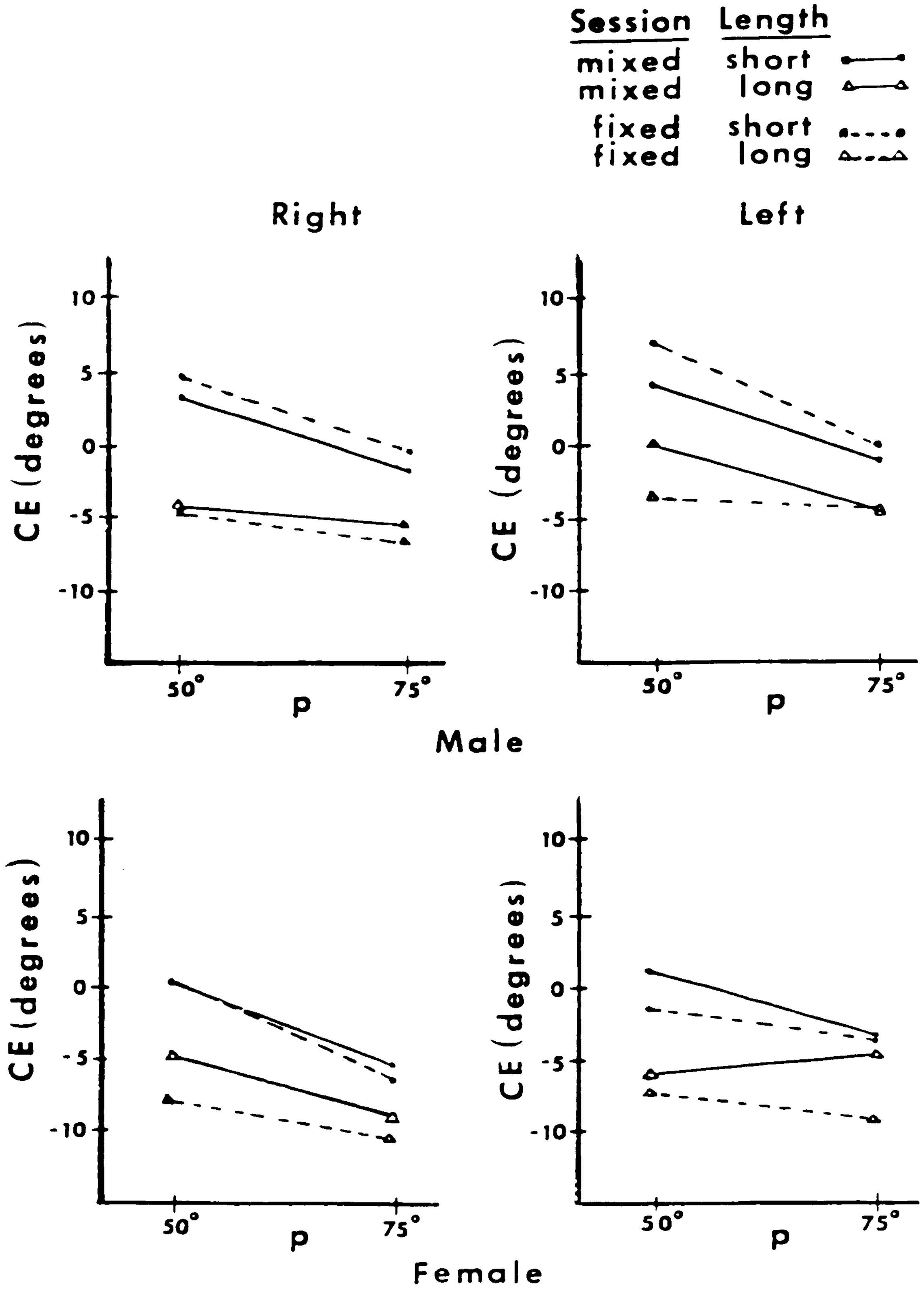
Length	Session Mixed	Session Fixed
Short	-.50	-.03
Long	-4.80	-6.68

Table 3

Mean Constant Error in Degrees:
Position x Length Interaction

Length	50 deg Position	75 deg Position
Short	+2.16	-2.69
Long	-4.73	-6.74

Figure 2. Session Type x Arm x Position x Length x Sex interaction for matched short (5 sec) retention interval trials: Mean constant error (CE = mean constant error; P = target end position).


Session Length
mixed short
mixed long
fixed short
fixed long
Right
Left
CE (degrees)
10
5
0
-5
-10
50°
75°
p
Male
Female

The 5-way interaction may be interpreted this way: the Position x Length interaction across the Session Types for males reflects a more positive mean CE for the left arm, with a long excursion, to a lateral (50°) end position in the Mixed Session than in the Fixed Session, resulting in a positively shifted fourth order difference score. The Position x Length interaction across the Session Types for females reflects a more positive mean CE for the left arm, with a long excursion, to a medial (75°) end position in the Mixed Session than in the Fixed Session, resulting in a negatively shifted fourth order difference score. First order difference scores for Session Type (see Appendix G) show that the greatest CE shift in the Mixed as compared to the Fixed Session for males is positive and occurs with the left arm and a long target excursion at the lateral (50°) end position. For females, the largest CE shift in the Mixed as compared to Fixed Session is positive and occurs with the left arm and a long target excursion, at the medial (75°) position. A smaller positive CE shift is seen for females, also, with the right arm at the lateral (50°) position.

To assess whether individual subject scores reflected the means for the 5-way interaction, individual fourth order difference scores were derived by subtracting the mean third order difference score of the opposite sex from the individual scores (see Table 4). Eleven out of twelve males had a fourth order difference score that was more positive

Table 4

Individual Fourth Order Difference Scores in Degrees Minus Mean Fourth Order Difference Score of Opposite Sex

Subject Male	Individual Dif. Score	$\bar{X}$ Diff. Score Female	Difference
1	+25.29	-7.77	+33.06
2	+ .64	-7.77	+ 8.41
3	- 5.40	-7.77	+ 2.37
4	+ 9.00	-7.77	+16.77
5	+11.94	-7.77	+19.71
6	+ 7.58	-7.77	+15.35
7	-11.00	-7.77	- 3.23
8	+20.25	-7.77	+28.02
9	- 4.33	-7.77	+ 3.44
10	+ 9.76	-7.77	+17.53
11	+ .25	-7.77	+ 8.02
12	+22.17	-7.77	+29.94

Subject Female	Individual Dif. Score	$\bar{X}$ Diff. Score Male	Difference
1	- 8.17	+6.83	-15.00
2	- 1.66	+6.83	- 8.49
3	-10.09	+6.83	-16.92
4	+ 2.76	+6.83	- 9.59
5	+ 7.43	+6.83	+ .60
6	+ .24	+6.83	- 6.59
7	- .74	+6.83	- 7.57
8	+18.75	+6.83	+11.92
9	-11.33	+6.83	-18.16
10	-26.68	+6.83	-33.51
11	-23.92	+6.83	-30.75
12	-19.66	+6.83	-26.49

than the mean fourth order difference score for females; ten out of twelve females had a fourth order difference score that was more negative than the mean fourth order difference score for males.

Variable Error

No main effects or interactions reached significance (see Appendix E).

Discussion of Experiment 1

Replication Excursion Length

Hypothesis 1, replication movement length was supported for medially directed movements concerning both arms and both sexes: the CEs of short projected excursions were shifted in a positive direction as compared to CEs of long projected excursions. This central tendency effect for movement replication has been reported by Marteniuk, Shields, & Campbell (1972) and Pepper & Herman (1970).

Proportionality between Absolute Error and Excursion Length

In this experiment,there was no main effect for length; AE was not found to be proportionate to replication excursion length so Hypothesis 2 was discarded.

Target End Position

Hypothesis 3 regarding the target end position was supported: with model movement excursion length held constant and end positions matched for projected replication movments, replication movements to lateral end positions were longer than replication movements to medial end positions; CE was shifted negatively for medial as compared to lateral positions. This was true for males and females alike. Thus, even with positions equated with regard to movement lengths, Nadler's (1983) results were confirmed.

Why should this effect consistently emerge? If Larish and Stelmach (1982) are correct, the ego reference system uses body reference points best in the frontal or facing portion of extrapersonal space. The body-based reference points (the shoulder joints, essentially, in the present experiment) would, therefore, have been used for medial targets, and distance cues might have been used for lateral targets. However, there is no *a priori* reason to suppose that distance cues had a more positive shift than position cues nor even that they were used, particularly since subjects were well informed that the use of distance cues would lead to error.

An alternative explanation may be that each arm has an optimal range in near extrapersonal space, perhaps due to experience and/or use of the shoulder joints as reference points, which is in the ipsilateral frontal hemispatial field. The inclination might exist to move an arm into, but not out of, this optimal range, a sort of 'comfort zone'. To use the terminology of Seligman (1970), initiation of movement into this zone is a 'prepared action', whereas movement out of it is counterprepared. Therefore, more lateral target end positions would be associated with a more positive excursion length (a medially-directed shift) than the medial target end positions.

Previous to the Nadler (1983) study this position effect had not been reported, most likely because of procedural differences across studies. Many studies required linear rather than curvilinear movements (e.g., Walsh et al., 1979). In others, the range of movements was not limited to the ipsilateral hemispace of the arm (e.g., Laabs, 1971) or extreme differences in excursion lengths were not equated across the various end positions (Wrisberg & Winter, 1985). Another variable of possible relevance is whether the movements are abductive of adductive. Both the Nadler and the present study employed adductive movements while other studies (e.g., Laabs, 1971) employed abductive movements. A small pilot study conducted prior to the present study examined abductive movements and failed to find a position effect. However, movements were limited to the ipsilateral hemispace for each arm and, therefore, the medial range (70° to 80°) was not tested using long excursions. Thus, this question requires further research.

Performance Asymmetry

Hypothesis 4, that performance would be better for the left than for the right arm, was supported in part: performance at the medial target position was better with the left than the right arm, as measured by AE. At the lateral position, however, performance was more accurate with the right than the left arm. These results are compatible with those of Nadler (1983). Although Nadler found a left arm advantage at all three end positions used, effects of different ranges of end position and excursion length could account for differences in performance between his and the present study.

Phillips and Summers (1954) hypothesized that movements of the left arm are better than those of the right arm at less familiar (lateral) positions. Since movements into medial extrapersonal space should be more familiar than those confined to lateral extrapersonal space for either arm, the data did not support the hypothesis of Phillips and Summers (1954): left arm movements were not more accurate than those of the right at the less familiar, lateral position.

For the medial positions, it may be that the egocentric reference system was used, just as Larish and Stelmach (1982) would predict, shifting the emphasis from kinesthetic to spatial abilities. Since the right hemisphere is believed to be superior to the left for spatiality this may have conferred the left arm advantage at the medial positions. For lateral positions, kinesthetic cues may have been emphasized, eliminating the right hemisphere advantage.

Temporal Uncertainty

Hypothesis 5, that temporal uncertainty would have an asymmetrical effect on AE performance, was disconfirmed. The left arm advantage at the medial position was independent of temporal uncertainty; it was observed in the fixed, as well as the mixed, retention interval session.

Two hypotheses about CE performance also concerned temporal uncertainty: Hypothesis 6 was that left and right arm performance as measured by CE would be differentially affected and Hypothesis 7 was that this asymmetry would be greater for males than for females. In fact, an asymmetry in performance and a more lateralized response for males than females was found, but these occurred only as part of the 5-way interaction. The greatest positive shift in CE, for the mixed as compared to the fixed condition, was seen for males at the most lateral position for the left arm, whereas for females, the greatest positive shift was seen at the medial position for the left arm with a lesser effect at the lateral position of the right arm.

Bryden (1979) stated that sex differences in performance may occur due to a) biological differences, b) different strategies, or c) an interaction of a) and b). To sort out these factors, it is necessary to examine the evidence linking temporal uncertainty manipulations to changes in arousal level.

Evidence is presented to support the view that the right hemisphere subserves a primarily receptive arousal system; the left hemisphere, a primarily motoric activation system. Furthermore, asymmetries in these systems may be attributed to characteristic or trait asymmetries in the biochemical and anatomical systems underlying arousal and activation. These asymmetries exist for groups, with individual variation superimposed, and interact with the dynamic processes involved in selection of task strategies.

Arousal. Arousal is the automatic, phasic, stimulus-event elicited receptivity of the organism. Pavlov (1927) was the first to observe that a newly selected stimulus elicited an unconditioned, attentional-type, "What is it?" response. Pavlov (1927) termed this behavior the orienting response (OR). Sokolov (1960, 1963) found that initial presentations of a stimulus of moderate intensity will result in a generalized, nonspecific OR, regardless of the sensory modality. What is important to elicit the OR or arousal is a stimulus which imparts novelty, adaptive value, surprisingness, significance or uncertainty. Even the absence of a stimulus can trigger an OR if the omission of an expected stimulus or the unexpected termination of a current stimulus leads to surprise.

Activation. Activation has been functionally defined in at least two distinct ways. Firstly, activation is defined as the motoric result of an arousal response and, therefore, coupled with arousal. Pavlov (1927) noted that the "What is it?" response or OR was followed by a "What's to be done?" reaction or activation. This is the meaning which Vinogrodova and Sokolov (1975), Luria (1973) and Heilman (1979) impart to activation. However, activation is also defined as a preparedness, a tonic readiness to respond, or vigilance (Pribram & McGuinness, 1975). This latter definition views arousal and activation as potentially decoupled. Failure to recognize the distinction has led to a controversy concerning whether activation has a right- or a left-brain bias. Heilman (1979) regards activation as right-brain biased, because the right hemisphere receptive arousal system has a motoric component to subserve the "What's to be done?" reaction to an arousing stimulus. Tucker and Williamson (1984), however, suggest that activation is left-brain biased when it is involved in preparedness and intention and is decoupled from arousal.

Characteristic arousal. Asymmetries of arousal can be task-dependent due to a lateralized stimulus or hemispheric function (Kinsbourne, 1974), or task-independent, due to neurochemical r other characteristic asymmetries (Levy, Heller, Banich, & Burton, 1983) Among dextrals, individual differences in the magnitude of asymmetry have typically been attributed to differences in hemispheric specialization but Levy et al. (1983) postulate that much of the variation is due to characteristic (trait) and task-independent asymmetries of hemispheric arousal.

The neglect syndrome provides evidence for asymmetry of the arousal system in humans. A lesion of the right hemisphere leads to a more profound neglect than a lesion of the left hemisphere, a finding not attributable to the extent of the lesion (Heilman & Valenstein, 1972). Right hemisphere neglect patients have depressed galvanic skin responses (GSRs) (Heilman, Schwartz, & Watson, 1977), and bilateral motoric slowness (Watson, Andriola & Heilman, 1977). Neglect due to a lesion of the right hemisphere is usually bilateral but most profound on the left.

Investigation of normal subjects also yields evidence to implicate the right hemisphere in arousal. Light stimuli presented in the right visual field (RVF) produce contralateral parietal desynchronization but if the stimuli are presented in the left visual field (LVF), the desynchronization is bilateral (Heilman & Van Den Abell, 1980). Parietal lesions may induce neglect due to destruction of the OR-type attentional cells which are believed to be more numerous in the right hemisphere of humans (Heilman & Valenstein, 1972).

Asymmetry in evoked potential research is associated with arousal: the early component of the contingent negative variation (O-wave) is believed to reflect the OR. The O-wave, itself, is divided into an early N3 and late N4 component. Rohrbaugh, Newlin, Varner, and Ellingson (1984) discovered that the N4 component was larger at the right than at the left frontal electrode and suggested that this asymmetry may reflect the right hemisphere predominance for arousal.

Evidence indicates that the right hemisphere has a bilateral capability to mediate arousal which increases activation. Heilman and Van Den Abell (1979) found that the LVF warning signals reduced right hand RT more than RVF warning signals reduced left hand RTs. Since right hemisphere arousal leads to left hemisphere arousal (Heilman & Van Den Abell, 1980), left hemisphere/right hand RT is improved.

The right hemisphere is bilaterally involved in the motoric component of arousal based on lesion sites of many neglect patients. Lesion sites which induce hypokinesia are almost always right-sided and these include frontal cortex (Heilman & Valenstein, 1972), striatum (Heir, Davies, Richardson, & Mohr, 1977; Valenstein & Heilman, 1981), and intralaminar nuclei (Watson & Heilman, 1979). This centre median-parafasicular complex has a higher concentration of NE on the right than on the left (Oke, Keller, Mefford, & Adams, 1978). Taken together, the evidence indicates that the motoric component of the arousal system also has a right-sided bias.

The conclusion drawn by Heilman (Watson & Heilman, 1979) from the above studies is that the left hemisphere subserves the contralateral (right) side but the right hemisphere with its subcortical components has a bilateral responsibility for arousal. In support of this view, Bowers and Heilman (1980) report that, in a tactually guided line-bisection task, performance is superior with the left than with the right hand and superior in the left than in the right hemispatial field. However, these results must be regarded as tentative at present because two independent studies failed to replicate (Bruder, personal communication, August 14, 1986; Hatter & Yamamoyto, 1986).

Watson and Heilman (1979) believe that hemispatial effects are subject to environmental influences: a lateralized attentional-arousal field can shift the functional midline (Bowers, Heilman, & Van Den Abell, 1981). Bowers et al. suggest that a dynamic realignment of perceptual space occurs with lateralized stimuli or responses wherein the body midline no longer serves as the division between left and right hemispace.

Characteristic activation. Asymmetry of activation may be expressed by the tendency of most people to veer to the right while walking or to choose the right stairway when given a right-left choice (Howard & Templeton, 1966).

Glick, Ross, and Hough (1982) analyzed human brains but were unable to report the handedness history related to the specimens. The dopamine level of the caudate and putamen was higher on the right while that of the globus pallidus was higher on the left. Thus, Glick et al. concluded that pallidal dopamine, greater on the left, is related to directional bias since it can be assumed that most people are right-handed. Glick et al. believe that in life these dopamine levels have a dynamic relationship with right-left asymmetry and depend on the activity of the whole system. Taken together with the results from animal reseach (see Appendix K), these asymmetries are believed to have functional significance.

In the Tucker and Williamson (1984) model of arousal and activation, activation has a left-brain bias and is tonic whereas arousal has a right-brain bias and is phasic. This model is consistent with a left hemisphere specialization for complex motor operations and a right hemisphere specialization for integrating bilateral perceptual input. Hughlings Jackson (Taylor, 1958) concluded that the left hemisphere is specialized for expressive funtions; the right hemisphere, for receptive functions. Arousal and activation underlie the specialization of motor and perceptual functions. The relevant neurotransmitters are also asymmetric: dopamine is left-biased and norepinephrine is right-biased. The attention required to maintain vigilance (activation) is basically different than an OR to a warning stimulus or other external event.

Levy et al. (1983) approached the problem of isolating characteristic arousal by including a performance rating in a laterality task. It is known that a search for a target letter within a vertically aligned array of letters is faster when the array comprises a word than when it forms a non-pronouncable nonword (Krueger, 1978). The closer to the bottom of the array that the target is, the greater will be the difference in search times for word and nonword arrays--the word superiority effect. Levy et al. (1983) noted that this increase in error with deepening position is due to a deterioration in LVF, but not RVF, performance. The performance of the RVF is stable from top to bottom so that it gains an increasing advantage with progressively lower placed letters of the word-array as LVF performance deteriorates. These differences are believed to result from a left hemisphere ability to use a linguistic name-code strategy along with a limited use of the non-linguistic feature extraction processes. The right hemisphere, however, must rely almost excusively on its feature extraction ability because, although it is capable of decoding or matching words for meaning, it cannot encode a nonsense word through name-code derivation. The outcome is that the right hemisphere processes the last letters much more slowly than the left hemisphere because it must analyze each letter singly.

In the Levy et al. (1983) experiment, dextral subjects performed a linguistic task which required identification of vertically aligned consonant/vowel/consonant nonsense syllables. The syllables were presented singly, near absolute threshold, and distributed over the two visual hemifields in a constrained-random order. Subjects also rated the correctness or incorrectness of their responses on a three point scale of confidence, yielding a performance discrimination measure and a bias about that measure. As predicted, last letter errors, with first letter correct, were more prevalent in the left than in the right visual field. First letter errors, with last letter correct, were more prevalent for the right visual field. Subjects were then divided into those with a strong right visual bias (Group S) and those with a weak or absent right visual bias (Group W). Whereas Group W performed better than Group S on first letters, Group S performed better than Group W on last letters. Interestingly, the relative shift of the two groups in asymmetry was stable regardless of lateralization of error types. That is, first letter errors occurred more in the RVF, although this effect was greater for Group W. For middle positioned errors, Group W showed a slight RVF increase; Group S showed a LVF increase. The last letter errors were predominently LVF errors for both groups but the greatest effect was seen for Group S. It appears that some general factor shifted the perception of Group W to the left. Levy et al. believe this factor to be a greater right hemisphere arousal for Group W than for Group S based on the arguments presented below.

Firstly, because both groups performed better on first letters in the LVF and on last letters in the RVF, no group differences in hemispheric specialization for name-code and feature analysis abilities can be inferred. Secondly, lateralization of metalinguistic skills is not believed to be responsible for the differences in performance. Because the magnitude of subject bias did not constrain the performance discrimination ability, performance discrimination could be viewed as a pure metalinguistic skill. Performance discrimination scores derived from subjects' judgments about performance accuracy, showed both groups to be equally capable of making LVF judgments. For Group W, though, LVF and RVF judgments were equivalent, whereas for Group S, the RVF judgments were superior to the LVF judgments. This is a similar pattern to that produced by the syllable identification task itself. The metalinguistic system, like the linguistic system has better access to information in the RVF, with a stronger effect for Group S than for Group W.

The right hemisphere is also believed to be differentially involved in emotion; high arousal of the right hemisphere is associated with positive affect and low arousal, with negative affect. If Group W has a higher right hemisphere arousal than Group S, then Group W should have more of a positive bias than group S. The results conformed to prediction. For the LVF, Group S bias was negative and Group W bias was positive. The two groups did not differ for the slight RVF bias.

Subjects returned for a final task, to examine pages with two mirror images of a composite face, one side smiling and the other side neutral. The first face, on a page, was placed above the second and the faces changed along with the direction of smiling side across the pages. By choosing the happier looking face, subjects could be scored for direction of attentional bias. As predicted, the RVF advantage for syllables was inversely related to leftward asymmetry on the perceptual face task, supporting the arousal asymmetry theory.

Individual differences in characteristic arousal asymmetry may lead to characteristic differences in strategies employed. For example, higher right hemisphere arousal could lead to a bias toward nonverbal processing and higher left hemisphere arousal toward a verbal bias. Diversities in strategy may be a consequence of asymmetric arousal which impact on utilization so that one develops a bias.

The asymmetric arousal, itself, may be the outcome of an asymmetric cerebral vascular supply. Carmon, Harishanu, Lowinger, & Lavy (1972) administered tritiated iodine intravenously to 85 normal subjects. The nondominant hemisphere showed higher irradiation curves, reflecting an asymmetrical blood supply: the left carotid artery stems directly from the aortic arch whereas the right carotid and subclavian arteries share a common trunk. Jutai (1984) suggests that the greater right than left hemisphere cerebral blood volume and flow predispose the right hemisphere to dominate in the early (arousal) stage of information processing.

Activation of a control center can 'prime' perceptual-cognitive mechanisms, perhaps through an attentional bias which Trevarthen (1972) would say is a subthreshold OR. Subvocalization improves an ability to detect right-side gaps in squares and gives a right visual field advantage to nonsense syllables (Kinsbourne, 1973). The increased arousal which primes the cognitive ability can be documented through EEG recordings. Ehrlichman and Wiener (1980) found subjects who showed a lateralization in the EEG activity due to cognitive tasks and then tested these subjects on covert verbal and visual tasks. Since movements were not involved, the EEG asymmetries reflect real asymmetries in cognitive function.

Kinsbourne (1979) views the two hemispheres, indeed each side of the whole neuraxis, as subserving orienting in its respective contralateral hemispace; right and left OR mechanisms are in a dynamic equilibrium at all levels of the nervous system. If one hemisphere is selectively engaged, an increase in the ipsilateral arousal/activation system or "homolateral orienting control center" (Kinsbourne, 1979, p. 355) induces a shift in the left-right orienting balance from midline to the contralateral hemispace. The arousal summoned forth to undertake a specialized cognitive task increases the arousal level of the hemisphere as a whole. The OR and attention are biased toward the contralateral hemispace even though it serves no adaptive purpose (Kinsbourne, 1970). Thus, Kinsbourne (1972) found, in dextrals, that verbal tasks induce a rightward visual OR whereas mathematical or spatial problems result in an upward or leftward visual OR, if the experimenter remains out of view of the subject (Gur, 1975).

Bowers and Heilman (1980) similarly suggest that alterations in asymmetry of arousal impact on the hemispatial body field or external space. The hemispatial field is an egocentric coordinate system, divided into left and right by the median plane of the body and as the body moves the hemispatial field is altered. Perception of this extracorporeal space is believed to have evolved from perception of corporeal space. Both are dependent on morphosynthesis, convergence of somesthetic and visual information (Denny-Brown & Banker, 1954; Denny-Brown, Meyer, & Horenstein, 1952).

Mesulam (1981, 1983) envisions three distinct representations of extracorporeal space: a limbic/motivational, a parietal/sensory spatial, and a frontal/motor mapping representation. Along with Bowers and Heilman (1980), Mesulam (1981, 1983) attributes the right hemisphere with a dominant, bilateral role in directing attention into space.

Bisiach and Lazzatti (1978) requested that right hemisphere-lesioned neglect patients describe Milan's Piazza de Duomo from two different perspectives. Unless prompted, patients omitted details from the imagined left hemispatial field, but not the right, regardless of the perspective imagined. A mental representation of extracorporeal space is apparently mapped across the brain, similar to Brain's (1941) concept of the body scheme.

Thus, asymmetries of arousal that shift the median plane of the coordinate system may be general, as typified by the neglect patient of Heilman and Valenstein (1979) or localized, as when engaging in a cognitive task.

Kinsbourne (1970) reasons that because verbal tasks are processed in the left hemisphere, for the most part, they produce a rightward OR and the symptoms of left-sided neglect are exacerbated. Visuospatial tasks will reduce the left-sided neglect. Heilman and Watson (1978) found support for this prediction. Right-lesioned neglect patients showed a greater decrement in performance on a crossing-out task if the stimuli were verbal than if visuospatial, due to a more severe left-sided neglect of stimuli in the verbal task. It was not clear, though, if the difference was due to verbal stimuli activating the left or visuospatial stimuli activating the right hemisphere more.

Extreme biases are prevented in the normal person by callosal inhibition and/or interhemispheric spread of arousal. At least for arousal, the callosal mechanism itself may be asymmetrical since arousal spreads much more from right to left than vice versa (Heilman & Van Den Abell, 1980).

In summary, there is good evidence that individual and, perhaps sexually differentiated, characteristic asymmetries of arousal and/or activation underlie lateralization of specific abilities and cognitive functions.

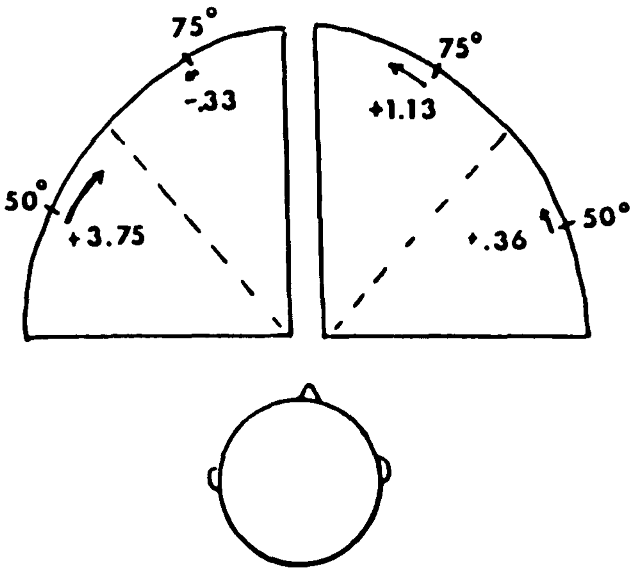
Temporal Uncertainty Revisited

Is the effect resulting from the temporal uncertainty manipulation due to changes in arousal, activation, strategies, or some combination of the three variables? It seems that two different foci for spatial orientation exist: the posterior parietal regions are concerned with extrapersonal space and the frontal lobes deal with personal, egocentric space, involving spatial discriminations of the body (Semmes, Weinstein, Ghent, & Teuber, 1963). These two different functional areas might be differentially and respectively involved in arm positioning and spatial location abilities. Moreover, parietal lesions of the right hemisphere produce greater deficits of extrapersonal spatial abilities than those of the left whereas frontal lesions of the left hemisphere produce greater deficits of egocentric spatial abilities than lesions on the right (Butters, Soeldner, & Fedio, 1972). In the present experiment, perhaps the males were more likely to treat the task as a replication of spatial location while the females attempted to replicate arm position. Then, the differences would be due to strategy or a strategy x biology interaction. This seems unlikely, because if the females were using a left hemisphere strategy, then the right arm response at the lateral end position should have shown an equivalent positive effect (if bilateral) or a larger effect (if unilateral), or no effect if the left hemisphere is unresponsive to temporal uncertainty manipulations.

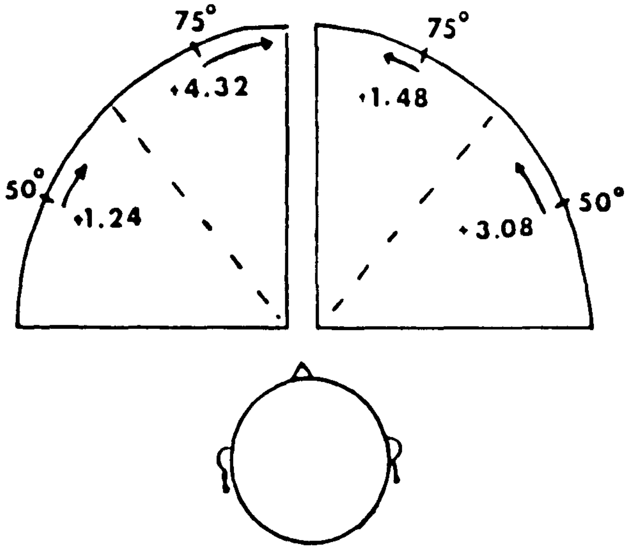
An arousal model would allow a different interpretation. Both arm positioning (left hemisphere-biased) and spatial location (right hemisphere-biased) abilities contribute to the position replication task and each may have a greater or lesser weighting, dependent on response demands and individual strategies. If the two sexes did use different strategies, matching trials across the two sessions should be the within-subject control to allow an arousal effect to emerge, if present. Also, unlike the RT task, the arm positioning task does not challenge the subject with a speeded response to measure preparedness so that a potential arousal response would not be obscured.

If manipulation of arousal is responsible for the significant 5-way interaction, males are most lateralized for right hemisphere arousal, since the positive increase was with the left arm and displaced to the most leftward position. For females, the displacement was shifted less but was bilateral; the most positive increase was with the left arm at the medial position but a less positive increase occurred with the right arm at the lateral position (see Figure 3). These results suggest the possibility of a sexually differentiated characteristic asymmetry of arousal. They also argue for an underlying biological or biology x strategy basis for some of the differences observed in spatial abilities.

Figure 3. Diagrammatic mapping of mean constant error difference scores (mixed minus fixed session/long target excursion) onto left and right hemifields of space.



Male



Female

CHAPTER III

EXPERIMENT 2

Introduction

The sequence of trials in Experiment 1 were not counterbalanced for the right and left arms. It was hypothesized, therefore, that the asymmetries found in the AE and CE analyses of variance might be due to a differential treatment of the two arms through inadvertent sequential effects. This hypothesis was based on reports that both RT and P3 are influenced by the preceding trials (Duncan-Johnson, Roth, & Kopell, 1981).

In an oddball (rarity) paradigm, trials with a rare (infrequent) stimulus can usually be differentiated from trials with a standard (frequent) stimulus by the amplitude of P3. However, about 19% of such trials are misclassified by P3 measurement (Squires, Wickens, Squires, & Donchin, 1976). These variations are apparently due to the particular sequential ordering of trials and do not reflect whether the target trial had a rare or frequent stimulus but rather whether a change occurred between the prior and present trial. A stimulus, rare or standard, which is preceded by a trial with a like stimulus is associated with greater expectancy than when preceded by a trial with an unlike stimulus. The influence of preceding trials extends to at least fourth order sequences but the largest effect is due to the most recent trials; memory decays as a function of time (Squires et al., 1976). Subjective sequential effects are similar to other probability effects in determining expectancy and P3 amplitude. Thus, P3 amplitude is increased by disconfirmation of expectancy due to sequential ordering as well as by a priori or conditional probability. An increase in both RT and P3 result (Squires et al., 1976).

For RT, the most prominent effect is a large increase in latency if the foreperiod of the preceding trial is larger than the foreperiod of the present trial (Niemi & Naatanen, 1981). Thus, the trial with a shorter foreperiod is more susceptible to surprise or disconfirmation of expectancy since it is more likely to be preceded by a trial having a comparatively longer foreperiod than is a long foreperiod trial. Sequential effects contribute to the foreperiod-RT relation just as does conditional or a priori probability.

The sequential foreperiod effect remains when time markers are employed to allow accurate estimation of the passage of time (Requin, Granjon, Durup, & Reynard, 1973; Stilitz, 1972). So, it is unlikely that the effect is due to overestimating a short foreperiod following a long foreperiod. It might be hypothesized that subjects anticipate foreperiod repetition rather than alternation. Peak readiness would then be premature or late depending on whether the foreperiod of the previous trial were short or long. Over trials, a mean foreperiod peak may be generated (Drazin, 1961). This hypothesis is weakened, however, by subject report; subjects generally expect alternation rather than repetition (Niemi & Naatanen, 1981). However, according to Kahneman (1973), the interpretation of Drazin (1961) still has merit because the OR, itself, is more primitive and may be at variance with verbal or conscious expectations about sequential order.

In support of Kahneman's (1973) view, Maltzman, Harris, Ingram, and Wolff (1971) found that the OR, as measured by the GSR, was greater for a stimulus change away from the initial stimulus level than for a stimulus change back to the initial stimulus level. Even though the alternating stimulus levels should lead to equivalent conscious expectancies, the OR-GSR displayed a primacy effect wherein the initial stimulus level became a referent by which to compare successive stimuli for differences.

Tueting, Sutton, and Zubin (1971) and Friedman, Hakerem, Sutton, and Fleiss (1973) found an inverse relationship between P3 amplitude and rareness of the stimulus event, although the subject was told in advance what stimulus would occur. Even in this 'certain' condition, the amplitude of P3 differentiated amongst stimuli of .20, .40, .60 and .80 _a priori_ probabiities. Tueting et al. (1971) similarly found an inverse relationship between P3 amplitude and probability of stimulus repetition in the certain condition; the subject knew that the stimulus would change, yet the rarer the event, the greater the P3 amplitude. It is now established that P3, maximal over centro-parietal scalp, is the waveform systematically associated with prior sequence of signals (Munson, Ruchkin, Ritter, Sutton, & Squires, 1984).

A variation of Drazin's (1961) hypothesis of a peak readiness on each trial is postulated by Alegria (1975): a waxing and waning of readiness occurs over the foreperiod. Peak preparations are said to rapidly fade in the absence of an imperative stimulus but new peaks (repreparations) develop during the foreperiod. Thus, RT will be lengthened if the imperative stimulus occurs before or in between the readiness peaks (Alegria, 1975). But, if the stimulus is coincident with a peak, especially the first peak, RT will be reduced. This hypothesis is supported by the finding of Loveless and Sanford (1974), that slow negative brain potentials, indicating heightened arousal or attention, occur during long intervals at the moments of potential stimulus occurrence.

In Experiment 1, it may be that the right and left hemispheres would have been equally responsive to the arousal effects of conditional probability had sequential ordering been equated for both arms. To test this possibility, a second experiment was performed in which the order of trials for the right arm in Experiment 1 became the order for the left arm in Experiment 2 and *vice versa*.

Method

Subjects. Subjects were ten male and ten female volunteers selected from the same subject pool and meeting the same requirements as those in Experiment 1. Their ages ranged from 17 to 27 years of age.

Apparatus and procedure. The apparatus and procedure were the same as those used in Experiment 1 except that the ordering of trials was changed: all right-arm trials of Experiment 1 became left-arm trials and all left-arm trials of Experiment 1 became right arm trials. Hence, sequential ordering effects were exchanged for the right and left arms between Experiments 1 and 2.

Response measures and data analysis. Response measures were those used in Experiment 1: AE, CE and VE. Separate analyses of variance were carried out for the data of these three measures, as in Experiment 1. Again, a $p \leq .01$ level of confidence was accepted as significant.

Results

Absolute error. The main effect of Length was significant ($p \leq .0002$; see Appendix F). Mean AE for short excursion trials was 6.55° and mean AE for long excursion trials was 10.03°.

Constant error. Main effects of Position and Length were significant ($p \leq .002$, & $p \leq .0001$; see Appendix G). For Position, mean CE was more negative at the medial (-7.34°) than at the lateral (-4.60°) end position. For Length, mean

CE was more negative for the long (-9.28°) than for the short (-2.63°) target excursion trials.

Variable error. There were no significant main effects. One 3-way interaction reached significance: Position x Arm x Sex ($p \leq .008$; see Appendix H). Mean VE was smaller at the lateral than at the medial end position for the right arm of females, whereas mean VE was smaller at the medial than at the lateral end position for the left arm of females and both arms of males (see Table 5).

Prior retention interval. To assess the first order sequential effects of prior retention interval on performance, the data from short retention interval, long excursion trials of Experiment 1 and Experiment 2 were combined and a 2 x 2 analysis of variance was performed with Arm and Prior Retention Interval (PRI) as factors. Only the long excursion trials were analysed for PRI because the short trials were not influenced by temporal uncertainty in experiment 1. There were no main effects. The 2-way interaction, Arm x Prior Retention Interval was significant (see Table 6). For the right arm, mean CE was similar for short (-7.21°) and for long (-7.51°) PRI trials. For the left arm, mean CE was different for the two PRI trial durations: mean CE for short PRI trials (-8.42°) was more negative than for long PRI trials (-5.15°). In other words, a long PRI served to decrease the CE negativity for the left arm.

Table 5

Experiment 2: Means of Variable Error Interaction of Position x Arm x Sex

	Male		Female	
Degrees	Right	Left	Right	Left
50	3.85	3.72	2.87	4.15
75	3.08	3.55	3.84	3.83

Table 6

Analysis of Variance of Constant Error for short Retention Interval Trials: Arm x Prior Retention Interval

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Prob. 1-tail
Arm	43.30	1	43.30	.78	n.s.
PRI	294.16	1	294.16	5.32	n.s.
Arm x PRI	486.01	1	486.01	8.79	$p \leq .01$
Error:	29866.53	540	55.31		

Discussion of Experiment 2

Absolute error. Absolute performance was significantly better for the short than for the long target excursion trials. Since the general trend was in the direction of undershooting (negative shift in CE), then a factor known to produce a positive shift should have improved performance. Short movements, within a certain range, lead to positively directed shifts, whereas long movements lead to negatively directed shifts (Marteniuk, Shields, & Campbell, 1972). This range effect for length was not seen in Experiment 1, due perhaps to the fact that the effects of sequential ordering of trials had a greater influence on left arm performance in Experiment 1 than Experiment 2 (see below), thus, obscuring the simple AE effect of Length. It is true that for Experiment 1, Length x Session Type did not reach significance at the $p \leq .01$ level but examination of the means of this interaction was helpful in attempting to explain the lack of consistency across the two experiments for the main effect of Length (see Table 7). The AE for short excursion movements did not differ between the fixed and mixed interval conditions, nor between Experiment 1 or 2. The AE for long excursion movements did not differ from AE for short excursion movements in Experiment 1 in the mixed interval condition, but was significantly greater than for short excursion movements in the fixed interval condition. In Experiment 2, AE for long excursion move-

Table 7

Means of Absolute Error for
Length x Session Type Interaction

Excursion	Experiment 1 Fixed Session	Experiment 1 Mixed Session	Experiment 2 Fixed Session	Experiment 2 Mixed Session
Short	6.68	6.72	6.71	6.39
Long	8.08	6.92	9.57	10.48

ments was greater than for short movements in both the fixed and mixed interval conditions. Therefore, it appears that decreased error for long excursions in the mixed session of Experiment 1 was responsible for the absence of a significant main effect for Length.

Since a main effect for Length was found in Experiment 2, Hypothesis 2, concerning a proportionate relationship between replication excursion length and magnitude of AE, could be examined. Therefore, scores in this experiment were transformed by dividing each AE score by the projected replication excursion length of its respective trial. A 2-tailed t-test for dependent means was performed comparing short and long replication excursion trials. The means were significantly different at the $p \leq .01$ level of confidence. The grand mean for short excursion proportionate scores (.32) was significantly larger than the grand mean for long excursion proportionate scores (.21). Thus, in this experiment, the magnitude of AE cannot be explained as being simply proportionate to excursion length.

<u>Constant error</u>. Two main effects reached significance: Position and Length. The discussion of these factors in Experiment 1 holds for Experiment 2. The 5-way interaction found in Experiment 1 was not confirmed in Experiment 2. It is possible that the significant 5-way interaction in Experiment 1 was a spurious result which led to the failure to replicate in Experiment 2. It was also considered possible that, between experiments, there was a differen-

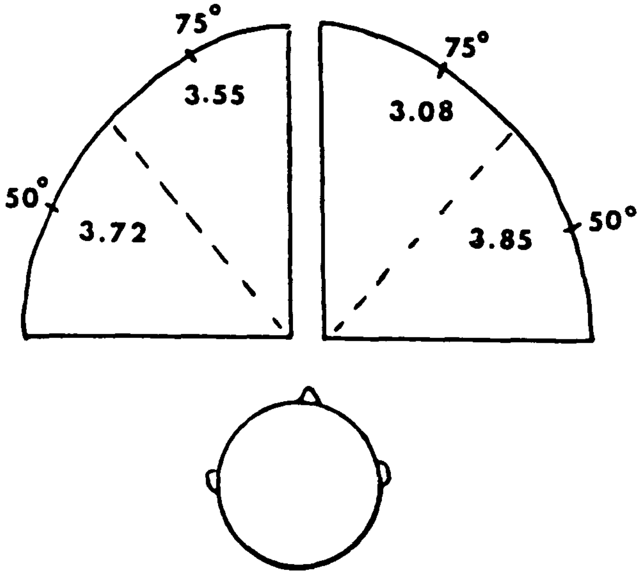
tial distribution of individuals with sinistral family members, and that this could have affected the results. However, this conclusion is unlikely because of the following: Six of the 24 subjects in Experiment 1 had a sinistral family member. To investigate the possible impact of familial sinistrality on the performance asymmetry for CE, the analysis of variance was repeated with their data excluded. With a reduced N of 18, The 5-way interaction remained significant ($p \leq .0004$), as did its η^2 value (.06).

A second explanation for the absence of a significant 5-way interaction in Experiment 2 is that it resulted from the sequential ordering manipulation. According to this view, the temporal uncertainty effect on left arm performance seen in Experiment 1, was dependent upon, or strengthened by sequential ordering factors. Since, a 5-way interaction was not found with involvment of the right arm in Experiment 2 to mirror that of the left arm in Experiment 1, the left hemisphere is not responsive to the conditional probability and sequential ordering effects in the same way as the right hemisphere.

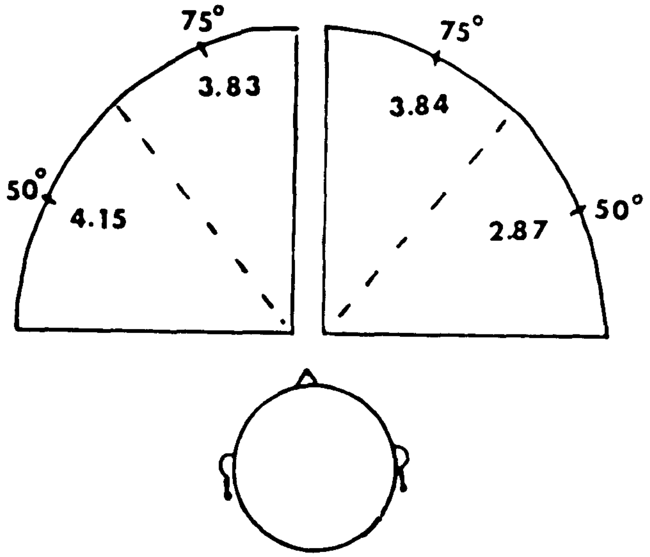
Variable error. One 3-way interaction, Position x Arm x Sex, reached significance ($p \leq .008$). For the males, VE performance was consistent across positions and arms. The males may have used a right hemisphere strategy (spatial location), making performance equally reliable across the two hemifields of space. But for the females, consistency was greatest at the most rightward position, equivalent for the medial positions, and least at the most leftward position (see Figure 4). Females may have used a left hemisphere strategy (arm positioning) to perform the task and, in fact, left hemisphere performance was most consistent in the contralateral hemifield.

Another interpretation is that, for the females, a right hemisphere strategy was more effective the more leftward the position. When the right hemisphere strategy proved less effective, then a left hemisphere strategy was used more. The left hemisphere strategy may be more resistant to procedural effects, such as temporal uncertainty or sequential ordering (see below) and, therefore, would lead to more consistent, though not necessarily more accurate, performance. According to this model, the males employ a right hemisphere strategy, bilaterally.

Figure 4. Diagrammatic mapping of mean variable error sccores across left and right hemifields of space.



Male



Female

CHAPTER IV

GENERAL DISCUSSION

There were three possible outcomes of the reverse sequential ordering paradigm with regard to the 5-way interaction: 1) The 5-way interaction could have emerged in Experiment 2 just as in Experiment 1. This would have indicated that right and left hemisphere are differentially sensitive to temporal uncertainty and that neither hemisphere is differentially affected by sequential ordering. 2) A mirror image 5-way interaction could have resulted in Experiment 2. This would have indicated that the two hemispheres are equipotential for temporal uncertainty and sequential ordering effects. 3) The 5-way interaction could have failed to occur, indicating that the two hemispheres are not equipotential for temporal uncertainty effects and, further, that the right hemisphere is differentially influenced by sequential ordering. This last possibility was, indeed, the outcome. This finding fits the right hemisphere arousal model and reflects a right hemisphere arousal bias for males and fmales, though less lateralized for females than for males.

The fact that the left arm temporal uncertainty effect was not seen when sequential ordering of trials was reversed led to the speculation that sequential ordering also contributes to temporal uncertainty effects. For this reason, trials were sorted, across the two experiments, according to PRI and arm. PRI was found to have a significant effect on left, but not right, arm performance. Thus, right hemiphere-left arm performance appears to be sensitive to sequential ordering manipulations, strengthening the arousal interpretation of the 5-way interaction of Experiment 1. This general right hemisphere-left arm bias due to temporal uncertainty and sequential ordering also supports the second interpretation of the significant 3-way interaction for VE (Position x Arm x Sex) in Experiment 2: females used a left hemisphere strategy for right hemifield/arm movements in this lower arousal condition (Experiment 2) but shifted to a more right hemisphere-dependent strategy in the higher arousal condition (Experiment 1). If females had used the left hemisphere for both hemifields/arms, then the temporal uncertainty manipulation of Experiment 1 would either have had no effect (indicating left hemisphere insensitivity to temporal uncertainty manipulations) or would have served to increase the positive shift of the left hemisphere/right arm performance more than that of the right hemisphere/left arm performance.

The strength of the arousal model to explain the overall results is that: 1) With a favorable sequential ordering of trials, temporal uncertainty predominantly effected left arm performance. 2) PRI was shown to produce a positive shift in left, but not right, arm performance. 3) The 5-way interaction of Experiment 1, involving the temporal uncertainty manipulation, led to the suspicion that other expectancy manipulations such as sequential ordering would also effect left arm performance. This was born out through examination of the interaction of PRI with performing arm. 4) The significant 3-way interaction for VE in Experiment 2, but not Experiment 1, can be explained on the basis that Experiment 2 reflects a lower arousal condition, due to an unfavorable sequential ordering, than does Experiment 1.

Buffery and Gray (1972) contended that the representation for spatial abilities in males is bilateral; for females, unilateral. Yet, McGlone's (1980) conclusion, based on a summary of a number of studies, was that males are more lateralized than females for spatial abilities. Can the present results contribute to resolving this discrepancy? Based on the 5-way interaction for mean CE of Experiment 1, both males and females showed a right hemisphere arousal effect on spatial performance which was strongly contralateral for males; for females, the arousal effect was bilateral and not as strongly displaced to the left as that of males. Since an arousal effect is believed to be involuntary, males are biologically more lateralized than females. Looking at the mean VE interaction of Experiment 2, wherein performance was shown not to be unduly influenced by expectancy effects, it appears that males use a right hemisphere strategy for both hemifields/arms. The performance of females is determined by the strategy of the hemisphere contralateral to the hemifield/arm of performance. This interaction may have been obscured in Experiment 1 due to an arousal-induced shift to right hemisphere processing in females. Thus, concerning sex differences in spatial abilities, Buffery and Gray may be correct as applied to the strategies employed and McGlone, for biological differences. Of course, without the use of experimental procedures to separate the two, spatial performance would be based on an interaction of the biological and cognitive sex differences in spatial abilities.

One unanswered question is why superior left arm performance (AE) was seen for the medial position in Experiment 1, but not Experiment 2. In part, this lack of congruence may be due to the sequential ordering of Experiment 2 which was shown to be unfavorable for the lateralized arousal effect. Although it is known that changes in both CE and VE influence AE, a strong correspondence is not always possible and this was true for the present experiments. Still, AE performance in the fixed condition showed a left arm advantage at the medial position for Experiment 1 but not Experiment 2. Since, no interval manipulation occurred between the fixed conditions of the two experiments, other sequential ordering effects must have been implemented. For example, is performance of right and left arm differentially affected by ipsi- versus contra-lateral arm of the previous trial(s)? This would reflect another form of expectancy manipulation, event uncertainty. Perhaps future work will address this issue.

A second question concerns why sex differences in AE were not found either in the Nadler (1983) or the present study despite the fact that sex differences on a spatial task are generally expected. Perhaps, if subjects had been sorted on the basis of maturational history, group differences would have emerged, since maturational rate is known to influence spatial abilities (Newcombe, 1982; Waber, 1976, 1977).

A third question concerns identification of the factors which led to different results concerning left arm superior performance between the study of Nadler (1983) and the present study. It is believed that visual imagery plays an important role in performance on arm positioning tasks (Colley & Colley, 1981) and since subjects were not tested for visual imagery, there may have been comparatively more high imagery subjects in the Nadler study than in the present study. But it is more likely that procedural differences between the studies are responsible for the different results. Nadler had subjects give a verbal response to indicate the end of the replication movements, while in the present study, a nonverbal, chinlift response was used. Perhaps the verbal response interfered with right arm performance to allow a left arm advantage by default. A small study was conducted (N=5) to address this question. The main effect for response mode was significant at a .05 level of confidence: mean CE was shifted in a negative direction in the nonverbal, as compared to the verbal, response condition ($p \leq .03$). No laterality effect emerged, however, indicating that the verbal response neither primed nor interfered differentially with left hemisphere-right arm performance. Rather, it appears that subjects were able to simultaneously terminate their arm movements while preparing the verbal response but arm movements were brought to completion in advance of preparation of the chin-lift response. Thus, motor interference was greater for both arms from chin-lift than from the verbal response mode.

Therefore, the explanation of the different results between the the study of Nadler and the present study must look toward other variables. One possibility is that more spatial cues were allowed in the Nadler study than in the present study. For example, in the Nadler study, subjects were allowed to sit back between trials and may have used this opportunity to update their extracorporeal spatial schema. They may also have received auditory cues about end positions from the placement of the metal clamps along the band. These possible sources of information were controlled in the present study. Another speculation is that the Nadler study was conducted by a male psychology instructor on his students. It could be that the different sex of the experimenters and/or whether an instructor/student relationship existed between experimenter and subject affected the results. Since the present study has offered evidence that arousal differentially affects right hemisphere-left arm performance, these may be relevant variables. Fairweather (1976) has argued cogently that such uncontrolled experimental variables can determine the outcome of investigations into sex differences in spatial abilities.

One way to test the amount of involvement of each of these possible influences would be to replicate the Nadler study in every detail to obtain the left arm advantage. Then, each variable could be manipulated one by one until the left arm advantage disappeared. Many factors may participate to produce a cumulative effect but there is most likely a hierarchical ranking in terms of the influence each variable has. The most important single variable is probably whether subjects are allowed to sit back between trials. Even though they cannot see the end position stops, complex visual input from the surrounding environment may prime visuospatial mechanisms, thereby shifting strategy toward greater dependency on a visuospatial mode. Next in importance would be auditory cues from the end position stops which would also prime visuospatial mechanisms after intermodality transfer. Manipulation of retention intervals might be next in importance and, finally, the experimenter-subject relationship with regard to sex of experimenter and whether he is the subject's instructor.

Lastly, there is the question of whether asymmetries of performance on kinesthetic arm positioning tasks are due to asymmetry of input or of processing/output. The present study has shown that at least some of the performance asymmetry can be attributed to asymmetry of hemispheric arousal underlying processing/output. It has not been shown whether kinesthetic input might also be asymmetrical. Furthermore, hemispheric effects have not been examined independently to determine the relative role of each: the hemispheres can influence performance in contralateral hemispace (hemispatial perceptual field), through the sensory-motor field (motor input-output channel), or by direction of movement. Would the influence of temporal uncertainty on the right hemisphere arousal system be larger for leftward or rightward movements? Would the left sensory-motor field or left hemispatial field produce a more positive shift in response to arousal? The present results indicate that it would be profitable to reanalyze and reinterpret the results of much of the motor performance literature, taking into account unintentional arousal manipulations. It would be interesting to determine whether this task is sensitive to subclinical fluctuations in arousal level, such as might occur in the early stages of depression or manic episodes.

Summary

Evidence was presented in the present study to show that performance in an arm positioning task relies on both spatial and kinesthetic matching abilities. The relative contribution of these two strategies depends on the integrity of the kinesthetic system of the performing limb, past visual (visuospatial) experience, and task demands. The results of the present experiment indicate that the sex of the subject and expectancy manipulation also contribute to the final determination of strategy.

From Sokolov's (1963) work with rare and uncertain stimuli, which has been supported by physiological and behavioral data, it is concluded that arousal is inversely related to probability of stimulus occurrence. The physiologic, anatomic, and neurochemical evidence reviewed indicates that the receptive arousal system is generally right-brain biased and underlies many asymmetries of performance in both normal people and neurological (neglect) patients.

In Experiment 1, a design that matched subjects and trials between temporally certain and uncertain conditions, led to the positive shift in CE, resulting from manipulation of arousal. For males, this performance effect was found in the most leftward position: the lateral position of the left hemifield/arm. For females, the effect was bilateral and not shifted leftward, although the left hemifield/arm showed a greater effect than the right hemifield/arm.

The order of trials for the left arm of Experiment 1 became the order of trials for the right arm in Experiment 2. The purpose was to test the equipotentiality of the two hemispheres for temporal uncertainty and sequential ordering effects. The absence of a sigificant effect due to the expectancy manipulations indicated that the left hemisphere is not sensitive, as is the right, to temporal uncertainty. Finding a right hemisphere effect in Experiment 1, but not in Experiment 2, indicates that it is the right hemisphere, and not the left, that is sensitive to temporal uncertainty and sequential ordering effects.

Furthermore, under unfavorable sequential ordering conditions wherein the right hemisphere was not unduly influenced by expectancy (Experiment 2), males appeared to use a right hemisphere strategy bilaterally but females used a right hemisphere strategy for the left hemifield/arm and a left hemisphere strategy for the right hemifield/arm. Under conditions of increased arousal (Experiment 1), the female strategy shifts to, or interacts with, a bilateral right hemisphere functioning. Thus, males are more lateralized for the underlying biological arousal component of right hemisphere spatial abilities but females are more lateralized in terms of employing a right hemisphere strategy.

Appendix A

Handedness Inventory

Name..................... Age.... Sex.... Date......

Were you one of twins, triplets at birth or were you single born?..............

Which hand do you use:

1. to write a letter legibly?........
2. to throw a ball to hit a target?........
3. to hold a racket in tennis, squash or badminton?.......
4. to hold a match while striking it?........
5. to cut with scissors?........
6. to guide a thread through the eye of a needle (or to guide the needle onto the thread)?........
7. at the top of a broom while sweeping?........
8. at the top of a shovel when moving sand?........
9. to deal playing cards?........
10. to hammer a nail into wood?........
11. to hold a toothbrush while cleaning your teeth?........
12. to unscrew the lid of a jar?........

If you use the right hand for all of these actions, are there any one-handed actions for which you use the left hand which are not stated above?...........................

If you use the left hand for all of these actions, are there any one-handed actions for which you use the right hand which are not stated above?.........................

Is your father right-handed or left-handed?........

Is your mother right-handed or left-handed?........

Do you have any brothers or sisters? If so, are they right-handed or left-handed?.............................

If you are right-handed, was your writing hand switched from left to right in school?........

Inventory Selection

Oldfield (1971) has distinguished two different approaches to determine handedness. One is hand preference based on responses to a handedness questionaire. The other is manual performance, based on actual unimanual manipulations.

Hand preference appears to be distributed in a continuous, rather than a discrete, manner (Annett, 1970) but it is necessary to identify individuals who fall along different regions of the continuum, such as the strongly right-handed. Annett administered her handedness inventory to 2322 subjects and used association analysis to evaluate the twelve handedness questions. Six questions, primary questions, were highly associated with all others: writing, throwing, striking a match, using a toothbrush, using a racket, and using a hammer. The first four of these items were also found to be primary by Bryden (1977) who did a factor analysis of questions from the Crovitz-Zener and

Edinburgh Inventories. Five questions of the Annett Inventory, secondary questions, were less strongly correlated: using scissors, threading a needle, sweeping, shoveling and dealing cards. A terciary question, unscrewing a lid, had the lowest association. In agreement with these findings, McFarland and Anderson (1980), performed a factor analysis of questions on the Edinburgh Inventory and also found that questions such as sweeping and scissors were less stable predictors of handedness than primary questions such as writing.

Annett (1976) compared the hand preference responses to the results of a test of manual performance, speed of movement. Consistent right-handers were faster with the left hand. It was interesting that those who answered "right" to the primary questions but "left" to the secondary questions of sweeping, shoveling or threading, had a greater asymmetry of speed toward the right than those who answered "right" to all questions. For this reason and because these items were only moderately correlated with other handedness questions, Annett (1976) concluded that "left" responses to sweeping, shoveling or threading, by themselves, do not indicate greater left-hand skill and, in most cases, can be ignored. The question having the highest sum of associations with the other questions, and therefore, the best single criterion for right-handedness is hammering. When a single criterion is needed, hammering also has another advantage: it is less subject to training or cultural bias than an item such as writing. It is curious that the hammer question was deleted from the final, shortened version of the Edinburgh Inventory even though item-analysis by Oldfield (1971) and Briggs and Nebes (1975) showed this question to be the most consistent single predictor of handedness. In the Crovitz-Zener Inventory (1962), the hammer question was rephrased "holding nail to hammer", thus, making this item a catch question and denying it its value as a handedness question.

Briggs and Nebes (1975) modified the Annett Inventory by including strength of preference similar to the Edinburgh Inventory. The aim was to make the inventory more sensitive to varying degrees fo handedness within the middle range. The results of the scoring procedure of Briggs and Nebes were still strongly correlated with the original procedure of Annett (1970). Unfortunately, Briggs and Nebes also gave equal weight to the different questions. Equal weighting of questions was used by Oldfield in the Edinburgh Inventory and criticized by McMeekan and Lishman (1975) since some questions are consistently better predictors than others.

McMeekan and Lishman (1975) generated retest reliabilities and discussed the advantages of the Annett and Edinburgh Inventories. Reliability was no better for one or the other, in general. However, the Edinburgh Inventory included a measure of strength of preference and 82.7% of those surveyed made at least one quantitative change upon retesting. Two major advantages of the Annett Inventory emerged. Firstly, the questions of the Annett Inventory are ranked according to their relative importance and, secondly, the Annett Inventory is easier to administer due to its simple instructions. So, based on the conclusions of McMeekan and Lishman (1975), the Briggs and Nebes modification (1975) of the Annett Inventory probably was not an improvment for most purposes.

Raczkowski, Kalat, and Nebes (1974) tested the reliability and validity of a list of handedness questions common to the Hull, Oldfield and/or Annett Inventories. All of Annett's (1970) questions were included in the group deemed most reliable after retesting and most valid by comparison to performance tasks.

Johnstone, Galin, and Herron (1979) compared the two approaches using the twelve items of the Annett Handedness Inventory and three performance criteria: strength, speed, and dexterity. Johnstone et al. found that different items on the questionaire correlated most strongly with different performance tests. The hammer and raquet questions represented strength; writing, drawing, and dealing cards related more to speed of dexterity.

Handedness may be defined by performance or hand preference but the hemisphere which predominates for a particular task may be determined by factors like cognitive style, regardless of which hemisphere is the most competent for a particular task. Johnstone et al. (1979) have found that the questionaire method is more comprehensive than individual performance tasks and is more highly correlated with predicted handedness based on EEG asymmetries, recorded during cognitive tasks such as a block design task and oral presentation of stories from memory.

Based on the above information, the simplified form of the Annett Inventory, Questionaire 3 (Annett, 1970) was chosen for this study. One subject answered 'both' to one primary question. This was the only instance of a 'non-right' answer to a primary question.

Additionally, questions were included about handedness of the subject's nuclear family. There are some difficulties with the use of subject report of familial sinistrality in determining handedness: a) Porac and Coren (1979) found that subjects' reports of parental handedness under-represented sinistrality in parents by 50%, b) McManus (1979) accrued evidence both by direct testing and by evaluating results of other studies that while direction of handedness may be inherited, strength of handedness is not. This view is supported by Searleman, Tweedy, and Springer (1979) who found familial sinistrality to be unrelated to strength of handedness. Thus, parental handedness may not be as important as actual self-reports and/or performance in the determination of handedness. At any rate, Briggs and Nebes (1975) found that family history has no gross effects on pattern of hand preference, based on analysis of individual items. Therefore, right-handers with familial sinistrality are behaviorally similar to right-handers without this history, c) the number of left-handed siblings reported is influenced by family size. So, a person with a large number of siblings is more likely to have a sinistral family member than a person with few or no siblings (Varney & Benton, 1975).

Along with McManus (1979) and McRae, Branch, and Milner (1968), this experimenter became concerned with 'forcing' as a strong environmental influence on innate direction of handedness since pilot studies showed this phenomenon in several interviewed subjects. Therefore, one question asked whether writing hand had been switched in school. No one who reported a forced switch of writing hand was included in this study.

Appendix B

Sample Data Collection Sheet

Name.................. Sex...... Age...... Date.........
Session....Calibration: Width....Left Arm....Right Arm....
Hand Preference..... Handedness Score: R.... L.... B....

Trial	Arm	Retention Interval (Seconds)	Model Start Position (Degrees)	Model End Position (Degrees)	Replicate Start (Degrees)
1.	L	20	40	75	25
2.	L	20	15	50	30
3.	R	20	15	50	30
4.	R	20	40	75	25
5.	L	5	15	50	30
6.	R	20	40	75	55
7.	R	5	15	50	30
8.	L	5	40	75	25
9.	R	20	40	75	25
10.	L	5	15	50	30
11.	R	5	40	75	55
12.	L	20	40	75	20
13.	L	20	15	50	0
14.	R	5	40	75	25
15.	L	20	40	75	55
16.	R	5	15	50	0
17.	R	20	15	50	30
18.	R	20	15	50	0
19.	L	5	40	75	55
20.	L	20	15	50	30
21.	R	20	15	50	0
22.	L	5	15	50	0
23.	L	20	15	50	30
24.	L	5	40	75	55
25.	R	5	15	50	0
26.	L	20	40	75	25
27.	R	5	40	75	55
28.	L	5	15	50	0
29.	L	20	15	50	0
30.	L	5	15	50	30
31.	R	20	40	75	55
32.	L	20	40	75	55
33.	L	5	40	75	25
34.	R	5	15	50	30
35.	L	20	40	75	55
36.	R	5	40	75	55

Trial	Arm	Retention Interval (Seconds)	Model Start Position (Degrees)	Model End Position (Degrees)	Replication Start (Degrees)
37.	R	5	40	75	25
38.	R	20	40	75	25
39.	L	5	15	50	0
40.	R	5	15	50	0
41.	R	20	15	50	30
42.	L	5	40	75	55
43.	R	20	15	50	0
44.	L	20	15	50	0
45.	L	5	40	75	25
46.	R	5	40	75	25
47.	R	20	40	75	55
48.	R	5	15	50	30

Appendix C

Experiment 1: Analysis of Variance of Absolute Error

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Tail Probability
Sex (S)	58.89	1	58.89	1.19	.29
Error	1089.07	22	49.50	----	--
Type Session (T)	29.99	1	29.99	3.39	.08
T x S	17.55	1	17.55	1.98	.17
Error	194.55	22	8.84	----	--
Arm (A)	3.86	1	3.86	.27	.61
A x S	.14	1	.14	.01	.92
Error	314.14	22	14.28	----	--
A x T	10.32	1	10.32	1.72	.20
A x T x S	3.24	1	3.24	.54	.47
Error	132.17	22	6.01	----	--
Position (P)	.03	1	.03	.00	.97
P x S	80.26	1	80.26	4.29	.05
Error	411.30	22	18.70	----	--
P x T	.55	1	.55	.19	.67
P x T x S	1.09	1	1.09	.38	.55
Error	63.69	22	2.89	----	--
P x A	121.48	1	121.48	23.86	.0001*
P x A x S	.68	1	.68	.13	.72
Error	111.99	22	5.09	----	--
P x A x T	.86	1	.86	.31	.58
P x A x T x S	19.42	1	19.42	7.07	.014
Error	60.48	22	2.75	----	--
Length (L)	61.94	1	61.94	1.27	.27
L x S	179.20	1	179.20	3.66	.07
Error	1076.88	22	48.95	----	--
L x T	34.40	1	34.40	4.17	.05
L x T x S	18.60	1	18.60	2.26	.15
Error	181.45	22	8.25	----	--
L x A	2.45	1	2.45	.16	.69
L x A x S	2.08	1	2.08	.14	.72
Error	334.40	22	15.20	----	--
L x A x T	.53	1	.53	.09	.77
L x A x T x S	13.07	1	13.07	2.22	.15
Error	129.75	22	5.90	----	--
L x P	38.13	1	38.13	3.25	.09
L x P x S	16.44	1	16.44	1.40	.25
Error	258.37	22	11.74	----	--
L x P x T	16.47	1	16.47	2.42	.13
L x P x T x S	3.07	1	3.07	.45	.51
Error	149.93	22	6.81	----	--
L x P x A	2.44	1	2.44	.43	.52
L x P x A x S	42.60	1	42.60	7.47	.012
Error	125.52	22	5.70	----	--
L x P x A x T	.29	1	.29	.04	.84
L x P x A x T x S	.79	1	.79	.12	.73
Error	143.82	22	6.54	----	--

Appendix D

Experiment 1: Analysis of Variance of Constant Error

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Tail Probability
Sex (S)	1430.71	1	1430.71	5.65	.03
Error	5574.47	22	253.39	----	--
Type Session (T)	48.24	1	48.24	2.07	.16
T x S	100.32	1	100.32	4.30	.05
Error	513.04	22	23.32	----	--
Arm (A)	167.55	1	167.55	3.96	.06
A x S	3.58	1	3.58	.08	.77
Error	929.94	22	42.27	----	--
A x T	5.08	1	5.08	.32	.58
A x T x S	1.30	1	1.30	.08	.78
Error	350.66	22	15.94	----	--
Position (P)	1125.90	1	1125.90	33.01	.0000*
P x S	10.97	1	10.97	.32	.58
Error	750.46	22	34.11	----	--
P x T	.13	1	.13	.02	.90
P x T x S	1.23	1	1.23	.15	.70
Error	174.44	22	7.93	----	--
P x A	8.40	1	8.40	.78	.39
P x A x S	84.99	1	84.99	7.92	.0101
Error	236.21	22	10.74	----	--
P x A x T	.62	1	.62	.07	.80
P x A x T x S	7.47	1	7.47	.80	.38
Error	206.33	22	9.38	----	--
Length (L)	2874.32	1	2874.32	36.95	.0000*
L x S	42.09	1	42.09	.54	.47
Error	1711.48	22	77.79	----	--
L x T	131.61	1	131.61	10.26	.004*
L x T x S	13.14	1	13.14	1.02	.32
Error	282.24	22	12.83	----	--
L x A	6.27	1	6.27	.34	.57
L x A x S	8.90	1	8.90	.48	.49
Error	404.72	22	18.40	----	--
L x A x T	1.73	1	1.73	.31	.58
L x A x T x S	5.17	1	5.17	.94	.34
Error	121.56	22	5.53	----	--
L x P	193.13	1	193.13	15.30	.0007*
L x P x S	3.70	1	3.70	.29	.59
Error	277.79	22	12.63	----	--
L x P x T	3.49	1	3.49	.31	.58
L x P x T x S	22.51	1	22.51	2.02	.17
Error	244.98	22	11.14	----	--
L x P x A	1.48	1	1.48	.13	.73
L x P x A x S	2.63	1	2.63	.22	.64
Error	260.22	22	11.83	----	--
L x P A x T	.33	1	.33	.04	.84
L x P x A x T x S	79.63	1	79.63	9.73	.005*
Error	180.09	22	8.19	----	--

Appendix E

Experiment 1: Analysis of Variance of Variable Error

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Tail Probability
Sex (S)	1.48	1	1.48	.12	.73
Error	264.46	22	12.02	----	--
Type Session (T)	.01	1	.01	.00	.96
T x S	7.62	1	7.62	1.50	.23
Error	112.13	22	5.10	----	--
Arm (A)	1.62	1	1.62	.32	.58
A x S	.0005	1	.0005	.00	.99
Error	110.60	22	5.03	----	--
A x T	.02	1	.02	.00	.95
A x T x S	2.10	1	2.10	.42	.53
Error	110.90	22	5.04	----	--
Position (P)	1.31	1	1.31	.29	.59
P x S	2.09	1	2.09	.47	.50
Error	97.99	22	4.45	----	--
P x T	13.14	1	13.14	4.96	.04
P x T x S	.01	1	.01	.00	.95
Error	58.28	22	2.65	----	--
P x A	.04	1	.04	.01	.92
P x A x S	6.81	1	6.81	1.57	.22
Error	95.12	22	4.32	----	--
P x A x T	2.03	1	2.03	.34	.57
P x A x T x S	.34	1	.34	.06	.81
Error	130.63	22	5.94	----	--
Length (L)	.21	1	.21	.07	.80
L x S	.08	1	.08	.03	.87
Error	68.81	22	3.13	----	--
L x T	.07	1	.07	.02	.89
L x T x S	1.89	1	1.89	.58	.45
Error	71.92	22	3.27	----	--
L x A	6.49	1	6.49	2.47	.13
L x A x S	8.12	1	8.12	3.10	.09
Error	57.73	22	2.62	----	--
L x A x T	.96	1	.96	.11	.74
L x A x T x S	20.75	1	20.75	2.47	.13
Error	184.57	22	8.39	----	--
L x P	.07	1	.07	.02	.89
L x P x S	3.81	1	3.81	1.17	.29
Error	71.70	22	3.26	----	--
L x P x T	2.03	1	2.03	.88	.36
L x P x T x S	5.12	1	5.12	2.22	.15
Error	50.71	22	2.31	----	--
L x P x A	.53	1	.53	.12	.73
L x P x A x S	.12	1	.12	.03	.87
Error	94.42	22	4.29	----	--
L x P x A x T	6.71	1	6.71	1.60	.22
L x P x A x T x S	18.35	1	18.35	4.37	.05
Error	92.43	22	4.20	----	--

Appendix F

Mean Constant Error Difference Scores in Degrees for Session Type x Arm x Position x Length x Sex Interaction

First Order Difference: Short Minus Long Excursion Length

Sex	Session	Arm	End Pos. Degrees	Short	Long	Difference
Male	Mixed	R	50	+ 3.09	- 4.26	+ 7.35
Male	Mixed	R	75	- 1.65	- 5.33	+ 3.68
Male	Mixed	L	50	+ 3.90	+ .19	+ 3.71
Male	Mixed	L	75	- 1.06	- 4.68	+ 3.62
Male	Fixed	R	50	+ 4.72	- 4.62	+ 9.34
Male	Fixed	R	75	- .08	- 6.47	+ 6.39
Male	Fixed	L	50	+ 7.03	- 3.56	+10.59
Male	Fixed	L	75	+ .03	- 4.35	+ 4.38
Female	Mixed	R	50	- .52	- 4.64	+ 4.12
Female	Mixed	R	75	- 5.22	- 8.83	+ 3.61
Female	Mixed	L	50	+ .92	- 6.01	+ 6.93
Female	Mixed	L	75	- 3.43	- 4.81	+ 1.38
Female	Fixed	R	50	- .45	- 7.72	+ 7.27
Female	Fixed	R	75	- 6.26	-10.31	+ 4.05
Female	Fixed	L	50	- 1.44	- 7.25	+ 5.81
Female	Fixed	L	75	- 3.81	- 9.13	+ 5.32

Second Order Difference: Lateral (50 deg) Minus Medial (75 deg) End Position

Sex	Session	Arm	50 Degrees	75 Degrees	Difference
Male	Mixed	R	+ 7.35	+ 3.68	+ 3.67
Male	Mixed	L	+ 3.71	+ 3.62	+ .09
Male	Fixed	R	+ 9.34	+ 6.39	+ 2.95
Male	Fixed	L	+10.59	+ 4.38	+ 6.21
Female	Mixed	R	+ 4.12	+ 3.61	+ .51
Female	Mixed	L	+ 6.93	+ 1.38	+ 5.55
Female	Fixed	R	+ 7.27	+ 4.05	+ 3.22
Female	Fixed	L	+ 5.81	+ 5.32	+ .49

Third Order Difference: Mixed Minus Fixed Retention Interval Session

Sex	Arm	Mixed	Fixed	Difference
Male	R	+ 3.67	+ 2.95	+ .72
Male	L	+ .09	+ 6.21	- 6.12
Female	R	+ .51	+ 3.22	- 2.71
Female	L	+ 5.55	+ .49	+ 5.06

Fourth Order Difference: Right Minus Left Arm

Sex	Right	Left	Difference
Male	+ .72	- 6.12	+ 6.84
Female	- 2.71	+ 5.06	- 8.77

Appendix G

Mean Constant Error Difference Scores in Degrees for Session Type x Arm x Position x Length x Sex Interaction

First Order Difference: Mixed Minus Fixed Session

Sex	Length	Arm	End Pos. Degrees	Mixed Session	Fixed Session	Difference
Male	Short	R	50	+ 3.09	+ 4.72	- 1.63
Male	Short	R	75	- 1.65	- .08	- 1.57
Male	Short	L	50	+ 3.90	+ 7.03	- 3.13
Male	Short	L	75	- 1.06	+ .03	- 1.09
Male	Long	R	50	- 4.26	- 4.62	+ .36
Male	Long	R	75	- 5.33	- 6.47	+ 1.14
Male	Long	L	50	+ .19	- 3.56	+ 3.75
Male	Long	L	75	- 4.68	- 4.35	- .33
Female	Short	R	50	- .52	- .45	- .07
Female	Short	R	75	- 5.22	- 6.26	+ 1.04
Female	Short	L	50	+ .92	- 1.44	+ 2.36
Female	Short	L	75	- 3.43	- 3.81	+ .38
Female	Long	R	50	- 4.64	- 7.72	+ 3.08
Female	Long	R	75	- 8.83	-10.31	+ 1.48
Female	Long	L	50	- 6.01	- 7.25	+ 1.24
Female	Long	L	75	- 4.81	- 9.13	+ 4.32

Appendix H

Experiment 2: Analysis of Variance of Absolute Error

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Tail Probability
Sex (S)	26.89	1	26.89	.31	.59
Error	1571.57	22	87.31	----	--
Type Session (T)	7.08	1	7.08	.22	.65
T x S	1.67	1	1.67	.05	.82
Error	588.48	22	32.69	----	--
Arm (A)	35.07	1	35.07	2.60	.12
A x S	.51	1	.51	.04	.85
Error	242.85	22	13.49	----	--
A x T	.29	1	.29	.06	.81
A x T x S	20.56	1	20.56	4.22	.05
Error	87.60	22	4.87	----	--
Position (P)	195.64	1	195.64	4.05	.06
P x S	18.30	1	18.30	.38	.55
Error	869.06	22	48.28	----	--
P x T	.01	1	.01	.00	.97
P x T x S	14.31	1	14.31	1.85	.19
Error	139.17	22	7.73	----	--
P x A	.78	1	.78	.12	.74
P x A x S	.25	1	.25	.04	.85
Error	121.19	22	6.73	----	--
P x A x T	.24	1	.24	.05	.82
P x A x T x S	26.24	1	26.24	5.94	.03
Error	79.10	22	4.39	----	--
Length (L)	966.02	1	966.02	21.98	.0002*
L x S	2.66	1	2.66	.06	.81
Error	791.04	22	43.95	----	--
L x T	30.58	1	30.58	5.04	.04
L x T x S	12.27	1	12.27	2.02	.17
Error	109.18	22	6.07	----	--
L x A	20.00	1	20.00	3.02	.10
L x A x S	1.10	1	1.10	.17	.69
Error	119.08	22	6.62	----	--
L x A x T	2.94	1	2.94	.63	.44
L x A x T x S	7.46	1	7.46	1.59	.22
Error	84.66	22	4.70	----	--
L x P	51.93	1	51.93	3.69	.07
L x P x S	.001	1	.001	.00	.99
Error	253.19	22	14.07	----	--
L x P x T	3.04	1	3.04	.31	.59
L x P x T x S	7.02	1	7.02	.71	.41
Error	178.57	22	9.92	----	--
L x P x A	14.26	1	14.26	2.84	.11
L x P x A x S	1.18	1	1.18	.23	.63
Error	90.46	22	5.03	----	--
L x P x A x T	4.29	1	4.29	1.13	.30
L x P x A x T x S	9.01	1	9.01	2.38	.14
Error	68.18	22	3.79	----	--

Appendix I

Experiment 2: Analysis of Variance of Constant Error

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Tail Probability
Sex (S)	244.39	1	244.39	.96	.34
Error	4591.07	22	255.06	----	--
Type Session (T)	65.48	1	65.48	1.84	.19
T x S	2.51	1	2.51	.07	.79
Error	639.99	22	35.56	----	--
Arm (A)	.05	1	.05	.00	.97
A x S	2.81	1	2.81	.11	.75
Error	48.65	22	26.70	----	--
A x T	2.96	1	2.96	.28	.60
A x T x S	6.49	1	6.49	.61	.44
Error	190.56	22	10.59	----	--
Position (P)	1056.15	1	1056.15	13.68	.002*
P x S	24.79	1	24.79	.32	.58
Error	1389.61	22	77.20	----	--
P x T	10.67	1	10.67	.75	.40
P x T x S	16.44	1	16.44	1.16	.30
Error	255.98	22	14.22	----	--
P x A	62.63	1	62.63	6.81	.02
P x A x S	4.23	1	4.23	.46	.51
Error	165.59	22	9.20	----	--
P x A x T	1.74	1	1.74	.24	.63
P x A x T x S	29.91	1	29.91	4.11	.06
Error	130.96	22	7.28	----	--
Length (L)	3525.51	1	3525.51	41.65	.0000*
L x S	.67	1	.67	.01	.93
Error	1523.72	22	84.65	----	--
L x T	2.20	1	2.20	.19	.67
L x T x S	40.48	1	40.48	3.48	.08
Error	209.49	22	11.64	----	--
L x A	54.59	1	54.59	6.20	.02
L x A x S	2.47	1	2.47	.28	.60
Error	158.51	22	8.81	----	--
L x A x T	.14	1	.14	.04	.85
L x A x T x S	19.70	1	19.70	5.01	.04
Error	70.73	22	3.93	----	--
L x P	34.18	1	34.18	2.05	.17
L x P x S	19.42	1	19.42	1.16	.29
Error	300.23	22	16.68	----	--
L x P x T	53.29	1	53.29	3.56	.08
L x P x T x S	1.95	1	1.95	.13	.72
Error	269.43	22	14.97	----	--
L x P x A	.07	1	.07	.01	.92
L x P x A x S	1.50	1	1.50	.24	.63
Error	114.42	22	6.36	----	--
L x P x A x T	4.57	1	4.57	.57	.46
L x P x A x T x S	.30	1	.30	.04	.85
Error	143.94	22	8.00	----	--

Appendix J

Experiment 2: Analysis of Variance of Variable Error

Source	Sum of Squares	Degrees Freedom	Mean Squares	F	Tail Probability
Sex (S)	1.32	1	1.32	.15	.70
Error	157.81	22	8.77	----	--
Type Session (T)	1.51	1	1.51	.42	.53
T x S	26.23	1	26.23	7.31	.015
Error	64.58	22	3.59	----	--
Arm (A)	12.81	1	12.81	6.08	.02
A x S	4.27	1	4.27	2.03	.17
Error	37.91	22	2.11	----	--
A x T	1.40	1	1.40	.30	.59
A x T x S	.39	1	.39	.08	.78
Error	84.49	22	4.69	----	--
Position (P)	.43	1	.43	.07	.79
P x S	12.49	1	12.49	2.05	.17
Error	109.64	22	6.09	----	--
P x T	1.60	1	1.60	.55	.47
P x T x S	3.48	1	3.48	1.20	.29
Error	52.02	22	2.89	----	--
P x A	2.45	1	2.45	1.22	.28
P x A x S	18.16	1	18.16	9.04	.008*
Error	36.17	22	2.01	----	--
P x A x T	.75	1	.75	.19	.67
P x A x T x S	4.85	1	4.85	1.25	.28
Error	69.96	22	3.89	----	--
Length (L)	.00002	1	.00002	.00	.998
L x S	8.35	1	8.35	3.36	.08
Error	44.67	22	2.48	----	--
L x T	5.25	1	5.25	1.47	.24
L x T x S	.04	1	.04	.01	.91
Error	64.16	22	3.56	----	--
L x A	.04	1	.04	.01	.91
L x A x S	5.93	1	5.93	2.05	.17
Error	52.16	22	2.90	----	--
L x A x T	9.82	1	9.82	3.01	.10
L x A x T x S	.94	1	.94	.29	.60
Error	58.75	22	3.26	----	--
L x P	10.67	1	10.67	3.00	.10
L x P x S	2.05	1	2.05	.57	.46
Error	64.08	22	3.56	----	--
L x P x T	9.68	1	9.68	2.05	.17
L x P x T x S	1.72	1	1.72	.36	.55
Error	84.85	22	4.71	----	--
L x P x A	.04	1	.04	.01	.92
L x P x A x S	.13	1	.13	.04	.85
Error	63.52	22	3.53	----	--
L x P x A x T	4.86	1	4.86	1.73	.20
L x P x A x T x S	7.05	1	7.05	2.51	.13
Error	50.54	22	2.81	----	--

Appendix K

Sexual Differentiation In The Central Nervous System

Neural Sex Differences Underlie Dimorphic Reproductive Behavior

Based on sexual dimorphism in the pattern of gonadotropin release (Pfeifer, 1936), and in reproductive behavior (Phoenix, Goy, Gerall, & Young, 1959), differences in the central nervous system (CNS) have been inferred (Kelly, 1981). These differences in the CNS appear to be the outcome of gonadal hormone exposure during a critical period (cp) of development (Arnold, 1980; Arnold & Gorski, 1984; Baum, 1979; Kelly, 1981; McEwen, 1981; Wilson, George, & Griffen, 1981).

Until recently, it was believed that in mammals, the organism would develop as a female unless a masculine course was imposed through steroid exposure. Alpha-fetoprotein, present in the neonate of most vertebrate species, was believed to protect the fetus from the mother's circulating estrogen by binding to it. However, Toran-Allerand (1984) has found alpha-fetoprotein intraneuronally which indicates a mediator and modulator role of the protein in the transport of estrogen or other steroids in the CNS. Therefore, it seems likely that feminization, as well as masculinization, is an active process requiring induction by steroids.

One explanation for the CNS organizational effect is that neural ciruitry is structurally altered by perinatal hormone exposure: the number, size, or pattern of connectivity of neurons is modified. A second explanation is that hormonal sensitivity of the CNS is sexually dimorphic (Breedlove, 1983). Thus, an important correlate to the study of CNS sexual differentiation in animal research is gonadal hormone manipulation.

Investigation of CNS sex differences in animal research is also aided by reliable criteria to identify male and female behavior. Copulatory postural adjustments are such gender-specific behaviors: their similarity is much stronger within the sexes and across species than between the sexes within species (Kelly, 1981). Thus, mounting is typically a marker for masculine neural organization and lordosis (or presenting) is typically a marker for feminine neural organization.

Three neural systems have been extensively studied. Each has a well-documented sexually dimorphic organization which can be related to sexually dimorphic behaviors (Arnold & Gorski, 1984). One is the vocal control system of the songbird. Another is the spinal nucleus of the bulbocavernosus (SNB). The last is the hypothalamic preoptic area (POA) along with other related hypothalamic and limbic areas.

Bird song. The vocal control system in the songbird involves several nuclei. The highest neural control originates with the hyperstriatum ventrale, pars caudale (HVc) which projects to the nucleus robustus archistriatalis (RA). The RA projects to two lower brain areas, the dorsomedial intercollicularis complex (DM/ICo) and the tracheosyringeal portion of the hypoglossal nucleus (nXIIts). The nXIIts, which also receives input from DM/ICo, innnervates the vocal organ, the syrinx (Gurney, 1981).

Testosterone is crucial for the development of courtship song in the male songbird (Nottebohm & Arnold, 1976). In both canary and zebra finch, sexual dimorphism occurs in the neural circuitry which controls song. Adult male canaries and zebra finches acquire a complex repertoire of songs by imitating other conspecific males. Female canaries will sing only if treated in adulthood with testosterone and this song is much less complex than that of the male. Female zebra finches do not sing even with testosterone treatment in adulthood (Nottebohm & Arnold, 1976). However, if the female zebra finch is treated with a gonadal hormone at hatching, plus testosterone in adulthood, the bird will sing (Gurney & Konishi, 1980).

The HVc, RA and nXIIts are all larger in males than in females. Also, these dimorphic differences in volume are greater in the zebra finch than in the canary, a finding consistant with the complete inability of the normal female zebra finch to sing (Nottebohm & Arnold, 1976).

The HVc and RA, but not the nXIIts, binds more testosterone in the male than in the female. This differential hormone sensitivity is believed to underlie sex differences by facilitation of cell growth and synaptogenesis in HVc and RA (Arnold & Saltiel, 1979).

Gurney (1981) was able to dissociate developmental factors in the RA. Treatment with 5,alpha-dihydrotestosterone (DHT) at hatching increased cell number in RA while treatment with another androgen, testosterone, altered somal size by changing small diameter cells to large diameter cells. Gurney suggests that this latter phenomenon is an induction process: the neurons assume either a male state (large) or a female state (small).

The spinal nucleus of the bulbocavernosus. The SNB is a nucleus which is located in the ventral horn of the fifth and sixth lumbar segments of the spinal cord in the rat. The SNB exists in the neonatal rat of both sexes but only in the male adult. In the male adult, SNB neurons innervate the penile muscles, levator ani and bulbocavernosus, and they readily take up androgen but not estrogen (Breedlove & Arnold, 1983b). Arnold and Gorski (1984) were able to dissociate development of number and size of SNB neurons just as Gurney (1981) has done in the RA of the songbird. The number of SNB cells was increased most by testosterone treatment and the cp for neuronal number ended on the sixth postnatal day; the size of SNB neurons was most increased by DHT and its cp continued past postnatal day eleven. Therefore, regulatory controls on cell size and number in the SNB are independent. Mitotic division in SNB is completed by gestational day fourteen. Yet, testosterone treatment on gestational day sixteen increases cell number in female neonates (Breedlove & Arnold, 1983a), indicating that, in the normal female rat, SNB cell death may occur due to the absence of testosterone. Alternatively, the SNB neurons may make connections to sites which change their morphology and position, since the penile muscle complex is atrophied in the female and cannot receive the SNB axons.

Preoptic area. The hypothalamic POA, which contains several nuclei and diffusely organized cells, comprises the most rostral portion of the third ventrical periventricular gray (Carpenter, 1978). The POA is involved in the regulation of masculine behavior, feminine behavior and gonadotropin release (Nordeen & Yahr, 1983).

The neuropil of POA is one site in which anatomical sex differences have been found. Raisman and Field (1971) eliminated limbic amygdalar projections to POA in the rat by sectioning the stria terminalis. Degeneration of the amygdalar input allowed greater visibility of the non-amygdalar contacts in the strial input area of POA. In the male, almost all non-amygdalar afferents made synaptic contact directly onto dendritic shafts; in the female, a large proportion of contacts were made onto dendritic spines. Regardless of the genetic sex of the rat, perinatal exposure to testosterone produced a strial POA with few axospinous synapses; eliminating testosterone during the cp would allow the female pattern of axospinous synapses to develop (Raisman, 1974). Since amygdalar stimulation is believed to trigger onset of puberty and ovulation in the female rat (Critchlow & Bar-Sela, 1967), Raisman and Field (1971) believe that the axodendritic versus axospinous contacts represent the tonic (male) versus cyclic (female) pattern of gonadotropin release.

Greenough, Carter, Steerman, & DeVoogd (1977) found in the POA of the hamster that dendritic densities were concentrated ventrally in the male, while in the female, heavier concentrations occurred dorsolateral, ventral and medial to the area of male concentration.

Toran-Allerand (1976) exposed in vitro brain slices of neonatal mouse to estradiol. Steroid-sensitive neurons of the hypothalamic POA proliferated with outgrowths of neurites. Thus, the POA neuropil is differentially affected by sex steroids even in the absence of extrinsic neuronal connections.

Gorski, Gordon, Shryne, & Southam (1978) found a sexual dimorphism in cell volume within the medial preoptic nucleus of POA in the rat. Both the absolute nuclear volume and nuclear volume relative to whole brain weight were greater for males than for females. This sexually dimorphic nucleus of the POA (SDN-POA) was dependent upon perinatal exposure to gonadal hormones, but was independent of hormonal exposure in adulthood. Although neonatally gonadectomized males and neonatally androgenized females both had larger SDN-POA than control females, the male group had the largest SDN-POA. Therefore, the cp for sexual differentiation of the SDN-POA appears to begin prenatally. Jacobson, Shryne, Shapiro, and Gorski (1980) found that the male SDN-POA grew in volume over the first ten postnatal days but in the female, SDN-POA began to shrink. Also, the development of the SDN-POA in the female began and ended earlier with a smaller posterior area than in the male (Jacobson & Gorski, 1981).

Swaab and Fliers (1985) examined 13 male and 18 female brains of humans between 10 and 93 years of age. The SDN-POA could be distinguished from POA by darker staining, larger cell bodies and higher cell density. Total cell number, SDN-POA volume and cross-sectional area were significantly larger in males than in females. In the adult rat, sex hormone treatment does not alter SDN-POA size (Arnold & Gorski, 1984) and this appears to be true also for humans; one female had been virulized by an adrenal cortical tumor yet her SDN-POA was of normal female size. No possible laterality differences were examined and the function of the SDN-POA is, as yet, unknown.

Sex differences in steroid receptor binding have been found in POA. Using brains of intact adult rabbit, rat, mouse, and even fetal human, Naftolin, Ryan, Davis, Reddy, Florer, Petro, Huhn, White, Takaoka, & Wolin (1975) exposed in vitro tissue slices to the androgen, androstenodione. Aromatization of androstenedione into the estrogen, estrone, was twice as great in male, than in female hypothalamus. This sex difference in aromatization of hypothalamus was shown to be the result of a very strongly differentialted POA and anterior hypothalamus; the other hypothalamic areas did not contribute appreciably to the effect.

The POA involvement in three separate reproductive functions of the rat may be paralleled by three separate populations of POA neurons since estrogen induces lordosis and cyclicity of gonadotropin release in the female but mounting in the male. Nordeen and Yahr (1983) examined the temporal aspects of estrogen binding in gonadectomized rats in an attempt to separate the populations. A sex difference was found in the post-injection time course for binding estrogen; male rats bound more estrogen at 30 min post-injection while at 60 min post-injection the opposite was true. The estrogen-sensitive POA neurons involved in masculinization appear to have a briefer time course for binding estrogen than those involved in feminine behavior and gonadotropin cylicity.

Fischette, Biegon, and McEwen (1983) found that the rate of serotonin (5HT) binding is greater in male POA than in female POA of gonadectomized rats. However, estrogen treatment produced an increase in female, but not male, lateral POA binding of 5HT so that female binding was greater.

Other areas related to POA by their involvement in gonadotropin release, onset of puberty, or sexual activity, are also found to show sex differences. These include the hypothalamic ventromedial nucleus (Rainbow, Parsons, & McEwen, 1982) and arcuate nucleus (Arai & Matsumoto, 1978; MacLusky, Chaptal, & McEwen, 1979; Matsumoto & Arai, 1980), the pituitary (Whalen & Massicci, 1975), the amygdala (Naftolin et al., 1975), and mesencephalic central gray (Sakuma & Pfaff, 1981).

The purpose of the initial investigations of CNS sex differences was to relate neural structures to reproductive functions. It was confirmed that CNS sex differences do occur in the size of neural structures, cell size and number, synaptology, electrophysiology, steroid hormone binding, neurotransmitter binding, and even in whether a structure is present or absent. Most recent have been the discoveries of sex-related asymmetries in the neural control of gonadal function. In intact female rats, luteinizing hormone releasing hormone (LHRH) content is higher on the right side of the mediobasal hypothalamus (MBH) (Gerendai, Rotztejn, Marchetti, Kordon, & Scapagnini, 1978). A unilateral ovariectomy increases LHRH in ipsilateral MBH. Bilateral ovarectomy produces a decrease in LHRH of MBH but only in the right half (Wheaton & McCann, 1976). Intact adult male rats have a symmetrical LHRH distribution in MBH (Mizunuma, DePalatis, & McCann, 1983), yet, a functional asymmetry may exist because only the combined right hemiorchidectomy-right hypothalamic deafferentation would block the hemiorchidectomy-induced follicle stimulating hormone. In females, the compensatory hypertrophy of the remaining ovary after a unilateral ovarectomy, regardless of the side, is prevented by a right, but not a left, lesion to locus coeruleus (Gerendai, 1984). However, sex-related neural asymmetries are not limited to gonadal function. This work points the way for exploration of CNS sex differences in sexually dimorphic non-reproductive functions, which, similarly, are emerging in a variety of ways.

Neural Sex Differences Underlie Dimorphic Non-reproductive Behavior

Sexual dimorphism or variation in behaviors not involved directly in reproduction are typified by asymmetrical cognitive functions (McGlone, 1980). One cognitive function is spatial ability, including exploratory behavior (Denenberg, 1984), which requires the participation of the hippocampus (O'Keefe & Nadel, 1978); the corpus striatum (Potegal, 1972); and the cerebral cortex (DeRenzi, 1979).

Since the brain of the rodent is similar to the human brain in that spatial functions show a male superiority (Beatty, 1979) and a right hemisphere dominance (Denenberg, 1984)[1], the rodent has been a useful model to examine sexual variation in spatial structure-function relationships

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[1] Benton (1979) would add the word 'simple' to spatial functions which are lateralized to the right hemisphere, such as the ability to appreciate the directional orientation of lines. Along with an increase in spatial task complexity, in humans, such as in spatial organizational constructive tasks, left hemisphere involvement increases.

(Beatty, 1980).

The hippocampus is specialized for spatial mapping (O'Keefe & Nadel, 1978). In support of the superior male spatial performance, Diamond, Murphy, Akiyama, and Johnson (1982) found that rat hippocampi of males are larger on the left. Also, if Schaffer collaterals of *in vitro* hippocampal slices are stimulated, estradiol facilitates spike discharges in the male, but not in the female (Teyler, Vardaris, Lewis, & Rawitch, 1980).

Sex steroids are believed to affect synaptogenesis in the hippocampus, as well. If septal projections to the hippocampus are lesioned, a typical sprouting response of sympathetic axons into the area occurs. For mature rats, but not for neonatal rats, this sprouting is more limited in the male (Loy & Milner, 1980; Milner & Loy, 1982). Neonatal castration of male rats produces a female sprouting response while testosterone treatment of the neonatal female or castrated male restricts the growth. The site of testosterone action is believed to be either the presynaptic neurons of the septum of hippocampus, both of which have estrogen and testosterone receptors.

The corpus striatum of the rat is involved in 'egocentric localization' (Potegal, 1972) and directional bias (Hyde & Jerussi, 1983). Female rats rotate more than male rats (Glick, Schonfeld, & Strumpf, 1980), due apparently to a functional difference of the presynaptic dopmaine receptors of striatum.

The cerebral cortex is necessary for the ability to imagine space; spatial exploration, spatial perception, spatial memory and elaboration of spatial information are all dependent on cortex and are asymmetrically represented (DeRenzi, 1979).

Diamond (1984) and Diamond, Dowling, & Johnson (1981) examined lateral differences in surface thickness of cortex in the rat. Intact female rats showed few lateral asymmetries and only one area, area 39, was larger on the right. But, this was a temporary developmental asymmetry. Male rats, on the other hand, showed right dominant asymmetry in almost all areas tested. The occipital cortex was larger on the right in the intact male, the gonadectomized male or female, and in older female rats which have reduced ovarian hormones, but not in intact young adult females (Diamond, 1984). Cortical areas 2 and 3 were thicker on the right in intact males but thicker on the left in intact females and orchidectomized males. The absence of estrogen seems to be necessary for right dominant asymmetry to develop. In addition, this asymmetry is heightened by raising the male rat in an enriched environment (Diamond, 1976).

In part, this estogen effect may occur by differential facilitation of maturation in the two hemispheres. Curry and Heim (1966) found that neonatal estrogen treatment in the rat facilitates myelination of sensory-motor cortex. Gregory (1975) examined the layer 5 pyramidal cells in somatosensory cortex of the rat and discovered that between 25 and 35 postnatal days, male cell somas were larger. Since the developing neuron accumulates water, increasing its volume, Gregory interpreted this difference in somal size to indicate that male, but not female, pyramidal cells are still developing during this postnatal period.

The general conclusion is that both cortex (Ross & Glick, 1981) and hippocampus (Diamond et al., 1982) modulate striatal-induced directional bias and both structures are usually thicker on the right in males and thicker on the left in females. That cortical, but not hippocampal, thickness is altered by neonatal gonadal hormones and environment, reflects the phylogenetic age of these structures; the more recently evolved cortex is more responsive to the environmental mileiu.

A final consideration is the need to distinguish between asymmetry of general arousal and asymmetry due to specialized functions. These asymmetrical anatomical sites which participate in spatial abilities also have a direct role in arousal. Research with humans (See text) has been most successful in addressing this issue.

Non-reproductive sexually dimorphic asymmetry of function. That individuals differ in magnitude and direction of arousal/activation asymmetries is supported by investigation of side preferences in animals. In rodents, directional bias in activation and its magnitude can be measured by nocturnal locomotor rotation (Zimmerberg, Glick, & Jerussi, 1974); arousal-induced rotation (Glick, 1973; Glick & Jerussi, 1974); postural asymmetry (Moslobodsky & Braum, 1981); strength of paw preference for lever pressing under amphetamine (Glick, Jerussi, & Zimmerberg, 1977); or by selection of the right or left arm of a T-maze (Zimmerberg et al., 1974). Activation asymmetry for most rodents has a stable direction. However, across individuals, the direction and its magnitude differ (Glick, Jerussi, & Zimmerberg, 1977).

The underlying cause of directional bias is a left-right asymmetry in the nigrostriatal dopamine system (Zimmerberg et al., 1974) which is critical for the arousal-activation system. Therefore, directional bias can be altered or enhanced by increasing the asymmetry in dopamine levels. A unilateral lesion of the nigrostriatal system will produce ipsiversive turning which is greatest if the high-dopamine side remains intact (Glick et al., 1977). Stimulation of the caudate nucleus produces contraversive rotation (Zimmerberg & Glick, 1967). Arousal-inducing agents, such as amphetamine, tail shocks or air puffs, in general, increase activation and lead to rotation contralateral to the side with the higher dopamine level. This rotation apppears to be an exaggerated, stereotyped form of a normal spatial preference.

At first, it appeared that the differences in direction or degree of right-left bias were randomly distributed across individuals but more recent work suggests a complex, but largely determined, pattern (Glick & Shapiro, 1984). Factors which are implicated in directional variation are the strain of a species (Brass & Glick, 1981; Denenberg, Rosen, Hofmann, Gall, Stockler, & Yutzey, 1982); sex or perinatal sex hormone exposure (Brass & Glick, 1981; Crowley, O'Donahue, & Jacobowitz, 1978); and postnatal handling and environment (Denenberg, Garbanati, Sherman, Yutzey, & Kaplan, 1978). Higher order interactions have been found amongst these variables.

For example, handling, environment and hemisphere interact to influence activity level (Denenberg et al., 1978). Since activity level is inversely related to strength of side preference (Glick et al., 1977), activity can be used as a measure of amount of directional bias or laterality. Male Purdue-Wistar rats were raised either with or without handling and with or without an enriched environment until day 70. At 165 days of age the rats received either a right or a left hemisphere lesion. In the non-handled animals with or without enrichment, a lesion of either hemisphere increased activity. This was true as well for handled rats with a right hemisphere lesion. But if the left hemisphere was lesioned (right hemisphere intact), the handled rats with an enrichment history showed inhibited activity. It seems that the right hemisphere is the focus for environmental interactions.

The variable of sex (or perinatal sex hormone exposure) was overlooked in earlier studies which examined either all males (e.g., Denenberg et al., 1978) or all females (e.g., Glick et al., 1977). But sex differences abound in the nervous system and in more recent studies which match for sex, interesting results have emerged.

Sex differences in directional bias vary across strains of rats. For example, newborn male and female Purdue-Wistar rats have a leftward-biased tail posture (which indicates that they should rotate to the left) but the females are more biased than the males (Denenberg, Rosen, Hofmann, Gall, Stockler, & Yutzey, 1982). In Sprague-Dawley pups, females are right-biased while males are unbiased (Ross & Glick, 1981; Ross, Glick, & Meibach, 1981). Rosen, Berrebi, Yutzey, and Denenberg (1983) exposed female Purdue-Wistar pups to male steroids prenatally. It was found that testosterone shifted tail posture away from the strong leftward position. Also, Glick and Shapiro (1984) report that the similarity of female offspring to their mothers for rotational bias diminishes with increase in number of male littermates, indicating, again, the influence of perinatal testosterone exposure.

Sex also interacts with strain and exposure to different dopamine-altering drugs (Brass & Glick, 1981). Amphetamine, which releases presynaptic dopamine, increases rotation much more in females than in males of either Sprague-Dawley or Fischer strains. Consistant with this finding, in vivo female sex steroids, but not those of the male, regulate in vitro release of dopamine in response to amphetamine (Crowley, O'Donahue, & Jacobowitz, 1978). Apomorphine increases rotation more for male than female Sprague-Dawley rats but has no differential effect on male and female Fischer rats. Apomorphine binds both the D3 presynaptic dopamine receptor and the D4 postsynaptic dopamine receptor. The D3 receptor bound more apomorphine in the female than in the male rat and binding was greatest ipsilateral to the side of rotation (Glick & Shapiro, 1984) which could explain why rats tend to rotate in the opposite direction after apomorphine or amphetamine administration. Since male Sprague-Dawley rats rotate more in response to apomorphine than their female counterparts and females of both Sprague-Dawley and Fischer strain rotate more in response to amphetamine than the males, different mechanisms predominate to produce directional bias in the two sexes (Brass & Glick, 1981). The site for sexually differentiated responses to dopaminergic agonists appears to be the presynaptic dopamine receptors (Glick & Shapiro, 1984) but these vary across strains. For both sexes, the left-rotators have an equivalent amount of apomorphine binding of D3 receptors on either side whereas right-rotators have a greater binding on the right.

Glick, Hind, and Shapiro (1983) found that cocoaine induced greater rotation in female than in male Sprague-Dawley rats. However, a sex by directional bias interaction was observed under the influence of cocaine. Right-biased females rotated more than left-biased females and left-biased males rotated more than right-biased males. Because cortex (Ross & Glick, 1981) and hippocampus (Glick et al., 1980) both modulate the intensity of rotation, and cortex (Diamond, Dowling, & Johnson, 1981) and hippocampus (Diamond, Murphy, Akiyama, & Johnson, 1982) both are thicker on the right in males and thicker on the left in females, these structures may contain the site(s) of cocain affinity.

Myslobodsky and Braum (1981) found an interaction amongst sex, directional bias and handling. Prior to and after administration of amphetamine, Wistar rats were placed in a rotometer to judge rotational bias. This bias could be predicted by tail pinch posture in females, in castrated and estrogen treated males, but not in untreated, sham-operated males unless they had been handled. Unhandled males showed no correlation between the postural asymmetry and rotation. Because handling of the normal male leads to the same behavioral outcome as found in unhandled females or estrogen-treated males, more than one system must be involved in modulation of postural adjustments.

Sherman, Garbanati, Rosen, Yutzey, and Denenberg (1980) found a cerebral involvement in the sex x directional bias x handling interaction. Intact male Purdue-Wistar rats showed no bias if unhandled but handled rats developed a leftward directional bias. However, if the nonhandled group received a left hemisphere ablation, a stronger ipsilesional rotation resulted than for a right hemisphere lesion. A lesion of either hemisphere in the handled group produced no significant difference in strength of directional bias. Sherman et al. (1980) conclude that in the intact nonhandled males the right hemisphere has a potential for a stronger influence on turning than the left hemisphere but that the right is inhibited by the left. In other words, in the nonhandled male, the right hemisphere induces a leftward directional bias that the left hemisphere opposes. In the handled males, the right hemisphere is not inhibited and controls spatial preference producing a leftward bias.

Glick, Meibach, Cox, and Maayani (1979) looked at asymmetrical activation of several structures involved in directional bias of female Sprague-Dawley rats by measuring deoxyglucose uptake. Direction of rotation was consistantly related to asymmetry of midbrain and striatal activity; activity was greater contralateral to side of rotation. Frontal cortex and hippocampus were more active on the left and if the higher activity was contralateral to direction of rotation (rightward bias) then the directional bias was stronger than if the cortico-hippocampal activity was higher ipsilateral to bias (leftward bias). Amphetamine reversed the cortico-hippocampal asymmetry and increased striatal activity contralateral to the rotational bias. Although thalamic and hypothalamic activity were not predictive of direction of rotation, their absolute asymmetries in activity were positively correlated with the magnitude of rotation. Glick et al. (1979) conclude that different functional asymmetries exist, a cortico-hippocampal left-right asymmetry, a midbrain-striatal directional asymmetry, and thalamo-hypothalamic asymmetry.

Many of the above studies (Denenberg et al., 1978; Myslobodsky & Braum, 1981; Sherman et al., 1980; Glick et al., 1979) support the view that the cerebral cortex, and in particular, the frontal lobes modulate striatal activity. Other evidence adds weight to this argument. Contralateral neglect and ipsiversive turning result from a unilateral lesion to the dopaminergic striatal system in cats (Frigyesi, Ige, Iulo, & Schwartz, 1971) and rats (Marshall & Teitelbaum, 1977). Bianchi (1895) discovered in monkeys and dogs that a unilateral lesion to frontal granular cortex resulted in ipsiversive rotation and contralateral neglect syndrome, signs common to a unilateral lesion of the nigrostriatal system. Also, monkeys with neglect due to frontal arcuate lesions rotated toward the side of lesion with apomorphine (Valenstein, Van Den Abell, Tankle, & Heilman, 1980).

There are two major differences between arousal/activation asymmetry of the rat and human. Firstly, women are less lateralized than men, as a general rule (see text), but for rats, females appear more lateralized than males. These may be real differences. However, the enrichment studies have shown that the male asymmetry is altered by stimulation so that male and female asymmetry are comparable (Myslobodsky & Braum, 1981; Sherman et al., 1980). If the normal housing for a laboratory rat is really a deprived environment, then normal laterality has yet to be studied in the male rodent. Perhaps future experiments (with field rats?) will resolve the discrepancies between human and rodent laterality research or determine if the differences are genuine.

Secondly, in humans with non-anomolous dominance, the arousal and activation systems oppose each other in their asymmetry: the left hemisphere emphasis is on activation and the right hemisphere, on arousal. Some sorting of these systems is apparent in rodents since Glick et al. (1979) found underlying anatomical arousal/activation asymmetries for the cortico-hippocampal and midbrain-striatal systems. However, the dissociation of arousal and activation asymmetries in the rodent is not as apparent as in the human.

Reference Notes

1. Sutton, S. Letter to Julian Silverman. July 26, 1968.

2. Naatanen, R. Brain mechanisms of attention-switching to unattended stimuli. Colloquium, Queens College March 10, 1986.

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