Evolutionary Psychology

www.epjournal.net – 2007. 5(3): 653-665

Original Article

Testing Predictions from the Hunter-Gatherer Hypothesis – 1: Sex Differences in the Motor Control of Hand and Arm

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Abstract: Here, in the first of two reports that test predictions from the hunter-gatherer hypothesis, we focus on sex differences in motor control. Published evidence confounds the cognitive demands, the muscles used and the spatial location in which tasks are performed. To address these issues our participants used hand or arm movements to track a moving target within near space. Study 1 identified an optimal level of task difficulty for the differentiation of male and female performance and showed that women tracked better using their hands and men using their arms. Employing the optimal level of task difficulty, Study 2 replicated the findings of Study 1 and, for men, demonstrated a significant correlation between arm tracking and performance on the nonmotor sex-dimorphic Mental Rotations task. This correlation suggests that the same or related events are responsible for the development of sex differences in motor and cognitive systems. The distal (hand) muscles are controlled by the primary motor cortex via two dorsolateral corticospinal tracts whereas the proximal (arm) muscles are controlled via two ventromedial corticospinal tracts. Our findings point to possible sex differences in these two neural pathways and they are compatible with an evolutionary origin as predicted by the hunter-gatherer hypothesis.

Keywords: hunter-gatherer hypothesis; sex differences; motor control; hand and arm; neural bases; near space.

Introduction

The hunter-gatherer hypothesis was proposed by Silverman and Eals (1992) as an evolutionary explanation for sex differences in spatial ability. The core idea is that sex differences in task performance have arisen from a process of natural selection that favored hunting-related skills in men and gathering–related skills in women. While the hypothesis cannot be tested directly, we can test its predictions and we have adopted this approach in a series of studies aimed to generate predictions that are novel and testable. In this, the first of two reports, we focus on predicted sex differences in the motor control of the hand and arm. In the second report we have addressed sex differences in visual processing (Sanders, Sinclair and Walsh, 2007). In both cases we were able to demonstrate the predicted sex differences and to identify from the literature potential neural bases for those differences.

We began with the premise that selection for hunting skills would favor men with good processing of visual input from far (extrapersonal) space for detecting suitable prey and accurately aiming a missile, together with good proximal arm muscle performance for throwing the missile at the prey. On the contrary, selection for gathering skills would favor women with good processing of visual input from near (peripersonal) space for the detection of appropriate items together with good distal hand muscle performance for grasping those items. Thus for motor performance we would expect an interaction between Muscle and Sex with women performing better with their hand and men with their arm. Of the motor tasks that might test these hand/arm predictions, two with good ecological validity that show sex differences are targeted throwing at which men excel (Watson and Kimura, 1991) and fine motor movement at which women excel (Nickolson and Kimura, 1996; Sanders and Kadam, 2001). Both tasks are dependent on aspects of hand-eye co-ordination but they fail to pinpoint the basis of the sex difference because of confounds. In addition to the task demands, published studies of sex differences in motor performance (see Kimura, 1999 for a review) confound the subdivisions of the motor and visuospatial components. Targeted throwing uses the proximal muscles of the arm and is directed into far (extrapersonal) space while fine motor movement uses the distal muscles of the hand and is performed in near (peripersonal) space.

Here we report two studies that focused on fine, distal (hand) and gross, proximal (arm) muscle use. To control for the confounds identified above we designed a computerized tracking task that participants performed using either distal hand muscle movements or proximal arm muscle movements. To avoid confounds between extrapersonal/ peripersonal space, performance was restricted to near (peripersonal) space. We predicted a Muscle*Sex interaction arising from women performing better with the hand and men with the arm.

STUDY 1

Studies aiming to demonstrate and identify the bases of sex differences are beset with task selection problems. Tasks must be appropriate not only in terms of the ability they target but also in their level of difficulty because sex differences may be readily masked by using tasks that are too easy or too difficult to differentiate between the performances of men and women (Sanders, Sjodin and de Chastelaine, 2002). Therefore, in Study 1, we used four levels of difficulty, and tested both preferred and non-preferred limbs, in order to maximize the chance of finding support for our prediction that there will be an interaction between Muscle and Sex.

Materials and Methods

Participants

The study used 128 right-handed participants, 64 men (mean age 23.59 ± 2.50 years) and 64 women (mean age 24.09 ± 2.51 years). No participant had sustained an injury to his or her upper limbs in the previous twelve months. The study was approved by the London Metropolitan University Psychology Department Ethics Committee. All participants gave informed written consent and were aware that they could withdraw from the study at any time. None withdrew.

Task

Participants performed a computerized tracking task in which they attempted to keep a cursor in contact with a moving target (diameter 5 mm). Task difficulty was manipulated by using combinations of two circular target paths (simple or complex) and two target speeds (slow or fast). The simple path was a circle with a radius of 30 mm. The complex path was an undulating circle with six peaks and troughs that deviated 5 mm without and within an imaginary circle with a radius of 30 mm. At the slow speed the target completed one revolution in 12 seconds. At the fast speed the target completed one revolution in 6 seconds. Each participant was assigned to one of four levels of difficulty: Level 1 used the slow speed and simple trajectory; Level 2 used the slow speed and complex trajectory; Level 3 used the fast speed and simple trajectory; Level 4 used the fast speed and complex trajectory.

The tracking task was performed under two conditions, Hand and Arm. For each condition the computer screen was placed at a distance of 600 mm, i.e. in peripersonal (near) space, in order to avoid near/ far space confounds. In the Hand condition participants operated a joystick with their distal, hand and wrist, muscles while in the Arm condition they used the proximal, upper arm and shoulder, muscles. For the Hand condition the forearm of the participants was retrained by strapping it to the table to prevent arm movements and they were instructed to track the moving target by manipulating a short (70 mm) joystick with wrist and finger movements. The maximal movement of the top of the short joystick was 42 mm in any direction from its central position. For the Arm condition the same joystick was moved from the table to the floor and its length extended to 1200 mm by attaching a rod. Participants were instructed to hold a 49 mm diameter ball at the top of the rod in the palm of their hand, to keep their wrist locked and to use their upper arm and shoulder muscles to perform the tracking task. The size of the ball and length of the rod encouraged, and the instructions ensured, that finger and wrist movements were effectively eliminated and that the extended joystick was manipulated by the proximal muscles of the upper arm and shoulder only. The maximal movement of the top of the long joystick was 600 mm in any direction from its central position. Maximal movement of both the short and long joystick produced the same 37.5 mm on screen movement of the cursor.

Procedure

We used a mixed design with independent groups of 16 men and 16 women randomly allotted to each of the four levels of task difficulty (Level 1 slow/ simple, Level 2 slow/ complex, Level 3 fast/ simple or Level 4 fast/ complex) and repeated measures on the Hand/ Arm and Non-preferred/ Preferred Limb factors. Participants were tested first using their non-preferred left limb and then their preferred right limb with the order of the Hand and Arm conditions counterbalanced. Both limbs were tested in order to manipulate task difficulty and to include the possibility of replicating any finding. Each test began with a 5 second practice followed by a 30 second test. Performance was recorded as the percentage of the 30 second period that the participant succeeded in keeping the cursor in contact with the target. Data were subjected to appropriate analyses of variance and significant interactions were explored with t-tests using 1-tailed tests for directional predictions and 2-tailed tests for other comparisons.

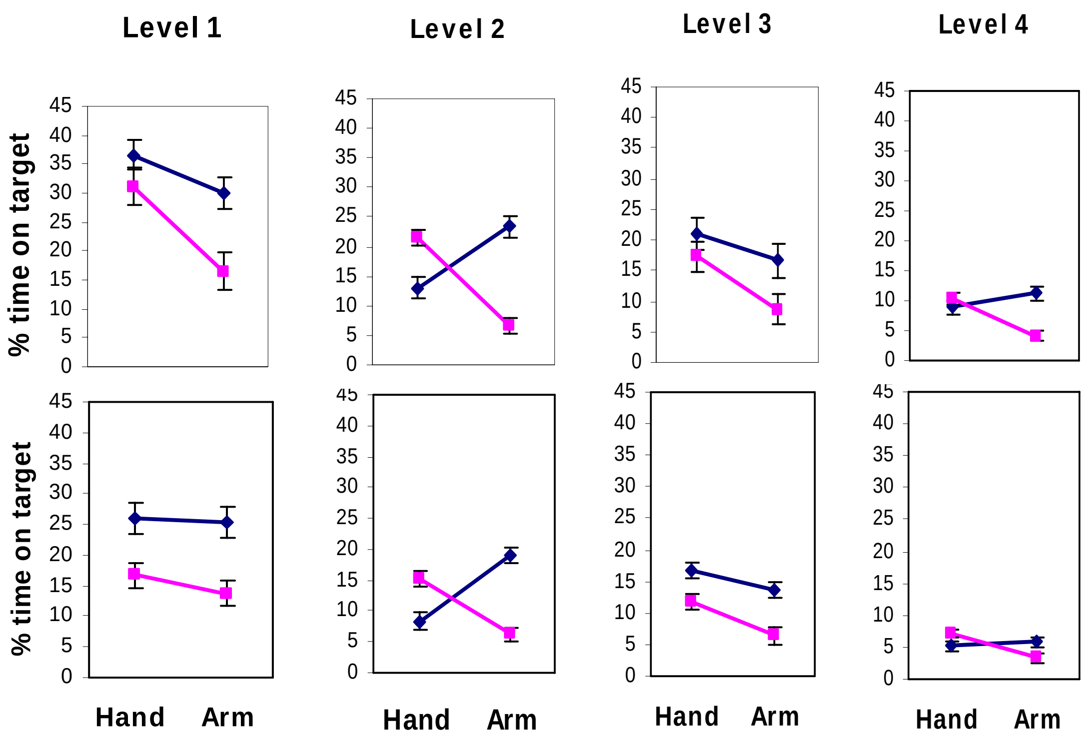
Results and discussion

Figure 1 shows that the patterns of performance obtain with the preferred right and non-preferred left limbs were remarkably similar although the time on target was higher with the preferred limb (grand mean 17.32% right, 12.54% left). Men tended to perform better than women when the target followed a simple circular trajectory (Level 1 and 3) but the predicted Muscle*Sex interaction appeared with the complex undulating trajectory (Levels 2 and 4). Data from the preferred and non-preferred limbs were analyzed separately.

Preferred right limb

The three-way interaction between the Sex, Muscle and Level was significant ($F_{3,120} = 8.16$, $p<0.001$) so separate two-way ANOVAs were conducted for Levels 1 to 4. At Level 1 the Muscle*Sex interaction was significant ($F_{1,30} = 4.53$, $p = 0.042$) because women ($t_{30} = 7.32$, $p = 0.001$, two-tailed) but not men ($t_{30} = 2.02$, $p = 0.061$, two-tailed) scored significantly lower with the arm. The predicted Muscle*Sex interaction appeared at Level 2 ($F_{1,30} = 84.23$, $p<0.001$). In the Hand condition, women achieved time on target scores that were higher than those of men ($t_{30} = 4.21$, $p<0.001$, two-tailed) and higher than their own scores in the Arm condition ($t_{15} = 10.07$, $p<0.001$, one-tailed). Conversely, in the Arm condition, men achieved time on target scores that were higher than those of women ($t_{30} = 8.25$, $p<0.001$, two-tailed) and higher than their own scores in the Hand condition ($t_{15} = 4.49$, $p<0.001$, one-tailed). At Level 3 the Muscle*Sex interaction was not significant but the predicted interaction appeared again at Level 4 ($F_{1,30} = 16.71$, $p<0.001$) because women scored significantly lower with the arm than with the hand ($t_{15} = 4.28$, $p = 0.001$, one-tailed) and significantly lower with the arm than men ($t_{30} = 4.65$, $p<0.001$, two-tailed). However, for men, the hand and arm scores did not differ significantly in this condition. A similar picture emerged from performance with the non-preferred left limb.

Figure 1. Study 1. Performance measured as percentage time on target (Mean ± SEM) using distal muscles (Hand condition) and proximal muscles (Arm condition). Eight independent groups (n = 16) completed the task at one of four levels of difficulty: Level 1 – slow simple; Level 2 – slow complex; Level 3 – fast simple and Level 4 – fast complex. Upper row – preferred right limb; lower row – non-preferred left limb; pink/ lighter grey lines and squares – women; blue/ darker grey lines and diamonds – men.



Non-preferred left limb

The three-way interaction between the Sex, Muscle and Level was a significant ($F_{3,120}$ = 11.33, p<0.001) so separate two-way ANOVAs were conducted for Levels 1 to 4. The two-way interaction was not significant at Levels 1 and 3 but at Level 2 the predicted Muscle*Sex interaction was again significant ($F_{1,30}$ = 86.76, p<0.001). In the Hand condition, women achieved time on target scores that were higher than those of men (t_{30} = 3.36, p = 0.002, two-tailed) and higher than their own scores in the Arm condition (t_{15} = 5.01, p<0.001, one-tailed). Conversely, in the Arm condition, men achieved time on target scores that were higher than those of women (t_{30} = 7.65, p<0.001, two-tailed) and higher than their own scores in the Hand condition (t_{15} = 9.57, p<0.001, one-tailed). Finally, the predicted interaction appeared again at Level 4 ($F_{1,30}$ = 8.83, p = 0.006) because women scored significantly lower with the arm than with the hand (t_{15} = 4.17, p = 0.001, one-tailed) and significantly lower with the arm than men (t_{30} = 2.50, p = 0.018, two-tailed). However, for men, the hand and arm scores did not differ significantly in this condition.

Hence, with the previous confounding variables of task demands and spatial location controlled, Study 1 confirmed our prediction from the hunter/gatherer hypothesis that women would perform better with their hand and men with their arm. It is notable that the pattern of performance obtained with the preferred right limb was replicated with the non-preferred left limb (Fig. 1). The data also show the importance of level of difficulty with the complex undulating circular pathway (Levels 2 and 4) revealing the predicted Muscle*Sex interaction and only Level 2 (slow/complex) optimally differentiating the opposite patterns of male and female performance. Consequently, the Level 2 tracking task was selected for use in Study 2.

STUDY 2

Here we aimed both to replicate the interaction between Sex and Muscle that we found in Study 1 and also to demonstrate correlations between performance on the tracking task and performance on five other sex-dimorphic motor and nonmotor cognitive tasks. We predicted that tracking with the hand would correlate positively with female favoring tasks and negatively with male favoring tasks whereas tracking with the arm would correlate negatively with female favoring tasks and positively with male favoring tasks.

Materials and Methods

Participants

The study used 100 right-handed participants, 50 men (mean age 22.74 ± 2.68 years) and 50 women (mean age 21.48 ± 2.35 years). The participants all had English as their first language and none had sustained an injury to his or her upper limbs in the previous 12 months. The study was approved by the London Metropolitan University Psychology Department Ethics Committee. All participants gave informed written consent and were aware that they could withdraw from the study at any time. None withdrew.

Tasks

We used the Level 2 (slow/complex) tracking task from Study 1 and five established sex-dimorphic motor and nonmotor cognitive tasks. The three motor tasks were the male-favoring Targeted Throwing (Watson and Kimura, 1991) which emphasizes gross, proximal muscle activity and the female-favoring Purdue Pegboard Single Peg Condition with the left and right hands (Tiffin, 1987), which emphasizes fine, distal muscle activity. We used a modified version of the throwing task in which participants directed six Velcro covered table tennis balls one at a time, using an underarm throw, to towards the centre of a 1450 mm square cloth target placed 1500 mm away and we recorded performance as mean radial error in cm. We used the standard Purdue pegboard single peg condition in which participants fit single pegs vertically into a column of holes on a horizontal board and performance is recorded separately for the left and right hands as the total number of pegs correctly placed in 30 seconds. The two cognitive tasks were the female-favoring Controlled Associations (Ekstrom, French, Harman, and Dermen, 1976) and the male-favoring Mental Rotations (Vandenberg and Kuse, 1978). We used a reduced version of the Controlled Associations task in which participants had 4 minutes to write down as many words as they could think of with the same or similar meaning to the target word “weak” and performance was recorded as the total number of correct words. In the Vandenberg and Kuse mental rotations test participants are required to select, from four figures, the two that match a given example but are rotated. Six minutes were allowed for the completion of the 20 items and performance was the recommended measure, correct responses adjusted for guessing.

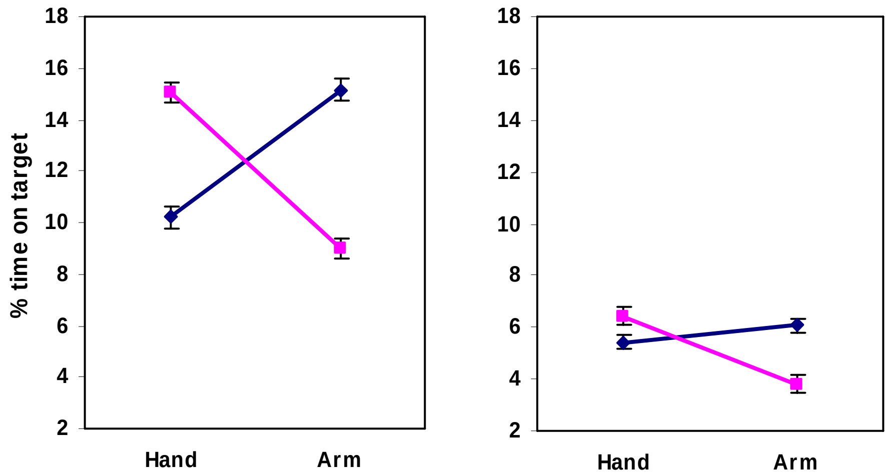
Procedure

We used a mixed design with independent groups of 50 men and 50 women and repeated measures on the tasks. The tracking task (Level 2 slow/complex) was administered as in Study 1. On completion of the tracking task the five sex-dimorphic motor and nonmotor cognitive tasks were completed in the following order: Purdue Pegboard Single Peg Condition first with the left non-preferred and then with the right preferred hand; the Controlled Associations; Mental Rotations; and Targeted Throwing. Data were subjected to appropriate analyses of variance and significant interactions were explored with t-tests using 1-tailed tests for directional predictions and 2-tailed tests for other comparisons and correlations.

Results and discussion

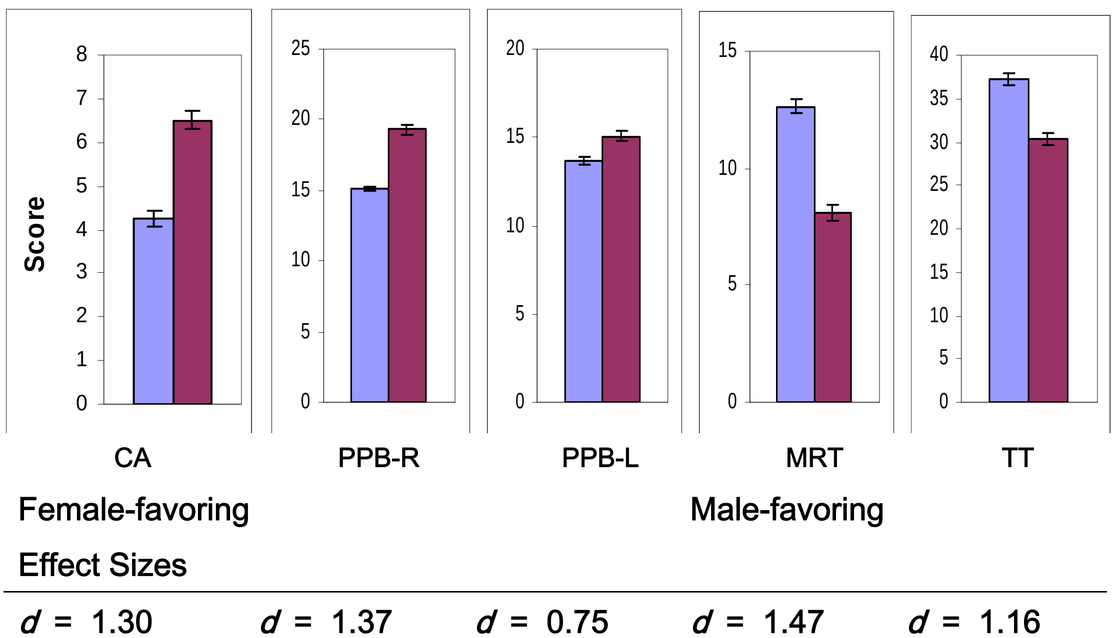
First, as seen in Figure 2, Study 2 confirmed the findings of Study 1. Once again the predicted Muscle*Sex interaction was significant for both the preferred ($F_{1,98} = 174.27$, $p<0.001$) and the non-preferred ($F_{1,98} = 28.85$, $p<0.001$) limbs. Preferred limb performance showed that women scored higher than men in the Hand condition ($t_{98} = 8.39$, $p<0.001$, two-tailed) and higher than their own scores in the Arm condition ($t_{49} = 10.17$, $p<0.001$, one-tailed). Conversely, men scored higher than women in the Arm condition ($t_{98} = 10.19$, $p<0.001$, two-tailed) and higher than their own scores in the Hand condition ($t_{49} = 8.49$, $p<0.001$, one-tailed). A similar picture emerged from performance with the non-preferred limb.

Figure 2. Study 2. Percentage time on target (Mean ± SEM) recorded by 50 men (blue/ darker grey lines and diamonds) and 50 women (pink/ lighter grey lines and squares) using distal muscles with a short joystick (Hand condition) and proximal muscles with an extended joystick (Arm condition). All completed the Level 2 (slow complex circle) tracking task from Study 1. Left panel – preferred right limb; right panel – non-preferred left limb.



Second, as illustrated in Figure 3, the widely reported sex differences for each of the five sex-dimorphic tasks were confirmed at $p<0.001$ and with substantial effect sizes (*d*). Women scored higher than men on each of the three female-favoring tasks: Controlled Associations ($t_{98} = 8.54$, $p<0.001$); Purdue Pegboard Single Peg Condition, non-preferred left hand ($t_{98} = 4.00$, $p<0.001$) and preferred right hand ($t_{98} = 9.41$, $p<0.001$). Conversely, men scored higher than women on the two male-favoring tasks: Mental Rotations Task ($t_{98} = 10.94$, $p<0.001$) and Targeted Throwing ($t_{98} = 7.07$, $p<0.001$).

Figure 3. Scores (Mean +/- SEM) from men (blue/ lighter grey) and women (pink/ darker grey) on five sex-dimorphic tasks. Female-favoring tasks: Controlled Associations (CA) number of words generated; Purdue Pegboard Right Hand (PPB-R) and Left Hand (PPB-L) number of correctly peg fitted. Male-favoring tasks: Mental Rotation Task (MRT) number of items correct adjusted for guessing; Target Throwing (TT) an accuracy score calculated by subtracting the male and female mean error scores in cm from their sum.



Finally, using the preferred limb data from the total sample we looked at correlations between performance on the tracking task and performance on the five sex-dimorphic motor and nonmotor cognitive tasks. Using the whole group data we found, as predicted, that tracking scores from the Hand condition correlated positively with female-favoring task performance and negatively with male-favoring task performance while the reverse was true for tracking scores from the Arm condition, all with Pearson correlations at $p<0.022$ or beyond (Table 1). However, given the marked sex differences that were recorded for these tasks (Figures 2 and 3) significant correlations with the combine male and female data are to be expected as for each task female scores will tend to be high and male scores low or vice versa. Consequently, real interest centers on the within-sex correlations of which only one was significant. Men showed a positive correlation between their scores for tracking in the Arm condition with the preferred right limb and the Mental Rotation Task ($r = 0.287$, $p = 0.043$). It is notable that this correlation is in the predicted direction and that it occurred between tracking and a nonmotor cognitive task suggesting the same factor(s) predispose the development of sex dimorphic patterns of performance for both types of task, at least in males. Why tracking with the arm and mental rotation should provide the only significant within-sex correlation is not clear especially as the other within-sex correlations were all small (the majority were less than r = 0.1 and p>0.500) although the effect size of the sex difference for mental rotation was 7% to 21% greater than for any of the other tasks.

Table 1: Pearson correlations Between Tracking and Sex-dimorphic Tasks Using Performance with the Preferred Right Limb (probabilities are two-tailed)

	Female-favoring		Male-favoring	
	Motor	Non-Motor	Motor	Non-Motor
	Purdue Pegboard	Controlled Association	Target Throwing	Mental Rotations
Hand tracking	r = +0.451 p < 0.001	r = +0.491 p < 0.001	r = -0.228 p = 0.022	r = -0.540 p < 0.001
Arm tracking	r = -0.549 p < 0.001	r = -0.416 p < 0.001	r = +0.392 p < 0.001	r = +0.404 p < 0.001

General discussion

Behavioral sex differences

As noted in the Introduction, published studies of sex differences in motor performance confound the motor and visuospatial subdivisions as well as task demands. The present investigation was designed to avoid these confounds. Male and female performance with hand and arm were compared using the same tracking task performed in near space so that both task demands and spatial location remained constant. The data from Study 1 confirmed our prediction from the hunter-gatherer hypothesis. With the previous confounds avoided there was an interaction between Muscle and Sex that arose because women performed better with their hands and men better with their arms (Fig. 1). We used four levels of difficulty in Study 1 in an attempt to avoid tasks that were too easy or too difficult to differentiate the performances of men and women. As seen in Figure 1, the interaction that we predicted appeared only with an appropriate level of tracking difficulty (Levels 2 and 4, slow and fast complex) in which frequent changes of direction were required. However, only Level 2 fully differentiated male and female performance. Consequently in Study 2 we used the same level of difficulty and replicated the finding of opposite patterns of performance in women and men with both the preferred right and non-preferred left limbs (Fig. 2).

Neural sex differences

The reality of such sex differences as those we have demonstrated for the control of distal hand and proximal arm muscles would be reinforced by the presence of separate underlying neural mechanisms for each of the behaviors. Separate mechanisms would provide neural bases for the differential development of male and female brains to support better hand than arm performance in women and the reverse in men. Studies with monkeys (Lawrence and Kuypers, 1968a; 1968b) have demonstrated that the neural mechanisms for distal and proximal muscle control are distinct. The distal (hand) muscles are controlled by the primary motor cortex via two dorsolateral corticospinal tracts whereas the proximal (arm) muscles are controlled by the primary motor cortex via two ventromedial corticospinal tracts. Our current behavioral findings point to the potential existence of sex differences in those dorsolateral and ventromedial motor systems.

Of course, other sex-dimorphic brain mechanisms may also contribute to male/ female differences in motor performance. For example, there is evidence that motor skills are more disrupted in men by lesions to the posterior cerebral cortex whereas in women anterior cortical lesions are more disruptive (Kimura, 1977, 1983). It was suggested that the posterior cortex is particularly important in men for the integration of visual and motor systems that would allow superior performance of tasks such as targeted throwing directed into extrapersonal space. However, our tracking task was performed in peripersonal space, thus holding spatial location constant, so the present data point specifically to sex differences in the dorsolateral and ventromedial pathways, and their associated cortical areas, that exercise distal and proximal muscle control.

Correlations between tracking and established sex-dimorphic tasks

In Study 2 we also replicated the reported sex differences for three motor and two nonmotor tasks. These tasks were included because we were interested in possible correlations between tracking scores and performance on sex-dimorphic tasks. In each case we found that the female-favoring Hand tracking correlated positively with the other female-favoring tasks but negatively with the male-favoring ones whereas for the male-favoring Arm tracking correlations were positive with the other male-favoring tasks and negative with the female-favoring ones (Table 1). However, given the marked sex differences recorded for each of the tasks it is not surprising that significant correlations were found for all comparisons using the combined male and female data because, for any one task, female scores will tend to be high and male scores low or vice versa. Consequently, of greater note is the within sex finding that for men there was a significant correlation between Arm tracking and performance on the Mental Rotations, a nonmotor cognitive task. This finding suggests that the same or related events are responsible for the development of complementary sex differences in the motor and cognitive systems, although the absence of similar correlations between tracking and the other tasks is puzzling (see final paragraph of Study 2, Results and discussion).

Implications for the hunter-gatherer hypothesis

The hunter-gatherer hypothesis (Silverman and Eals, 1992) points to an evolutionary selection for hunting-related skills in men and gathering–related skills in women. In addition, men would have been the primary defenders and women the primary carers. Hunting and defending would require, among other things, skilled use of the proximal, arm and shoulder, muscles for targeted throwing and for striking powerful blows with or without a weapon. In contrast, gathering and caring would require skilled use of the distal, hand and wrist, muscles for fine motor movement. Our present data are compatible with the hunter-gatherer hypothesis. In both Study 1 (Fig. 1, Level 2) and Study 2 (Fig. 2), where the previous confounds created by task demands and spatial location were avoided, women performed the tracking task better with their hand than with their arm while men performed better with their arm than with their hand.

A related prediction from the hunter-gather hypothesis concerns visual processing. As the predominant hunters, men should perform better with visual input from far (extrapersonal) space. Conversely, women as the predominant gatherers, should perform better with visual input from near (peripersonal) space. In a parallel paper (Sanders, Sinclair and Walsh, 2007), we have reported a demonstration and two replications of this predicted sex difference in visual processing. Finally, taken together the motor and spatial location studies not only confirm predictions from the hunter/gatherer hypothesis but they also suggest that studies in which known sex-dimorphic tasks are deconstructed to isolate subcomponents of the tasks provide a fruitful approach to a further understanding the nature of sex differences and their underlying neural basis.

Acknowledgements: This paper is dedicated to my colleague and collaborator, Tom Walsh, who sadly died in the late summer of 2006 before this manuscript was completed for publication. In addition to the close collaboration that I enjoyed with Tom Walsh, I am grateful to John Robinson who wrote the program for the tracking task and to Stephano Del Bianco and Hardeep Sambi who collected the data for Studies 1 and 2 respectively. Some of the data reported here were presented as a poster at the 28th Annual Meeting of the International Academy for Sex Research, Hamburg, 19-22 June 2002.

Received 7 June 2007; Revision submitted 2 September 2007; Accepted 3 September 2007

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