INFLUENCE OF TASK COMPLEXITY ON MANUAL ASYMMETRIES

Markus Hausmann, Ian J. Kirk and Michael C. Corballis

(Department of Psychology, and Research Centre for Cognitive Neuroscience, University of Auckland, Auckland, New Zealand)

ABSTRACT

The degree of manual asymmetry is generally assumed to vary with task complexity. However, task complexity as a factor in manual asymmetries has rarely been examined directly. Further, the results of psychophysical studies indicate that manual asymmetry increases with task complexity, while physiological studies consistently report a reduction of manual asymmetries in more complex tasks. The use of different tasks (rather than different complexity levels within a given task) in many psychophysical studies might result in this inconsistency. This study investigated the influence of task complexity on manual asymmetries in 70 right-handed subjects. We used three complexity levels within a finger-tapping paradigm. A strong advantage of the preferred hand was particularly pronounced in the simple finger-tapping task. When the task was more complex, the advantage of the preferred hand, and thus, the manual asymmetry significantly decreased or disappeared. These results support previous suggestions that simple motor tasks involve localised neural networks confined to one cerebral hemisphere, while complex motor tasks are controlled by more widely distributed neuronal assemblies that involve both hemispheres. However, the influence of task complexity on manual asymmetry seems not to be monotonic.

Key words: finger tapping, functional cerebral asymmetry, lateralization, motor asymmetry, sex differences

INTRODUCTION

On most manual tasks the preferred hand, usually the right, is more skilled than the non-preferred hand. The degree of manual asymmetry varies from task to task, but the basis of this variation is not well understood (Bryden, 2000). One aspect of a task that seems to affect the degree of asymmetry, however, is its complexity, and it is broadly accepted that the more complex the task the stronger the preference and the greater the preferred hand advantage (Borod et al., 1984; Flowers, 1975; Provins and Magliaro, 1993, for review, see Bryden, 2000). However, it should be noted that no explicit definition of 'task complexity' exists, although intrinsic task demands (e.g. multiple postures or multi-joint actions) and extrinsic task demands such as the spatial complexity of an action might be relevant (e.g. Bryden et al., 2002; Elliott et al., 1999). Moreover, task complexity as a factor in manual asymmetries has received little attention and has rarely been examined directly (Bryden, 2000; Steenhuis, 1996).

There is some evidence from brain imaging that task difficulty strongly influences hemispheric involvement in motor preparation and programming (Colebatch et al., 1991; Pulvermüller et al., 1995; Rao et al., 1993; Roland et al., 1980; Seitz et al., 1992; Solodkin et al., 2001) but the results of these studies point in the opposite direction to that suggested by the psychological evidence; that is, they suggest that asymmetry decreases with task complexity. For example, the fMRI study of Rao et al. (1993) showed that simple finger movements activated the contralateral primary motor cortex, whereas complex movements were associated with additional foci of activity in the supplementary motor cortex, the premotor cortex bilaterally, and the contralateral somatosensory cortex. The somatosensory cortex was bilaterally activated in some participants. A small degree of activation was also observed in the ipsilateral primary motor cortex during the complex movement conditions. In sum, Rao et al. (1993) indicate that in simple movement tasks cortical activation tends to be unilateral, whereas in more complex motor tasks activation is more bilateral.

Even in the few psychophysical studies that have examined the effects of complexity, there has been little attempt to vary complexity or difficulty in manual tasks in a quantitative fashion (Bryden, 2000). Typically, the tasks that are compared differ not only in complexity, but also in the abilities they draw on; for example, rhythmic tapping has been compared with manual aiming (Flowers, 1975), and grip strength with handwriting (Provins and Magliaro, 1993). As Bryden (2000) points out, manual asymmetry in these cases is potentially dependent on the nature of the task, and not just on its complexity.

In this study, we analyse the influence of task complexity on manual asymmetry in finger tapping. By using different finger sequences, our aim was to generate different complexity levels within one basic motor function. Overall finger-tapping rate and intertap variability provided measures of complexity level under each experimental condition. Lateralization indices were then computed to provide measures of functional cerebral asymmetries that were independent of overall performance. Since there is evidence that men are more lateralized than women (e.g. Hausmann et al., 1998; 2002; Hausmann and Güntürkün, 1999; McGlone, 1980; Voyer, 1996), as well as evidence

Cortex, (2004) 40, 103-110

that women are superior to men in fine motor tasks (e.g. Halpern, 2000; Kimura, 1999), we were also alert to possible gender differences.

METHODS

Subjects

Seventy right-handed subjects (38 women and 32 men) were recruited from the student body of a variety of faculties. The handedness of all subjects was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), which yields a laterality quotient (LQ) that can vary from – 100 for maximum left-handedness to + 100 for maximum right-handedness. The mean LQ was + 89.1 (SD = 13.4; range from + 52.9 to + 100) for the women and + 82.0 (SD = 24.0; range from + 20.0 to + 100) for the men. The mean age was 27.7 years (SD = 7.1, range: 20-45 years) for the women and 27.7 years (SD = 7.7, range: 20-47 years) for the men. They were recruited by advertisement and were paid for their participation.

Procedure and Materials

The finger-tapping apparatus consisted of four micro-switches, each mounted on a magnetic base so that it could be located in any position on a metallic platform. This system allowed fine positioning of each micro-switch to the subject's individual posture and size of the fingers and hand. The micro-switches were connected to the parallel port of a personal computer to record the sequence of taps on the switches. The sampling rate was at least 1 msec. We used three levels of task complexity. In the simple tapping condition subjects were instructed to press the button with the index finger (tapping finger 2) as fast as possible in a time interval of 15 sec. In one complex tapping condition (complex 1) subjects were instructed to repeatedly press the buttons in the sequence: index finger, middle finger, ring-finger, and little finger (finger sequence: 2, 3, 4, 5) as fast as possible within a 15 sec time interval, but to avoid making errors. In the second complex tapping task (complex 2) the tapping sequence was index finger, ring finger, middle finger, small finger (finger sequence: 2, 4, 3, 5). We expected the complex 2 sequence to be the most demanding task.

The subjects were seated during the whole experiment. During practice they could look at the keys, but during test trials an occluding screen was installed so that the tapping had to be executed without any visual feedback. Moreover, the subjects were asked to keep the palm of the hand pressed flat on the board while they were tapping to reduce any effects due to differential typing or piano-playing experience (Lomas and Kimura, 1976). They repeated each condition 5 times with each hand. Each 15-sec trial was followed by a short break. The order of the 6 conditions was counterbalanced across subjects. For each hand, the tapping rate was assessed by the mean number of correct taps of the five trials under each condition. The time interval between two correct successive taps (intertap time) was recorded and for each trial the standard deviation of the intertap intervals was calculated. For each hand, intertap variability was measured as the mean, over 5 trials, of the standard deviations of intertap time intervals on each trial.

For the purposes of the analysis, the dominant hand (DH) was determined from the Edinburgh Handedness Inventory (Oldfield, 1971). The manual asymmetries under each level of task complexity were measured by the ratio of the differences between the hands (DH – non-DH, for tapping rate; and non-DH – DH, for intertap variability) to overall performance (DH + non-DH). This ratio was used to correct for differences in overall performance, and was adapted from Schmidt et al. (2000).

Overall performance and manual asymmetry measures of tapping rate and intertap variability were analysed using repeated-measures ANOVAs (multivariate tests) with 3 levels of complexity (simple, complex 1, complex 2) as a within-subject factor and sex as a between-subject factor. For all tests, significance level of 5% (two-tailed) was used. The statistical analyses of the complex 1 condition are based on 68 participants, of the complex 2 condition on 69 participants, due to erroneous recordings. The analyses of the simple condition are based on all participants ($n = 70$).

As a check on whether previous experience might influence the results, all subjects were asked about fine motor skills that involved tapping movements, such as typing or playing the piano. The numbers of years of experience in each activity were then summed to provide an overall measure. For example, a subject who had regularly used a typewriter for 4 years and played the piano for 8 years would receive a score of 12. A subject who had had no such experience would receive a score of 0. Since the scores were positively skewed, and deviated significantly from a normal distribution (Kolmogorov-Smirnov goodness-of-fit, $Z = 1.54$, $N = 70$, $p < 0.05$), they were subjected to a square-root transformation. The transformed scores ranged from 0 to 6.16 (mean: 2.31, standard error: 0.20).

RESULTS

Motor Experience and Overall Performance

There were significant correlations between motor experience and overall tapping rate under the two complex conditions (for complex 1, r (68) =

TABLE I

Correlation coefficients of the relationships between motor experience and overall performance or manual asymmetry for tapping rate (TAP) and intertap variability (VAR) under different task complexity levels (S – simple, C1 – complex 1, C2 – complex 2)

	Condition	Motor experience
Overall Performance	TAP-S	– .03
	TAP-C1	**.37****
	TAP-C2	**.42*****
	VAR-S	– .09
	VAR-C1	**– .31****
	VAR-C2	– .22$^+$
Manual Asymmetry	TAP-S	– .11
	TAP-C1	– .10
	TAP-C2	– .17
	VAR-S	– .06
	VAR-C1	.08
	VAR-C2	.08

***p < 0.001; **p < 0.01; *p < 0.05; $^+$p < 0.10

TABLE II

Mean tapping rates (and standard error means) for the dominant (DH) and the non-dominant hand (Non-DH) and both genders under three task complexity conditions (tappings/15 sec)

	Simple		Complex 1		Complex 2	
	DH	Non-DH	DH	Non-DH	DH	Non-DH
Males (n = 32)	80 .00 ± 1.35	74.09 ± 1.47	51.28 ± 1.92	49.97 ± 2.06	45.84 ± 1.93	43.84 ± 2.26
Females (n = 38)	69.00 ± 1.74	61.32 ± 1.88	46.00 ± 2.19	43.62 ± 1.72	43.49 ± 2.20	40.63 ± 2.05
All (n = 70)	74.03 ± 1.30	67.16 ± 1.44	48.49 ± 1.49	46.57 ± 1.37	44.58 ± 1.48	42.10 ± 1.52

.37, p < .01; for complex 2, r (69) = .42, p < .001), but the correlation with simple tapping rate was not significant [r (70) = – .03]. Similarly, the correlation between motor experience and overall intertap variability was significant for the complex 1 condition [r (68) = – .31, p = 0.01] and approached significance for the complex 2 condition [r (69) = – .22, p = 0.07], but did not approach significance in the simple tapping condition [r (70) = – .09, n.s.]. Correlation coefficients are shown in Table I.

Motor Experience and Manual Asymmetries

None of the correlations between motor experience and manual asymmetry (in tapping rate or intertap variability) approached significance (all rs < .17, n.s.), so motor experience was not considered in any of the subsequent analyses (Table I).

ANOVA Results

Overall Performance

Mean tapping rates for each hand and for each gender under three complexity conditions are shown in Table II. ANOVA for overall performance in tapping rate revealed a highly significant main effect of task complexity [F (2, 64) = 147.53, p < 0.0001], indicating a strong reduction in tapping rate with increasing complexity of the task (Figure 1a). The analysis of the main effect of gender showed the well-known (Bornstein, 1986; Ruff and Parker, 1993; Schmidt et al., 2000) higher tapping rate in males [F (1, 65) = 9.45, p < 0.01], which may be a peripheral effect of testosterone on muscle fibres (Schmidt et al., 2000). The interaction between task complexity and sex also reached significance [F (2, 64) = 4.90, p < 0.01]. Males showed a higher tapping rate than females, but with increasing complexity of the motor task the difference decreased (Figure 2). Post hoc t-tests revealed a significant sex difference in the simple condition [t (68) = 5.46, p < 0.0001]. With a Bonferroni- adjustment for post hoc testing (Holm, 1979), the sex difference in the complex 1 condition was marginally significant [t (66) = 2.13, p = 0.037], while in the complex 2 condition it did not approach significance [t (67) = 0.91, n.s.].

There was also a significant effect of task complexity on intertap variability [F (2, 64) = 37.49, p < 0.0001], with least variability in the simple tapping condition (Figure 1b). Neither the effect of sex [F (2, 64) = 2.10, n.s.] nor the interaction between task complexity and sex [F (2, 64) = 0.94, n.s.] were significant. Post hoc t-tests revealed that the differences in overall performance between each complexity condition was highly significant for the tapping rate (all ts > 5.39, p < 0.0001) as well as for the intertap variability (all ts > 4.86, p < 0.0001) (Figure 1a, b).

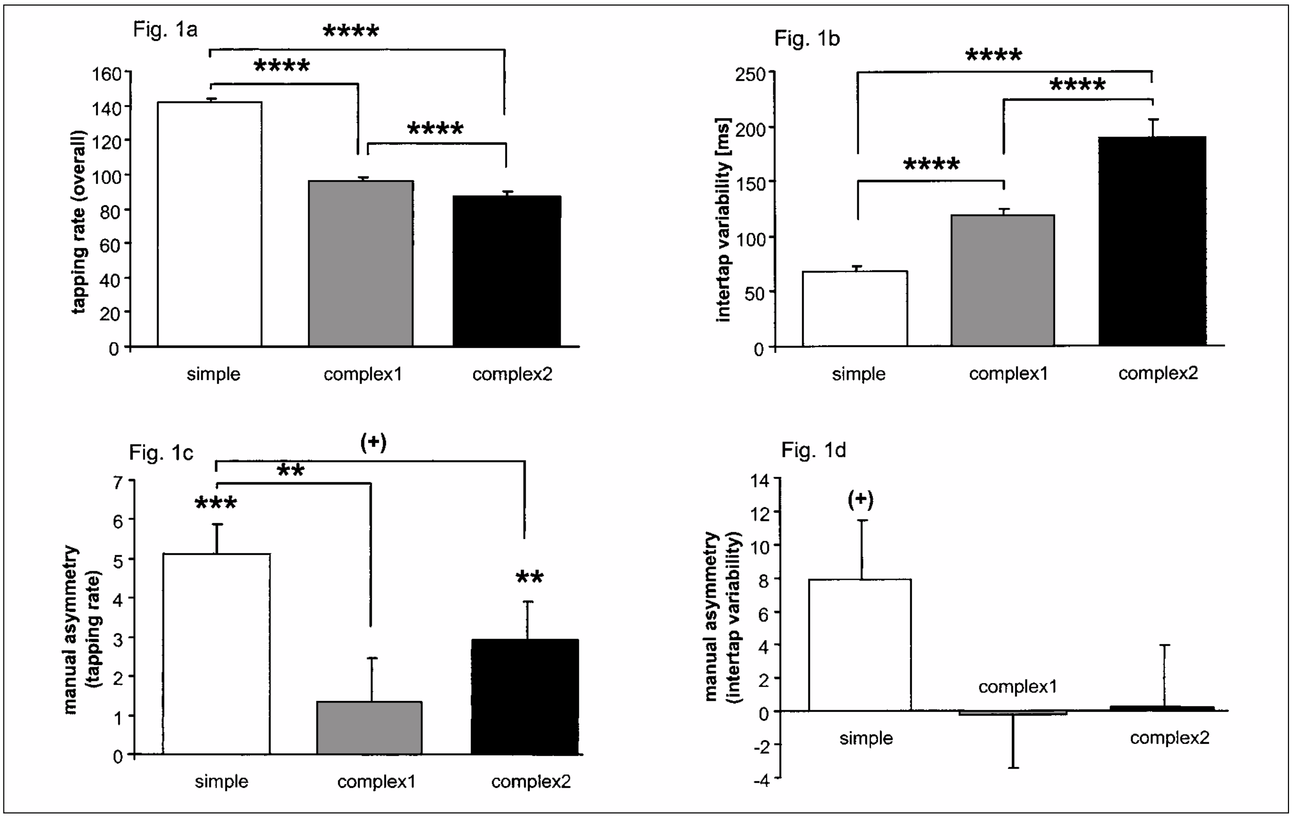

Fig. 1 – *Upper figures show overall performance of tapping rate (Fig. 1a) and intertap variability (Fig. 1b) in the simple, complex 1, and complex 2 condition. Bottom figures show the manual asymmetry in tapping rate (Fig. 1c) and intertap variability (Fig. 1d) for three complexity levels.*

*Significance: $p < 0.0001$ ****, $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *, $p < 0.10$ (+)*

Manual Asymmetry

For manual asymmetry in tapping rate, there was a significant main effect of task complexity [F (2, 64) = 4.75, $p < 0.02$]. The manual asymmetry was strongest in the simple condition (Figure 1c). Neither the main effect of sex [F (1, 65) = 0.73, n.s.] nor the interaction of sex with task complexity [F (1, 65) = 0.28, n.s.] approached significance. Post hoc t-tests revealed the only highly significant difference in manual asymmetry of the tapping rate between the simple and the complex 1 condition [t (67) = 3.19, p = 0.002]. The difference between the simple and complex 2 conditions showed only a slight trend [t (68) = 1.70, p = 0.095], whereas the two complex conditions did not differ significantly [t (66) = – 1.32 , n.s.] (Figure 1c).

ANOVA of the manual asymmetry in intertap variability revealed no significant effects or interactions (all Fs < 1.85, n.s.) (Figure 1d)[1].

In addition, the degree of manual asymmetries was analysed to reveal which complexity levels produced lateralized tapping performance that differed significantly from zero (symmetry). For this we computed one-sample t-tests which compared the manual asymmetry ratios with a symmetry score of 0. The simple [t (69) = 7.05, $p < 0.0001$] as well as the complex 2 conditions [t (68) = 3.19, p = 0.002] showed significant departures from functional symmetry, but the complex 1 condition did not [t (67) = 1.27, n.s.] (Figure 1c). As for the intertap variability, the manual asymmetries showed a trend toward significance only for the simple condition [t (69) = – 1.87, p = 0.066]; neither complex condition deviated significantly from zero asymmetry (0.24 > t > – 0.24, n.s., in all cases) (Figure 1d).

To analyse whether the preferred or the non-preferred hand was more affected, we computed the percentage of decrease (D) in tapping rate of the left (D_L) and the right hand (D_R) for all tapping conditions (S, C1, C2). The tapping rate of the simple condition (S), complex 1 condition (C1), respectively, was used as 100% for each subject. The following example shows the formula which was used to analyse the percentage decrease (D) of C1 relative to S for the left hand: $D_L = 100 - ((C1_L / S_L) \times 100)$. This was done for C1 relative to S, for C2 relative to S, and for C2 relative to C1, respectively. In the next step, the relative

---

[1] This study has replicated and extended the results of a previous study (unpublished data). In the previous study 37 participants (19 women, 18 men) were investigated with two complexity levels, the simple repetitive finger-tapping task (S) and the complex sequential finger tapping task (C2) using the identical experimental setup. The manual asymmetry in tapping rate was less strong in the complex tapping condition (C2) [F (1, 34) = 7.78, $p < 0.01$], although the manual asymmetry in C2 was still different from the virtual symmetry score of 0 [T (35) = 2.38, p = 0.02]. In agreement with this study the manual asymmetry in intertap variability did not deviate significantly from virtual symmetry for both complexity levels (both Ts (35) < – 0.73; n.s.).

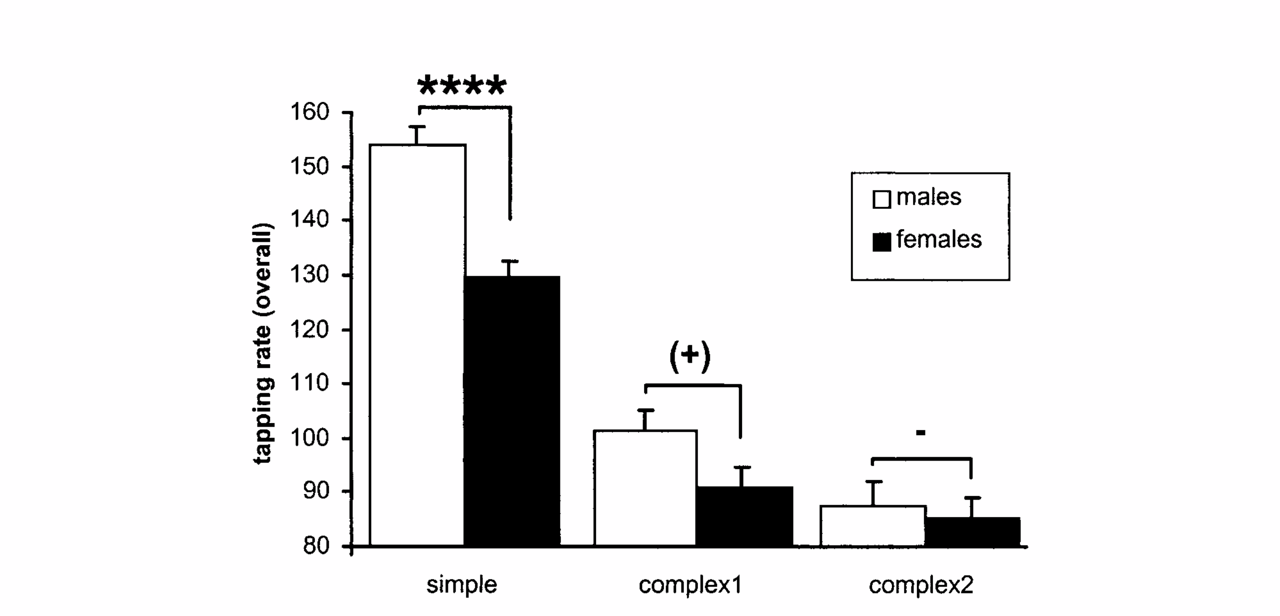

Fig. 2 – *Significant interaction between task complexity (simple, complex 1, and complex 2) and sex in tapping rate (overall). Males showed a higher tapping rate than females particularly in simple finger tapping. Sex differences in tapping rate decreased with increasing complexity of the motor task.*
*Significance: p < 0.0001 ****, p < 0.001 ***, p < 0.01 **, p < 0.05 *, p < 0.10 (+)*

decrease of tapping rate of the left and the right hand was compared, resulting in 3 comparisons. Paired t-tests revealed a significant stronger decrease in tapping rate from S to C1 when the right hand was used [t (67) = – 3.23, p = .002]. A similar result was obtained when tapping rate of C2 was compared relatively to S. The decrease was again stronger for the right hand [t (68) = – 2.20, p = .03]. No significant difference between both hands was obtained when the decrease in tapping rate of C2 relative to C1 was analysed [t (66) = 1.39, n.s.].

Discussion

The most notable result was the significant effect of task complexity on manual asymmetries. A very strong advantage of the preferred hand was particularly pronounced in the simple repetitive finger-tapping task. When the finger-tapping task was more complex and included sequencing of different movement elements at different levels of difficulty, the advantage of the preferred hand, and thus the manual asymmetry, significantly decreased or disappeared. The analyses of intertap variability showed into the same direction, however, task complexity as a factor in the statistical design was not significant. Previous studies (e.g. Lomas, 1980; Lomas and Kimura, 1976; Thornton and Peters, 1982) have found a significant asymmetry in sequential finger tapping tasks. However, Lomas and Kimura (1976) showed that the superiority of the right hand was particularly pronounced in simple repetitive finger tapping. This is in agreement with the results reported here. A superiority of the preferred hand was observed for all conditions, and was even clearly significant in the complex 2 condition. It was strongest, however, in the simple repetitive finger tapping task. These results strongly support the notion that cortical contribution is predominantly unilateral during simple motor tasks, but increasingly bihemispheric in the more complex tasks.

The results are in agreement with physiological findings of studies using EEG (Pulvermüller et al., 1995) or PET and fMRI measures (Colebatch et al., 1991; Roland et al., 1980; Seitz et al., 1992; Solodkin et al., 2001). Pulvermüller and Mohr (1996) speculate that higher cognitive functions, as well as motor programs with a certain degree of complexity, are represented in transcortical cell assemblies, while simple representations are organized as local assemblies of neurons. "This would suggest, for example, that a simple movement is controlled by the activation of a small cortical area [particularly in the left hemisphere]... while more complex sequential movements requiring a certain degree of planning and coordination are controlled by more widely distributed assemblies including neurons of both hemispheres" (Pulvermüller and Mohr, 1996, p. 562). In support of this view, PET and fMRI measures (Colebatch et al., 1991; Roland et al., 1980; Seitz et al., 1992; Solodkin et al., 2001), showing a strongly reduced or bilateral activation during complex sequential finger movements but only unilateral activation patterns in the motor and pre-motor cortices during simple repetitive finger movements.

The relative contribution of open- and closed-loop motor control processes provides a complementary explanation of the results observed in the current study. On the basis of clinical studies of patients with injury to one hemisphere, Haaland and Harrington (1989a; 1989b; Harrington and Haaland, 1991) propose that the left hemisphere is specialized for controlling open-loop movements, which are rapid, programmed movements performed with little or no modification by sensory input. This seems consistent with many findings related to left-hemisphere specialization for sequencing movements of the limbs and articulatory muscles (Hausmann et al., 1998; Hellige, 1993). In contrast, Haaland and Harrington (1989b) report evidence for right-hemispheric control in programming closed-loop movements, which are slower and modified from moment to moment by sensory feedback. In another study (Harrington and Haaland, 1991) they showed that right-hemisphere stroke patients began to show programming deficits during movement, but only for heterogeneous sequences. However, the authors themselves suggest an interesting alternative explanation for this finding. They noted that "impaired visuospatial skills in right-hemisphere stroke patients may affect programming processes, …when sequences are spatially more complex" (Harrington and Haaland, 1991, p. 161).

It is possible to describe the simple and complex motor tasks of this study as tasks that are based on open- and closed-loop movements, respectively. Although all subjects were denied visual feedback, the sensory feedback necessary for accurate closed-loop monitoring in complex tapping would have been available from proprioception. If this increased the degree of right-hemispheric involvement, it might explain why asymmetry also decreased for the complex tasks. In this regard, right dorsolateral prefrontal, and right posterior parietal cortices have been implicated in the integration of intention, action and proprioceptive and visual feedback in tasks similar to those employed here (Fink et al., 1999).

Despite being generally consistent with a variety of previous studies discussed above, the current results are in contrast to the broadly accepted assumption that the more complex the task the stronger the preference and the greater the preferred- hand advantage—as reported in several psychophysical studies (Borod et al., 1984; Flowers, 1975; Provins and Magliaro, 1993, for review, see Bryden, 2000). The contradictory results might be due to the fact that most of these studies investigated manual asymmetries in simple and complex tasks that were not directly comparable, such as rhythmical tapping and manual aiming (Flowers, 1975), or grip strength and handwriting (Provins and Magliaro, 1993). Differences in manual asymmetries in these tasks might be due to the different abilities required, rather than the differing degrees of complexity.

It should also be noted that when a verbal task was added to the tapping paradigms in the Lomas and Kimura (1976) study discussed above, tapping rates were significantly reduced in both the left and right hands for a single-finger tapping task, and the number of correct sequences in a sequential tapping task was significantly reduced for the right hand only. This pattern of results is inconsistent with the interpretation presented here, and by the authors' own admission is a puzzling result. It also contradicts the majority of evidence from such dual-task studies (see discussion in Kinsbourne and Hiscock, 1983). In addition, Sergent et al. (1993) have suggested that diminished tapping rates during a concurrent verbal task may reflect interference of a non-lateralized time-keeping mechanism, whereas a separate motor-sequencing or motor-implementation mechanism may be the substrate of hand asymmetries in the types of task used here.

This study shows a very strong and robust decrease in manual asymmetries for the more complex sequencing tapping tasks. Nevertheless, it could be argued that this was due, not to complexity per se, but to the incorporation of extra fingers into the two complex tasks. If these other fingers involve some degree of ipsilateral control, then this might also reduce the manual asymmetry. Although crossed pathways are the principle mechanism for controlling rapid and complex movements of all limbs (Todor et al., 1982), a study investigating the extent of ipsilateral control of fingers in callosotomized patients (Trope et al., 1987) has shown that there is a substantial amount of potential ipsilateral control, and that the fingers do differ in this respect. However, an ipsilateral contribution was clearly evident only for the thumb and the index finger. In the present study, this should have served to attenuate the asymmetry in the simple repetitive tapping condition, since the complex conditions included extra fingers (middle, ring, and little finger) for which there is little if any ipsilateral control. It is therefore unlikely that the variation in asymmetry that we observed was due to varying degrees of ipsilateral control.

Substantial differences between the fingers in overall tapping speed were also found by McManus et al. (1986) who presume that this is due to different structure on the peripheral level (musculature and tendons) used for moving the separate fingers. Nevertheless, one experiment in the study by McManus et al. (1986) showed an interaction between hand use and fingers, indicating differences between the hands being greater for the index finger than for the ring or little finger. Thus, when all fingers are used in a task, the observed asymmetry might be reduced. However, the overall conclusion of McManus et al. (1986) was that the difference between the preferred and non-preferred hand was approximately the same for all fingers.

The degree of prior learning or experience in a task may also account for contradictory reports in the literature regarding the degree of asymmetry observed in particular tasks. Bryden (2000) concludes in her review that the largest differences between hands are found in highly learned tasks that require complex sequencing, visual feedback and precise control of motor output. The simple and complex finger-tapping tasks used in our study were not highly learned, and there was only a short practice session. This might further explain why manual asymmetries in the complex conditions were significantly reduced. It would be interesting to investigate potential changes in the manual asymmetries of complex finger-tapping tasks as a function of extended practice using this experimental paradigm. We would assume that if a specific complex motor task is well practiced, the corresponding motor program becomes more efficient and needs fewer cortical assemblies of neurons, and thus might be localized unilaterally within the left-hemisphere. A TMS study (Tinazzi and Zanette, 1998) has shown evidence of increased excitability of cortical motor outputs targeting the unmoving muscles during contralateral complex sequential finger movements (but not during the execution of simple repetitive movements) which disappeared with over-training of the specific motor task. These physiological data support the assumption of an increasing manual asymmetry in complex tasks that are well practiced. The authors conclude that during motor learning there is an interhemispheric transfer of information, possibly in order to inhibit the opposite hemisphere from interfering when a unimanual movement is required. Unfortunately, only right-handed finger movements were investigated. A use-dependent functional reorganisation in the motor system is also reported by Jäncke et al. (2000), who found that cortical activation in primary and secondary motor areas for complex bimanual movements was smaller in professional pianists than in controls. The authors suggest that "long lasting extensive hand skill training of the pianists leads to a greater efficiency which is reflected in a smaller number of active neurons needed to perform given finger movements" (Jäncke et al., 2000, p. 177).

In the current study, the motor experience of the subjects was perhaps not specific enough to the tasks employed to affect laterality observations. In any case, McManus et al. (1986, p. 472) showed that "hand differences in tapping are not a consequence of differential practise between hands". However, more motor experience was related to a higher overall tapping rate and a reduced overall intertap variability in complex sequential finger tapping. Hence, the effect of practice and /or experience on manual asymmetries remains unclear.

Sex differences were also observed in this study. Overall, men tapped more rapidly and more regularly than women, which is strongly supported by other studies (Bornstein, 1986; Peters, 1980; Peters and Durding, 1979; Ruff and Parker, 1993; Schmidt et al., 2000) and is presumably a result of sex hormone-related effects on the size of fast-twitch fibers in muscles (Schmidt et al., 2000). An explanation for the significant interaction between task complexity and sex in tapping rate might be that the impact of a peripheral physiological advantage in males during a simple motor task is increasingly balanced by the advantage of females in motor tasks with a higher complexity level. Sex differences in manual asymmetries were not found. Unexpectedly, the reduction of manual asymmetry in complex finger tapping was particularly pronounced in the less demanding of the two complex tasks (complex 1 condition). That is, although the overall performance, as reflected in tapping rate and intertap variability, was significantly higher in the complex 1 condition than in the complex 2, manual asymmetry was more pronounced in the complex 1 condition. This might indicate that the relationship between task complexity and manual asymmetry is not monotonic, and/or that additional properties of the task affect the influence of task complexity on manual asymmetry.

Acknowledgements. This work is supported by grant HA 3285/1-1 of the Deutsche Forschungsgemeinschaft (DFG).

REFERENCES

BORNSTEIN RA. Normative data on intermanual differences on the tests of motor performance. *Journal of Clinical and Experimental Neuropsychology, 8:* 12-20, 1986.

BOROD J, CARON HS and KOFF E. Left-handers and right-handers compared on performance and preference measures of lateral dominance. *British Journal of Psychology, 5:* 177-185; 1984.

BRYDEN PJ. Lateral preferences, skilled behavior and task complexity: Hand and foot. In: MK Mandal, MB Bulman-Fleming and G Tiwari (Eds), *Side Bias: a Neuropsychological perspective.* Dordrecht: Kluwer Academic Publishers, 2000, pp. 225-248.

BRYDEN PJ, PRYDE KM and ROY EA. A performance measure of the degree of hand preference. *Brain and Cognition, 44:* 402-414, 2002.

COLEBATCH JG, DEIBER MP, PASSINGHAM RE, FRISTON KJ and FRACKOWIAK RSJ. Regional blood flow during voluntary arm and hand movements in human subjects. *Journal of Neurophysiology, 65:* 1392-1401, 1991.

ELLIOTT D, HEATH M, BINSTEAD G, RICKER KL, ROY EA and CHUA R. Goal directed aiming: Correcting a force-specification error with the right and left hands. *Journal of Motor Behavior, 31:* 309-324, 1999.

FINK GR, MARSHALL JC, HALLIGAN PW, FRITH CD, DRIVER J, FRACKOWIAK SJ and DOLAN RJ. The neural consequences of conflict between intention and the senses. *Brain, 122:* 497-512, 1999.

FLOWERS K. Handedness and controlled movement. *British Journal of Psychology, 66:* 39, 1975.

HAALAND KY and HARRINGTON D. Hemispheric control of initial and corrective components of aiming movements. *Neuropsychologia, 27:* 961-969, 1989a.

HAALAND KY and HARRINGTON D. The role of hemispheres in closed loop movements. *Brain and Cognition, 9:* 158-180, 1989b.

HALPERN DF. *Sex Differences in Cognitive Abilities.* Mahwah: Lawrence Erlbaum Associates, 2000.

HARRINGTON DL and HAALAND KY. Hemispheric specialization for motor sequencing: Abnormalities in levels of programming. *Neuropsychologia, 29:* 147-163, 1991.

HAUSMANN M, BEHRENDT-KÖRBITZ S, KAUTZ H, LAMM C, RADELT F and GÜNTÜRKÜN O. Sex differences in oral asymmetries during word repetition. *Neuropsychologia, 36:* 1397-1402, 1998.

HAUSMANN M, ERGUN G, YAZGAN Y and GÜNTÜRKÜN O. Sex differences in line bisection as a function of hand. *Neuropsychologia, 40:* 235-240, 2002.

HAUSMANN M and GÜNTÜRKÜN O. Sex differences in functional cerebral asymmetries in a repeated measures design. *Brain and Cognition, 41:* 263-275, 1999.

HELLIGE JB. *Hemispheric asymmetry: what's right and what's left.* Cambridge: Harvard University Press, 1993.

HOLM S. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6:* 65-70, 1979.

JÄNCKE L, SHAH NJ and PETERS M. Cortical activation in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cognitive Brain Research, 10:* 177-183, 2000.

KIMURA D. *Sex and cognition.* Cambridge: MIT Press, 1999.

KINSBOURNE M and HISCOCK M. Asymmetries of dual task performance. In JB Hellige (Ed), *Cerebral Hemisphere Asymmetry: Method, Theory and Application*. New York: Praeger, 1983, pp. 255-334.

LOMAS J. Competition within the left hemisphere between speaking and unimanual tasks performed without visual guidance. *Neuropsychologia, 18:* 141-149, 1980.

LOMAS J and KIMURA D. Intrahemispheric interaction between speaking and sequential manual activity. *Neuropsychologia, 14:* 23-33, 1976.

MCGLONE J. Sex differences in human brain asymmetry: A critical survey. *Behavioral and Brain Sciences, 3:* 215-263, 1980.

MCMANUS IC, KEMP RI and GRANT J. Differences between fingers and hands in tapping ability: Dissociation between speed and regularity. *Cortex, 22:* 461-473, 1986.

OLDFIELD RC. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia, 9:* 97-113, 1971.

PETERS M. Why the preferred hand taps more quickly than the non-preferred hand: three experiments on handedness. *Canadian Journal of Psychology, 34:* 62-71, 1980.

PETERS M and DURDING B. Left-handers and right-handers compared on a motor task. *Journal of Motor Behavior, 11:* 103-111, 1979.

PROVINS KA and MAGLIARO J. The measurement of handedness by preference and performance tests. *Brain and Cognition, 22:* 171-181, 1993.

PULVERMÜLLER F, LUTZENBERGER W, PREISSL H and BIRBAUMER N. Motor programming in both hemispheres: An EEG study of the human brain. *Neuroscience Letters, 190:* 5-8, 1995.

PULVERMÜLLER F and MOHR B. The concept of transcortical cell assemblies: A key to the understanding of cortical lateralization and interhemispheric interaction. *Neuroscience and Biobehavioral Reviews, 20:* 557-566, 1996.

RAO SM, BINDER JR, BANDETTINI PA, HEMMEKE TA, YETKIN FZ, JESMANOWICZ A, LISK LM, MORRIS GL, MUELLER WM, ESTKOWSKI LD, WONG EC, HAUGHTON VM and HYDE JS. Functional magnetic resonance imaging of complex human movements. *Neurology, 43:* 2311-2318, 1993.

ROLAND PE, LASSEN B, LASSEN NA and SKINHOJ E. Supplementary motor area and other cortical areas in organization of voluntary movements in man. *Journal of Neurophysiology, 43:* 118-136, 1980.

RUFF M and PARKER SB. Gender-and-age-specific change in motor speed and eye-hand coordination in adults: Normative values for the finger tapping and grooved pegboard tests. *Perceptual and Motor Skills, 76:* 1219-1230, 1993.

SCHMIDT SL, OLIVEIRA RM, KRAHE TE and FILGUEIRAS CC. The effects of hand preference and gender on finger tapping performance asymmetry by the use of an infra-red light measurement device. *Neuropsychologia, 38:* 529-534, 2000.

SEITZ RJ and ROLAND PE. Learning of sequential finger movements in men: A combined kinematic and positron emission tomography (PET) study. *European Journal of Neuroscience, 4:* 154-165, 1992.

SERGENT V, HELLIGE JB, CHERRY B. Effects of responding hand and concurrent verbal processing on time-keeping and motor-implementation processes. *Brain and Cognition, 23:* 243-262, 1993.

SOLODKIN A, HLUSTIK P, NOLL DC and SMALL SL. Lateralization of motor circuits and handedness during finger movements. *European Journal of Neurology, 8:* 425-434, 2001.

STEENHUIS RE. Hand preference and performance in skilled and unskilled activities. In: D Elliott and EA Roy (Eds) *Manual asymmetries in motor performance*. Boca Raton, CRC Press, 1996, pp. 123-142.

THORNTON CD and PETERS M. Interference between concurrent speaking and sequential finger tapping: Both hands show a performance decrement under both visual and non-visual guidance. *Neuropsychologia, 20:* 163-169, 1982.

TINAZZI M and ZANETTE G. Modulation of ipsilateral motor cortex in man during unimanual finger movements of different complexities. *Neuroscience Letters, 244:* 121-124, 1998.

TODOR JI, KYPRIE PM and PRICE HL. Lateral asymmetries in arm, wrist and finger movements. *Cortex, 18:* 515-523, 1982

TROPE I, FISHMAN B, GUR RC, SUSSMAN NM and GUR RE. Contralateral and ipsilateral control of fingers following callosotomy. *Neuropsychologia, 25:* 287-291, 1987.

VOYER D. On the magnitude of laterality effects and sex differences in functional lateralities. *Laterality, 1:* 51-83, 1996.

Markus Hausmann, Biopsychology, Institute for Cognitive Neuroscience, Faculty of Psychology, Ruhr-University Bochum, GAFO 05/620, D-44780 Bochum, Germany. e-mail: markus.hausmann@ruhr-uni-bochum.de

(*Received 21 August 2002; reviewed 2 October 2002; revised 2 January 2003; accepted 16 January 2003; Action Editor Henry A. Buchtel*)