Motor control and cerebral hemispheric specialization in highly qualified judo wrestlers

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Abstract

With the purpose of investigating motor and cognitive lateralization profiles associated with long-term motor training, we investigated differences in hemispheric specialization between proficient judo sportsmen and controls through the assessment of a number of handedness and footedness items including postural preferences as well as dichotic listening and lateralized visual field tests. Our data show that: (1) the different handedness and footedness items did differently relate to each other within the athlete and control groups as revealed by a principle component analysis (PCA); (2) stand side correlated differently to these motor profile factors in athletes and controls; (3) athletes preferred more frequently to perform certain movements with the left hand than controls, although overall right-handed; (4) this was especially true for athletes which proved to be most proficient/skilled; and (5) in a lateralized verbal listening task and a lateralized visual field task athletes revealed enhanced right-hemispheric involvement relative to controls. Our results suggest that during motor and postural skill acquisitions (long-term judo training) lateral preferences are modified, probably due to neuroplasticity. Moreover, the present findings support the multidimensional view of handedness by Steenhuis and Bryden [Cortex 25 (1989) 289] and the notion of a right-hemispheric "praxis system" involved in skilled action routines within peripersonal space [Brain and Cognition 23 (1993) 181]. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Right-hemispheric praxis; Motor profile; Postural and cognitive asymmetry; Training; Skill; Plasticity

1. Introduction

The majority of motor asymmetries in right-handed human subjects indicates left-hemispheric motor dominance [21,28], which is also evidenced by the fact that apraxias are almost exclusively seen after damage to the left hemisphere [16,20,22,39]. The most intense investigated motor asymmetry is handedness, and right-handedness has closely been related to left-hemispheric language dominance. More recently, however, it has been postulated that postural asymmetry, and not handedness, is the better predictor for language lateralization [8,11], but see [38] for the close relationship between postural and manual asymmetries. One important aspect of handedness, which contradicts the view that manual preferences are exclusively governed by one neural system within the left hemisphere, lies in the fact that handedness is multidimensional and can lateralize differently for certain actions in the same subject (e.g. distal–proximal, unimanual–bimanual actions) [15,36]. Already Geschwind emphasized the sparing of axial movements in left hemisphere damaged patients with ideomotor apraxia [14] and much earlier Jackson noted the dissociation between “voluntary” versus “automatic” movements in apraxia [19], suggesting that axial and “automatic” movements can be governed by separate neuronal systems. Indeed, automatic whole-body movements are far from being consistently lateralized. A slightly more frequent rightward bias in the “stepping test” [29], no side preference in rotation behavior [4] and a left-sided predominance for turns during physical exercise [35] have been reported. Moreover, the existence of a specific “praxis system” of the right hemisphere for over-trained, “automatic” actions has been proposed by Rapcsak et al. [30]. These authors presented a patient with extensive damage to the left, language dominant hemisphere who was severely impaired in pantomiming transitive gestures with the left hand. However, the patient’s...
Such a priori selection might be based on neuro-anatomical factors or the low frequency of non-right-handers in the overall population, latter making encounters with non-right-handers relatively infrequent and, thus, more unfamiliar for the opponent (“unfamiliarity effect” leading to a fitness advantage for non-right-handers) [12,18,31]. In the present study, athletes matched controls regarding overall hand and foot laterality scores. Non-right-handedness was not more frequent in the athlete group also according to the subjects’ self-classification. A priori selection of left-handedness/ambidexterity in sports is, thus, unlikely to confound our results. Accordingly, group differences of our study are likely to depend on experience.

Taken together, the present study was designed to investigate if highly qualified sportspersons, i.e. judo wrestlers, reveal different motor profiles and lateral preference patterns than untrained controls, and thus, to add further evidence on functional reorganization with respect to lateralization due to over-training. Since athletes have previously been reported to show better spatial information processing than non-athletes [33], we also investigated training-related changes of hemispheric specialization with respect to cognition, namely visuo-spatial and verbal functions through visual hemifield and dichotic testing. Finally, neural correlates of visuo-spatial functions have been reported to differ between left- and right-handed athletes. Left-handed/standed fencers exhibit shorter latencies of visually evoked potentials than right-handed/standed fencers [37]. For this reason, we also included comparisons between left- and right-standed athletes.

2. Methods

2.1. Subjects

A total of 34 black-belted male judo wrestlers (range: 16–35 years; mean ± S.D. = 25 ± 6.71) and 35 healthy male controls (range: 18–40 years; mean ± S.D. = 28 ± 6.03) without significant sport training and experience were tested. In the control group, there were two left-handers by self-report, while in the athlete group there was only one. The remaining participants were right-handed by self-report.

2.2. Lateralization measures for motor acts and cognition

2.2.1. Stand side

Every subject had to indicate the stand in which they wrestle: left (−1), either (0), or right (1). All athletes provided immediate and concrete answers. When controls hesitated, they had to show with which shoulder they would try to knock in a closed door or to push a huge heavy object. The pushing shoulder was considered as coinciding with stand side.

2.2.2. Handeness

Subjects (SS) were asked which hand they use to write, to draw, to throw a ball, to sweep a floor, to hold a spoon, a
Hammer, scissors, a comb, a toothbrush, a knife, a screwdriver, a tennis racket, to strike a match, to open a tube, to deal cards, or to thread a needle. The performing hand was considered to be the preferred one. Additionally, SS were asked to perform the following actions: applauding—the hand which carries out the striking movement is considered the dominant one; clasping the fingers—the thumb of the dominant hand is in the upper position; folding the arms in front of the chest—the arm situated on top of the other arm is the dominant one. Movement accuracy was one in strength for more than 20 kg (sum of all three trials for each hand—the hand exceeding the other three times for each hand—the hand exceeding the other). If dots made by both hands were partly or completely inside or outside the 10 cm radius, neither hand was labeled dominant. If all dots made by one hand were located within a 10 cm radius from the center, this hand was judged to be dominant. If dots made by both hands were partly or completely inside or outside the 10 cm radius, neither hand was labeled dominant.

2.2.3. Footedness

To determine the dominant leg the following tests were applied: SS were asked with which leg they kick a ball, push in a long jump (the pushing leg) and wag up in a high jump (the wagging leg). Additionally, SS were asked to perform the following actions: crossing legs—the dominant leg being the upper one; place a knee on a chair; take a step forward and backward—the dominant leg starts the step; write with one foot words on the floor—the dominant leg. Finally, SS had to walk blind-folded forward and backward—the dominant leg is the performing one. Finally, SS had to walk blind-folded forward (5 m)—the leg opposite to the deviation direction was the performing one. Finally, SS had to walk blind-folded forward (5 m)—the leg opposite to the deviation direction was labeled dominant.

2.2.4. Dichotic testing

SS were simultaneously offered two different words (nouns of one syllable), one word to each ear by headphones. A total of 94 pairs of words were presented in series (16 series of 4 pairs and 5 series of 6 pairs). The interval between word pairs was 0.5 s and between series 40 s. Before being tested, every subject received a routine tonal audiogram. SS with an auditory deficit were excluded from further investigation.

Every subject was instructed to listen attentively to the words presented to the left and right ear (without accentuating attention on any ear), and to try to remember as many words as possible. Between two series, SS were asked to recall as many words as possible in any order. Two runs of all 21 series were conducted in each subject. After the first 21 series, headphones were inverted and the experiment was started again. All words were now presented in the same order to the other ear. In order to familiarize subjects with the experimental condition, a practice trial of 12 word pairs was presented in advance.

2.2.5. Visual hemifield testing

2.2.5.1. Stimuli. Sixteen black and white line drawings were used consisting of eight 3–10 edged rectilinear regular polyhedrons and eight 3–10 rectilinear regular ray stars. The surface was identical for all figures and their mean diameter (circumscribed circumference) was approximately 4.7. Thirty-six drawing pairs were constructed in a way that the number of sides/rays in each pair differed by no more than 30%.

2.2.5.2. Procedure. SS had to fixate during 500 ms a black dot presented on a white background in the center of a computer screen. The screen was located 60 cm from the subject’s eyes. Each drawing pair was presented for 80 ms on the white background in a bilateral presentation mode, with the two stimuli projected simultaneously to the left and right visual fields (L VF/R VF), respectively. The center of the test picture and the central fixation dot were separated by 5.5°. Each presentation was immediately followed by a full screen pattern mask consisting of overlapping polyhedrons and stars. After each presentation, all stimuli were presented simultaneously on the screen and SS had to indicate which figure has been presented on the left and right to the fixation point. Afterwards, the black dot reappeared for 500 ms before the next drawing pair was presented. Each test pair had its mirror reflection in the same series. The sequence of test series was identical for all subjects.

2.2.6. Proficiency

Proficiency of the wrestlers was evaluated according to the following classification: (1) prize-winners of the city championship once or several times (n = 6); (2) prize-winners of the city championships constantly during sport career (n = 18); (3) prize-winners of the national championships of Russia (n = 10).

2.3. Laterality index scores

The following laterality scores were calculated for further statistical analysis.

2.3.1. Handedness

Hand asymmetry was determined by the laterality index LQH:

LQH = \( \frac{\sum r - \sum l}{\sum r + \sum l} \times 100 \), \( -100 \leq LQH \leq +100 \)

whereby “\( \sum r \)” (“\( \sum l \)” represents the sum of all handedness items (see Section 2.2.2) for which the right (left) hand
was preferred. A “LQ DL”-value higher than +15% was considered to reflect right-handedness, lower than −15% to reflect left-handedness and values between −15 and 15% as mixed-handedness, respectively [5,27].

2.3.2 Footedness

Foot asymmetry was determined by calculating an analog laterality index as for handedness (LQ F) including all nine footedness items (see Section 2.2.3).

2.3.3 Dichotic listening

The right- or left-ear advantage (REA/left-hemisphere advantage or LEA/right-hemisphere advantage) was determined through a lateral ear preference index (LQ VH) using the conventional formula:

$$LQ_{VH} = \frac{\sum_{m=1}^{3} \text{cr}_m - \sum_{m=1}^{3} \text{cl}_m}{\sum_{m=1}^{3} \text{cr}_m + \sum_{m=1}^{3} \text{cl}_m} \times 100$$

whereby a negative (positive) “LQVH”-value means that the hit rate in the LVF (RVF) (i.e. right (left) hemispheric dominance) is higher than in the RVF (LVF). Those cases in which the coefficient was between −15 and +15 were considered to be symmetric in visuo-spatial functions.

2.4 Statistical analysis

Lateral preference has usually been determined unfactorially (laterality index scores) [27] and multifactorially by grouping interrelated parameters into factors [36]. For the present study, both statistical approaches were applied. First, laterality index scores (handedness, footedness, dichotic listening and visual hemifield testing) were compared between groups (control group versus athletes; left-standed athletes versus right-standed athletes) using Mann–Whitney U-tests. Second, principal component analyses (PCA) with Varimax rotation were conducted for handedness and footedness items, respectively. Factor loadings greater than 0.7 were considered salient for analysis. Only factors with eigenvalues greater than one were interpreted. Data were factor-analyzed for controls and athletes separately. The motor profile items, which had a low variability in the examined groups or lead the matrices to become singular, were excluded from further statistics. This reduction resulted in 11 handedness items (throwing a ball, holding a hairbrush, a knife, a hammer, a screwdriver, threading a needle, hand clapping, holding a broom, hand strength and accuracy) and six footedness items (pushing leg, wagging leg, kicking a ball, placing a knee on a chair, writing by foot, walking with eyes closed) for the PCA.

According to the results of the PCA, the between groups differences were reassessed. For each factor, frequency distribution of lateral preferences was compared between groups using one-sampled Chi-square tests. Differences of laterality index scores recalculated for each of the factors were evaluated using Mann–Whitney U-tests.

In addition, to evaluate directional dependencies of wrestling stand side with motor and cognitive specialization measures, we intercorrelated stand side with the motor and cognitive parameters within groups using the Kendall tau (τ) index.

3 Results

3.1 Group differences

3.1.1 Differences of laterality index scores in athletes versus controls and frequency distribution

The laterality index scores for handedness (LQ H) and footedness (LQ F) did not differ significantly between controls (LQ H: mean = 59.2; S.E. = 4.75; range: −32 to 93.26; LQ F: mean = 33.2; S.E. = 5.64; range: −73 to 72.73) and athletes (LQ H: mean = 61.8; S.E. = 4.23; range: −27 to 95.5; LQ F: mean = 26.7; S.E. = 5.69; range: −64 to 81.8)

The statistics on the dichotic listening scores (LQ VH) as well as the visual hemifield testing (LQ VH) both revealed significant differences between controls (LQ VH: mean = 19.0; S.E. = 2.2; range: 0−61; LQ VH: mean = 6.7; S.E. = 3.71; range: −59 to 24) and athletes (LQ VH: mean = 8.88; S.E. = 2.95; range: −20 to 60; LQ VH: mean = 17.8; S.E. = 3.84; range: −71 to 33; LQ VH: U = 382; P = 0.02; LQ VH: U = 408; P = 0.025). Table 1 shows that controls have a clear right-ear advantage in dichotic listening (left-ear versus right-ear advantage = 0.77% of all controls), and a slight LVF advantage in visual processing (LVF versus RVF advantage: 37.17% of all controls). They, thus, show a specialization of the left hemisphere for verbal functions, and a slight
advantage of the right hemisphere for visuo-spatial functions, as would be expected. In athletes as compared to controls, the right-ear advantage (left-hemispheric dominance for verbal functions) is reduced, and the LVF advantage (right-hemisphere advantage for visuo-spatial functions) is enhanced (Table 1: left-ear versus right-ear advantage = 18:47% of all athletes: LVF versus RVF advantage: 62:9% of all athletes). Thus, both lateralized cognitive tasks suggest a shift towards more right-hemispheric involvement in athletes relative to controls.

3.1.2. Difference of laterality index scores and proficiency level in left-standed athletes versus right-standed athletes

Comparisons of the laterality indices LQH, LQF, LQDL, and LQVH between right- and left-standed athletes were all not significant (all U > 102; all P > 0.23). A significant difference between right- (mean = 1.94; S.E. = 0.15) and left-standed athletes (mean = 2.46; S.E. = 0.18) was found for proficiency level only (U = 69.5; P = 0.02), showing that left-standed athletes are more proficient.

3.2. Factor analysis

3.2.1. PCA for handedness

In controls, a two factor solution best fitted the data and accounted for 78% of the variance in hand preference, while in athletes, a three-factor solution best fitted the data which accounted for 73% of the variance (Tables 2 and 3). Items of the first and second factors in athletes are different regarding the space towards which the actions are directed. Most of the items of factor 1 are directed to a goal in peripersonal space, while all three actions of factor 2 are centered on the body (personal space). In controls, these items form a single factor. In other words, the items compounding the first factor in controls are separated into two factors in athletes loading “peripersonal” items on the first and “body-centered” manipulations on the second factor (Table 3).
3.2.2. PCA for footedness

In controls, a two-factor solution best fitted the data and accounted for 65% of the variance (Tables 4 and 5). In athletes, a three-factor solution best fitted the data which accounted for 60% of the variance (Tables 4 and 5). Factor 1 of controls contains proximal actions, which require maximal or sub-maximal effort for performance. Factor 2 unites finer leg actions for which less effort, but more precision is needed. In athletes, the “striking a ball” task loads on the same factor as fine movements (“placing knee on a chair”; “writing with a foot”), probably indicating that for more experienced athletes this is a task of precision rather than strength. The fact that the “wagging leg” loads on a separate factor in athletes could be due to the necessary coincidence of the wagging leg with the stand side for wrestling biomechanics (see Section 4).

3.3. Reassessing of group differences according to the PCA results

To calculate the indices LQH and LQF, a multitude of handedness and footedness items were taken into account. That is, items that are usually strongly lateralized (e.g., tool items) were mixed with less clearly lateralized items (e.g., clapping fingers, crossing arms). This might confound possible differences in hand/foot laterality between groups. The PCA, reordering items according to their degree of lateralization, indeed indicated that several subgroups of items might be distinguished. Some items clustered differently in controls and athletes, although there was considerable overlap between the groups, at least for the handedness items (see Table 3). The handedness items of factor 1 in controls correspond largely to the handedness items collapsed over factors 1 and 2 in athletes. The remaining handedness factors with only few items (factor 2 in controls and factor 3 in athletes) also overlap between controls and athletes in having their main item (hand accuracy) in common. To further test for group differences in lateral hand preferences, frequency distributions and laterality indices were compared between controls and athletes for all factors of overlap separately (factor 1 (controls) versus factor 1 (athletes); factor 1 (controls) versus factor 2 (athletes); factor 2 (controls) versus factor 3 (athletes)). Since there were no strong overlaps regarding foot factors, no comparisons on lateral foot preferences were performed between these two groups. Comparisons were also performed between left- and right-standing athletes.

3.3.1. Lateral preferences in controls and athletes for each factor

Fig. 1A depicts the frequency distribution for the main overlapping factors (factor 1 in controls and factors 1 and 2 in athletes). Chi-squares showed that there is a statistically significant shift towards more left-sided choices in athletes (factor 2) when compared to controls (factor 1) (Chi-square = 19.7; \( P < 0.0001 \)). No other comparison was significant.

This difference also proved to be significant for the laterality index LQH collapsed over factor 2 (athletes) versus factor 1 (controls) (U = 276; \( P = 0.00013 \)), indicating more left-sided choices in athletes. No other comparison was significant. For mean values and standard errors of LQH, see Table 7.

It might be argued that the hand difference between athletes and controls reported above is strongly influenced by hand clapping (i.e. a rather uncommon handedness item), since this item loaded only in athletes on the factor included in the comparison (factor 2 (athletes) versus factor 1 (controls), see Table 3). To make sure that hand clapping is not the sole source of the hand difference, factors were compared between groups without the finger clapping data. The hand difference between athletes and controls remained qualitatively unchanged (Fig. 1B) and statistically significant (Chi-square = 5.9; \( P = 0.01 \)).
3.3.2. Lateral preferences in right- and left-stanced athletes for each factor

Differences between left- and right-stanced athletes are most obvious for the first handedness factor (goal oriented actions in peripersonal space) and the third footedness factor (the wagging leg) (Fig. 2). These two factors represent in left-standers those lateral preferences with an increased left-sided or no lateral bias compared to right-standers. Left or no side preference for items of the first handedness factor amounted to 21% for left-standers versus 3.7% for right-standers. For the third footedness factor, the proportion of left or no side preference was 60% in left-standers versus 11% in right-standers. Chi-square comparisons for hand preference and side of stand revealed that the left hand was significantly more often preferred in left-standers (n = 13) than in right-standers (n = 2) (Chi-square = 9.48; P = 0.002). A similar comparison for foot items almost reached significance (left-side preference in right-standers versus left-standers n = 2 versus n = 7) (Chi-square = 2.96, P = 0.08). No other comparisons proved to be significant.

The LQs, recalculated according to the results of the PCA, revealed a significant difference for the third footedness factor (the wagging leg), i.e. left-standers (mean ± S.E. = −6.7 ± 24.8) chose less often the right leg than right-standers (mean ± S.E. = 77.8 ± 15.2) (U = 71; P = 0.005).

3.4. Correlation dependencies

3.4.1. Relationships of wrestling stand with handedness items

In athletes, significant correlations were found for wrestling stand and “peripersonal” tasks (holding a knife, a hammer, a screwdriver, a broom, see Table 8). Thus, the stand side in athletes is exclusively correlated with lateralization of items belonging to “peripersonal” actions, while correlations with items of both “peripersonal” and “body-centered” actions were observed in controls (see Table 8). Correlations for the remaining handedness items were not significant (all τ < 0.29; P > 0.068).

Table 8

<table>
<thead>
<tr>
<th>Group</th>
<th>Test items</th>
<th>Correlation coefficient (τ)</th>
<th>P-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Controls</td>
<td>Throwing a ball</td>
<td>0.60</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Holding a toothbrush</td>
<td>0.49</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Holding a hairbrush</td>
<td>0.37</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Holding a knife</td>
<td>0.36</td>
<td>0.003</td>
</tr>
<tr>
<td>Athletes</td>
<td>Holding a knife</td>
<td>0.34</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Holding a hammer</td>
<td>0.34</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Holding a screwdriver</td>
<td>0.20</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Holding a broom</td>
<td>0.27</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>The wagging leg</td>
<td>0.47</td>
<td>0.0008</td>
</tr>
<tr>
<td></td>
<td>Proficiency</td>
<td>−0.32</td>
<td>0.009</td>
</tr>
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</table>

Table 6

<table>
<thead>
<tr>
<th>Factor comparisons</th>
<th>Preference</th>
<th>Left</th>
<th>No</th>
<th>Right</th>
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<tbody>
<tr>
<td>Factor 1 (C)</td>
<td>15</td>
<td>18</td>
<td>247</td>
<td></td>
</tr>
<tr>
<td>Chi-square</td>
<td>0.85</td>
<td>1.16</td>
<td>0.0001</td>
<td></td>
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<tr>
<td>P-value</td>
<td>0.35</td>
<td>0.28</td>
<td>0.98</td>
<td></td>
</tr>
<tr>
<td>Factor 2 (A)</td>
<td>23</td>
<td>2</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td>Chi-square</td>
<td>&lt;0.0001</td>
<td>0.10</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td>P-value</td>
<td>0.02</td>
<td>0.17</td>
<td>0.12</td>
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</table>

Table 7

<table>
<thead>
<tr>
<th>Factor</th>
<th>Mean (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 factor (controls)</td>
<td>81.9 (7.6)</td>
</tr>
<tr>
<td>2 factor (controls)</td>
<td>57.7 (9.8)</td>
</tr>
<tr>
<td>1 factor (athletes)</td>
<td>83.3 (7.7)</td>
</tr>
<tr>
<td>2 factor (athletes)</td>
<td>50.9 (6.3)</td>
</tr>
<tr>
<td>3 factor (athletes)</td>
<td>25 (7.7)</td>
</tr>
</tbody>
</table>
3.4.2. Relationships of wrestling stand with footedness items

In controls, no significant correlations were found for wrestling stand and footedness items (all $\tau < 0.31$; all $P > 0.087$). For athletes, stand side was significantly correlated to the wagging leg (Table 8). Correlations for the remaining footedness items and wrestling stand in athletes were not significant (all $\tau < 0.25$; all $P > 0.11$). Given the fact that in athletes the “wagging leg” is emerging in a separate factor (see PCA, Table 5) and is strongly correlated to stand side, the “wagging leg” was analyzed in relation to another fundamental footedness parameter: the pushing leg. The wagging and the pushing leg were significantly negatively correlated in controls ($\tau = -0.30; P = 0.01$), but not in qualified athletes ($\tau = 0.16; P = 0.69$).

3.4.3. Relationships of wrestling stand with proficiency level and cognitive specialization measures

The only significant correlation between motor profile parameters and individual proficiency was found between stand side and proficiency ($\tau = -0.32; P = 0.009$) (Table 8), indicating that left-standers are more proficient. No significant relationship was found between either visual laterality testing or dichotic testing and wrestling stand side (all $\tau < 0.11$; all $P > 0.32$).

4. Discussion

The present study investigated differences in motor profiles, hemispheric specialization and postural preferences, namely the wrestling stand, between proficient judo sportsmen and controls. A number of handedness and footedness items as well as dichotic listening and lateralized visual hemifield tests were assessed and compared between and within experimental groups.

The main findings can be summarized as follows: (1) the different handedness and footedness items did differently relate to each other within the athlete and control groups as revealed by a PCA; (2) stand side correlated differently to these motor profile factors in athletes and controls; (3) athletes preferred more frequently to perform certain movements with the left upper limb than controls, although overall right-handed; (4) this was especially true for left-standed athletes which proved to be most proficient/skilled; and (5) that in a lateralized verbal listening task and a lateralized visual pattern task athletes revealed enhanced right-hemispheric involvement relative to controls. Overall, our results are indicative of an enhanced right-hemispheric involvement in highly qualified judo athletes not only regarding motor acts but also other cognitive functions.

4.1. Differences in laterality preference patterns and motor profiles between wrestlers and controls: effect of a priori selection or over-training?

Of the 11 handedness items retained for the PCA, three handedness items (factor 2) were more often associated with left-hand use in athletes as compared to controls. In addition, six of these handedness items (factor 1) more often engaged the left hand in the most proficient/skilled (left-standed)
sportsmen. Regarding the dichotic verbal task, around 20% of the athletes showed a left-ear (right-hemisphere) advantage versus 0% in controls. Furthermore, the visuo-spatial task revealed a LVF (right-hemisphere) advantage in around 60% of the athletes, but only in 35% of the control subjects. The most straightforward interpretation of these lateralization differences between athletes and controls is that long-term training in judo is associated with more right-hemispheric involvement. Yet, there is a major confounding mechanism, which is a priori selection for left-handed subjects to become proficient athletes due to a neuro-anatomical advantage or their rarity in the population (effect of unfamiliarity for encounters with left-handers) [12,18,31]. This mechanism would also be expected to lead to lateralization differences between athletes and controls, which however would be unrelated to over-training.

An overrepresentation of left-handed athletes due to a priori selection, however, is unlikely to confound our results. In fact, most of our subjects including athletes were right-handed/right-footed and there was no overall handedness/footedness difference between athletes and controls (~95% versus 90% right-handers, ~70% versus 85% right-footers, Table 1). In addition, all athletes except one classified themselves as right-handed. Significant differences between sportmen and controls were only found when handedness/footedness was compared on items collapsed over specific factors, but these differences were fine-grained and interrelated with specific wrestling characteristics, i.e. most likely conditioned by judo experience (see paragraph below). Thus, although significant, the increased use of the left hand/foot in our athletes is unlikely to be biased by a priori selection of left-handers/ambidexters in sports.

Several aspects of our results are in keeping with the notion that the athletes’ motor profiles have been shaped by their judo experience. First, as shown by the PCA, the majority of handedness parameters formed a single factor in the untrained control group, while a different picture emerged for athletes. The handedness parameters of the latter group loaded on more and different factors than in controls, most likely reflecting a finer and more experienced regulation of motor activities in athletes. With this respect, it is noteworthy how these handedness factor solutions are characterized. In athletes, actions directed to objects in peripersonal space and actions centered on the body loaded on different factors, while in controls these actions compounded a single factor. More importantly, several items belonging to the factor peripersonal, goal-oriented actions correlated in athletes, but not controls with wrestling stand, while no correlation with items of the “body-centered” factor was observed. It is conceivable that actions dealing with objects in peripersonal space and stand side become functional entities through wrestling training, since both are closely linked to how to face an “opponent” in near-space. In other words, our data suggest that within the process of skill improvement, i.e. the formation and perfectioning of new automatisms, the individual motor profiles are influenced in a way that a number of “peripersonal” actions and stand side begin to correspond with respect to lateralization. Second, the view that the motor profiles of our wrestlers may be due to dynamic modifications through practice is further supported by the wrestler-specific relationship between stand side and wagging leg. The coincidence of the wagging leg and the stand side is a necessary component of wrestling biomechanics. It is conceivable that the training process influenced the preference for the wagging leg, the latter becoming dependent on the laterality of the acquired posture (stand) through practice. Note that this also explains the emerging of the “wagging leg” in a separate factor in athletes. Another argument supporting this suggestion is that the negative correlation between pushing and wagging legs does exist only in controls, but not in athletes. This correlation can mean that the former subjects mostly use the stronger (pushing) leg to stand on when wagging. In athletes, on the contrary, probably due to the obligatory shift of the wagging leg towards the stand side and consequent to their experience in the wag inertia use (judo skills contain plenty of wags) the stronger leg can also be preferred for a wag.

It is, thus, suggested that the laterality and motor profiles of our athlete group have evolved through motor adaptations influenced by external factors, namely long-term training. This is compatible with reports that motor profiles and cortical motor representations in healthy subjects do adapt under the influence of long-term experience [9,23,34]. This also agrees with the fact that even in chronic stroke patient, reduced cortical representations of an affected body part can be enlarged in space and increased in excitability by motor rehabilitation procedures [26]. Similarly, it has been shown that motor and perceptual representations in animals are not fixed entities, but rather dynamic and continuously modifiable through experience [6].

4.2. Increased left-hand/foot use with over-training: evidence for a right-hemispheric involvement in praxis

The finding that athletes revealed comparatively more left-sided choices than controls for some actions which are usually driven by the left hemisphere/right hand (factor 2 in athletes, factor 1 in most proficient (left-standed) wrestlers) indicates an enhanced right-hemispheric involvement in motor control. This group difference is in line with (1) Rapcsak’s hypothesis [30] that the right hemisphere has a similar capacity in controlling well-trained movements as the left-hemisphere, and (2) earlier findings showing that motor preferences are multi-dimensional and depend on motor complexity (skill needed for performance) and on participating muscle groups [15,36]. More specifically, Rapcsak et al. [30] proposed that the right hemisphere may have the potential to program and execute familiar, well acquired (automatic) movements for direct manipulations of objects (tools) in peripersonal space, i.e. depending on the context. With this respect, the emerging of “peripersonal actions” in a separate factor in the athletes’ PCA is of
particular interest, since these actions depend on context. They become senseless without direct (muscular, proprioceptive) contact with the concrete object or opponent in the peripersonal space. These actions do lateralize more to the left hand in the most over-trained/proficient athletes (left-handers). Our data, thus, support the view that the right hemisphere plays a role in certain aspects of praxis, namely in the well-acquired manipulation of “objects” in peripersonal space.

In other words, our data suggest that these actions are less dependent on left-hemispheric control than would be expected for “abstract”, non-context-dependent, purposeful movements or learning of new motor sequences [30]. Note in this respect that our results do not disagree with Liepmann’s view that the left hemisphere predominates for praxis [24] and further investigations revealing that left-hemispheric lesions are associated with a disability to acquire motor skills, e.g., action sequences [16,17,20,22,39]. Note also in this regard that our findings do not necessarily generalize to all motor skills. The way over-training affects laterality profiles is expected to depend on the degree of left-hemispheric control for performance of the skill. In contrast to wrestling, tennis and fencing to indicate depend more on dexterity of hand and forearm and playing a musical instrument more on fine-tuned finger sequences. Moreover, movements in tennis and fencing also involve less bimanual coordination. Since such aspects of praxis are strongly controlled by the left hemisphere in right-handed subjects, over-training of these skills would not necessarily be expected to be associated with more left-hand involvement.

4.3. Possible mechanisms of changes in lateral preference with experience: a hypothetical model of right-hemispheric release

It is conceivable that in right-handers the left hemisphere exerts control over all actions of the left hand by suppressing the right hemisphere’s independent capacity for motor control [30]. A possible mechanism for such control of left over-right-hemispheric functions may be transcallosal inhibition [7]. Note that the characteristics of this model does not contradict the proposition that the right hemisphere possesses a “praxis system”. Indeed, a recent transcranial magnetic stimulation study has reported decreased inter-hemispheric inhibition in well-trained musicians [32]. Moreover, Andres et al. [1] found via EEG coherence measures an increased inter-hemispheric coupling during bimanual as compared to unimanual skill acquisition and a decrease when skill was over-learned. Thus, it might be speculated that a decrease in inter-hemispheric inhibition evolving during the process of skill acquisition enables the right hemisphere to influence motor processes to a greater extent than under-trained conditions. As soon as the new skill is over-learned motor programs may be stored in both hemispheres becoming increasingly independent from callosal involvement [13].

Taken together, our data show that highly skilled and over-trained judo wrestlers realize hand and foot actions as well as postures through more right-hemispheric involvement than controls, suggesting a decreased asymmetry regarding motor functions in these athletes. Zaidel and Sperry [40] already proposed that the motor control of acquired automatic movements is likely to be bilaterally represented. In addition, our results suggest that the increased left-hand (left-foot) use in over-trained, highly proficient judo wrestlers applies predominantly for goal-directed movements in peripersonal space reflecting a right-hemispheric role in the control of these kinds of motor acts.

Acknowledgements

This work was in part supported by the “Institut für Grenzgebiete der Psychologie und Psychiatrie”, Freiburg, Germany (Grant no. 690/610 to Christine Mohr), and by the Swiss National Science Foundation (Grant no. 823A-061230 to Gregor Thut).

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