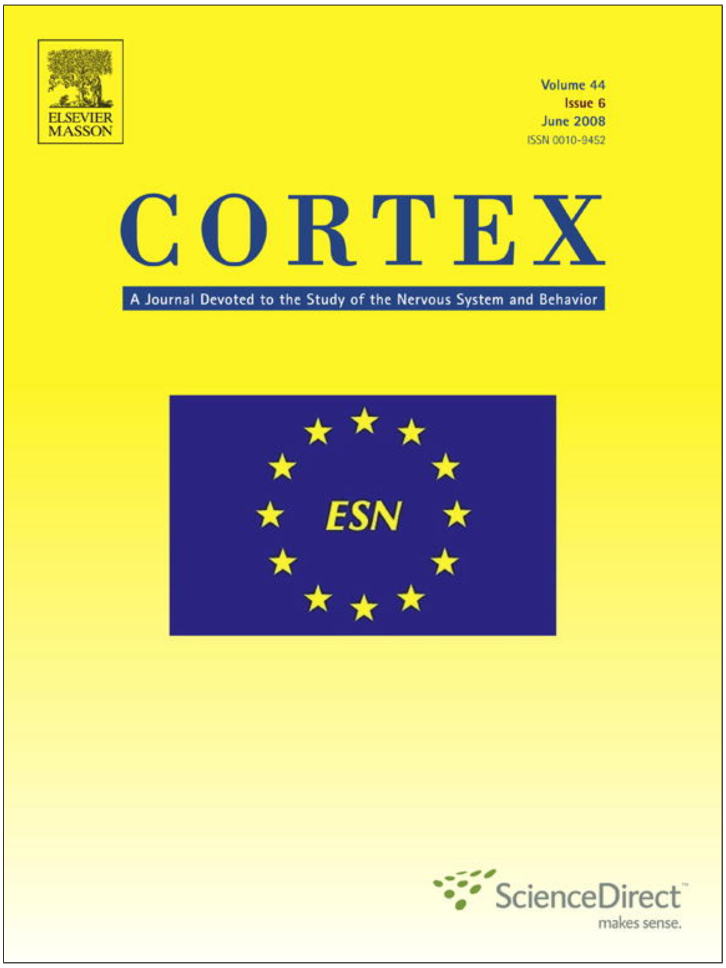
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Note

Categories of manual asymmetry and their variation with advancing age

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ABSTRACT

Manual asymmetries were analyzed in 18- to 63-year-old right-handers in different motor tasks. This analysis aimed at describing the asymmetry profile for each task and assessing their stability across ages. For this purpose, performance of the right and left hands were analyzed in the following aspects: simple reaction time, rate of sequential finger movements, maximum grip force, accuracy in anticipatory timing, rate of repetitive tapping, and rate of drawing movements. In addition, stability of manual preference across ages was assessed through the Edinburgh inventory (Oldfield, 1971). The results indicated different profiles of manual asymmetry, with identification of three categories across tasks: symmetric performance (asymmetry indices close to zero), inconsistent asymmetry (asymmetry indices variable in magnitude and direction), and consistent asymmetry (asymmetry indices favoring a single hand). The different profiles observed in the young adults were stable across ages with two exceptions: decreased lateral asymmetry for maximum grip force and increased asymmetry for sequential drawing in older individuals. These results indicate that manual asymmetries are task specific. Such task specificity is interpreted to be the result of different sensorimotor requirements imposed by each motor task in association with motor experiences accumulated over the lifetime. Analysis of manual preference showed that strength of preference for the right hand was greater in older individuals.

1. Introduction

Results from neuroimaging studies have indicated that the right-handers' left cerebral hemisphere has structural properties that may be correlated with the superior performance of their right hand on a number of motor tasks. In a recent study, Hervé et al. (2005) correlated the central sulcus gray matter volume of the cerebral hemispheres with performance asymmetry on maximum tapping rate in right-handers. They observed that performance of the right hand correlated positively with the left central sulcus gray matter volume. This result suggests a left hemisphere specialization for fast repetitive movements in right-handers. Further investigation has also found increased cortical representation in the somatosensory (Sörös et al., 1999) and in the primary motor (Volkmann et al., 1998) areas of the left hemisphere in right-handers. Yet, Volkmann et al. observed the structural asymmetry detected in the primary motor cortex correlated with performance asymmetry in tasks requiring wrist and finger movements. Namely, the greater the right-hand advantage

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in motor performance the larger the difference in size favoring the left in comparison with the right primary motor area. These results suggest that metric structural asymmetries favoring the left cerebral hemisphere may underlie the right-hand advantage observed in a number of motor skills in right-handers. However, evidence has been presented that manual control is not exerted exclusively by the contralateral cerebral hemisphere. In a study using functional magnetic resonance imaging of cerebral activity, Verstynen et al. (2005) found that while performance of a simple repetitive tapping task was accomplished with lower ipsilateral hemispheric activation, performance on sequential or chord tapping tasks was found to require significantly higher ipsilateral activation. This finding suggests that the right and left cerebral hemispheres interact in different ways, depending on the particular functional requirements of each motor task.

Task-related functional interlateral asymmetry has been observed also in motor behavior. Analysis of performance asymmetries across different motor tasks has revealed distinct profiles. In fast repetitive tapping tasks, for example, a consistent right-hand advantage has been reported. Superior performance of the preferred right hand has been detected early in childhood (Bruml, 1972; Fagard, 1987; Ingram, 1975) and in young adults (Agnew et al., 2004; Hammond et al., 1988; Lutz et al., 2005; Schmidt et al., 2000; Teixeira and Paroli, 2000; Truman and Hammond, 1990). When fast sequential movements are performed with different fingers, on the contrary, a similar (symmetric) performance between hands has been found (Denckla, 1974; Hausmann et al., 2004). These results are in agreement with the pattern of inter-hemispheric cerebral activation observed by Verstynen et al. (2005). Somewhat analogous results have been found for reaction time. In choice (Barthélémy and Boulinguez, 2002; Boulinguez et al., 2000; Carson et al., 1995) or simple (Barthélémy and Boulinguez, 2001) reaction time tasks requiring spatial analysis to detect the imperative stimulus, presented at different spatial locations, a faster response of the left in comparison with the right hand has been observed. Conversely, for simple reaction time tasks without spatial uncertainty as to the site of stimulus presentation similar delays for the two hands have been reported (Carson et al., 1995; Teixeira et al., 1999). These results suggest right hemisphere dominance for visuospatial attention, leading to shorter latencies of the left hand to initiate movements requiring more complex spatial analysis, while initiation of pre-programmed movements seems to be accomplished equally well by both cerebral hemispheres.

It is apparent from the results commented upon thus far that there exists a consistent right or left hand advantage for some motor tasks, while others are characterized by symmetric performance. In the group of tasks featured by right hand advantage are included handwriting (Blank et al., 2000; Provins and Glencross, 1968; Rigal, 1992), aiming at static targets (Boulinguez et al., 2000; Morange-Majoux et al., 2000; Sainburg, 2002), throwing for distance (Teixeira and Gasparetto, 2002; Watson and Kimura, 1989), and manual strength (Finlayson and Reitan, 1976; Ingram, 1975; Rigal, 1992). Symmetric performance between the hands has been observed in tasks requiring anticipatory timing (Teixeira, 2000), grasping moving objects (Teixeira, 1999), and in industrial tasks such as bolt twisting and drilling (Salazar and Knapp, 1996). The third manual asymmetry profile, marked by left hand advantage, has been observed in hand posture tasks (Ingram, 1975; Kimura and Vanderwolf, 1970). Such diversity of between-hand performance profiles indicates that manual asymmetry is task specific, being dependent on the particular functional requirements of each motor action, rather than a general component of motor behavior (see Mamolo et al., 2004, for analogous task specificity in manual preference).

In addition to the particular neural functions required by each motor task, another element that seems to modulate manual asymmetries of performance corresponds to the age-related changes taking place during the lifespan. This assumption has emerged from a number of studies reporting modification of manual asymmetries during early stages of life. For inter-tasks comparisons, it has been found that while timed tapping (Fagard, 1987) and global body coordination actions (Denckla, 1974) are characterized by decreased manual asymmetry, handwriting (Rigal, 1992) is characterized by increased manual asymmetry as children get older. For intra-task comparisons, analysis of handwriting from childhood to adolescence has also revealed variations of manual asymmetry. Blank et al. (2000) observed age-related reduction of performance asymmetry for wrist linear movements, with increased asymmetry for finger linear movements (see also Bryden and Roy, 2005; Roy et al., 2003; Singh et al., 2001). These results suggest that structural and experiential factors taking place during the lifetime are able to modify intrinsic dispositions in the brain configuration associated with manual asymmetry.

Looking at the other extreme of the lifespan developmental spectrum, some age-related changes in brain structure and function are potentially able to lead to global modifications of performance asymmetry in the elderly. In this regard, Dolcos et al. (2002) have summarized evidence for two models of hemispheric asymmetry associated with aging: the right hemisphere-aging model and the hemispheric asymmetry reduction in old adults model. The former proposes that the right cerebral hemisphere shows greater age-related decline than the left hemisphere. In this case, one should observe a faster decline of the processing functions mediated by the right hemisphere as a function of age, including motor control of the left hand. From this perspective, an overall magnification of motor asymmetries would be expected with advancing age. The latter model, on the other hand, proposes that frontal activity during cognitive performance tends to be less lateralized in older than in younger adults. Recent evidence from a neuroimaging study (Hutchinson et al., 2002) has indicated that similar reduction of lateralization of cerebral activity is observed also in movement control. A possible behavioral consequence of a predominant bihemispheric cerebral activation in the elderly would be an overall change of manual asymmetries, but now with reduction of performance asymmetries between the right and the left hand. Modification of the structure of the corpus callosum with aging is a further element possibly affecting manual asymmetry overall in the elderly. The corpus callosum has been found to decline in size (Hayakawa et al., 1989; Suganthy et al., 2003; Weis et al., 1991) and to be altered in its microstructural characteristics (O'Sullivan et al., 2001; Sullivan et al., 2001; Sullivan et al., 2006) in older individuals. As the corpus callosum is the main commissure linking the two cerebral hemispheres, this structural degradation may underlie the observed longer periods for inter-hemispheric communication (Jeeves and Moes, 1996). If results from a computational model of lateralization in cortical maps (Levitan and Reggia, 2000) are applicable to biological systems, decline in communication between cerebral hemispheres should lead to a more symmetric work between the hemispheres as a function of reduced inhibitory callosal interactions. In this case also, a global reduction of manual asymmetries would be predicted as a result of aging.

The issue of variation of manual asymmetries in the elderly has been investigated by Francis and Spirduso (2000). In this investigation they compared motor asymmetries between young adults and elderly individuals in five motor tasks: turning small disks, peg-moving, manual stability, drawing, and repetitive tapping. The results indicted significant between-age differences in two tasks: the elderly group presented a more asymmetric performance on the drawing task, while their performance was more symmetric on the peg-moving task as compared with the young group (cf. Beaton et al., 2000, for contradictory findings). In the other three tasks a right-hand advantage was observed, but no significant age-related difference was found. These results indicate that, contrary to what would be expected from the above reported changes in brain function and structure with aging, there was not an overall modification of manual asymmetry across tasks. Rather, Francis and Spirduso presented some evidence for task-specific changes in manual asymmetry. In this study, however, the authors limited their analysis to the comparison of average indices of lateral asymmetry between ages and tasks. As this analysis does not allow one to differentiate interindividual profiles of manual asymmetry between tasks (cf. Teixeira and Paroli, 2000), important age-related changes in manual asymmetries may have been masked. Additionally, Francis and Spirduso used only tasks characterized by superior performance of the preferred right hand. Since a number of motor tasks are executed with symmetric performance between the hands, as indicated in this review, an aspect of interest about age-related changes of performance asymmetries is whether aging leads to modifications of manual asymmetries in this category of tasks as well.

In the present investigation the experimental strategy consisted of assessing manual asymmetries in right-handed adults, from early to late adulthood, in the performance of motor tasks of different natures. Tasks were selected on the basis of previous studies, with some showing a predominantly symmetric profile and others yielding a right-hand advantage. Among the tasks that have previously been observed to lead to symmetric performance simple reaction time, anticipatory timing, and sequential finger movements were chosen. Among the tasks that have been marked by right-hand advantage manual strength, fast repetitive tapping, and drawing were selected. The main purposes of the study were to identify the profiles of performance asymmetry in the selected motor tasks and compare these profiles across ages. As overall modification of manual asymmetry might potentially lead to modification also of manual preference, a further issue addressed in this study was variation of strength of manual preference across ages.

2. Methods

2.1. *Participants*

Fifty-four healthy males and females participated in the experiment, forming three age groups: 20 (10 male, 10 female; age range: 18–23 years; mean: 20 years), 40 (10 male, 7 female; age range: 36–43 years; mean: 39 years), and 60 (7 male, 10 female; age range: 56–63 years; mean: 59 years) years. University students formed the youngest group, and voluntary participants of physical activity programs of the University of São Paulo composed the other groups. Participants had at least 8 years of formal education, and reported no history of diseases which might impair their performance in the experiment. Assessment of manual preference using the Edinburgh handedness inventory (Oldfield, 1971) indicated that all participants had consistent preference for the right hand across tasks. Experimental procedures were approved by the local Ethics Committee, with participants signing an informed consent form to be admitted in the experiment.

2.2. *Tasks*

The motor tasks employed in the study were as follows.

2.2.1. *Reaction time*

In this task participants were to react as fast as possible to an auditory stimulus, and then perform a fast aiming movement to a solid object. This task was performed using a reaction timer apparatus (Lafayette Instruments Co., model 63017) composed by a control device and two telegraph-like switches. Participants initially held down one of the switches by depressing it with their index finger. In the sequence, a prompt visual signal (LED lighting) was seen, and then after a foreperiod of 2–4 sec (randomized across trials) the imperative stimulus was presented. The imperative stimulus was a loud sound emitted by the control device located near the participant. The task consisted of losing contact with the home switch as fast as possible and then aiming at the spatial target. The time interval between onset of the imperative stimulus and the moment at which contact with the home switch was lost corresponded to reaction time (results from the aiming movement are not reported).

2.2.2. *Sequential finger movements*

This task consisted of touching alternately the thumb with the other four fingers in sequence, starting with the index finger, then the middle, the ring, and the little finger, as fast as possible. The aim in this manual dexterity task was to complete 10 series of finger movements (1 series = one touch to each of the four fingers), in the shortest period of time. On each trial the experimenter prepared the participant through a verbal prompt and, after a regular period of 1 sec, an imperative vocal stimulus was presented. Time to complete the 10 series was measured manually using a stopwatch, starting at the moment that the experimenter provided the imperative stimulus and stopping at the moment that the last between-finger touching was made.

2.2.3. Anticipatory timing

In order to assess temporal accuracy in anticipatory timing a Bassin anticipation timer (Lafayette Instruments Co., model 50575) was used. This apparatus consists of a 152-cm long metallic trackway, holding LEDs spaced by 4.5 cm on its surface. A control device produced a sequenced incandescence of the LEDs, generating the perception of a luminous red spot moving at 2 m/sec from the far to the proximal end of the trackway. Participants stood upright at the proximal end, holding in their hand a switch connected to the equipment through a cable. The task consisted of pressing the switch with the thumb simultaneously with the arrival of the luminous stimulus at the proximal end of the trackway. Temporal accuracy was measured as the modular difference between the time at which the switch was pressed and the time of arrival of the moving stimulus at the criterion position (absolute error).

2.2.4. Maximum grip force

For this task a digital handgrip dynamometer (Takei Kiki Co., Japan) was used. Participants stood upright, keeping their active arm stretched down vertically close to the body. In this position, they were to exert the maximum grip force, by applying a single discrete pull on the dynamometer.

2.2.5. Tapping

In order to assess the capacity to produce fast oscillatory movements at the wrist a mechanical tapping counter was used. This equipment consisted of a small wooden basis of support, and a 6 cm-long vertical metallic stick joined to the basis. The stick was grasped with the thumb, the index and the medium finger, employing a manual prehension similar to that used for handwriting, while the other hand was used to hold the basis of support, keeping it motionless. In order to move the stick vertically up and down, participants had to perform extension and flexion movements at the wrist. The aim in this task was to perform 30 taps as fast as possible, with performance indexed by the time taken to complete a whole sequence of taps. Time was manually measured with a stopwatch.

2.2.6. Drawing

This task consisted of drawing circles of approximately 1 cm in diameter, as fast as possible. More specifically, participants had to draw a sequence of 10 circles in a row on a sheet of paper, within squares printed on the sheet to delimit the space reserved for drawing each circle. Participants moved from the center (sagittal axis) to the left for left-hand movements and from the center to the right for right-hand movements. The aim in this task was to complete the series of 10 circles as fast as possible. The measurement of the time taken to complete a whole sequence of circles in a series was made by using a stopwatch.

2.3. Procedures

Participants filled out the Edinburgh inventory (Oldfield, 1971) in order to assess the magnitude of their manual preferences. Evaluation of motor performance was divided into two sessions, which were conducted on different days. On the first session participants carried out the following tasks: sequential finger movements, drawing, and maximum grip force. On the second session they performed the remaining tasks: reaction time, anticipatory timing, and repetitive tapping. The tasks were performed in the order they were presented here.

For all tasks there were familiarization trials both for the right and the left hand. They had the purpose of introducing participants to the task and reducing performance variability characteristic of initial trials. Given the particular demands of each task, different numbers of familiarization trials were employed: a single trial for maximum handgrip force, and five trials for sequential finger movements, drawing and repetitive tapping. For the reaction time and anticipatory timing tasks 10 trials were provided. The main trials were performed immediately after the corresponding familiarization trials, with five trials for the right hand and five trials for the left hand on each motor task. For familiarization trials knowledge of results was provided immediately after each execution, while in the main trials no knowledge of results was provided. Order of hands was the same across tasks for each participant, and order of right/left hands was counterbalanced across participants. There were intervals of approximately 10 sec between trials for each task, and a longer rest interval of approximately 2 min between one task and the following one.

2.4. Data analysis

Analysis of the results was conducted for the average of the five trials performed with either hand on the main trials. Analysis of lateral asymmetries across ages was made through two-way {3 (age) × 2 (hand)} analyses of variance[1] with repeated measures on the second factor. This statistical model was applied separately for each task. Post hoc comparisons were made through Newman–Keuls procedures. The level of significance was set at $p < .05$ (two tailed test). Further analyses of manual asymmetry were conducted through algebraic and absolute indices of lateral asymmetry. The algebraic index takes into consideration both magnitude and direction of the difference between scores achieved by each hand. Positive signs indicate better performance of the right hand and negative signs indicate better performance of the left hand. Values with similar magnitude but opposite signs nullify each other, resulting in an average value close to zero; this is valid for computation of individual as well as of group averages. The formula used to calculate this index was the following:

$$\left\{ \sum [(L_i - R_i)/(L_i + R_i)]/n \right\} \times 100,$$

where L_i corresponds to each value observed for the left hand; R_i is the corresponding value for the right hand; and n is the number of trials. The order of L_i and R_i in the equation was inverted for maximum grip force, in order to obtain positive values in situations of superior performance of the right hand.

The absolute index of lateral asymmetry was achieved by transforming the results of the subtraction of R_i from L_i in the equation above into modulus, which is simply the index without regard to sign. With this procedure the actual magnitude of performance asymmetry, independent of the

[1] Preliminary analyses were performed including gender as a factor, but no significant effect was found. For this reason, this factor was not considered in the final analyses.

particular direction (right–left) of lateral asymmetry, was calculated. As there are only positive signs in this score, such a variable indicates the average magnitude of lateral asymmetries. For the analysis of both algebraic and absolute indices two-way {3 (age) $\times$ 6 (tasks)} analyses of variance were employed.

3. Results

3.1. *Manual asymmetry in individual tasks*

3.1.1. *Reaction time*

A significant main effect was found only for age [$F(2,51) = 9.04$, $p < .001$]. Post hoc comparisons indicated significant lower reaction times at the ages of 20 ($M = 292.15$ msec) and 40 ($M = 303.18$ msec) years in comparison with the age of 60 years ($M = 328.96$ msec). Absence of significant effects for hand and for the hand by age interaction revealed symmetric performance across ages (Fig. 1a).

3.1.2. *Sequential finger movements*

The analysis indicated a significant main effect for age [$F(2,51) = 6.55$, $p < .005$]. Post hoc comparisons indicated a significantly shorter time to complete the task at the age of 20 years ($M = 10.46$ sec) in comparison with the ages of 40 ($M = 12.45$ sec) and 60 ($M = 12.75$ sec) years, which did not differ. As neither a significant main effect for hand nor a hand by age interaction was found, these results indicate that performance was consistently symmetric across ages (Fig. 1b).

3.1.3. *Maximum grip force*

The analysis indicated a significant main effect for hand [$F(1,51) = 29.06$, $p < .0001$], due to overall higher values for the right ($M = 33.32$ kgf) than for the left ($M = 30.87$ kgf) hand. The age by hand interaction was found to be at the borderline of significance [$F(2,51) = 3.06$, $p = .056$]. As represented in Fig. 1c, this interaction was a consequence of superior values for the right hand at the ages of 20 (right = 34.31 kgf; left = 30.69 kgf) and 40 (right = 35.32 kgf; left = 32.54 kgf) years,

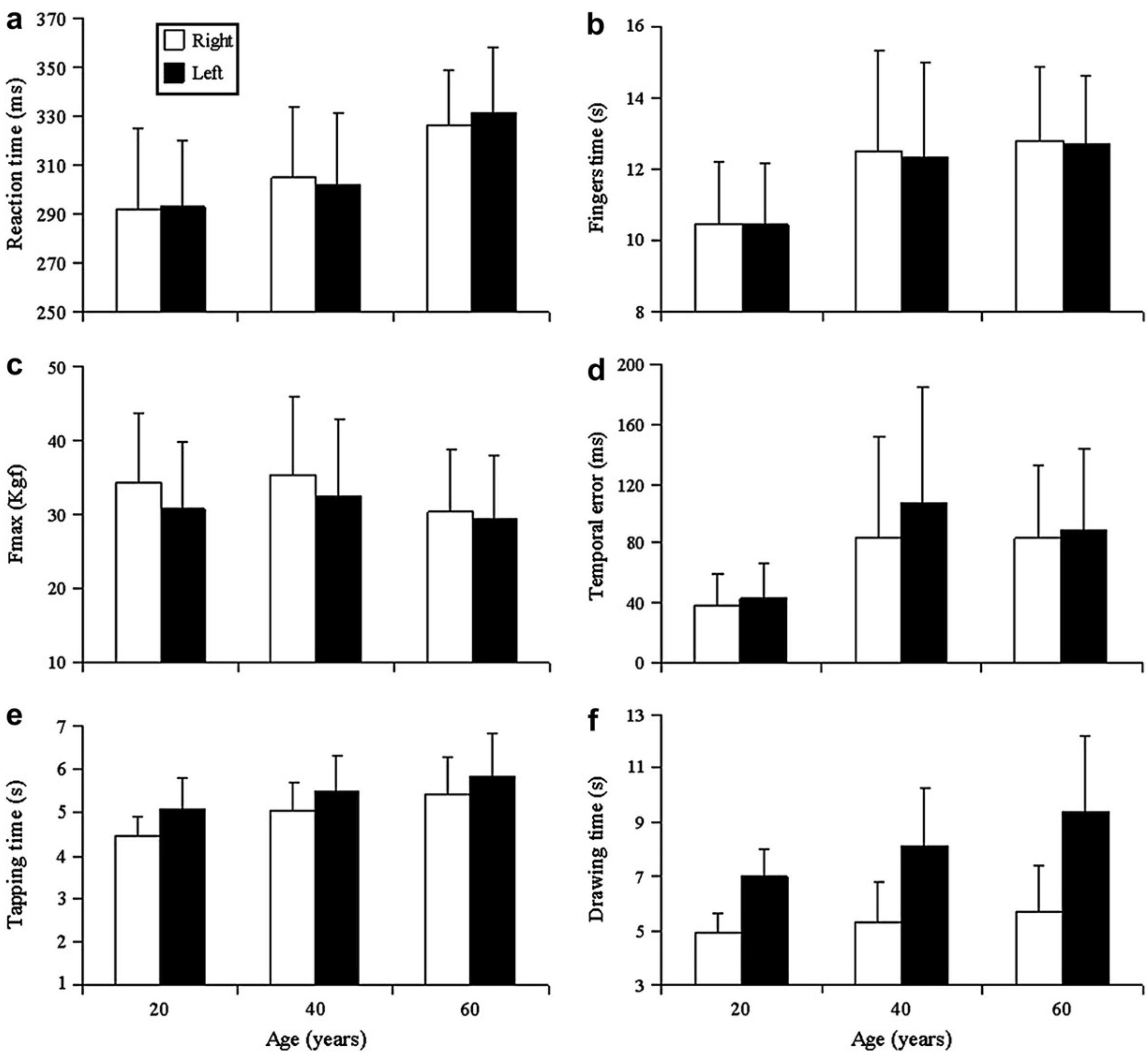

Fig. 1 – Averages for the right and the left hand on the following tasks: (a) reaction time, (b) sequential finger movements, (c) maximum grip force, (d) anticipatory timing, (e) repeated tapping, and (f) drawing; standard deviation represented by vertical bars.

while at the age of 60 years (right = 30.32 kgf; left = 29.38 kgf) no significant asymmetry was detected. Abolition of lateral asymmetry was caused by a greater decline of performance in the right than the left hand from 40 to 60 years.

3.1.4. *Anticipatory timing*

Significant main effects for age [$F(2,51) = 6.94$, $p < .005$] and hand [$F(1,51) = 4.47$, $p < .05$] were detected. The main effect for age was due to fewer temporal errors at the age of 20 years ($M = 40.77$ msec) in comparison with the ages of 40 ($M = 95.57$ msec) and 60 ($M = 86.09$ msec) years, which did not differ. The significant main effect for hand was due to overall fewer errors for the right ($M = 68.52$ msec) in comparison with the left ($M = 79.77$ msec) hand (Fig. 1d).

3.1.5. *Tapping*

Significant main effects for age [$F(2,51) = 6.91$, $p < .005$] and hand [$F(1,51) = 45.05$, $p < .0001$] were detected. The significant main effect for hand indicated a consistent superiority of the right ($M = 4.97$ sec) over the left ($M = 5.47$ sec) hand. Post hoc comparisons for the main effect of age indicated a significantly lower time to complete the task for the age of 20 years ($M = 4.76$ sec) as compared with the ages of 40 ($M = 5.28$ sec) and 60 ($M = 5.62$ sec) years, which did not differ. Although no significant difference was detected between the ages of 40 and 60 years, there was a trend toward progressive decline of performance as a function of age in both the right and left hands, as depicted in Fig. 1e.

3.1.6. *Drawing*

Significant main effects for age [$F(2,51) = 4.28$, $p < .05$] and hand [$F(1,51) = 306.89$, $p < .0001$], and a significant interaction [$F(2,51) = 7.77$, $p < .005$] were found. The significant main effect for hand was due to a faster performance of the right ($M = 5.32$ sec) in comparison with the left ($M = 8.18$ sec) hand. Post hoc comparisons indicated that the significant main effect for age was due to a longer time to complete the task at the age of 60 years ($M = 7.55$ sec) in comparison with the age of 20 years ($M = 5.96$ sec), while the age of 40 years ($M = 6.74$ sec) was not significantly different from any of the other age groups. Contrasts for the interaction effect indicated significant differences between all ages in the comparisons within the left hand, revealing a continuous decline of performance as a function of age ($M = 7.02$, 8.13, 9.39 sec, respectively for the ages of 20, 40, and 60 years). Performance of the right hand, however, was found to be poorer at the age of 60 years ($M = 5.71$ sec) in comparison with the age of 20 years ($M = 4.90$ sec), while no significant difference was detected in the comparison with the age of 40 years ($M = 5.34$ sec). These results, hence, indicated greater manual asymmetry in older individuals as compared with their younger counterparts (Fig. 1f).

3.2. *Comparison of manual asymmetries across tasks and ages*

Fig. 2a shows the algebraic index of manual asymmetry for every task across ages. As is apparent from this figure, there was a consistent and distinctive superior performance of the right hand for drawing across ages, while in the other tasks the indices of performance asymmetry were lower. This observation was corroborated in the analysis of variance by a significant main effect for task [$F(5,255) = 22.48$, $p < .0001$], with a significantly higher index for drawing in relation to all other tasks. A higher index for anticipatory timing as compared to sequential finger movements and reaction time tasks was also detected. The absolute index of performance asymmetry, as depicted in Fig. 2b, was characterized by a reversal of the order between the drawing and anticipatory timing tasks. Analysis of variance indicated a significant main effect for task [$F(5,255) = 253.91$, $p < .0001$], with post hoc contrasts pointing out the following relationship among the tasks: anticipatory timing > drawing > the other tasks. No significant age-related effect was detected in either analysis.

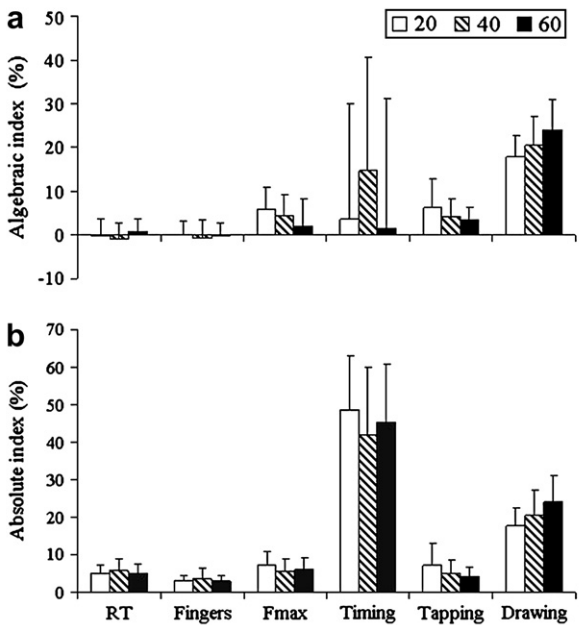

Fig. 2 – Average algebraic (a) and absolute (b) indices of performance asymmetry for the six motor tasks across ages; standard deviation represented by vertical bars.

Analyses conducted so far suggest the existence of three categories of performance asymmetry: symmetric performance, inconsistent asymmetry, and consistent asymmetry. The former category refers to similar performance in the intraindividual comparison between hands, so that performance of the left is similar to that achieved by the right hand. In this category are the sequential finger movements and reaction time tasks. The second category, inconsistent asymmetry, is characterized by high absolute indices of performance asymmetry associated with much lower algebraic indices, when the average for the group is analyzed. This is due to a large interindividual variance, with individual algebraic values varying in the range between large asymmetry favoring the left hand and large asymmetry favoring the right hand. Performance on the anticipatory timing task presented this profile. The third category is characterized by a consistent asymmetric manual performance, so that all or the large majority of individuals in a group perform better with the right than with the left hand. The tasks showing this profile were repetitive tapping and drawing. The single case of transition between such categories across ages was observed for maximum grip force, with a shift from consistent asymmetry at the age of 20 years to symmetric performance at the age of 60 years. Fig. 3 presents histograms for absolute frequency of individual algebraic indices, comparing the asymmetry profiles observed in all ages studied, on tasks representative of each proposed category: sequential finger movements, for symmetric performance; anticipatory timing, for inconsistent asymmetry; drawing, for consistent asymmetry; and maximum grip force, for the transition from an asymmetric to a symmetric profile across ages.

3.3. *Between-hand correlation and manual preference*

In addition to analysis of manual asymmetry, correlation between performance of the right and left hands was assessed for each task across different ages using the Pearson test. The results indicated a significant correlation between the right and the left hand in all analyses ($ps < .05$), with most r^2 scores being higher than .5. Table 1 shows a complete description of the observed values. A closer observation of the indices indicates that there was no overall trend either toward increment or decrement of the correlation scores across ages.

Table 1 – Correlation (r^2) between the right and the left hand for each task across ages

	Age		
	20	40	60
Reaction time	.56	.62	.52
Fingers	.86	.83	.83
Grip force	.88	.92	.83
Anticipatory timing	.21	.64	.35
Tapping	.60	.67	.90
Drawing	.69	.74	.71

Analysis of manual preference was conducted on the basis of the laterality indices derived from the Edinburgh inventory, through a one-way analysis of variance for repeated measures contrasting the three ages. The results indicated a significant age effect [$F(2,51) = 4.38$, $p < .05$], which was due to a stronger preference for the right hand at the age of 60 years ($M = 83.68$, $SD = 13.19$) in comparison with the age of 20 years ($M = 61.74$, $SD = 25.84$), while the index observed for the age of 40 years was intermediate ($M = 72.60$, $SD = 25.61$) although not reaching significance in the comparisons with the other ages.

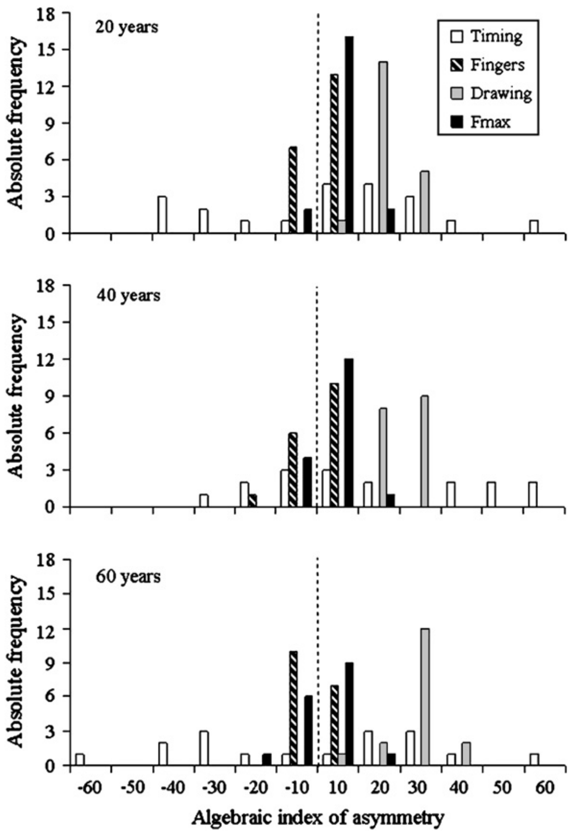

Fig. 3 – Absolute frequency of individual algebraic indices of performance asymmetry for the three age groups in representative tasks of the identified profiles of manual asymmetry: anticipatory timing, for inconsistent asymmetry; sequential finger movements, for symmetric performance; sequential drawing, for consistent asymmetry; and maximum grip force, for transition from asymmetric to symmetric performance.

4. Discussion

Analysis of the results revealed a diversity of manual asymmetry profiles, with some of them varying with age. Among the tasks studied, performance on the repetitive tapping and drawing tasks was found to be consistently asymmetric; anticipatory timing was characterized by interindividual inconsistent asymmetry, with large variation of magnitude and direction of manual asymmetries; and for the sequential finger movements and simple reaction time tasks a symmetric profile was identified, with only small individual advantages favoring either the right or the left hand. For maximum grip force a transition between manual asymmetry categories was observed, with a shift from consistent asymmetry early in adulthood to symmetric performance in the oldest group. These findings suggest that manual asymmetries in human motor control are not determined by a few components in the brain determining general asymmetry of function. Rather, it seems to be a result of the combination of many sensorimotor components in neural organization of behavior that influence human laterality in specific ways.

For repetitive tapping the present results indicate an intrinsic advantage lateralized to the right hand/left cerebral hemisphere system. This conclusion is drawn from the stable superiority of the right over the left hand observed across all ages. It is also in agreement with previous findings, as lateral asymmetry in repetitive tapping has been consistently observed early in motor development (e.g., Fagard, 1987), as well as in young adults (e.g., Lutz et al., 2005). Additionally, movements of the preferred right hand have been shown to be not only faster, but also less variable than left-hand movements over a series of fast repetitive movements, even after extensive practice (Peters, 1981). In a series of experiments, Peters (1980) showed that lateral asymmetry in this task is not related to muscular aspects, like fatigue, but to a superior modulation of force between antagonist muscles in the right hand. This factor seems to be responsible for faster cycles of contraction–relaxation of distal muscles, which enables one to produce flexion–extension movements at a higher frequency in the preferred right hand. In this regard, a complementary piece of information was provided by the present results by showing that performance asymmetry between the right and the left hand in repetitive tapping is highly consistent across young as well as older individuals.

In spite of being marked by a consistent manual asymmetry, as observed for repetitive tapping, performance on the drawing task was found to exhibit a particular characteristic: increased asymmetry in older ages. This finding is analogous to developmental changes of manual asymmetry detected in children (Rigal, 1992), which seems to be particularly due to the increment of the differential dexterity of linear finger movements of the right over the left hand (Blank et al., 2000). The present results are consistent also with findings by Francis and Spirduso (2000), showing a higher manual asymmetry for drawing in older as compared with younger adults. Taking these results as a whole, there seems to be a continuous increment of manual asymmetry in handwriting-related tasks as an individual gets older. In this regard, attention should be drawn to the fact that this was the only task, among those studied here, which is regularly practiced throughout most of the lifespan. It is apparent that the extensive motor experience accumulated over most of the lifetime has an important role in preserving performance specifically for the practiced limb, while performance with the non-practiced limb declines linearly with age. From this observation, the capacity of the non-practiced limb to take advantage from unilateral practice with the opposite active hand on handwriting-related tasks, as identified in young individuals (Latash, 1999), seems to be ineffective in preventing the increment of performance asymmetry as an individual advances in age. From these results, greater manual asymmetry favoring the right hand in older adults for drawing might be thought of as due to differential practice over many years, reinforcing innate manual dominance.

A different sort of manual asymmetry was observed for the anticipatory timing task. A remarkable variation of individual indices of manual asymmetry was observed in this task, ranging from individuals with large asymmetry favoring the right hand to individuals showing a large asymmetry favoring the left hand. In other words, the results did not indicate a definite direction of lateral asymmetry for the sample studied. Therefore, the right-hand advantage indicated by the analysis represents only a trend for the group as a whole, which is not consistent between individuals. Such an observation suggests that performance asymmetries on tasks of this nature are not established by a particular structural arrangement of the neural architecture favoring performance of one hand in particular. In this regard, it should be noticed that the motor component of the anticipatory timing task employed was quite simple, requiring only a short thumb flexion movement in order to press a hand-held switch. The perceptual component, on the other hand, was more critical to skilled performance, given the importance of estimation of time of stimulus arrival to a temporally accurate response. Considering that the timing component of motor actions has been shown to be relatively independent of the effector system (cf. Franz et al., 1992; Keele et al., 1985), synchronization of motor acts of the right hand with environmental events seems not necessarily to be executed in the left cerebral hemisphere, nor left-hand movements in the right hemisphere. Indeed, absence of a consistent direction of manual asymmetry, as reported here, suggests that anticipation of coincidence is a component in movement organization that is not consistently lateralized either to the right or to the left cerebral hemisphere.

A counterpoint to manual asymmetry was the between-hand similarity of performance across ages on sequential finger movements and simple reaction time. Focusing first on the task of sequential finger movements, the present results are consistent with previous studies showing that this kind of motor action is characterized by symmetric performance (Hausmann et al., 2004). In agreement with these behavioral results, Verstynen et al. (2005) showed that, in addition to contralateral hemispheric activation, sequential and chord finger movements are performed with strong ipsilateral activation, which is especially pronounced in the left hemisphere during left-hand movements. In a fast repetitive tapping task, on the other hand, ipsilateral activation was less pronounced. These results suggest that simple motor actions involve neural networks restricted mainly to one cerebral hemisphere, while control of complex finger movements involves more widely distributed neural populations in both hemispheres. Performance on the simple reaction time task in the present investigation was also characterized by symmetry between the hands. Schluter et al. (2001), however, have shown that this behavior is achieved through asymmetric activation of cerebral hemispheres. Schluter used positron emission tomography to study cerebral activation in simple and choice reaction time tasks. The results indicated that while the right hemisphere was active when subjects used their left hand, left cortical areas were activated either when the right or the left hand was used. Associating the results from the present study with such results from neuroimaging investigations, it seems that the stable symmetric behavior observed both in sequential finger movements and simple reaction tasks across growing ages is achieved through distinct patterns of hemispheric activation.

Maximum grip force was the only task in which a transition between the identified profiles of lateral asymmetry as a function of age was observed. The significant lateral asymmetry characteristic of 20- and 40-year-old individuals gave place to a symmetric profile at the age of 60 years as a result of a more dramatic decline of handgrip force in the right hand. Therefore, aging seems to lead to a selective effect on the right hand, eliminating its advantage over the left hand as detected in early and middle adulthood. Previous studies have shown that there exists a natural reduction of muscular strength due to degeneration of neuromuscular structures with aging (see Rogers and Evans, 1993, for a review). In addition, reduction of manual asymmetry for muscular strength might be related to the fact that older individuals frequently reduce the amount and intensity of physical activities requiring application of muscular strength. The likely consequence of these structural and experiential factors is a decrement of muscular strength, which is expected to be more evident in the more developed muscular system at earlier ages.

An overall analysis of the present results, therefore, revealed different asymmetry profiles across tasks ranging from symmetric to consistent asymmetric performance. This finding supports the notion that manual asymmetry on a given task is not the result of a factor favoring motor control in general by the dominant left hemisphere/right hand system. Rather, manual asymmetries were found to be task specific, with variation of the asymmetry profile as a function of distinct sensorimotor requirements of each task. A variety of task requirements – such as fine motor control, movement speed, sensorimotor integration and so forth – are hypothesized to be dealt within the nervous system by activating neural assemblies responsible for the particular processing functions associated with task requirements. The neural assembly activated to perform a given task could be circumscribed to one cerebral hemisphere or, alternatively, spread over cerebral structures in both hemispheres. On the basis of this conceptualization, the diversity of manual asymmetries observed in this study is proposed to be a consequence of different factors. First, there are different capacities between hemispheres for each sensorimotor function. Some capacities are markedly superior in one hemisphere while for other capacities this advantage is smaller or even absent. Such brain asymmetries seem to be a consequence of inherited developmental dispositions molded by experience. From this perspective, depending on the main component required for movement control, a variety of manual asymmetries might be found across tasks. Second, in more complex neural coalitions using processing resources of both cerebral hemispheres, the relative importance of each sensorimotor function in a particular movement organization is conceived to modulate the asymmetry profile. On the basis of this proposition, variation of manual asymmetries could be thought of as deriving from different aspects of the interaction between cerebral hemispheres.

Results presented here showed that there was neither an overall decrease of manual asymmetries as a function of age – as expected from findings of increased bihemispheric activation (e.g., Hutchinson et al., 2002), and decline in size (e.g., Hayakawa et al., 1989) and in the microstructure (e.g., Sullivan et al., 2001) of the corpus callosum of elderly people as compared to young adults – nor an overall increase of performance asymmetry, as expected from the right hemisphere-aging model (cf. Dolcos et al., 2002). Hence, these data suggest that structural and functional changes taking place in the aged brain do not lead to global changes of manual asymmetry across different motor actions. Rather, the age-related changes of manual asymmetry seem to be related to extensive unimanual motor experiences that modulate over years innate handedness dispositions. Relevant additional data for this discussion were provided by the correlational analysis. In spite of the diversity of observed patterns of lateral asymmetries, significant indices of correlation between the right and the left hand across all tasks and ages were found.

A higher index of manual preference for the 60 year-old participants in comparison with the 20-year-olds indicates that strength of lateral preference increases with advancing age. As a significant increment of manual asymmetry favoring the right hand was detected only for sequential drawing, it was shown that the growing preference for the right hand is not based on a general enlarged advantage in the performance of the right over the left hand in older individuals. Therefore, stronger manual preference in the elderly seems to be the result of increased confidence in the preferred right hand rather than the result of a general modification of performance asymmetry.

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