# Age-Related Deterioration of Coordinated Interlimb Behavior

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Younger and older participants performed two-limb coordination patterns of homologous (similar) and nonhomologous (dissimilar) effectors during 1:1 synchronization, according to the in-phase or anti-phase mode. The aim of the study was to examine age-related changes during the production of these basic movement patterns and their relative stability difference. The findings revealed that the aging process modulated the coordination dynamics as a function of effector system characteristics. Whereas the homologous system was resistant to agerelated deficits, movements of the nonhomologous system showed coordinative degradation that was most apparent during execution of the anti-phase mode. The latter performance regression is argued to be an expression of age-dependent declines in cognitive regulation and afferent information processing. This implies that deterioration in coordinated behavior across the life span may be strongly task dependent because of a combined effect of cognitive and sensory components.

GING is often associated with a deterioration in motor Aperformance. One predominant characteristic is agerelated slowing in cognitive and motor processes (Birren, Woods, & Williams, 1980; Cerella, Poon, & Williams, 1980), which is reflected in longer reaction and movement execution times. There are various hypotheses concerning age-related slowing (Spirduso, 1995). One of them is that slowing occurs because of increased neural noise (i.e., signals are less well detected in the central nervous system), resulting in a reduced signal-to-noise ratio (Salthouse, 1982). Central and/or peripheral factors underlie this lowered signal-to-noise ratio and more time is needed to examine signals and discard neural noise, leading to increased processing demands. Age-related slowing in the execution of movement patterns has been an extensively investigated topic and an abundance of literature is available (for reviews, see Diggles-Buckles, 1993; Spirduso, 1995; Welford, 1984).

Clearly, behavioral slowing that refers to a modification in absolute timing represents an important feature of movement performance in older adults. Another temporal issue represents relative timing, that is, the ability to synchronize movement patterns. Not much is known about modifications in the quality of interlimb behavior across the life span. Inherent changes in the underlying coordination process due to degeneration of central or peripheral components may have significant functional consequences. Previously, studies involving postural requirements and manual actions have revealed that aging leads to declines in coordinated activities (Bennett & Castiello, 1994; Greene & Williams, 1996; Pohl, Winstein, & Fisher, 1996; Spirduso & Choi, 1993; Stelmach, Amrhein, & Goggin, 1988; Woollacott, Shumway-Cook, & Nashner, 1986). In addition, movement complexity represents a meaningful factor that contributes to motor deficits with age (Light & Spirduso, 1990). However, the control of rhythmical multilimb behavior and modifications due to age have not been explored in detail. This type of action that underlies daily life as well as social and recreational activities is a prototype of a complex task that demands attentional regulation and sensory monitoring of various sources. Therefore, it can be hypothesized that coordinated actions impose an additional load on older as compared with younger adults because of age-related declines in cognitive processing (Clark, 1996; Hasher & Zacks, 1988; McDowd, Vercruyssen, & Birren, 1991) and deterioration in sensory structures and function (Skinner, Barrack, & Cook, 1984; Schaumburg, Spencer, & Ochoa, 1983; Stelmach & Sirica, 1986).

Previously, research on coordinated interlimb behavior has demonstrated that certain movement patterns represent preferred modes of coordination that express the intrinsic behavior of the motor system (Kelso, 1984; Turvey, 1990). One such configuration is moving segments rhythmically with equal tempo according to the in-phase or anti-phase mode. When performed in the sagittal plane, these coordination modes can be associated with the directional requirements of the action pattern. In particular, segments move in the same direction in extrinsic space during in-phase, whereas they move in different directions during anti-phase (Baldissera, Cavallari, Marini, & Tassone, 1991).

Even though interlimb synchronization represents a primary constraint, it has been noticed that the movement dynamics depend on the type of coordination mode (in-phase vs. antiphase) as well as the type of limb combination (homologous vs. nonhomologous). First, in-phase movements are produced more successfully than anti-phase movements (e.g., Kelso, 1984). Commonly, this performance difference has been illustrated as an increased instability of the anti-phase mode when cycling frequency is increased until it can no longer be continued and a transition toward the inphase mode occurs. Applying an identical frequency scaling when moving according to the in-phase mode does not give rise to transitions. Second, isofrequency coordination is more successful for homologous (similar) than for nonhomologous (dissimilar) effectors. That 1:1 synchronization is less stringent for nonhomologous than for homologous limbs has been interpreted to result from natural frequency dissimilarities between the upper and lower limbs and from differences in afferent and/or efferent command structures (Kelso & Jeka, 1992; Serrien & Swinnen, 1997, 1998; Swinnen, Dounskaia, Verschueren, Serrien, & Daelman, 1995).

Provided that in-phase and anti-phase coordination are spontaneously generated movement patterns in human behavior, the question arises of how accurate and stable these configurations remain across the life span. The aim of the present study was to investigate age-related modifications in the production of these elementary coordination modes and their relative stability difference. In addition, because of the observed performance differences between homologous and nonhomologous conditions in young adults, it was also of interest to examine whether these dissimilarities remain present to the same degree in older adults. Accordingly, an experimental paradigm was set up in which two-limb coordination patterns were compared across younger and older participants. Our aim was to describe age-related changes in movement performance and to identify potential determinants that might be responsible for the reduced quality of coordinated interlimb behavior due to aging.

#### **METHODS**

#### **Participants**

A group of eight younger (mean age = 24 years; 5 women and 3 men) and eight older (mean age = 75 years; 5 women and 3 men) adults participated in the study. All were right-handed and had no history of neurological disease or skeletomotor dysfunction. None of the participants was taking any medication at the time of testing. The older adults were in good health, ambulatory, and lived independently either in the general community or in a retirement community. They were all involved in daily activities and hobbies. A variety of socioeconomic classes and educational levels were represented. Participants had not been involved in a similar experiment and were naive with respect to the purpose of the experiment. Informed consent was obtained from all participants.

#### Apparatus and Task

Participants were seated in a chair that allowed independent motion of the forearms and lower legs in the sagittal plane (Figure 1). The chair consisted of a welded steel frame, a wooden back support, and a seat that could be adjusted in the forward–backward direction. The upper and lower limbs were attached to levers which were 45 cm (18 in.) in length for the upper limbs and 65 cm (26 in.) for the lower limbs. Participants performed flexion and extension movements around the elbow and knee joints. The setup was built such that the horizontal axes of rotation of the levers could be aligned with the center of rotation of the elbow and knee joints. Joint angles were registered through built-in shaft encoders (Tamagawa, 4096 bits/revolution), mounted at the axis of rotation of each joint. The data were sampled at 150 Hz.



Figure 1. Side view of the experimental apparatus.

The task required cyclical flexion and extension movements with a 1:1 frequency ratio. There were six performance conditions: homologous (upper limbs, lower limbs), homolateral (right side, left side), and heterolateral (right arm/left leg, left arm/right leg). The coordination modes included in-phase (isodirectional) and anti-phase (nonisodirectional) movements.

## Procedure

The participants were seated in the chair and their limbs were attached to the levers. Shoes were removed to avoid additional loading of the legs. In the start position, the joint angle was approximately 90° in the lower limbs and 110° in the upper limbs. Before the experiment started, the participants were informed about the goal of the test. They were instructed to make cyclical two-limb movements across the total duration of a trial (15 s) at the pace provided by a metronome (60 beats/min). Participants were asked to preserve spatial and temporal requirements of the movement patterns within and between trials. Order of the trials was counterbalanced across participants, between and within limb combinations and coordination modes. Two trials per condition were performed, resulting in a total of 24 trials. Following a "ready" command, a 400-Hz tone was presented that led to initiation of a trial.

#### Measures

*Phase synchronization.*—Interlimb coordination was quantified by means of relative phase that represents the difference in phase angle between two segments moving concurrently. The phase angles for each segment were estimated from the phase plane trajectories that refer to position versus velocity at each instant. Normalizing both coordi-

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nates to the unit circle, the individual phase angles ( $\Phi$ ) were obtained through the following formula:  $\Phi = \tan^{-1} \left( \left[ \frac{dx}{dt} \right] \right)$ x), whereby x refers to the normalized position and dx/dt to the normalized instantaneous velocity (Scholz & Kelso, 1989). Velocity was obtained by differentiation of the displacement data. Amplitude rescaling was done for each half cycle: Positive amplitudes were divided by their peak positive amplitude, and negative amplitudes were divided by their respective peak negative amplitude score. The phase angles were subtracted for each data sample, resulting in a continuous estimate of relative phase, that is,  $\phi = \Phi_1 - \Phi_2$ . In addition, the absolute deviation from the intended relative phase (0° and 180°) was extracted at the two peak positions of flexion and extension, providing a measure of relative phase accuracy. The within trial standard deviation around the mean relative phase represented relative phase variability and is indicative of the stability with which the coordination pattern is executed. Moreover, a high degree of pattern stability (low variability) can be associated with a preferred behavioral state, whereas a decrease in pattern stability occurs when moving away from it. Mean deviation and variability scores were calculated for each trial and averaged across experimental condition.

*Cycle duration and amplitude.*—To examine the temporal and spatial parameters of movement organization, the cycle duration and amplitude of the limb trajectories were determined. Cycle duration was obtained by measuring the time that elapsed between two consecutive positive peaks. Amplitude was determined by calculating the absolute value of the peak-positive to peak-negative amplitude. For both timing and amplitude, within trial standard deviation was calculated to assess temporal and spatial variability, respectively. Mean and variability scores were calculated per trial and subsequently averaged for each segment across experimental condition.

## Data Analyses

The main phase analyses consisted of 2 (group)  $\times$  2 (coordination mode)  $\times$  3 (limb combination) analyses of variance (ANOVAs), with repeated measures on the last two factors. The first factor included the younger and older adults, whereas the second factor represented the coordination modes: in-phase and anti-phase. The third factor referred to the homologous, homolateral, and heterolateral limb combinations.

Additional phase analyses were conducted to examine coordination differences within effector combination. These consisted of separate 2 (group)  $\times$  2 (coordination mode)  $\times$  2 (limb condition) ANOVAs, with repeated measures on the last two factors. The first factor referred to the younger and older participants, whereas the second factor represented the in-phase and anti-phase coordination modes. The third factor included the conditions for the different limb combinations: upper versus lower limbs, right versus left side, right arm/left leg versus left arm/right leg.

The analyses for cycle duration and amplitude consisted of 2 (group)  $\times$  2 (coordination mode)  $\times$  3 (limb combination) ANOVAs, with repeated measures on the last two factors. The first factor represented the younger and older adults, whereas the second factor included the coordination modes: in-phase and anti-phase. The third factor referred to the homologous, homolateral, and heterolateral limb combinations.

## RESULTS

#### Phase-Synchronization

The mean deviation scores from the required relative phase showed a significant main effect of group, F(1,14) =30.4, p < .0001, coordination mode, F(1,14) = 11.5, p <.01, and limb combination, F(2,28) = 35.4, p < .0001. All two-way interactions were significant: Group × Coordination Mode, F(1,14) = 5.7, p < .05; Group × Limb Combination, F(2,28) = 21.7, p < .0001; and Coordination Mode × Limb Combination, F(2,28) = 9.3, p < .001. The Group × Coordination Mode × Limb Combination interaction also reached significance, F(2,28) = 9.8, p < .001. Figure 2 demonstrates that phasing accuracy did not differ between younger and older adults for homologous conditions (p >



Figure 2. The absolute deviation (AD) of relative phase for the different effector combinations during in-phase and anti-phase coordination for younger and older adults.

.05). Conversely, it deteriorated for the older adults during homolateral and heterolateral conditions and more strongly for anti-phase than in-phase coordination.

Relative phase variability revealed a significant main effect of group, F(1,14) = 16.4, p < .01, coordination mode, F(1,14) = 51.5, p < .0001, and limb combination, F(2,28) = 20.1, p < .0001. All two-way interactions were significant: Group × Coordination Mode, F(1,14) = 21.1, p < .001, Group × Limb Combination, F(2,28) = 9.6, p < .001, and Coordination Mode × Limb Combination, F(2,28) = 7.0, p < .01. The Group × Coordination Mode × Limb Combination, F(2,28) = 7.2, p < .01. Figure 3 shows that coordinative stability of the younger and older participants did not differ during homologous conditions. Conversely, relative phase variability increased for the older adults during homolateral and heterolateral conditions, especially during anti-phase movements.

Additional analyses of relative phase were conducted to examine differences within the limb combinations. For the homologous limbs, relative phase accuracy showed that younger adults ( $M = 8.3^{\circ}$ ) were more successful than older adults ( $M = 12.9^{\circ}$ ), F(1,14) = 5.8, p < .05. Also, in-phase coordination ( $M = 9.1^{\circ}$ ) was more accurate than anti-phase coordination ( $M = 12.1^{\circ}$ ), F(1,14) = 20.3, p < .001. In addition, upper limb movements ( $M = 6.8^{\circ}$ ) were performed with a higher degree of accuracy than lower limb movements ( $M = 14.4^{\circ}$ ), F(1,14) = 5.2, p < 05. The latter finding confirms previous data with the same task (Serrien & Swinnen, 1997). Relative phase variability revealed a main effect of coordination mode, F(1,14) = 41.8, p < .0001. The mean scores were 5.6° and 6.7° for in-phase and anti-phase movements, respectively.

For the homolateral limbs, relative phase accuracy showed a significant main effect of group, F(1,14) = 43.4, p < .0001, coordination mode, F(1,14) = 12.5, p < .01, and limb condition, F(1,14) = 7.3, p < .02. The Group × Coordination Mode interaction was significant, F(1,14) = 10.5, p < .01. This interaction indicated that phasing accuracy was similar across coordination modes for the younger adults ( $M = 12.1^{\circ}$  for in-phase,  $M = 13.8^{\circ}$  for anti-phase),

whereas it deteriorated for the older adults during anti-phase movements ( $M = 64.3^{\circ}$ ) as compared with in-phase movements ( $M = 25.9^{\circ}$ ). The Group  $\times$  Limb Condition interaction was also significant, F(1,14) = 5.3, p < .04. This interaction suggested that relative phase accuracy was similar for the younger adults on both sides of the body ( $M = 13.7^{\circ}$ for the left side,  $M = 12.3^{\circ}$  for the right side), whereas quality of performance decreased on the left side ( $M = 53.6^{\circ}$ ) as compared with the right side  $(M = 36.7^{\circ})$  for the older adults. Relative phase variability demonstrated a significant main effect of group, F(1,14) = 18.5, p < .001, and coordination mode, F(1,14) = 24.1, p < .001. The Group  $\times$  Coordination Mode interaction was significant, F(1,14) = 15.9, p < .01. This interaction revealed that phasing variability was similar across coordination modes for the younger adults ( $M = 7.1^{\circ}$  for in-phase,  $M = 9.1^{\circ}$  for anti-phase), whereas it increased for anti-phase movements ( $M = 27.9^{\circ}$ ) as compared with in-phase movements ( $M = 9.2^{\circ}$ ) for the older adults.

For the heterolateral limbs, relative phase accuracy showed that the older adults ( $M = 25.0^{\circ}$ ) were less successful than the younger adults ( $M = 14.3^{\circ}$ ), F(1,14) = 6.9,  $p < 14.3^{\circ}$ .02. Relative phase variability demonstrated significant main effects of group, F(1,14) = 5.4, p < .05, and coordination mode, F(1,14) = 9.9, p < .01. The main effect of limb condition was also significant, indicating that the right arm/left leg condition ( $M = 7.9^{\circ}$ ) was produced with higher stability than the left arm/right leg condition ( $M = 13.0^{\circ}$ ), F(1,14) = 8.6, p < .02. The Group × Coordination Mode interaction reached significance, F(1,14) = 4.8, p < .05. This interaction suggested that the younger adults performed the coordination modes with virtual equal degree of variability ( $M = 7.6^{\circ}$  for in-phase,  $M = 9.2^{\circ}$  for anti-phase), whereas it deteriorated during anti-phase movements (M =16.9°) as compared with in-phase movements ( $M = 8.4^{\circ}$ ) for the older adults.

## Cycle Duration

Mean cycle duration revealed that older adults (M = 1136.5 ms) produced slower cycles than younger adults (M = 1136.5 ms)



Figure 3. The standard deviation (SD) of relative phase for the different effector combinations during in-phase and anti-phase coordination for younger and older adults.

1002.0 ms) who complied more successfully with the imposed metronome pacing, F(1,14) = 6.9, p < .02. The main effect of limb combination was also significant, F(2,28) = 3.4, p < .05. The mean scores were 1015.0 ms, 1116.2 ms, and 1076.5 ms for the homologous, homolateral, and heterolateral limbs, respectively.

Temporal variability revealed a significant main effect of coordination mode, F(1,14) = 10.0, p < .01, and limb combination, F(2,28) = 5.0, p < .02. The two-way interactions of Group × Limb Combination, F(2,28) = 3.4, p < .05, and Coordination Mode × Limb Combination, F(2,28) = 6.6, p < .01, were significant. The Group × Coordination Mode × Limb Combination interaction was also significant, F(2,28) = 3.4, p < .05. Figure 4 shows that temporal variability increased substantially for the older as compared with the younger adults during nonhomologous conditions when anti-phase coordination was required.

## Amplitude

Mean amplitude showed a significant main effect of coordination mode, F(1,14) = 31.7, p < .01. The Group  $\times$ Coordination Mode interaction was significant, F(1,14) =11.8, p < .01. This interaction indicated that younger adults increased their amplitude during anti-phase coordination (M =110.0°) as compared with in-phase coordination (M =102.6°), whereas older adults maintained their amplitude during both configurations ( $M = 123.8^{\circ}$  for in-phase, M =124.3° for anti-phase). The Coordination Mode  $\times$  Limb Combination interaction was significant, F(2,28) = 6.0, p < 100.01. This interaction suggested that amplitude was equal for both coordination modes during homologous conditions (M =115.4° for in-phase,  $M = 114.1^{\circ}$  for anti-phase), whereas it was dissimilar during homolateral conditions ( $M = 111.1^{\circ}$  for in-phase,  $M = 118.3^{\circ}$  for anti-phase) and heterolateral conditions ( $M = 133.1^{\circ}$  for in-phase,  $M = 119.2^{\circ}$  for anti-phase).

Spatial variability was lower for the younger ( $\dot{M} = 5.2^{\circ}$ ) than for the older adults ( $M = 7.1^{\circ}$ ), F(1,14) = 8.9, p < .01. The main effect of limb combination was also significant, F(2,28) = 10.9, p < .001. The mean scores were 5.6°, 6.6°, and 6.3° for the homologous, homolateral, and heterolateral

limbs, respectively. In addition, in-phase movements ( $M = 5.7^{\circ}$ ) were less variable than anti-phase movements ( $M = 6.6^{\circ}$ ), F(1,14) = 9.4, p < .01.

## Phase Transitions

Even though in-phase and anti-phase movements are preferred coordination modes, fluctuations around their mean states are inevitable because of the systems' inherent noisiness. In this respect, relative phase variability is a relevant parameter to conceptualize coordinative stability and to effect phase transitions between patterns (Kelso, 1995). The smaller the fluctuations, the more stable the coordination mode and the more solid the coherence between the underlying components. Conversely, when coordinative variability is strongly increased, a phase transition is likely to occur toward a pattern with a relatively lower degree of fluctuations.

In view of the previously described differential level of stability between in-phase and anti-phase coordination and between both groups of adults, trials were counted in which phase transitions occurred. The results were consistent with the hypothesis that high variability underlies coordinative change. In particular, no transitions were observed for the younger adults or, during homologous conditions, for the older adults. During homolateral conditions, 25% of the trials produced by the older adults were characterized by a transition. The latter always occurred in trials during which the anti-phase mode was initially adopted, resulting in a change toward the in-phase mode. Moreover, older participants always started off appropriately in the anti-phase pattern, whereas a transition to the in-phase pattern was made after a few seconds of practice. All elderly adults except one participant experienced a pattern change in one or more trials. Therefore, it can be suggested that transitory events characterize coordinated behavior of older adults when task constraints become too demanding. During heterolateral conditions, phase transitions were noted in 3% of the older adults' trials. Also in this case, coordinative change always took place from an initially controlled anti-phase pattern toward an in-phase pattern.

The age-related deterioration during homolateral coordi-



Figure 4. The standard deviation (SD) of cycle duration for the different effector combinations during in-phase and anti-phase coordination for younger and older adults.

nation is exemplified in Figure 5. Displacement time profiles of right arm/right leg movements and the orthogonal plot of both displacement patterns (Lissajous figure) are displayed for a young and older participant. When inphase and anti-phase movements are performed correctly (i.e., relative phases of 0° or  $180^{\circ}$ ), the Lissajous figures result in a straight (diagonal) line configuration, oriented to the right or left. It can be observed that the plots of the young adult show consistent behavior during in-phase as well as anti-phase movements. Conversely, the relative motion plot of the older adult is more diffuse during the in-phase mode and is highly scattered and irregular during the anti-phase mode. In the latter case, there is no coordinative consistency and a transition from anti-phase to inphase is apparent.

#### DISCUSSION

Past research has shown that explicit constraints emerge during coordinated interlimb behavior, resulting in a preference to move effectors rhythmically with equal tempo (Kelso, 1995; Swinnen, Jardin, Meulenbroek, Dounskaia, & Hofkens-Van Den Brandt, 1997). Little is known about the extent to which these constraints change or become more challenging across the life span due to modifications in central or peripheral factors. The aim of this experiment was to investigate age-related changes in the coordination dynamics of homologous versus nonhomologous limbs during the production of 1:1 synchronization, according to the in-phase and anti-phase mode. The data revealed performance differences between younger and older participants that depended both on limb combination and coordination mode. These modifications due to aging are hypothesized to result from a conjunction of (a) deficits in afferent information processing for steering coordinated behavior and (b) declines in cognitive regulation, emerging from a deterioration of inhibitory mechanisms and a reduced optimal (attentional) monitoring of sensory feedback information.



Figure 5. Displacement time series and relative motion plots of homolateral coordination for a young (A) and older (B) participant.

## Age-Related Changes in Coordinated Behavior Depend on Limb Combination

All participants produced the required coordination modes more successfully with their homologous than with their nonhomologous limbs, confirming and extending previous findings in young adults (Serrien & Swinnen, 1997, Swinnen et al., 1995). This performance difference as a function of limb combination may be related to a distinction in organizational/control processes. In particular, it has been demonstrated that homologous segments form a tight synergy characterized by a high degree of converging afferent signals, an informational input which is of primary importance for realizing interlimb synchronization. Therefore, the capability to detect deviations from the required relative motion pattern through continuous kinesthetic monitoring is highly efficient during homologous conditions, securing the preservation of in-phase and anti-phase coordination. Conversely, nonhomologous effectors are associated with a less stringent type of synergy for which sensory information is less congruent. This may reduce optimal monitoring of afferent information and subsequent detection of errors in the ongoing movement pattern, affecting the quality of synchronized interlimb behavior (Serrien & Swinnen, 1998; Swinnen et al., 1995).

Because of the fact that aging induces an overall deterioration of sensory functions (Skinner et al., 1984; Stelmach & Sirica, 1986), it is suggested that a decline in the quality of afferent information from the periphery and/or an increase in threshold for its detection will change the available contextually related input for calibrating and steering coordinated behavior in an optimal manner. In the present study, age-related deficits were rather specific to nonhomologous conditions. This indicates that deficient sensory information processing has a stronger effect on loosely coupled control structures for which the ability to monitor afferent input is attenuated. In addition, it is likely that a decline in the processing of afferences is associated with an increased cognitive load for task production, that is, more conscious control and mental effort is required for the control of movement. The latter statement is supported by data from a deafferented patient. During dual task performance, the patient experienced more interference than controls and commented that combined tasks such as speaking and a manual action demanded substantial cognitive resources (Teasdale et al., 1994).

## *Complexity of the Coordination Mode: In-Phase Versus Anti-Phase Movements*

In support of previous work, the present findings indicated that directional requirements determine the quality of interlimb synchronization. In particular, in-phase (isodirectional) movements were easier to execute than anti-phase (non-isodirectional) movements and resulted in superior motor behavior (Kelso & Jeka, 1992; Serrien & Swinnen, 1997; Swinnen et al., 1995). The intrinsic nature of in-phase coordination was especially noted during homologous movements that were produced with a similar degree of success in both groups of participants. During homologous anti-phase movements, an age-related deterioration in synchronization capabilities was noticed, supporting earlier data on bimanual coordination (Greene & Williams, 1996; Serrien, Teasdale, Bard, & Fleury, 1996). A more pronounced performance regression became apparent when executing the anti-phase mode with a combination of the upper and lower limbs. Older adults experienced a great deal of difficulty during nonhomologous anti-phase as compared with in-phase movements. We hypothesize that this finding can be explained by a compound effect of loosely coupled nonhomologous effectors (as discussed previously) and dissimilar feedback mechanisms subserving in-phase and antiphase patterns. In particular, Baldissera and colleagues (1991) examined nonhomologous coordination and suggested that in-phase movements require limited feedback control, whereas anti-phase movements undergo refined processing, relying on increased monitoring and attentional resources.

The latter statement is supported by recent functional imaging data. In particular, it has been demonstrated that anti-phase movements demand more pronounced neural processing than in-phase movements (Goerres, Samuel, Jenkins, & Brooks, 1998; Sadato, Yonekura, Waki, Yamada, & Ishii, 1997; Stephan et al., 1999). Also, the antiphase mode necessitates a suppression of the elementary inphase mode (Sadato et al., 1997). Consequently, anti-phase coordination requires selective attention to inhibit conflicting neural commands. As the capacity of the attentional system to suppress patterns of interference and/or dominant responses becomes deficient with age (Clark, 1996; Dempster, 1992; Hasher & Zacks, 1988; West, 1996), it is reasonable to assume that the performance of the anti-phase mode will deteriorate as a function of age. Because of reduced inhibitory control, a bias toward the more basic in-phase mode emerges. In this respect, phase transitions from antiphase to in-phase were regularly observed for the older adults during nonhomologous conditions, especially when homolateral effectors were involved. The diminished capacity to repress intrinsic coordination tendencies as a function of age was also noticed in a learning experiment in which a 90° out of phase pattern was to be acquired with the upper limbs (Swinnen et al., 1998).

Weakened inhibitory mechanisms in older participants may also contribute to impaired sustained attention (Chao & Knight, 1997). In the present context, this suggests that cognitive processing that is required to produce coordinated actions will be subject to age-related declines. Less capacity can be directed to monitoring the trajectories of the coordinative task, resulting in a greater vulnerability to inefficient behavior. The latter is likely to be more prominent for antiphase than in-phase movements because of the higher mental effort that is required, a distinction that can be associated with the concepts of controlled or effortful processing versus automatic processing (Hasher & Zacks, 1979; Schneider & Shiffrin, 1977). Furthermore, Summers, Byblow, Bysouth-Young, and Semjen (1998) examined the cognitive demands during bimanual isofrequency coordination by including a supplementary task. The authors noticed that secondary task performance did not affect in-phase movements but resulted in a deterioration of anti-phase movements when cycling at high frequencies. This discrepancy of cognitive requirements between both coordination modes has received support from functional imaging work. In particular, it has been shown that neural activation in the prefrontal cortex and midbrain occurs during anti-phase patterns that does not emerge during in-phase patterns. Sadato and colleagues (1997) stated that this extra activation is indicative of additional attentional requirements, reflecting on-line monitoring due to augmented spatial attention and spatial working memory during anti-phase coordination. However, Fink and colleagues (1999) claimed that this prefrontal activation can be specifically related to sensory(motor) integration. The authors suggested that frontal monitoring serves an executive function, allowing active supervision of the task. The observation that the prefrontal cortex appears to be more sensitive to age-related deterioration than other areas of the cortex (Mielke et al., 1998; Raz et al., 1997) is likely to contribute to cognitive processing deficits in older adults. As stated previously, extra attentional resources are probably required because of insufficient sensory regulation, suggesting that an impairment in cognitive monitoring as a function of age may play a determining factor in the quality of multilimb coordination. This is in line with earlier data that have demonstrated that cognitive declines due to age may introduce significant consequences for motor behavior (Kluger et al., 1997).

The coordinative difficulties that were observed during two-limb motion patterns were supported by the cycle duration data. Whereas movements of homologous limbs and nonhomologous limbs according to the in-phase mode were produced in harmony with the tempo of the metronome, movements of nonhomologous limbs in the anti-phase mode were performed with a high degree of temporal variability. Increased kinematic variability due to aging has been observed repeatedly, a finding that can be associated with agerelated neuromuscular changes (Cooke, Brown, & Cunningham, 1989; Seidler & Stelmach, 1995; Spirduso, 1995). In addition, older as compared with younger participants produced large delays from the target tempo provided by the metronome. It is hypothesized that the older persons slowed their motion patterns as an adaptive strategy to cope more successfully with the task requirements. Behavioral slowing may also be related to the fact that the older participants depended more on visual feedback to guide their movement patterns because of a reduced reliance on proprioceptive information. Therefore, the temporal constraints associated with the visual feedback's detection or adjustment processes might necessitate a reduction in movement speed.

In conclusion, the present data have revealed that the process of aging induces modifications of the interlimb coordination dynamics as a function of effector combination. Whereas the homologous system that is characterized by tight neural networks shows resistance to age-related declines, the more loosely coupled nonhomologous system is susceptible to performance deterioration that is most prominent for anti-phase coordination. This may result from a combined effect of age-dependent deficits in afferent information processing and cognitive regulation.

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