Movement-Related Sensory Feedback Mediates the Learning of a New Bimanual Relative Phase Pattern

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ABSTRACT. On the basis of findings emphasizing the role of perceptual consequences in movement coordination, the authors tested the hypothesis that the learning of a new bimanual relative phase pattern would involve the matching of the movement-related sensory consequences (rather than the motor outflow commands) to the to-be-learned pattern. Two groups of participants ($n = 10$ in each) practiced rhythmically moving their forearms with a phase difference of 30°. In 1 group, a difference in the arms' eigenfrequencies was imposed such that synchronous generation of the left and right motor commands resulted in the required relative phase (30°), yielding incongruence between the motor commands and their sensory consequences. In the other group, the experimenter imposed no eigenfrequency difference so that the sensory consequences were congruent with the motor commands. Throughout the practice period, performance of both groups was assessed repeatedly for the congruent situation (i.e., no eigenfrequency difference). On those criterion tests, both groups performed the required pattern equally well. The authors discuss that result, which corroborated the hypothesis, from a dynamical systems perspective.

Key words: coordination dynamics, ideomotor hypothesis, motor learning

In the dynamical systems approach to movement coordination, scientists studying rhythmic bimanual movements have focused on the stability characteristics of coordination patterns and how those characteristics may result from interactions between the limbs (e.g., Beek, Peper, & Stegeman, 1995; Haken, Kelso, & Bunz, 1985; Kelso, 1995; Peper, Daffertshofer, & Beek, 2004). As a consequence, that theoretical approach has also instigated new developments in the study of motor learning by revealing that the intrinsic stability features that arise from inherent coordination tendencies have a marked influence on how new coordination patterns are acquired (e.g., Lee, 1998; Schöner, Zanone, & Kelso, 1992). In particular, as has been shown in many studies on 1:1 frequency coordination, spontaneous attraction to in-phase and antiphase coordina-

tion (i.e., the two intrinsically stable coordination patterns involving 0° and 180° of relative phase between the limbs) impedes the acquisition of new relative phase patterns (e.g., Fontaine, Lee, & Swinnen, 1997; Lee, Swinnen, & Verschueren, 1995; Swinnen et al., 1998; Zanone & Kelso, 1992). The learning rate and the nature of the learning process (e.g., abrupt vs. gradual) are dependent on the interplay between the to-be-learned pattern and the intrinsic coordination tendencies (Kostrubiec & Zanone, 2002; Wenderoth, Bock, & Krohn, 2002; Zanone & Kelso, 1992, 1997). Learning a new pattern, in turn, can affect the stability of the intrinsic dynamics (Amazeen, 2002; Zanone & Kelso, 1992, 1997), although that effect may only be temporary (Fontaine et al.). Thus, it has become clear that during the learning process, the coordination dynamics, as a real-time phenomenon, results from the interactions between the individual's intrinsic dynamics and the pattern to be acquired. Within the dynamical framework, the latter influence has been conceptualized as *behavioral information* (i.e., a specific phase relationship stipulated by the environment, memory, or intention; Schöner, 1989; Schöner & Kelso, 1988; Schöner et al., 1992), which captures the contribution to the coordination dynamics that attracts the behavior to the to-be-learned pattern. Because learning involves an evolution of the initial intrinsic dynamics toward a desired dynamics, learning has been conceived of as the process by which the behavioral information specifying a to-be-learned pattern becomes memorized or internalized (Kostrubiec & Zanone; Schöner; Schöner & Kelso).

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In sum, the basic concepts and insights provided by the dynamical systems approach have resulted in new developments in the study of motor learning. In a similar vein, more recent advances in the study of bimanual rhythmic coordination may also have implications for this field of study. In that regard, indications that perception may play an important role in the stabilization of coordination patterns are a particularly interesting development. That notion was underscored, for instance, by Mechsner, Kerzel, Knoblich, and Prinz (2001), who showed that a coordination pattern that involved a 3:4 frequency ratio between the hands (which is known to be rather difficult to perform; e.g., Deutsch, 1983; Summers, Rosenbaum, Burns, & Ford, 1993) was acquired relatively easily if the visual consequences of the movements were transformed into a simple 1:1 frequency pattern. Likewise, Bogaerts, Buekers, Zaal, and Swinnen (2003) demonstrated that one may enhance performance of less stable coordination patterns (e.g., antiphase) by providing visual feedback manipulations that result in coherently grouped visual motion structures.

Such influences of the perceived consequences of motor performance may be associated with the by now well-documented observation that both visual and proprioceptive perception of relative phase are characterized by a variability structure that resembles the stability features of interlimb performance of relative phase patterns (Bingham, Schmidt, & Zaal, 1999; Bingham, Zaal, Shull, & Collins, 2001; Wilson, Bingham, & Craig, 2003; Zaal, Bingham, & Schmidt, 2000). In particular, irrespective of the actual level of phase variability, the relative phasing between two oscillating signals was judged to be least variable for relative phases of 0° and 180° (corresponding to the intrinsically stable coordination patterns), with 180° being judged to be more variable than 0° (corresponding to the differential stability of those two coordination patterns). Moreover, for intermediate relative phases, variability judgments increased as a function of their distance to 0° and 180° (corresponding to the instability of those intermediate patterns). The striking similarity between perceptual variability judgments and the stability of the corresponding coordination patterns has led to the suggestion that the stabilization of those patterns is dependent (in part) on the perceived variability of relative phase (e.g., Bogaerts et al., 2003; Zaal et al., 2000).

The understanding that perceptual consequences of motor performance may affect the stability of bimanual coordination patterns evokes the question of the extent to which movement-related sensory feedback is essential in the acquisition of a to-be-learned coordination pattern. Indeed, the results of several studies have underscored the finding that augmented feedback, which may improve the perception of the bimanually performed relative phase, enhances the learning process (e.g., Hodges, Chua, & Franks, 2003; Swinnen, Lee, Verschueren, Serrien, & Bogaerts, 1997; Wenderoth et al., 2002), indicating that the perceived consequences of the motor performance affect the acquisition of a new coordina-

tion pattern. That observation can be related to the key role ascribed to sensory feedback, together with knowledge of results (KR), in the formation of sensory schemata for the control of movement, such as the perceptual trace postulated in Adams's (1971) closed-loop theory of learning or the recognition schema in R. A. Schmidt's (1975) schema theory. According to that perspective, the constructed perceptual trace (or recognition schema) serves as a foundation for online movement corrections on the basis of comparison with actual feedback signals. An alternative account of the role of sensory feedback is founded on the ideomotor hypothesis proposed by James (1981, 1890; see e.g., Greenwald, 1970). In that account, the selection of a particular motor response is based on the anticipated sensory consequences of the resulting movements. Recently, several experiments have provided support for the notion that expected perceptual consequences influence the preceding response selection (e.g., Elsner & Hommel, 2001; Knuf, Aschersleben, & Prinz, 2001; Kunde, 2001, 2004; Kunde, Hoffmann, & Zellmann, 2002). For example, Kunde (2001) showed that the reaction times in response to a color stimulus were affected by the correspondence between the location (or force) of the response and the location (or intensity) of the resulting visual (or auditory) sensory effect. According to that view, motor learning primarily entails establishing how the to-be-learned coordination pattern is represented by the ensuing sensory experiences. In that manner, the learning process results in an integrated representation that relates the sensory consequences to the required movement pattern, allowing for adequate selection of motor outflow commands on the basis of their expected sensory effects (cf. Elsner & Hommel).

With regard to the topic in the present study, that is, the acquisition of a new bimanual relative phase pattern, those considerations fuel the expectation that the learning process is primarily dependent on the sensory effects that are associated with the required coordination pattern. In relation to the dynamical systems account as formulated by Schöner and Kelso (1988; see also Schöner, 1989; Schöner et al., 1992), we therefore propose that such sensory information plays an essential role in the internalization or memorization of behavioral information. More specifically, one may expect that learning a new relative phase pattern (primarily) involves matching the perceived relative phasing of the limb movements (i.e., the perceptual consequences) to the required relative phase pattern as specified by the behavioral information. To examine that hypothesis, we designed an experiment in which we evaluated that prediction against the contrasting possibility that an individual acquires a new coordination pattern by establishing a correspondence between the relative phasing of motor outflow commands to the musculature of the two moving limbs and the relative phasing specified by the behavioral information.

To dissociate between those two general possibilities, we performed an experiment in which the relative phasing of the motor outflow commands and the perceived relative phasing

of the movements were either congruent or incongruent. In a natural learning situation during which motor outflow commands and movement-related sensory information are congruent, the two identified possibilities for the memorization of behavioral information cannot be dissociated. However, one may gain more insight into their relative prominence by inducing an incongruence between the outflow commands and the movement-related sensory information. To that end, we devised a task environment in which the resulting relation between the motor outflow commands and the behavioral information was incongruent, whereas congruence was preserved between their sensory consequences and the behavioral information (see the following). If learning a coordination pattern is based on matching the phasing of the motor outflow commands to the specified task goal, then one may expect that the pattern practiced under such conditions (i.e., with the phasing of the motor outflow commands being incongruent with the pattern specified by the behavioral information) cannot be performed when the incongruence is removed (i.e., no transfer of learning to the congruent situation would be expected to occur). In contrast, if, as we hypothesize, learning is based on matching the sensory information about the performed coordination pattern to the specified task goal, then the pattern practiced under such conditions would be expected to transfer to the congruent situation because in both situations adequate performance implies that the required coordination pattern is specified by the sensory consequences of the movements.

In the experiment reported here, we created an incongruence between the relative phasing of the motor outflow commands and the actual (and, thus, the perceived) phasing of the movements by introducing a difference in eigenfrequency between the two moving limbs. The results of several studies have indicated that relatively small differences in eigenfrequency between the moving limbs induce slight deviations away from in-phase and antiphase coordination during isofrequency coordination (e.g., Jeka & Kelso, 1995; Peper, Nooij, & Van Soest, 2004; Rosenblum, & Turvey, 1988; R. C. Schmidt, Beek, Treffner, & Turvey, 1991; R. C. Schmidt & Turvey, 1995; Sternad, Turvey, & Schmidt, 1992; Turvey, Rosenblum, Schmidt, & Kugler, 1986). Thus, by breaking the symmetry between the oscillating components, one can induce systematic differences between the intended and the performed coordination patterns. We exploited that insight by manipulating the degree of symmetry breaking (i.e., the size of the eigenfrequency difference) in such a way that the pre-existing attractor for in-phase coordination shifted toward the to-be-learned pattern (i.e., 30° of relative phase between the limbs). To that end, we submitted the left forearm to inertial loading, whereas we left the right arm unloaded. In doing so, an incongruence was created between the relative phasing of the motor outflow commands associated with the movements of the two limbs and the sensory (i.e., proprioceptive and visual) information specifying the relative phasing of those movements. In that situation, performance of the to-be-learned relative phase (here 30°, specified by an auditory metronome) requires a rel-

ative phasing of approximately 0° between the motor outflow commands. Note that the inertial loading of the left arm may induce small changes in the timing of the motor commands associated with that arm, resulting in a small deviation from the exact 0° phase difference. For our present purposes, however, it was not the precise relative phasing between those commands that was essential but rather the fact that that relative phasing was incongruent with the resulting phase difference specified by the generated sensory signals.

In sum, our main expectation was that participants who practiced (and acquired) the to-be-learned pattern in the described incongruent situation would show positive transfer of learning to performance of the same pattern in the congruent situation, that is, without an externally imposed asymmetry between the limbs. As we have just argued, a finding such as that would indicate that during the learning process, participants internalized the behavioral information by matching the sensory information about the performed relative phase pattern to the specified required coordination pattern. The absence of such a positive transfer would contradict our hypothesis, indicating that the key to learning resides in matching the motor outflow commands to the specified relative phasing pattern. To assess the degree of transfer, we compared the performance of the participants who practiced in the incongruent situation with that of participants who practiced in the congruent situation (i.e., in the absence of symmetry breaking).

Method

Participants

All participants were self-proclaimed right-handers. During the selection procedure, we carried out a so-called scanning run (see Procedure) to assess the intrinsic dynamics of the candidate participants. Individuals with bistable dynamics, that is, individuals who could perform only two coordination patterns in a stable fashion, corresponding to relative phases (RPs) of 0° and 180°, respectively, were invited to participate in the experiment, whereas those who could perform more patterns in a stable fashion were excluded. Out of 29 volunteers, we selected 20 participants (aged 21–26 years) and randomly assigned them to two groups: an incongruent (IC) group (5 men and 5 women) and a congruent (C) group (3 men and 7 women).

Apparatus

Participants sat on a modified chair. Each forearm rested comfortably in a premolded carbon filter splint mounted on a vertical axis; the splint was fitted into a slider, allowing precise positioning of the epicondilus medialis of the participants' elbow above the center of rotation. The splint allowed for flexion and extension around the elbow in the horizontal plane only, in a range of about 120°. Using a motor (developed by Fokker Aerospace for flight simulators), which was connected to the rotation axle of the left splint, we could add an inertial load to the left manipulandum, resulting in an inertial asymmetry (difference in

eigenfrequency) between the arms. We measured the angular position of each axle with a hybrid potentiometer (22HHPS-10; Sakae, Kawasaki, Japan). A digital actuator controller (also developed by Fokker Aerospace) yielded positional data with an accuracy of 0.2°. We used a sampling rate of 200 Hz in all trials.

We specified the required RP by using an auditory metronome that was controlled by a microcomputer. We presented the metronome signals (with each single beep pulse lasting for 50 ms) by means of two speakers that were positioned, respectively, to the right and the left sides of the participant. They differed in tone: The high (440 Hz) tones of the right speaker specified the required movements of the right arm, and the low (200 Hz) tones of the left speaker those of the left arm. For all trials, we fixed the frequency of the successive beeps of either signal at 1 Hz. By varying the time interval between the onsets of the two signals, we were able to generate various relative phases. During the practice trials, participants received KR on a computer screen positioned in front of them (see Figure 1).
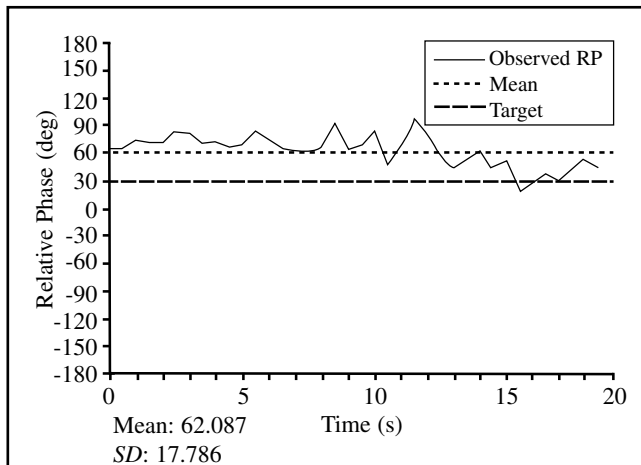
Task

We instructed participants to perform the pattern as specified by the auditory metronome by rhythmically moving both arms, with flexion of the right arm corresponding to the beeps presented through the right speaker and flexion of the left arm corresponding to the beeps presented through the left speaker.

Procedure

We provide a summary of the full experimental design in Table 1. Practice was distributed across 3 consecutive days. Before those practice sessions began, but after familiarization with the task and the experimental set-up, we per-

FIGURE 1. Example of the knowledge of results display as presented after each practice trial. The cycle-by-cycle relative phase (observed RP, solid curve), mean (dotted curve), and 30° target (dashed line) are plotted as a function of time. The within-trial mean and standard deviation of RP (here, 62.087° and 17.786°, respectively) are also shown (bottom, left).

formed two tests (see Table 1, Preparation). First, we assessed the initial coordination tendencies of each participant by probing performance for 25 equidistant RPs, ranging from 0° to 360° (cf. Table 1, Scan). For each participant, the required RPs involved in that so-called scanning procedure were presented in a unique random order. The duration of each trial was 20 s. No KR was provided during or after the scanning trials. We used the results of that first scanning session to match the two groups according to their intrinsic dynamics. We included in the experiment only those participants whose performance abilities were limited to in-phase (RP = 0°) and antiphase (RP = 180°) coordination, that is, those with bistable dynamics. Such bistability was characterized by minimal values for the error and variability at required RPs of 0° and 180°. In addition, other required RPs resulted in either a bias of the actually produced RPs toward those two RPs or in high RP variability (i.e., the transformed circular variance [*TCV*] of the produced RP [see Data Analysis] was higher than 25), or both. For each individual participant of the IC group, we administered a second test before the practice sessions started to determine the level of inertia that was required to induce a phase shift of approximately 30° between the rhythmically moving arms (cf. Table 1, Load level). We achieved that level by presenting a range of inertial loads (0–1,500 kg.m², in randomized steps of 250 kg.m²) to the left arm while we instructed the participant to perform (during 20 s) the in-phase pattern in a comfortable fashion (i.e., without offering resistance to

TABLE 1. Summary of Experimental Design

Task	Number of trials	Knowledge of results	Duration per trial(s)
Day 1			
Preparation			
Scan	25	No	20
Load level[a]	Variable	No	20
Days 2–4			
Practice session (1–3)			
Criterion test (pretest[b])	1	No	40
Practice	15	Yes	20
Criterion test	1	No	40
Practice	15	Yes	20
Criterion test	1	No	40
Scan[c]	25	No	20
1 week later			
Recall session			
Scan	25	No	20
Criterion test	1	No	40

[a]Conducted only for the incongruent group. [b]Conducted only for Practice Session 1. [c]Conducted only for Practice Session 3.

the applied inertia). We selected the load that effectively produced an RP near 30° (± 10°) for the practice sessions. No KR was provided during those load level trials.

We began the first practice session (cf. Table 1, Practice session) with a criterion test in which both groups produced the 30° pattern with symmetric coordination dynamics (i.e., in the absence of asymmetric inertial loading). The criterion test lasted 40 s and consisted of two parts: During the first 10 s, the participant had to produce the required pattern (30°) specified by the metronome (pattern-specification part). Then, the participant had to continue the pattern for 30 s in the absence of the metronome (criterion test proper). No KR was provided during or after the criterion test. We carried out subsequent criterion tests in the middle and at the end of each session. Thus, at the end of the third session, participants had produced seven criterion tests.

Each daily practice session comprised 30 learning trials (lasting 20 s each), in which a required RP of 30° was practiced. For each member of the IC group, we loaded the left arm with the individually determined level of inertia, whereas the members of the C group were not submitted to such a manipulation. After each practice trial, both qualitative and quantitative KR regarding the produced RP was provided to the participant (see Figure 1). We concluded the third session with a scanning run (see the preceding for a description; we again fully randomized the presentation of the RPs) to probe the resulting underlying dynamics (cf. Table 1).

One week later, in a recall session, we conducted one criterion test and one scanning run to determine the long-term effects of practice (see Table 1, Recall session).

Data Analysis

We low-pass filtered the signals with a recursive second-order Butterworth filter that we applied back and forth to negate the phase shift (Lees, 1980), and we used a peak-finding algorithm to identify maximal extension and flexion for each cycle. We adapted the length of the analyzed part of the trials to the trial length in question; that is, we analyzed the last 17 s of the scans and the practice trials, the first 3 s and the last 3 s of the pattern-specification part of the criterion test (with metronome), and the last 20 s of the criterion test proper (without metronome).

We determined the main dependent variable—the point estimate of the actually produced RP—by using the peak excursions in the recorded right (R) and left (L) arm movements. RP was determined for every peak (i.e., for both peak extension and peak flexion), resulting in two estimates of relative phase for each movement cycle. Those were defined as $(t[L_n] - t[R_m])/(t[R_{m+1}] - t[R_m]) \cdot 180°$, where t refers to the moment in time at which a given peak was attained and m and $m + 1$ index the two peaks in the right arm signal between which the considered peak in the left arm signal (indexed by n) was situated in time. L_1 and R_1 were both flexion peaks; therefore, we could determine RP unambiguously on the basis of the subsequent peak numbers (n, m). For each trial, we calculated mean relative phase ($RP_{perfomed}$)
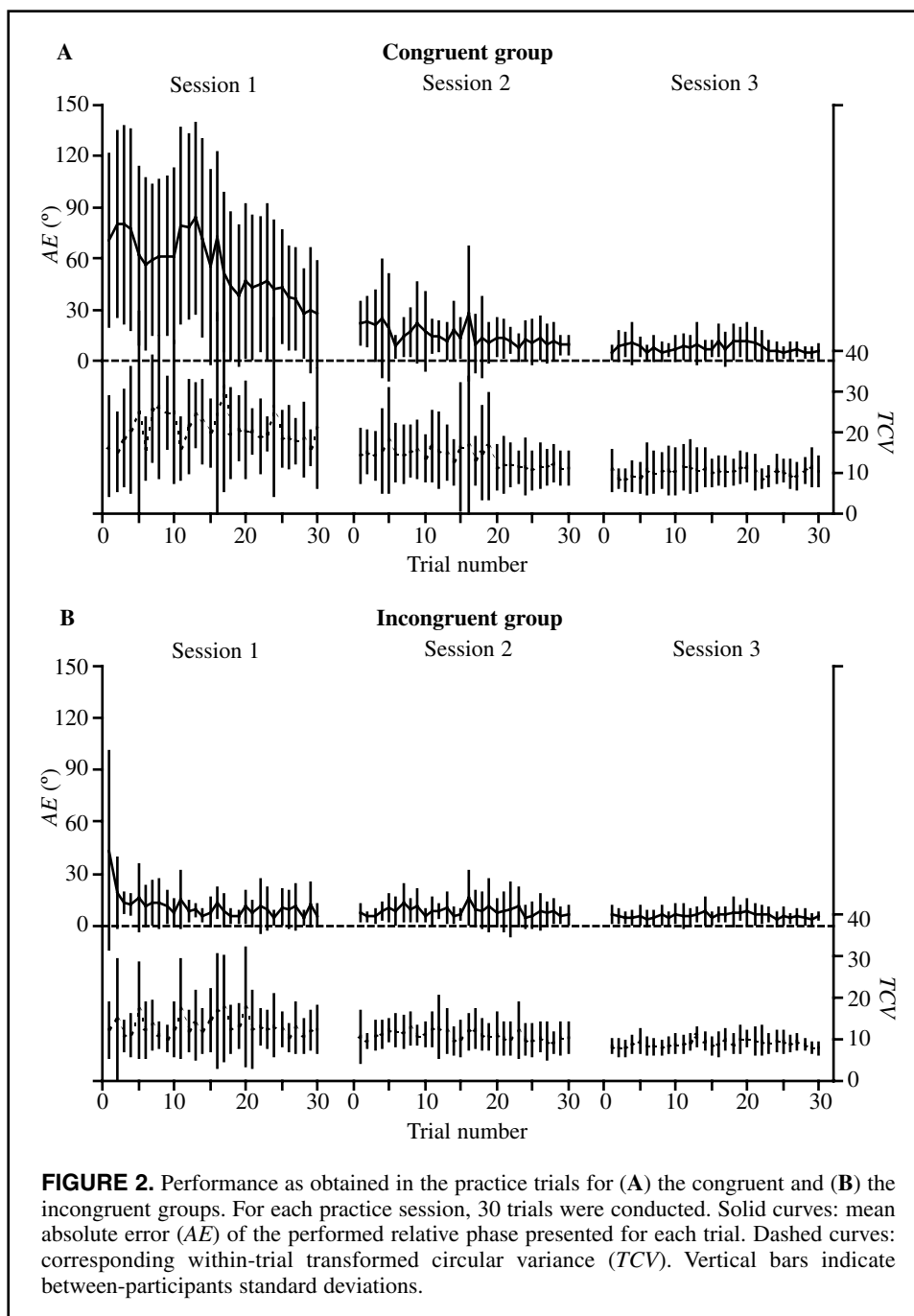
as well as *TCV* (a measure of variability resembling the ordinary standard deviation, with large values reflecting high variability) by using circular statistics (Mardia, 1972). Depending on the purpose of the analysis, we considered the absolute error ($AE = |RP_{performed} - RP_{required}|$) for the practice trials, scans, and criterion tests proper, whereas we examined the constant error ($CE = RP_{performed} - RP_{required}$) for the pattern-specification phase of the criterion test.

Results

The results are presented in three sections. First, we compare the changes in performance during the practice trials for the two groups (IC and C) in terms of the learning rates that were achieved. In the second section, we address our main research question by analyzing the results obtained for the criterion tests. In those tests, both groups performed the to-be-learned pattern (30°) in the congruent situation (i.e., in the absence of asymmetric inertial loading). We expected that a comparison of the performance of the two groups (who practiced under different circumstances) would provide information about the relative importance of matching either the required phasing of the motor outflow commands or the movement-induced phasing of sensory signals to the externally specified relative phase pattern. In the final section, we present the modifications of the coordination dynamics for both groups, as revealed by the three scanning probes.

Practice Trials

In Figure 2, we provide a general picture of the evolution of performance with practice under congruent (Figure 2A) and incongruent conditions (Figure 2B). For both groups, a clear decrease in both *AE* and *TCV* can be observed. The decreases were corroborated statistically by the results of an analysis of variance (ANOVA) with a 2 (group: C vs. IC) × 3 (session: 1, 2, 3) × 30 (trial: 1–30) factorial design in which group was the between-participants factor and session and trial were the within-participants factors. Significant effects were obtained for *AE* for both session and trial as well as for their interaction, $F(2, 36) = 27.26$, $p < .001$, $F(29, 522) = 4.54$, $p < .001$, and $F(58, 1044) = 2.26$, $p < .05$, respectively. For *TCV*, we found significant main effects of only session and trial, $F(2, 36) = 55.77$, and $F(29, 522) = 2.03$, respectively, both $ps < .001$. Moreover, Figure 2 reveals clear differences in performance (with respect to both *AE* and *TCV*) between the groups; in general, the IC group was more accurate and less variable than the C group. That observation was supported by the significant main effect of group on both dependent variables—for *AE*, $F(1, 18) = 15.58$, $p < .005$; for *TCV*, $F(1, 16) = 5.72$, $p < .05$. The most salient difference between the groups concerned the evolution of *AE* with practice (top, solid curves in Figures 2A and 2B); the IC group quickly established a rather low *AE*, whereas the C group started out with a considerably higher *AE* and improved at a much slower rate. The significant interactions between group and session, $F(2, 36) = 18.41$, $p < .001$, and between group and trial, $F(29, 522) = 2.26$, $p < .05$, highlighted that difference. Comparison of the

FIGURE 2. Performance as obtained in the practice trials for (**A**) the congruent and (**B**) the incongruent groups. For each practice session, 30 trials were conducted. Solid curves: mean absolute error (*AE*) of the performed relative phase presented for each trial. Dashed curves: corresponding within-trial transformed circular variance (*TCV*). Vertical bars indicate between-participants standard deviations.

TCV obtained for the two groups (bottom, dashed curves in Figures 2A and 2B) showed a similar difference between the groups, which was corroborated by a significant Group × Session interaction, $F(2, 36) = 11.49$, $p < .001$.

Thus, the results showed that during the practice trials, both groups improved their performance in terms of accuracy (*AE*) as well as variability (*TCV*). However, the shape of the learning curves differed considerably over the two groups.
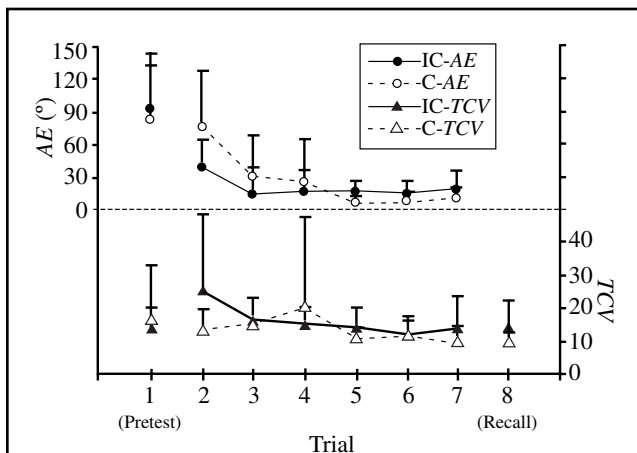
Criterion Tests

Examination of the transfer of the IC group from the incongruent to the congruent situation enabled us to assess the extent to which learning depended on matching movement-related sensory information or, alternatively, the phasing of the motor outflow commands to the presented behavioral information. Therefore, we compared the performances of the IC and the C groups on the criterion tests. To examine how well the two groups could perform the practiced 30° pattern, we focused in that analysis on the second part of the criterion trials during which the metronome signals were removed, that is, the criterion test proper (note that during the practice trials, the metronome was present throughout the trial). We conducted an ANOVA on *AE* and *TCV* with a 2 (group: C vs. IC) × 8 (trial: 1–8) factorial design in which group was the

between-participants factor and trial was the within-participants factor. The evolution of RP performance (AE and TCV) as obtained for the criterion test proper is shown in Figure 3. For both groups, AE decreased significantly as a function of trial, $F(7, 126) = 21.33$, $p < .001$. However, no differences between the two experimental groups were observed for either dependent variable. Therefore, it appeared that irrespective of the differences in the practice situation (for the C group, both the motor outflow commands and their perceptual consequences were congruent with the specified pattern, whereas for the IC group, only the sensory signals were congruent with that pattern), the rate of learning and the performance of the learned pattern were identical for both groups. To further examine eventual differences between the two groups, we performed additional analyses in which we focused on the initial part of the criterion tests, that is, the pattern-specification part.

Because Criterion Tests 2–7 were conducted directly after a series of practice trials, it is not unlikely that the performance during the initial part of the criterion tests was influenced by the learning situation at hand (which differed between the two groups). Therefore, we analyzed that part of the criterion test (during which the pattern was specified by the metronome) in more detail. Specifically, we focused on the changes in performance during the first 10 s of the trials by comparing the first 3 s to the last 3 s (henceforth referred to as the *first* and the *last epochs*). We performed an ANOVA with a 2 (group: C vs. IC) × 8 (trial: 1–8) × 2 (epoch: first, last) factorial design in which group was a between-participants factor and trial and epoch were within-participants factors for both CE and TCV. In Figure 4, we show the evolution of performance (CE and TCV) for the first epoch (Figure 4A) and the last epoch (Figure 4B) for the C group (dashed curves) and

the IC group (solid curves). The main effects of trial revealed that the changes in CE (directed toward 0°) as well as the decrease in TCV were statistically significant, $F(7, 126) = 8.42$, $p < .001$, and $F(7, 126) = 3.9$, $p < .005$, respectively. The effects of epoch were also significant—for CE, $F(1, 18) = 17.36$, $p < .005$; for TCV, $F(1, 18) = 24.26$, $p < .001$—as was the interaction between trial and epoch for CE, $F(7, 126) = 3.03$, $p < 0.01$. Most interesting, there was a significant effect of group, which was accompanied by significant interactions with trial as well as with epoch for CE, $F(1, 18) = 11.47$, $p < .005$, $F(7, 126) = 2.17$, $p < .05$, and $F(1, 18) = 19.99$, $p < .001$, respectively. Concerning the Group × Epoch interaction, we conducted post hoc analyses (paired t tests, $p < .05$) to compare the two epochs between and within groups. For the C group, we found no significant difference between the first and last epochs, whereas for the IC group, the difference was significant. For the latter group, the CEs of the first epoch were systematically smaller than 0° (tending toward –30°; cf. Figure 4A, solid curve), whereas the corresponding CEs of the last epoch were close to or slightly larger than 0°. Furthermore, the post hoc tests revealed that although the groups differed with respect to the CEs obtained for the first epoch

FIGURE 3. Performance as obtained in the criterion test proper (i.e., without metronome) for the congruent (C) group (dashed curves) and the incongruent (IC) group (solid curves). Circles: mean absolute error (AE) of the performed relative phase for the eight criterion trials. Triangles: corresponding within-trial transformed circular variance (TCV). Vertical bars denote between-participants standard deviations.
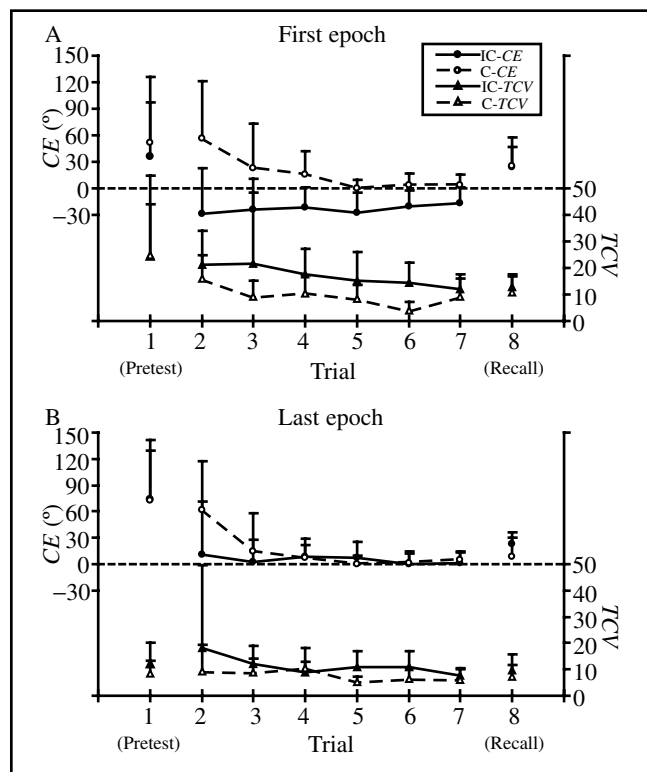
FIGURE 4. Evolution of performance for the first epoch (**A**) and last epoch (**B**) of the pattern-specification part of the criterion test for the congruent (C) group (dashed line) and the incongruent (IC) group (solid line). Circles: mean constant error (CE) of the performed relative phase for the eight criterion trials. Triangles: corresponding within-trial transformed circular variance (TCV). Vertical bars denote between-participants standard deviations.
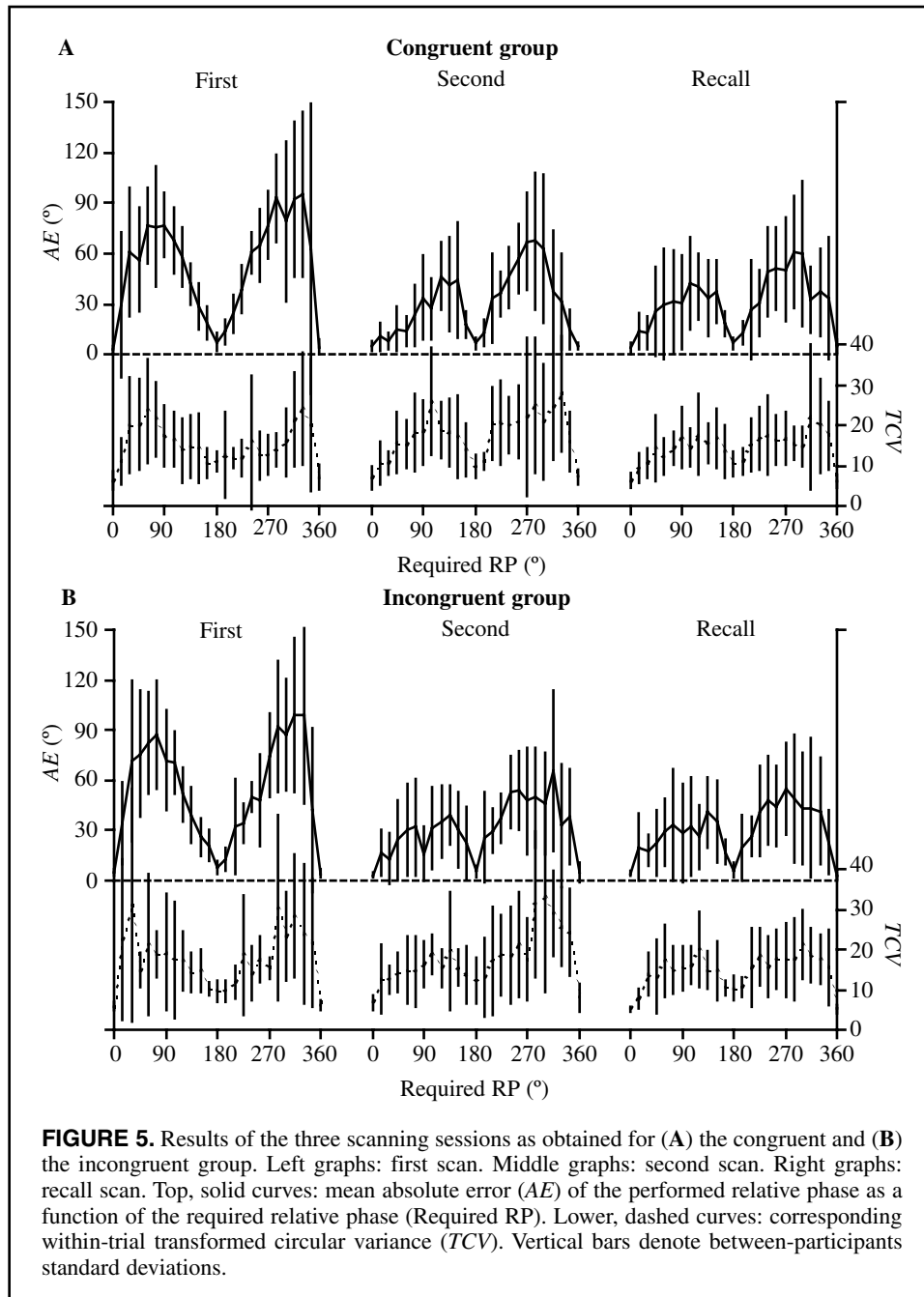
(cf. Figure 4A), that difference was no longer present for the last epoch (Figure 4B).

Thus, whereas we observed no differences between the groups on the criterion tests proper (i.e., with the metronome turned off), the performances of the two groups were clearly different during the initial part of the criterion tests (during which the required pattern was specified with a metronome). In all likelihood, that result reflects the influence of the different learning conditions as applied in the practice trials.

Scanning

To assess the manner in which the coordination dynamics changed with practice, we performed an ANOVA with a $2 \times 3 \times 25$ factorial design with the between-participants factor group (C, IC) and the within-participants factors scan (1, 2, 3) and RP (0, 15, 30, . . . , 360) on AE and TCV, as obtained for the scanning sessions. In Figure 5 are the results for the three probes carried out before and after the learning procedure as well as 1 week later (recall) for the C and IC groups (Panels A and B, respectively). The results clearly showed that performance (as indexed by both AE and TCV) largely depended on the required RP. Common features observed in all scans were the low AE and TCV for the RPs of 0° (360°) and 180° relative to intermediate values. The significant main effects of RP underscored that aspect of the scans: For AE and TCV, Fs(24, 432) = 23.89

FIGURE 5. Results of the three scanning sessions as obtained for (**A**) the congruent and (**B**) the incongruent group. Left graphs: first scan. Middle graphs: second scan. Right graphs: recall scan. Top, solid curves: mean absolute error (*AE*) of the performed relative phase as a function of the required relative phase (Required RP). Lower, dashed curves: corresponding within-trial transformed circular variance (*TCV*). Vertical bars denote between-participants standard deviations.

and 13.38, respectively, both ps < .001. Moreover, the change in the global form of the AE and TCV curves over the subsequent scans (left, middle, and right graphs) resulted in a main effect of scan for both dependent variables: AE, $F(2, 6) = 48.96$, $p < .001$; TCV, $F(2, 36) = 4.02$, $p < .05$.

As expected, the initial scan (left graphs in Figures 5A and 5B) revealed that the coordination dynamics were characterized by attraction to in-phase and antiphase (i.e., the dynamics were bistable) for both groups. The second scans revealed that the subsequent 3 days of practice had affected the initial coordination dynamics (middle graphs in Figure 5A and B), especially around the to-be-learned pattern (i.e., 30°). Indeed, the ANOVA showed a significant Scan × RP interaction for both AE and TCV, Fs(48, 864) = 7.62 and 2.36, respectively, both ps < .001. We conducted post hoc analyses (paired t tests, $p < .05$) to compare the three scans. Only the comparison between the first and the second scans yielded significant results, indicating a decrease in the AEs obtained for the RPs between 15° and 120° and between 270° and 330°. Moreover, the only significant difference between those two scans with regard to TCV concerned a significant decrease from the first to the second scan for the 30° pattern (i.e., the pattern practiced in the intermediate practice sessions). The ANOVA did not yield any significant effects associated with group.

In sum, with respect to the changes in the coordination dynamics as a result of learning, we obtained no systematic differences between groups, even though the practice situation differed (being either congruent [C group] or incongruent [IC group]). The changes in the coordination dynamics indicated stabilization of the practiced pattern (i.e., 30°) characterized by a decrease of both AE and TCV. Those changes appeared to be relatively permanent, because significant differences between the second scan and the recall scan were absent.

Discussion

Our aim in the present experiment was to gain more insight into how behavioral information about a new coordination pattern might be internalized or memorized so that it becomes part of the coordination dynamics. Our hypothesis was that individuals accomplish the memorization of behavioral information predominantly by matching the sensory information about the performed coordination pattern (rather than the phasing of the associated motor outflow commands) to the required pattern (as specified by behavioral information). To that end, we created incongruence between the motor outflow commands and the phasing of the resulting sensory signals by using inertial loading to break the symmetry between the two coordinated limbs. In the following, we first discuss the effects of introducing that incongruence on practicing a new coordination pattern and on the practice-induced changes in the overall coordination dynamics. Next, we discuss the implications of the findings for our main research question regarding the manner in which behavioral information becomes memorized, and we finish with a discussion of associated corollaries for the dynamical systems approach.

The participants who practiced under the incongruent condition (the IC group) could perform the required 30° pattern by generating roughly synchronous motor outflow commands (i.e., with a relative phasing of approximately 0°), thanks to the imposed asymmetry between the coordinated lower arms. Analysis of the practice trials indicated that right from the start, the performance of the IC group was closer to the required RP of 30° and improved much quicker during the subsequent practice trials than did that of participants with congruent information (the C group). The analyses conducted on the modifications of the coordination dynamics (based on the scans), however, revealed no significant differences between the two groups. Thus, despite the differences in the performance curves during the practice trials, the practice-induced changes in coordination dynamics were similar after practice was completed. Note that during the scanning trials, the inertial loading was not applied to the IC group, rendering the situation identical for the two groups.

Throughout the experiment, we carried out criterion tests to compare the abilities of the two groups to perform the 30° pattern under the congruent condition. The results showed that during the initial part of the criterion test (i.e., during the first 3 s of pattern specification), the CE obtained for the IC group was systematically negative, reflecting a bias toward the 0° pattern (i.e., CE tended toward –30°), whereas that bias was absent in the C group. This initial bias in performance was consistent with the fact that during IC practice, the generation of roughly synchronous motor outflow commands resulted in the required 30° pattern because of the imposed asymmetric inertial load. Most interesting, the IC participants were able to correct that initial tendency within 7 s. Thus, even though they did not actively practice the required relative phasing of the motor outflow commands, they required only 7 s to perform the 30° pattern equally well as the C group did after removal of the inertial loading of the left arm. The fact that the groups did not differ with regard to their performance on the criterion test proper also underscores the positive transfer.

The positive transfer observed for the IC group clearly corroborates our hypothesis that during the learning process participants memorized behavioral information (specifying the to-be-learned pattern) by matching the sensory information about the performed relative phase to the specified coordination pattern. As argued in the introductory comments, that result can be readily understood in relation to the ideomotor hypothesis, according to which the expected sensory consequences play an essential role in the selection of motor outflow commands. The remarkably quick adjustments made by the IC group in the pattern-specification phase of the criterion tests and the fact that both groups performed equally well on the criterion test proper suggest that when an action is represented in terms of its anticipated perceptual consequences, the actual transformation of those consequences into appropriate motor commands is relatively straightforward. In other words, if behavioral information is memorized on the basis of the movement-induced sensory

signals, then one may expect it to be effective in all situations requiring a similar phasing of the resulting sensory signals, regardless of the corresponding characteristics of the associated motor outflow commands.

The interpretation that behavioral information is memorized on the basis of its correspondence to the perceptual consequences of the performed movements underscores the relevance of linking the abstract coordination dynamics to underlying system properties and processes (Beek, Peper, Daffertshofer, Van Soest, & Meijer, 1998; Peper, Daffertshofer, & Beek, 2004; Peper, Ridderikhoff, Daffertshofer, & Beek, in press) because the current definition of behavioral information (purely in terms of a potential attracting the behavior to the specified pattern) does not address the mechanisms or processes that mediate its influences on the coordination dynamics. Although modeling by means of potentials provides an interesting account of the stability characteristics of the coordination dynamics that result from the interplay between an individual's intrinsic dynamics and specific behavioral information, it does not allow investigation of how that interplay between those two cornerstones of the coordination dynamics is realized.

Relatedly, the present results may suggest that further conceptualization of the dual notions of competition and cooperation (cf. Schöner et al., 1992) should be sought primarily in terms of the degree of correspondence between the perceptual consequences of task execution and the provided behavioral information. In the current experiment, a situation of cooperation was created for the IC group in which the manipulated coordination dynamics corresponded to the required coordination pattern. That situation readily enabled adequate performance of the required pattern, resulting in sensory signals that matched the behavioral information. The correspondence between signals and behavioral information appeared to facilitate the learning process because the IC group performed more accurately than the C group did during the first practice sessions. Similarly, the competition between the intrinsic dynamics and the behavioral information that characterized the practice conditions of the C group complicated the generation of sensory signals corresponding to the behavioral information because the intrinsic dynamics hindered performance of the required pattern.

Before closing, it is useful to qualify the implications of the present results on learning for current investigations of the perceptual basis of rhythmic bimanual coordination. First of all, our findings do not elucidate which modalities of the sensory information are instrumental in the learning process because we did not manipulate the availability of the visual and proprioceptive information sources. Second, although the present results emphasize the key role of perceptual consequences in learning a new bimanual coordination pattern, they do not necessarily imply that the stability characteristics of real-time rhythmic interlimb coordination are fully or even primarily determined by perceptual processes. As explained in the introduction, a number of studies involving specific perceptuomotor transformations or incongruences have revealed that perception of relative phase may influence the stability of rhythmic coordination patterns (e.g., Bogaerts et al., 2003; Mechsner et al., 2002) or have indicated that particular interlimb interactions may be based on visual information (Weigelt & Cardoso de Oliviera, 2003). However, that finding does not, in itself, imply that the stability features observed in the absence of such perceptuomotor manipulations also mainly originate from perceptually mediated processes, as opposed to processes that are independent of the perception of the performed relative phasing between the limbs (e.g., processes associated with "neural cross-talk" or the central generation of the required temporal patterning of the motor outflow command; cf. Peper et al., 2004). Thus, although inducing perceptuomotor incongruences provides an expedient means for uncovering the role of perceptual factors in movement coordination, there remains a clear need to determine their importance relative to other aspects of the coordination process.

In sum, the present results underscore the role of the perceptual consequences of performance in acquiring a new coordination pattern, a finding that can be readily related to the ideomotor hypothesis. From the dynamical systems perspective, they indicate how behavioral information is incorporated into the coordination dynamics because the present results suggest that matching the sensory consequences of the movements to the specified coordination pattern mediates that process.

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