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Do Muscles Matter for Coordinated Action?

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This article investigates coordination stability when 2 fingers of each hand periodically tap together. The main question concerns the functional origin of the symmetry tendency, which has widely been conceived as a bias toward coactivation of homologous fingers and homologous muscular portions. In Experiment 1, the symmetry tendency was independent of finger combination. In Experiment 2, virtually identical stability characteristics were revealed under full vision and no vision. In Experiment 3, symmetrical and parallel visual labels on the fingers neither stabilized nor destabilized symmetrical and parallel tapping patterns. In Experiment 4, in which the relative position of the hands was varied, it revealed that the observed stability characteristics are to be defined in a hand-centered reference frame. Because the symmetry tendency was always independent of finger combination, the authors suggest that it is not a bias toward coactivation of homologous muscle portions but instead originates on a more abstract, functional level.

When a person moves his or her limbs simultaneously, there is a tendency toward synchronizing the displayed movement patterns in time and space. This tendency toward bimanual congruency is particularly strong in periodic movements. In bimanual oscillatory movements, mirror symmetry with regard to the midsagittal plane is the preferred, and the most stable, movement mode. With increased movement speed, involuntary transitions from asymmetrical to symmetrical patterns occur. Inspired by the seminal articles by Cohen (1971), Kelso (1981, 1984), and Haken, Kelso, and Bunz (1985), much experimental and theoretical research has been devoted to the differential stability and transition behavior in bimanual oscillatory movements. The experimental paradigms included bimanual hand circling (e.g., Semjen, Summers, & Cattaert, 1995), bimanual wrist oscillation (e.g., Carson, Riek, Smethurst, Lison-Parraga, & Byblow, 2000), interlimb coordination between hand and foot (e.g., Baldissera, Cavallari, & Civaschi, 1982), and intralimb coordination (e.g., Carson, Goodman, Kelso, & Elliot, 1995), among others.

The classic bimanual index finger oscillation paradigm has gained special prominence, because it was a focus of the landmark papers by Kelso (1984) and Haken et al. (1985), putting forward the so-called synergetic or dynamic systems approach to human movement coordination. The participant places both arms in parallel to each other, in a sagittal direction. There are only two stable patterns of bimanual index finger oscillation in the transverse plane. The symmetrical pattern is characterized by periodic mirror-symmetrical finger movements toward and away from the sagittal body midline. The parallel pattern is characterized by one finger moving away from the sagittal midline along with the other finger moving toward it, and vice versa. At a slow speed, most people are able to successfully produce the symmetrical as well as the parallel pattern. However, when oscillation speed is increased, only the symmetrical pattern can be performed up to the highest possible frequencies. The parallel pattern, in stark contrast, cannot be maintained with increasing speed. Spontaneous transitions to a symmetrical oscillation pattern are often observed.

Cohen (1971) and Kelso (1984) emphasized that the symmetrical coordination mode is characterized by coactivation of homologous muscles, suggesting that the symmetry advantage might arise because of this coactivation. As such, the symmetry advantage is open for various interpretations concerning the functional locus of its emergence. Three main possible interpretations have been proposed over the years. First, the symmetry advantage might be executional, or motoric, in nature (i.e., it might reflect cross talk in efferent neuronal structures; see Carson et al., 2000; Cattaert, Semjen, & Summers, 1999). Second, the symmetry advantage might be due to bimanual interference during parameterization of the bodily characteristics of movements (see Heuer, 1993; Heuer, Kleinsorge, Spijkers & Steglich, 2001). Third, the symmetry advantage might not be canonically bound to the body but be even more abstract in nature, reflecting interference in connection with specification of intended movement goals (see Diedrichsen, Hazeltine, Kennerly, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerly, & Cohen, 2003). In the present article, we focus on the basic dichotomy between the first interpretation, which claims that interference takes place on the level of motor commands, and the second and third interpretation, which both suggest that interfer-

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ence originates on a more abstract level of movement organization processes that use perceptual codes.

The experimental evidence so far suggests that perceptual factors certainly can play a role in spontaneous bimanual coordination dynamics. For example, two people looking at each other tend to synchronize their swinging legs or handheld pendulums. Even spontaneous transitions from parallel to symmetrical oscillations occur in these situations (R. C. Schmidt, Bienvenu, Fitzpatrick, & Amazeen, 1998; R. C. Schmidt, Carello, & Turvey, 1990; R. C. Schmidt & O'Brien, 1997). Similarly, two people looking at each other tend to synchronize periodic flexion and extension movements of the index fingers into synchronous flexion and synchronous extension (Oullier, DeGuzman, Jantzen, & Kelso, 2002). There is a symmetry tendency between unilateral limb movements and moving objects (Wimmers, Beek, & van Wieringen, 1992). Intrapersonal oscillations of ipsilateral hand and foot are preferably synchronized in parallel in the parasagittal plane, independent of a prone or supine position of the forearm (Baldissera et al., 1982; Carson et al., 1995). Tactile feedback can stabilize, destabilize, and even reverse the preferred coordination mode in periodic bimanual finger flexion and extension (Kelso, Fink, DeLaplain, & Carson, 2001). In the light of these and similar results, several researchers have assumed that bimanual coordination might generally be informational or abstract in nature (e.g., Kelso, 1994; Saltzman, 1995). If we understand these proposals correctly, this would mean that perceptual codes would generally be of primary and crucial relevance in bimanual coordination. Perceptual factors of any modality (vision, kinesthetics, touch, audition, etc.) and of many kinds might play a role in spontaneous and voluntary coordination, in view of the multitude of perceptual grouping principles proposed by researchers in the Gestalt tradition (see Köhler, 1947, 1971).

A tendency toward coactivation of homologous muscles may be open to possible perceptual anticipatory explanations. It might be that coactivation of homologous muscles leads consistently to perceptual effects that are preferably tuned. Strictly speaking, one could argue in this case that it is not muscular homology but the respective perceptual features that are the basis of coordination processes.

It is important, however, that a coactivation tendency of homologous muscles would be open to a nonperceptual explanation as well, in terms of interference between homologous motor command pathways. Several researchers embrace this position and suggest that in the special, but most important, case of bimanual movements of homologous limbs, there might be a general and strong tendency toward coactivation of homologous muscles (e.g., Swinnen, 2002; Swinnen et al., 1997, 1998). Bilateral cross talk in neuronal command streams or other tendencies leading to a preferred coactivation of homologous motor pathways would provide a plausible nonperceptual mechanism, as a rather general tendency in efferent neuronal structures (Cattaert et al., 1999; Swinnen, 2002).

In the present experiments, we investigate the locus of the symmetry tendency in a bimanual four-finger tapping paradigm, with two fingers of each hand involved. Can the symmetry tendency plausibly be understood as a tendency toward coactivation of homologous muscles or muscular portions, which might be understood as a tendency toward coactivation of homologous efferent command streams? Or is this coordination tendency caused by perceptual characteristics that can be dissociated from muscular homology?

To our knowledge, the four-finger tapping paradigm has not been experimentally addressed in a systematic way until recently (Mechsner, Kerzel, Knoblich, & Prinz, 2001). However, even without sophisticated experimentation, the symmetry tendency in bimanual four-finger tapping is immediately obvious. The participant places the hands parallel to each other on a desk, both in a sagittal direction, with the index and middle fingers stretched out (Figure 1A). He or she taps in the following way as if playing a virtual piano. First the left index finger is moved down synchronously with the right middle finger. Then the left index finger is lifted together with the right middle finger and, at the same time, the left middle finger is moved down synchronously with the right index finger. This parallel tapping pattern is repeated periodically, at a slow pace. Then the speed is increased while one tries to maintain the parallel pattern. Most likely, one will be able to do so only up to a certain maximal speed, beyond which one will fall spontaneously into a symmetrical pattern, with both index fingers tapping synchronously in alternation to both middle fingers. One will realize that the symmetrical pattern can be maintained rather easily, virtually up to the highest possible tapping frequencies. Moreover, it is difficult to adopt any other tapping pattern at fast speed.

Actually, the evident, and surprising, phase transition from parallel toward symmetrical tapping in this paradigm inspired Kelso (1984) to explore dynamical systems phenomena in human finger movement patterns. Until this time, the dynamic systems approach to biological movements had mainly been applied to phenomena such as gait transitions in horses and humans.

Kelso and his coworkers (Haken et al., 1985; for a review, see Kelso, 1995) extensively investigated the bimanual index finger oscillation paradigm, as a simplified version of the task, but did not, at least to our knowledge, return to his first inspiration (i.e., the four-finger tapping paradigm). MacKay and Soderberg (1971) studied other bimanual multifinger tapping paradigms with more than four fingers involved. Consistent with Kelso's (1984) later observations, these experiments revealed a tendency toward synchronous taps of anatomically homologous fingers even if this was contrary to the instructed tapping pattern. The authors called this phenomenon a tendency toward *homologous intrusion*.

On closer inspection, the four-finger tapping paradigm does not correspond as closely to the index-finger wiggling paradigm as had originally been assumed by Kelso (1984). This is mainly because in the four-finger tapping paradigm, there is not such a perfect one-to-one relationship of the muscles and digits involved in the task. The most prominent finger flexors, namely flexor digitorum profundus and flexor digitorum superficialis, are located in the forearm. Both muscles contribute to the flexion of index, middle, ring, and little fingers, as they have four tendons each that individually attach to the four digits. Reilly and Schieber (2001) provided evidence that flexor digitorum profundus is divided into compartments, which are devoted to the flexion of separate fingers. However, the compartmentalization is not perfect. Thus, contraction of a certain muscular portion usually contributes to the flexion of more than one finger. This behavior, which might also hold for flexor digitorum superficialis, seems one of the main reasons for the observation that voluntary movements of one finger

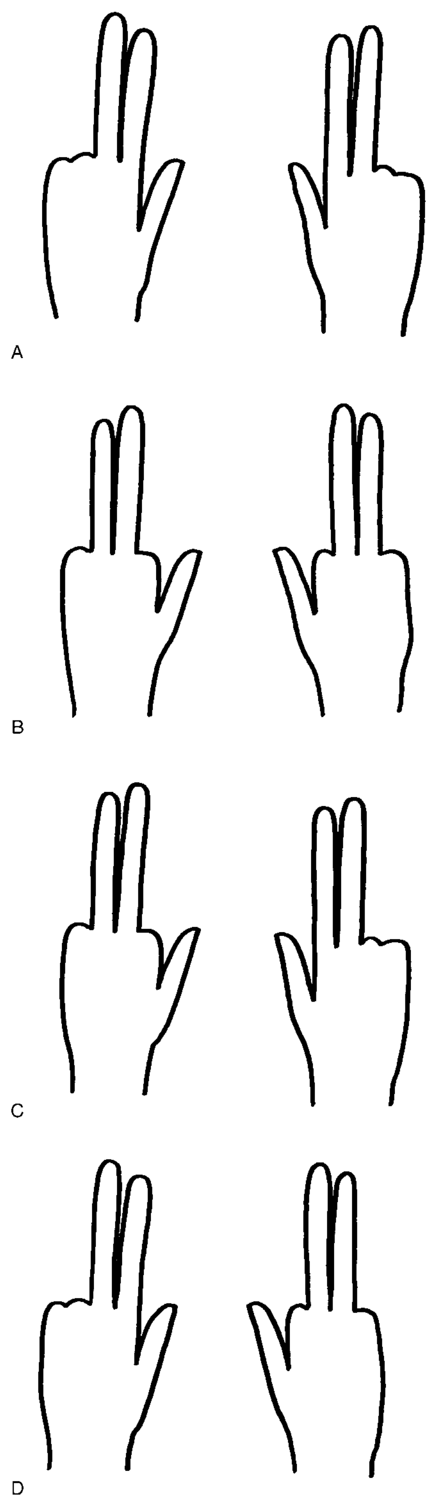


Figure 1. Instructed finger combinations. A and B: Congruous combinations with the same two fingers selected in both hands. C and D: Incongruous combinations with different fingers selected in both hands.

usually are accompanied by nonintended movements of other fingers (Hager-Ross & Schieber, 2000). It should be noted here that flexion of a digit is even more complicated because of the involvement of muscles that are internal to the hand, which are also engaged in finger adduction and abduction (for details concerning the functional anatomy of the hand and arm, see Eaton, 1997).

In the light of these considerations the homologous muscle approach to the symmetry tendency should be somewhat reformulated by pointing out that homologous muscular portions might be coactivated in synchronous flexion of homologous fingers. The corresponding hypothesis thus claims that the symmetry tendency has to be understood as resulting from a tendency toward coactivation of homologous muscular portions and, thus, may be a tendency toward coactivation of efferent motor command streams. As stated above, perceptual factors also might be of relevance, which normally result in coactivation of homologous fingers and muscular portions but can, in principle, be dissociated from muscular homology. Specifically, it might be that the symmetry tendency is toward perceptual spatial mirror symmetry rather than toward coactivation of homologous muscular portions. Applied to the four-finger tapping paradigm, this would mean that there is a tendency to synchronously tap the fingers close to the midline (i.e., inner fingers) in alternation to the fingers apart from the midline (i.e., outer fingers). Recently, Mechsner et al. (2001) provided experimental results suggesting that the symmetry tendency in four-finger tapping is indeed toward spatial symmetry, independent of the fingers involved. They suggested that the symmetry tendency originates on a more abstract level, in connection with planning processes that use perceptual codes.

Further support for this notion may be taken from a related line of research, which investigated whether there is a reaction time (RT) advantage for successive or synchronous taps of homologous fingers. Wakelin (1976) found an RT advantage for successive taps of homologous fingers compared with nonhomologous fingers. Interestingly, it seems to be crucial for this advantage that the pair of fingers to be used is not known by the participant in advance (Heuer, 1986). Actually, the RT advantage for pairs of homologous fingers disappeared if participants were informed prior to the task, or "precued" (Rosenbaum, 1980, 1983), which fingers to use (Heuer, 1985). The RT advantage disappeared as well if the selected finger pairs were constant across blocks, and, thus, their prespecification was possible (Heuer, 1982a, 1982b, 1982c; Rosenbaum & Kornblum, 1982; for a review, see Heuer, 1993). Heuer concluded that the RT advantage is only transient. He proposed that homologous coupling might occur on a level at which movement parameters are planned and specified, rather than on a level of efferent motor execution. In the present study, we investigated the differential stability characteristics in the four-finger tapping paradigm more thoroughly than was done in Mechsner et al. (2001). Our first experiment is essentially a replication of the experiment on four-finger tapping reported in Mechsner et al., with the results analyzed in more detail. By varying the involved finger combinations, mirror-symmetrical tapping was dissociated from coactivation of homologous fingers. The main experimental questions were as follows: Would the symmetry tendency turn out to be a tendency toward spatial mirror symmetry, independent of the fingers and thus dominant muscular portions involved? Or would a tendency toward coactivation of homologous fingers occur, independent of whether the resulting most stable pattern was symmetrical or parallel?

Experiment 1

Participants performed four-finger tapping tasks as a variation of the standard paradigm described above. As an additional factor, different finger combinations were introduced (Figure 1). There were two types of finger combinations, denoting two levels of the factor congruency. In the congruous condition, the finger combinations were the same in both hands. It included the finger combinations (MI, IM; Figure 1A) and (RM, MR; Figure 1B). *I* denotes the index finger, *M* the middle finger, and *R* the ring finger. Inside the parentheses, the fingers are denoted from left to right (i.e., the left pair of characters denotes the finger combination in the left hand, whereas the right pair of characters denotes the finger combination in the right hand). In the incongruous condition, the finger combinations in both hands were different. It included the finger combinations (RM, IM; Figure 1C) and (MI, MR; Figure 1D).

In addition, there were two movement instructions. Symmetrical movements were executed by tapping the inner and outer fingers of the respective four-finger combination, in alternation. With *inner finger* we refer to the finger of each hand that is closer to the sagittal body midline. With *outer finger* we refer to the finger of each hand that is further away from the sagittal body midline. For example, for the congruous finger combination (MI, IM), symmetrical tapping was defined as periodically alternating synchronous bimanual taps of the form (_I · I_), (M_ · _M), (_I · I_), and so on.[1] For the incongruous finger combination (RM, IM), symmetrical tapping was defined as periodically alternating taps of the form (_M · I_), (R_ · _M), (_M · I_), and so on. Parallel movements were executed by tapping the outer finger of one hand synchronously with the inner finger of the other hand and vice versa, in alternation. To give an example, with the congruous finger combination (MI, IM), parallel tapping is defined as periodically alternating synchronous bimanual taps of the form (_I · _M), (M_ · I_), (_I · _M), and so on. With the incongruous finger combination (RM, IM), parallel tapping is defined as periodically alternating taps of the form (_M · _M), (R_ · I_), (_M · _M), and so on.

The hypotheses were as follows. For the congruous condition, we expected a replication of Kelso's (1984) original observation (i.e., stability of the symmetrical movement and corruption of the parallel movement with increasing frequencies, together with transitions from the parallel to the symmetrical pattern). For the incongruous condition, two alternative predictions were derived. If there is a dominant tendency toward coactivation of homologous fingers (as confounded with homologous muscular portions and motor commands), parallel movements should be more stable than symmetrical movements. This is because only parallel movements involve synchronous taps of homologous fingers, namely the middle fingers, whereas symmetrical movements do not. By contrast, if there is a dominant tendency toward spatial perceptual symmetry, symmetrical movements should be more stable than parallel movements.

Method

Participants. Twelve adults, 8 women and 4 men, ages 22–29 years ($M = 24.3$ years), participated in Experiment 1. All participants were right-handed according to self-report. Five additional participants were excluded from the experiment, because they were not able to perform parallel tapping even at low frequencies. The participants, most of them students at the Ludwigs-Maximilian-Universität, Munich, Germany, signed an informed consent prior to the experiment. None of them had previous experience with the task to be performed. Upon completion, they were informed about the purpose of the experiment if they desired. They received €8.50 (U.S.$8.50) for their participation.

Apparatus. The participants tapped with their fingertips on metal squares that had an area of 1.5×1.5 cm^2. The metal plates were attached, in pairs, on two movable tapping boards, one for each hand. The midpoints of the metal plates on one respective tapping board were 4 cm apart. The tapping boards were positioned on the table in a way that the fingers could comfortably touch the metal plates. They were slightly readjusted from trial to trial according to the participant's comfort. If the participants desired, their hands were supported by small foam cushions. For each touch of a finger on a metal plate, the time was registered (in milliseconds) using PsyScope (J. D. Cohen, MacWhinney, Flatt, & Provost, 1993) software and the PsyScope button box connected to a Macintosh computer.

Procedure. Participants were seated at the experimental table, with the computer monitor in front. Their hands were positioned in parallel, roughly sagittally, on the respective tapping boards in a way that the selected fingers could touch the metal plates as comfortably as possible. The experiment was conceived in a 2 (congruency) $\times$ 2 (movement) design. There were two types of finger combinations, as two levels of the factor congruency. The congruous condition included the finger combinations (MI, IM) and (RM, MR). The incongruous condition included the finger combinations (RM, IM) and (MI, MR). There were two movement instructions. Symmetrical movements were executed by tapping the inner and outer fingers of the respective four-finger combination, in alternation. Parallel movements were executed by tapping the outer finger of one hand synchronously with the inner finger of the other hand and vice versa, in alternation.

In each trial of 45-s duration, a computer-generated metronome pace continuously speeded up from 1 Hz to 3 Hz. Participants were requested to produce one full movement cycle per metronome beat. They selected and positioned the fingers according to the instructed finger combination and were requested to maintain the instructed movement pattern throughout the trial. However, if they felt the pattern begin to change, they were told to not resist but rather adopt the pattern that was most comfortable under the current conditions (see Kelso, 1995, p. 47). In other words, they were instructed to keep pace with the metronome beat in the first place, even if maintaining the requested pattern became impossible.

A printed label located in front of the participants was always visible and displayed the instructed movement pattern (symmetrical or parallel). The instructed finger combination was displayed on the computer monitor. The trials were presented in blocks of four trials each. In each block of four trials, all of the four possible finger combinations occurred once, in randomized order. Half of the participants performed the experiment with four blocks of symmetrical movements first, then four blocks of parallel movements, whereas the other half of the participants followed the reverse sequence. The experimenter started a trial after the participant's hands and fingers were well positioned. After each block, there was a pause of about 1–2 min. In addition, participants could take a rest whenever they needed.

[1] Here and in Experiment 4, the fingers applied in a given combination are symbolized from left to right. The fingers of the left hand are indicated to the left of the dot, and the fingers of the right hand are indicated to the right of the dot. An underscored blank denotes a lifted finger.

At the beginning of the session, all participants underwent a short training procedure to familiarize them with the different finger combinations and instructions. Then, in a practice block of eight trials, the experimental procedure was applied, with each finger combination and movement instruction executed once. The whole session, including practice and experimental trials, was completed in about 1 hr.

Data reduction. We analyzed the coordination between the fingers. First, we determined the time of touch onsets, individually for each finger involved in the task. Second, we determined for each single onset the respective onset on the tapping board for the other hand, which occurred with the minimal temporal distance. If this distance was not more than 80 ms, both taps were classified as one synchronous tap. The single onset, which occurred earlier in the synchronous tap, was taken as the onset of the synchronous tap. Each synchronous tap was categorized either as a symmetrical synchronous tap or as a parallel synchronous tap. The criterion for categorizing a synchronous tap as symmetrical was that either the inner or the outer fingers of both hands tapped together. The criterion for categorizing a synchronous tap as parallel was that the inner finger of one hand and the outer finger of the other hand tapped together. Single taps belonging to a symmetrical synchronous tap were called symmetrical taps. Single taps belonging to a parallel synchronous tap were called parallel taps. The remaining single taps were called unclassified taps.

To analyze the effects of frequency on coordination, in particular on pattern stability, each trial was separated into three intervals of equal length: 0–15 s (*M* frequency = 1.1 Hz), 15–30 s (*M* frequency = 1.5 Hz), and 30–45 s (*M* frequency = 2.7 Hz). The two dependent variables were the percentage of symmetrical and parallel taps for each condition and interval. The percentages of symmetrical and parallel taps were computed relative to the total number of single taps (i.e., symmetrical plus parallel plus unclassified taps) for the three time intervals and treated as quasicontinuous variables.

Results

Of all single taps, 91% were classified as either symmetrical taps or parallel taps (see the *Method* section). Because the percentage of unclassified taps was relatively small and did not systematically vary between the conditions and factors of interest, we do not report further analyses for this variable.

As the main dependent variable, the percentage of symmetrical and parallel taps for each interval was computed relative to the sum of taps in each interval (including unclassified). The upper panel in Figure 2 displays the percentage of symmetrical taps under the symmetry and parallel instructions, and for congruous and incongruous finger combinations, across the three intervals. The lower panel displays the percentage of parallel taps. The main outcome was that the results were almost identical under congruous and incongruous finger combinations.

When participants were instructed to tap symmetrically they produced, on average, a high percentage of symmetrical taps (87%) and virtually no parallel taps (5%). The percentage of symmetrical taps remained at a constant high level, even during the last interval. The overall stability results are quite different for the condition in which participants were instructed to tap in parallel. Participants produced a lower percentage of parallel taps (54%) and an amount of symmetrical taps (36%) that was much larger than the small amount of parallel taps produced under a symmetry instruction. The percentage of parallel taps decreased sharply across intervals. At the same time, the number of symmetrical taps increased in the same manner. Under the parallel instruction, the percentage of symmetrical taps increased to almost the same

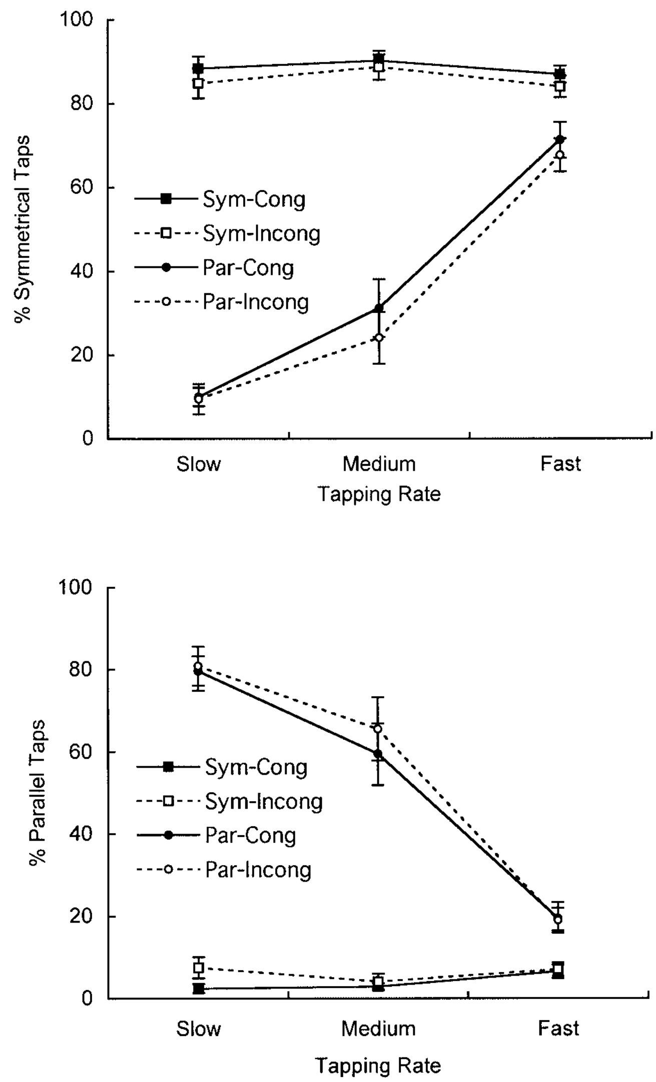


Figure 2. Results of Experiment 1. The upper panel displays the percentage of symmetrical taps under the parallel (Par) and symmetrical (Sym) instructions for congruous (Cong) and incongruous (Incong) finger combinations across the three time intervals. The lower panel displays the percentage of parallel taps. Error bars represent standard errors.

measure as under the symmetry instruction in the last time interval. In other words, the transition into symmetry was almost complete. This means, first, that there were very few trials, if at all, where such a transition did not occur and, second, that participants generally remained in the symmetrical mode after the transition. It is important to note that the results for the congruous and incongruous finger combination show the same overall pattern.

To statistically confirm these results, the percentages of symmetrical and parallel taps were entered into two 2 × 2 × 3 repeated measures analyses of variance (ANOVAs) with the factors instruction (symmetrical, parallel), congruency (congruous, incongruous), and interval (1, 2, 3). For symmetrical taps, this analysis revealed highly significant main effects for the factors instruction, $F(1, 11) = 168.0$, $p < .001$, and interval, $F(2, 22) =$

71.0, $p < .001$, and a highly significant Instruction × Interval interaction, $F(2, 22) = 77.0$, $p < .001$. The main effect for congruency was also significant, $F(1, 11) = 9.0$, $p < .05$. The remaining interactions were not significant. The ANOVA for parallel taps yielded the following results: There were main effects for instruction, $F(1, 11) = 113.0$, $p < .001$, and interval, $F(2, 22) = 79.0$, $p < .001$, and a significant Instruction × Interval interaction, $F(2, 22) = 95.0$, $p < .001$. The main effect for congruency was close to significance, $F(1, 11) = 4.0$, $p = .06$. The remaining interactions were not significant.

Discussion

The overall results of Experiment 1 replicate and thus confirm recent evidence by Mechsner et al. (2001). The stability characteristics of symmetrical and parallel tapping patterns, and in particular the symmetry tendency, were virtually independent of whether the finger combination was congruous or incongruous. This basic outcome suggests that the symmetry tendency in the investigated four-finger paradigm is not mainly due to coupling tendencies between homologous motor commands but instead indicates a perceptual preference.

One might argue that another classification procedure might have produced other proportions of symmetrical and parallel taps, leading to possibly different results. However, the low number of unclassified taps ensures that the results of Experiment 1 as well as of the following experiments are not artifacts of our classification procedure.

An additional outcome is that there seems to have been a slight stabilization of parallel patterns with incongruous finger combinations compared with congruous finger combinations. Before accepting this result, we looked for further confirmation in the following experiments, as it is well known that stability characteristics are very sensitive to instructional differences (Lee, Blandin, & Proteau, 1996) and, thus, possibly sensitive to many influences. We consider this issue further in the experiments that follow.

In summary, the symmetry tendency was toward spatial mirror symmetry, virtually without regard to the fingers and, thus, the muscular portions and motor commands involved. Therefore, the symmetry tendency plausibly arises on the level of perceptual anticipation and planning processes. However, the hands were always visible in Experiment 1. Therefore it is possible that the perceptual symmetry tendency was purely visual in nature, simply overriding an underlying tendency toward coactivation of homologous fingers, muscular portions, and/or motor commands. To address this problem, in Experiment 2 we investigated the influence of vision.

Experiment 2

We designed the second experiment in close analogy to Experiment 1. However, visibility was included as an additional factor. In the vision condition, the participants could see their hands, whereas in the no-vision condition, vision of the hands was occluded. If the tendency toward spatial symmetry observed in Experiment 1 was only a visual phenomenon, alternative coordination tendencies should become obvious in the no-vision condition. To be able to reveal minor differences between the visibility conditions, the number of participants as well as the number of trials were enhanced.

Method

Participants. Sixteen adults, 12 women and 4 men, ages 18–28 years ($M = 23.3$ years), participated in Experiment 2, under the same conditions as the participants in the previous experiment. Fourteen participants were right-handed, and 2 participants were left-handed according to self-report. Three additional participants were excluded because of finger movement difficulties.

Apparatus, procedure, and data analysis. These were the same as in Experiment 1 with the following modifications. On each of the two tapping boards, three aluminum rods, each 1 cm in diameter and 15 cm long, were vertically mounted beneath and between the tapping plates, perpendicular to the horizontal surface of the board. The rods served to haptically guide the tapping fingers, thus ensuring that participants were able to hit the metal plates without vision. In the vision condition the participants performed as in Experiment 1. In the no-vision condition, they wore a cap with a black visor attached, which prevented any view of the hands.

The experiment followed a 2 (congruency) × 2 (visibility) × 2 (movement) design. Every participant performed 64 trials total in two successive sessions of 32 trials each, which followed each other in about a week's period. The experimental conditions were blocked and counterbalanced across participants as in Experiment 1.

Results

Of all single taps, 98% were classified as either symmetrical taps or parallel taps. The upper and lower panels in Figure 3 display the percentage of symmetrical and parallel taps under the parallel and symmetry instructions, and for congruous and incongruous finger combinations, across the three intervals. Because the factor visibility virtually did not influence the results, this factor is omitted in Figure 3 (see below).

The overall pattern of results was very similar to that obtained in Experiment 1. When participants were instructed to tap symmetrically they produced a high percentage of symmetrical taps (91%) and virtually no parallel taps (7%). The percentage of symmetrical taps remained at a constant high level, even during the last interval. When participants were instructed to tap in parallel, they produced a lower percentage of parallel taps (69%) and an amount of symmetrical taps (29%) that was much larger than the small amount of parallel taps produced under a symmetry instruction. The percentage of parallel taps decreased across intervals and the number of symmetrical taps increased. There were no differences between the vision and the no-vision conditions, with one exception. When instructed to tap in parallel, participants in the no-vision condition had a somewhat higher percentage of symmetrical taps (69% vs. 65%) at the highest speed. The percentage of parallel taps was not affected by the visibility manipulation.

The percentages of symmetrical and parallel taps were entered into two 2 × 2 × 2 × 3 repeated measures ANOVAs with the factors visibility (yes, no), instruction (symmetrical, parallel), congruency (congruous, incongruous), and interval (1, 2, 3). For symmetrical taps, this analysis revealed no significant main effect for visibility, $F(1, 15) = 2.8$, $p = .12$. There were significant main effects for instruction, $F(1, 15) = 414.0$, $p < .001$; congruency, $F(1, 15) = 6.0$, $p < .05$; and interval, $F(2, 30) = 69.0$, $p < .001$.

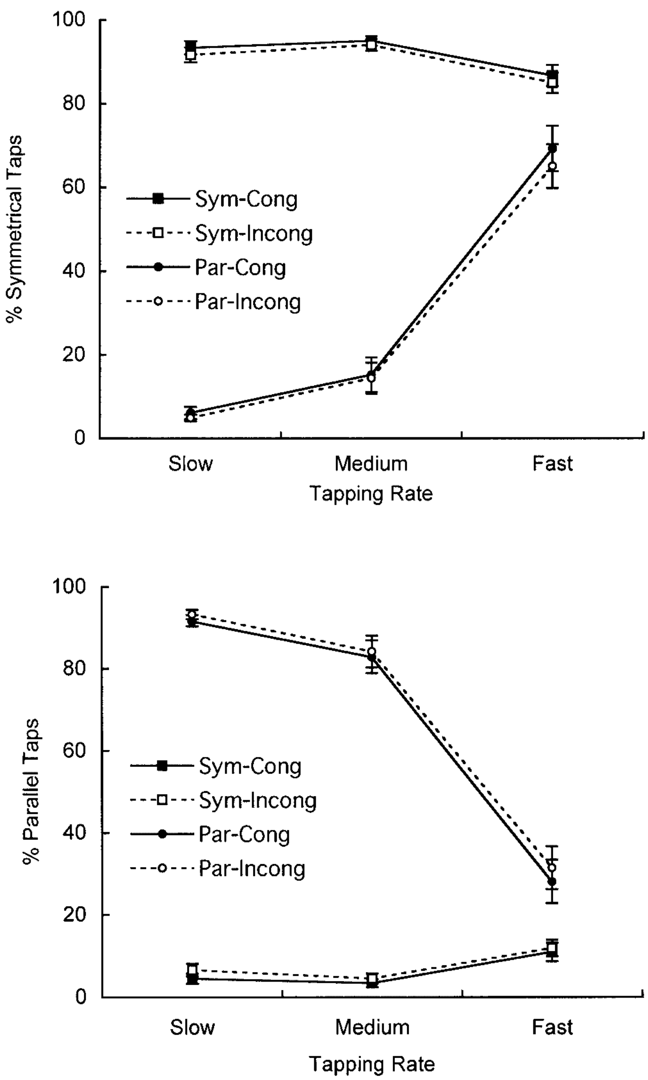


Figure 3. Results of Experiment 2. The upper panel displays the percentage of symmetrical taps under the parallel (Par) and symmetrical (Sym) instructions for congruous (Cong) and incongruous (Incong) finger combinations across the three intervals. The lower panel displays the percentage of parallel taps. Because there were virtually no effects of the factor visibility, they are not separately displayed here. Error bars represent standard errors.

In addition, there was a highly significant two-way Instruction × Interval interaction, $F(2, 30) = 147.0$, $p < .001$, and a significant three-way Visibility × Instruction × Interval interaction, $F(2, 30) = 5.0$, $p < .05$.

The ANOVA for parallel taps showed no significant main effect for visibility, $F(1, 15) = 1.4$, $p = .25$. There were significant main effects for instruction, $F(1, 15) = 434.0$, $p < .001$; congruency, $F(1, 15) = 7.0$, $p < .05$; and interval, $F(2, 30) = 74.0$, $p < .001$. In addition, there was a significant Instruction × Interval interaction, $F(2, 30) = 137.0$, $p < .001$. The remaining interactions were not significant.

Discussion

The overall results of Experiment 2 are very similar to those of Experiment 1. The stability characteristics of symmetrical and parallel tapping patterns, and in particular the symmetry tendency, were virtually independent of the finger combination and, thus, probably of the muscular portions and motor commands involved. This pattern occurred regardless of whether the participants could see their hands. Taken together, the results of the first two experiments suggest that the symmetry tendency is a perceptual preference toward spatial symmetry not only under vision but also under occluded vision. Under occluded vision, the perceptual modality mediating these effects is obviously kinesthetic proprioception, though visual imagination might play some additional role as well.

It is important to note that even subtle differences between the vision and no-vision conditions could not be revealed. The only exception is the significant three-way interaction among visibility, instruction, and interval for the percentage of symmetrical taps. Unfortunately, this interaction is difficult to interpret. It is based on the result that, under parallel instruction, participants in the no-vision condition had a somewhat higher percentage of symmetrical taps, at the highest speed. However, this does not mean that more switches from the parallel to the symmetric pattern took place, as the percentage of parallel taps was not affected by the visibility manipulation. One might argue that the overall accuracy of movements may have been enhanced by the no-vision condition, and thus the sum of classified taps was enhanced, whereas the ratio of symmetrical versus parallel taps was increased. However, this seems not to be the case because, first, the number of unclassified taps does not point to such an interpretation, and second, such a general improvement of accuracy was not observed in any other condition. The idea that only performance of symmetric taps was more accurate without vision can be doubted in an analogous way. In conclusion, we are reluctant to interpret this result, as it stands in isolation.

The congruency effect with regard to stability that was found in Experiment 1 was also present in Experiment 2, in the vision condition as well as in the no-vision condition. Thus, it might be that an instructed symmetrical tapping mode is slightly more stable with a congruous finger combination compared with an incongruous finger combination. Correspondingly, an instructed parallel mode might be slightly more stable with an incongruous finger combination compared with a congruous finger combination. As a caveat, however, one should note that the results of Experiment 3 point into the opposite direction (see the *Discussion* section of Experiment 3).

Whereas visibility does not seem to make any difference concerning the observed stability characteristics, it is possible that an influence of vision could be revealed with differential visual support of the to-be-performed movement patterns. In the next experiment, we labeled the fingers by symmetric versus parallel pairs of visual cues to examine whether enhanced visual feedback would influence the relative stability of the two tapping modes.

Experiment 3

In Experiment 3 we tested whether additional visual cues, which differentially emphasized symmetrical and parallel tapping patterns, would differentially stabilize or destabilize these patterns. There are clear hints in the literature that perceptual cues can influence coordination stability (for an overview, see Kelso et al., 2001). Although this issue has rarely been explored, the hypothesis seems plausible that compatible stimuli may stabilize the performed pattern, whereas incompatible stimuli may destabilize the performed pattern. To pursue this possibility, we attached a salient visual marker of green color to one of the tapping fingers on each hand (Figure 4). The possible bimanual combinations of visual markers resulted in two symmetrical and two parallel labeling patterns, in correspondence with the two possible symmetrical and the two parallel patterns of synchronous taps (see above).

Participants tapped with the hands sagittally stretched out, as in Experiments 1 and 2, and were again instructed to tap in symmetry or in parallel. They were requested to watch their hands at all times. The question of interest was whether symmetrical visual markers would stabilize symmetrical patterns and destabilize parallel tapping patterns and, correspondingly, whether parallel visual markers would stabilize parallel and destabilize symmetrical tapping patterns.

Method

Participants. Sixteen adults, 11 women and 5 men, ages 20–27 years ($M = 22.9$ years) volunteered to serve as participants in Experiment 3, under the same conditions as the participants in the previous experiments. Fourteen participants were right-handed, and 2 participants were left-handed according to self-report. Two additional participants were excluded because of finger movement difficulties.

Apparatus, procedure, and data analysis. The procedure was very similar to Experiments 1 and 2. Participants tapped under the same normal hand positions as in Experiments 1 and 2 (i.e., with the hands sagittally stretched out in parallel). In addition, movement instructions and finger combinations were varied analogously to Experiments 1 and 2, in eight blocks of four trials each. The crucial variation in contrast to the previous experiments was the addition of a mark in luminous and salient green, which was attached to one of the tapping fingers of each hand (Figure 4). The marks were 1×3 cm^2 in size and attached longitudinally on top of the phalanx proximalis (i.e., the most proximal phalanx). The resulting bimanual labeling patterns were as follows: symmetrical inward, symmetrical outward, parallel left, and parallel right. For the analysis, these four patterns were collapsed into the two visual cue conditions, symmetrical and parallel.

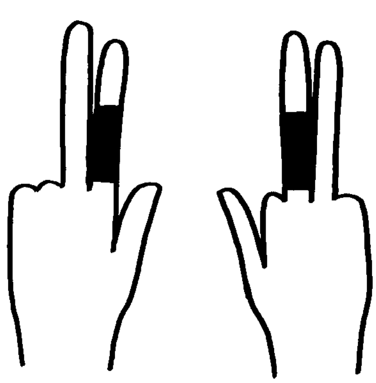


Figure 4. Symmetrical labeling pattern of an incongruous finger combination (as an example).

Participants were requested to watch their hands during tapping. The tapping boards were white in the previous experiments. This time, to make the green labels more visible, the tapping boards were black, except the metal plates displaying their natural copper color. For the same reason, participants wore black gloves. The fingertips of the gloves were open to ensure direct contact of the skin with the metal plates. However, the uncovered skin of the fingertips was hardly visible to the participants.

The experiment followed a 2 (instruction: symmetrical, parallel) × 2 (cue: symmetrical, parallel) × 2 (congruency: congruous, incongruous) × 3 (interval: early, middle, late) design. The four labeling patterns were counterbalanced across participants, together with movement instruction, in a Latin square design.

Results

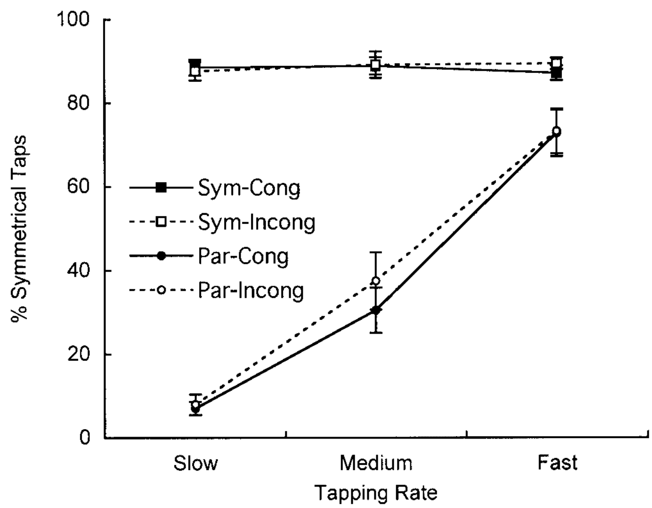
Of all single taps, 91% were classified as either symmetrical taps or parallel taps. Figure 5 displays the results. Because the results were virtually identical for the two different cue conditions, they are not displayed separately. The pattern of results is indistinguishable from the one obtained in the two preceding experiments. When participants were instructed to tap symmetrically, they produced a high percentage of symmetrical taps (88%) and very few parallel taps (3%). The percentage of symmetrical taps remained at a constant high level in all intervals. When participants were instructed to tap in parallel, they produced a lower percentage of parallel taps (51%) and amount of symmetrical taps (38%), which was much larger than the small amount of parallel taps produced under a symmetry instruction. The percentage of parallel taps decreased and the number of symmetrical taps increased across intervals. Moreover, during the middle interval, the percentage of symmetrical taps was lower and the percentage of parallel taps was higher when the finger combination was congruous.

The percentages of symmetrical and parallel taps were entered into two $2 \times 2 \times 2 \times 3$ repeated measures ANOVAs with the factors instruction (symmetrical, parallel), visual cue (symmetrical, parallel), congruency (congruous, incongruous), and interval (early, middle, late). For symmetrical taps, this analysis revealed significant main effects for the factors instruction, $F(1, 15) = 231.0$, $p < .001$, and interval, $F(2, 30) = 92.0$, $p < .001$, and a highly significant Instruction × Interval interaction, $F(2, 30) = 132.0$, $p < .001$. There were no significant main effects of cue, $F(1, 15) = 0.3$, $p = .62$, and congruency, $F(1, 15) = 0.5$, $p = .48$. In addition, the three-way Instruction × Congruency × Interval interaction approached significance, $F(2, 30) = 3.2$, $p = .05$. The remaining interactions were not significant.

The ANOVA for parallel taps revealed no significant main effect for visual cue, $F(1, 15) = 0.1$, $p = .71$. There were significant main effects of instruction, $F(1, 15) = 216.0$, $p < .001$, and interval, $F(2, 30) = 77.0$, $p < .001$, and a significant Instruction × Interval interaction, $F(2, 30) = 120.0$, $p < .001$. The main effect for congruency was not significant, $F(1, 15) = 1.0$, $p = .33$. However, there was a significant two-way Interval × Congruency interaction, $F(2, 30) = 3.3$, $p < .05$, and a significant three-way Instruction × Congruency × Interval interaction, $F(2, 30) = 3.4$, $p < .05$. The remaining interactions were not significant.

Discussion

In Experiment 3, we were not able to reveal any influence of symmetrical versus parallel visual labeling of the fingers on the



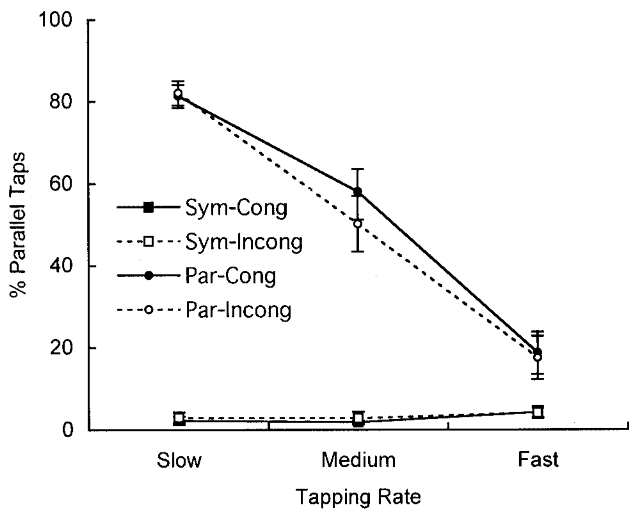


Figure 5. Results of Experiment 3. The upper panel displays the percentage of symmetrical taps under the parallel (Par) and symmetrical (Sym) instructions for congruous (Cong) and incongruous (Incong) finger combinations across the three intervals. The lower panel displays the percentage of parallel taps. Because there were virtually no effects of the factor cue, they are not separately displayed here. Error bars represent standard errors.

stability of symmetrical and parallel tapping patterns. This outcome was contrary to our expectations. Because the results of Experiments 1 and 2 suggest an overwhelming dominance of perceptual factors in constraining stability of bimanual four-finger tapping patterns, one would, at least, not be surprised if visual factors of this kind could easily influence these stability characteristics. However, this seems not to be the case. Two interpretations of this result seem plausible. First, it might be that the color cues were not strong enough to alter the visual appearance of the fingers in a functionally relevant way. Second, it might be that kinesthetic proprioception is clearly dominant in bringing about the observed stability characteristics and, in particular, the symmetry tendency.

The results regarding the effects of congruency on stability of the different coordination patterns point to an influence opposite to the influences revealed in Experiments 1 and 2. Whereas the latter results pointed to a possible (slight) stabilization of the parallel pattern under the incongruous finger combination, the results of Experiment 3 point to a possible (slight) stabilization of the symmetrical pattern under this finger combination. As mentioned above, additional analyses of the percentage of unclassified taps did not reveal an answer to the question of whether the factor congruency influences stability. Because of these inconsistencies we are reluctant to interpret these results.

Experiment 4

Experiments 1–3 clearly showed that the symmetry tendency in bimanual four-finger tapping occurs virtually without regard to the fingers involved and, thus, probably without regard to homologous motor commands and muscular portions. Instead, the results indicate a perceptual nature of the symmetry tendency. However, the exact kind and role of the perceptual principles of relevance are not obvious, because spatial mirror symmetry is confounded with other possible frames of reference and grouping principles. We considered two alternative hypotheses out of the several possible ones. The spatial symmetry hypothesis claims that those fingers that are closest to each other tend to tap synchronously, in alternation with those fingers that are most distant to each other. Alternatively, the anatomical symmetry hypothesis claims that those fingers that are anatomically closer to the thumb of the respective hand (or the ulnar fingers) tend to tap together in alternation with those fingers that are anatomically farther away from the thumb (or the radial fingers). In other words, the anatomical symmetry hypothesis claims that the symmetry tendency is associated with the serial position of the fingers in the hand. These two hypotheses are not mutually exclusive, as both a spatially defined as well as an anatomically defined symmetry tendency might be of influence.

To determine the relative influence of these two reference frames, we changed the spatial orientation and relative position of the hands and fingers. This was done in such a way that both arms were placed roughly perpendicular to the sagittal midline, whereas the fingertips were aligned in a row on the sagittal midline. Figure 6 shows this arrangement with the right hand "down" and the left hand "up" (*down* means closer to the body, and *up* means farther away from the body).

As in the previous experiments, the participants were instructed that one finger of the one hand should always tap synchronously

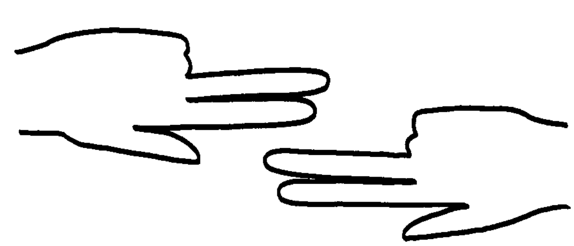


Figure 6. Finger position instructed in Experiment 4, with the right hand down and the left hand up.

with one finger of the other hand. There were two instructed tapping patterns. First, the fingers that were close to each other tapped in synchrony, in alternation to the fingers that were farther away from each other. This tapping pattern is spatially symmetrical, but anatomically parallel. Second, the fingers that were closer to the thumb of their respective hand tapped synchronously, in alternation to the two fingers that were farther away from the respective thumb. This tapping pattern is spatially parallel but anatomically symmetrical.

We assumed that it should not make much of a difference whether participants were instructed with regard to spatial patterns or anatomical patterns. However, preliminary observations led us to expect that an anatomically defined symmetry tendency (with regard to the serial position of fingers in the hands) would be much stronger than a spatially defined symmetry tendency (with regard to the sagittal fingertip positioning). Therefore, to emphasize a possible spatial symmetry tendency, participants were instructed in terms of the spatially defined pattern.

Method

Participants. Twelve adults, 6 women and 6 men, ages 21–34 years ($M = 25.4$ years) participated in Experiment 4, under the same conditions as the participants in the previous experiments. All participants were right-handed according to self-report. Five additional participants were excluded because of finger movement difficulties.

Apparatus, procedure, and data analysis. Participants tapped under similar conditions as in Experiment 1, with vision of the hands. This time, however, the arms and fingers were placed roughly perpendicular to the sagittal midline, whereas the fingertips were aligned in a row on the sagittal midline. The tapping boards were positioned correspondingly. The hand that was closer to the participant's body is referred to as the *down* hand, whereas the other hand is referred to as the *up* hand. Figure 6 shows this arrangement with the right hand down and the left hand up. Care was taken to ensure that the fingertips were aligned as exactly as possible in a midsagittal row. Whether this was the case was judged by the experimenter. Slight position adjustments were allowed if the participant had difficulties with the exact position. This happened only occasionally, especially with the congruous finger combination (RM, MR), which requires a relatively uncomfortable position of both hands to put the fingertips as exactly as possible in a row.

We varied the following factors. Movement instruction required either symmetrical or parallel tapping. As explained above, these instructions were defined with regard to the spatial position of the fingertips as aligned along the midsagittal line, relative to a transversal axis. Symmetrical tapping required synchronous tapping of the fingers that were close to each other, in alternation to the fingers that were farther away from each other. Parallel tapping required synchronous tapping of the fingers that were closer to the body, in alternation to the fingers that were farther away from the body. To give an example, consider the congruous finger combination (MI, IM), with the right hand in the down position. Spatially symmetrical tapping means (_I · _M), (M_ · I_), (_I · _M), and so forth, which is an anatomically parallel pattern. Spatially parallel tapping required (_I · I_), (M_ · _M), (_I · I_), and so forth, which is an anatomically symmetrical pattern.

Instructions and finger combinations were varied according to the same design as described in Experiment 1. The hand positions (one hand up and the other down) were varied from block to block. However, the factor hand position was not included into the following analyses because it had virtually no effect.

Results

Of all single taps, 88% were classified as either spatially symmetrical taps or spatially parallel taps. The upper and lower panels in Figure 7 display the percentage of spatially symmetrical and parallel taps under the spatially parallel and symmetry instructions, and for congruous and incongruous finger combinations, across the three intervals. Note that a spatial symmetrical tapping pattern is considered anatomically parallel, and vice versa. We instructed and analyzed the data with regard to the spatial pattern. When participants were instructed to tap in parallel they produced a high percentage of parallel taps (84%) and virtually no symmetrical taps (5%). The percentage of parallel taps remained at a constant high

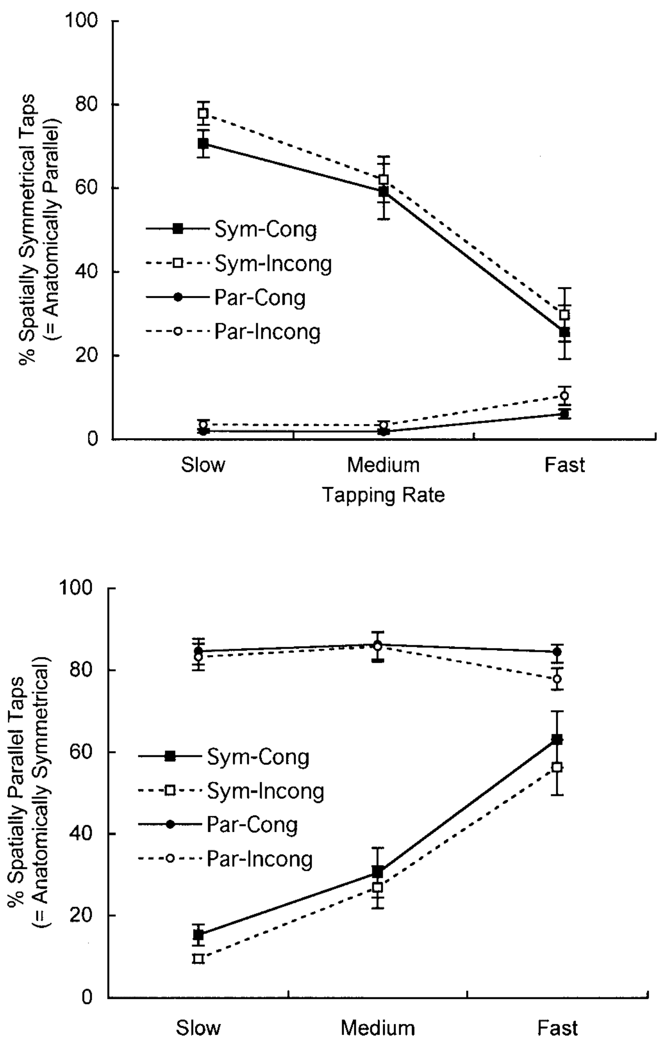


Figure 7. Results of Experiment 4. The upper panel displays the percentage of spatially symmetrical (i.e., anatomically parallel) taps under the spatially parallel (Par) and symmetrical (Sym) instructions for congruous (Cong) and incongruous (Incong) finger combinations across the three intervals. The lower panel displays the percentage of spatially parallel (i.e., anatomically symmetrical) taps. Error bars represent standard errors.

level across consecutive intervals. When participants were instructed to tap symmetrically, they produced a lower percentage of symmetrical taps (54%) and an amount of parallel taps (34%) that was much larger than the amount of symmetrical taps produced under a parallel instruction. The percentage of symmetrical taps decreased and the number of parallel taps increased across intervals. Under both instructions, the percentage of symmetrical taps was somewhat higher for incongruous finger combinations (31%) than for congruous finger combinations (28%), and the percentage of parallel taps was somewhat higher for congruous finger combinations (61%) than for incongruous finger combinations (57%).

The percentages of spatially symmetrical and spatially parallel taps were entered into two $2 \times 2 \times 3$ repeated measures ANOVAs with the factors instruction (symmetrical, parallel), congruency (congruous, incongruous), and interval (1, 2, 3). For symmetrical taps, this analysis revealed significant main effects for the factors instruction, $F(1, 11) = 128.0$, $p < .001$; interval, $F(2, 22) = 28.0$, $p < .001$; and congruency, $F(1, 11) = 17.0$, $p < .01$. In addition, there was a highly significant Instruction × Interval interaction, $F(2, 22) = 46.0$, $p < .001$. The remaining interactions were not significant. The ANOVA for parallel taps showed significant main effects for instruction, $F(1, 11) = 95.0$, $p < .001$; interval, $F(2, 22) = 28.0$, $p < .001$; and congruency, $F(1, 11) = 13.0$, $p < .01$. In addition, there was a highly significant Instruction × Interval interaction, $F(2, 22) = 43.0$, $p < .001$. The remaining interactions were not significant.

Discussion

The results of Experiment 4 provided no evidence for the spatial symmetry hypothesis, which claims that those fingers that are closest to each other tend to tap synchronously, in alternation with those fingers that are most distant to each other. Instead, the results support the anatomical symmetry hypothesis. This hypothesis claims that the symmetry tendency is toward anatomical symmetry, which is defined with regard to the serial position of the fingers in the hand. There was a strong tendency toward synchronous taps of those fingers that were closer to the thumb (i.e., the radial fingers) in alternation with the fingers which were farther away from the thumb (i.e., the ulnar fingers), regardless of which finger combination was selected.

How might this result be interpreted? Because the observed spontaneous coordination tendency was independent of the fingers, muscular portions, and, thus, the motor commands involved, we conclude, again, that it originates on a more abstract level, in connection with anticipatory and planning processes. However, what exactly is anticipated or planned here? The revealed preference for anatomically defined symmetry is reminiscent of the so-called orthogonal stimulus–response (S-R) compatibility, which has been demonstrated in experiments on spatial compatibility (Weeks, Proctor, & Beyak, 1995) as well as experiments on the Simon effect (Hommel & Lippa, 1995). S-R compatibility refers to the phenomenon that there is an RT advantage if the spatial position of the response corresponds to the spatial position of the imperative stimulus, that is, if a right-hand stimulus has to be responded to with a right keypress, compared with a left keypress. This advantage holds when the spatial position is a relevant stimulus feature (proper spatial compatibility; Fitts & Seeger, 1953) as well as when it is an irrelevant stimulus feature (Simon effect; see Simon & Rudell, 1967). If participants cross their hands such that the left button is pressed with the right hand, and vice versa, compatibility effects occur with regard to the response location and not to the responding effector (Wallace, 1971). Thus, the effect is clearly perceptually defined with little influence of motor characteristics, whether they are perceptual or not (see also Attneave & Benson, 1969; Wickens, 1938).

Interestingly, an orthogonal compatibility effect of the following kind can be found as well. If, for example, both responses have to be made with the right arm placed transversely pointing to the left, there is an RT advantage for an up answer if the imperative stimulus is presented to the right. Conversely, there is an RT advantage for a down answer if the imperative stimulus is presented to the left (Hommel & Lippa, 1995; Weeks & Proctor, 1990). A possible and plausible interpretation for this effect is that there is a frame of reference defining left and right with regard to the respective arm, independent of the actual arm position (Lippa, 1996).

A similar principle might apply to the spontaneous coordination tendency toward anatomically symmetrical oscillations, as observed in Experiment 4. In the most stable movement pattern, a tap of the right finger in one hand is synchronous to a tap of the left finger in the other hand, in arm-related coordinate systems. Thus there might be a tendency of right and left fingers tapping together. In accordance with the foregoing considerations, we propose that this tendency is perceptually defined in a hand-centered reference frame, involving similar mechanisms as the compatibility effects described above.[2] If so, one would not be surprised if other frames of reference also would be of some relevance, depending on the particular hand positions and instructions. However, this is an issue for further experiments.

General Discussion

In four experiments, we investigated bimanual coordination in a multifinger tapping task with two fingers of each hand. The main question was whether the strong stability advantage of symmetrical movements, and in particular the symmetry tendency, mirrors a tendency toward coactivation of homologous fingers. By systematically varying the finger combinations involved in the task, we revealed in Experiments 1 and 2 that the tendency to switch from an instructed parallel to a mirror-symmetrical tapping pattern is virtually independent of the particular fingers involved. The symmetry bias is thus not a bias toward coactivation of homologous fingers, muscular portions, or homologous neuronal motor pathways. Experiment 3 revealed that visual labels supporting either the symmetrical or parallel mode did not significantly influence the observed stability characteristics. Finally, in Experiment 4, we investigated whether the symmetry tendency is toward spatial mirror symmetry with regard to the sagittal midline or toward an anatomically defined symmetry, in terms of relative serial positions of the fingers of the hands. We varied the relative position and orientation of the hands to dissociate these two possible tendencies. The results suggest that the symmetry ten-

[2] We thank Herbert Heuer for pointing us to this interpretation.

dency is anatomically defined in hand-centered coordinates: Those fingers that are closer to the thumb (i.e., the radial fingers) tend to tap in alternation with those fingers that are farther away from the thumb (i.e., the ulnar fingers).

Because all of the observed stability characteristics were independent of the particular finger combination, we conclude that homology of fingers or homology of muscular portions is of little importance in defining the most stable mode, if at all. Thus it seems plausible that the symmetry tendency does not originate at the level of motor commands. We suggest that it instead originates on a more abstract level, in connection with planning processes by way of anticipation of the perceptual consequences of movements. The results of Experiment 3, in connection with Experiment 2, suggest that kinesthetic proprioception might be dominant over vision in bringing about this coordination tendency. If so, this goes against the general claim that vision dominates touch and proprioception (Posner, Nissen, & Klein, 1976; Rock & Harris, 1967; Rock & Victor, 1964). Experiment 4 reveals that symmetry tendency is not a well-defined concept, as it is confounded with many possible notions of how to describe the observed spontaneous coordination bias. One has to investigate carefully the frames of reference and the exact movement characteristics, which are of relevance in the particular task.

The interpretation that the observed stability characteristics originate at a planning level rather than at a level of motor commands gains plausibility if we compare our observations with results obtained in discrete RT tasks. As discussed above, our findings are reminiscent of earlier work on bimanual RT tasks (e.g., Heuer, 1993) as well as work on S-R compatibility (e.g., Fitts & Seeger, 1953; Weeks & Proctor, 1990). We propose that there is a stability advantage for bimanual tapping movements when compatible parameters are to be specified in discrete as well as in periodic patterns.

As a more general hypothesis, we propose that there is no level or stage in human motor control where coherent motor command or muscular activity patterns are organized as such, whether it be by forming and using muscle-oriented motor programs (e.g., R. A. Schmidt, 1982) or by tuning critical control parameters to stimulate self-organization of component muscular activities into suitable collective action (e.g., Haken et al., 1985). Instead we propose that movements are planned, executed, and stored in memory by addressing their anticipated, mentally represented, perceptual and conceptual effects, without any obligatory regard to the required muscular activity patterns, though such muscular patterns might be addressed now and then in the perceptual planning process, in particular situations.

We are not the first to suggest such a perceptual–cognitive principle of movement control. Our approach is largely consistent with a detailed multilevel framework proposed by Powers (1973) several decades ago as well as with ideas developed by Prinz (1997), Hommel (1998), and Hommel, Müsseler, Aschersleben, and Prinz (2001). Hoffmann (2003) introduced a learning framework of anticipatory behavioral control to account for voluntary action. In a similar vein, Prinz and colleagues (Knoblich & Prinz, in press; Wohlschläger & Prinz, 2003) proposed an *ideomotor* approach to human movement control, thereby recognizing and revitalizing similar ideas by Greenwald (1970) as well as much older ideas by Lotze (1852) and James (1890/1981). Essentially, this approach claims, first, that perceptual anticipation of movement effects are functional in organizing and bringing about the corresponding movement and, second, that such an anticipation is a necessary step in the organization of a movement. This hypothesis is different from the better known and widely spread *sensorimotor* approach, which implies that patterns of motor commands or muscle activity can directly be elicited by stimuli—external or internal—of any kind associated to them. We take the results of our present study as support for the ideomotor approach. Accordingly, we consider the symmetrical and parallel tapping patterns in the paradigm investigated here to be controlled by anticipatory, perceptual–cognitive, reference structures, or "event files" (Hommel, 1998; Hommel et al., 2001). We suggest that the symmetry advantage and the symmetry tendency in the four-finger tapping paradigm reflect organizational processes internal to these perceptual–cognitive reference structures.

The present experiments do not determine whether the symmetry bias originates at a canonical, body-bound, parameterization level or at a more general and abstract level of goal specification, or target selection. This is because all our movement instructions were defined with regard to the body and not to external goals. At first sight, the body parameterization hypothesis seems rather plausible, as one might assume that specifying bodily movement parameters in a complete and detailed way is a canonical, necessary step in movement performance, regardless of the goal of the movement. With "complete and detailed" parameterization we mean a parameterization that completely specifies the bodily movement characteristics in intrinsic coordinates, independent of what they are for.

Surprisingly, recent results by Diedrichsen and colleagues (Diedrichsen et al., 2001, 2003) tell a different story. These authors showed that higher RT costs, usually observed in asymmetrical movements compared with symmetrical movements, disappear if one instructs not movement parameters (i.e., amplitudes or directions) but instead presents the to-be-reached targets directly. Moreover, overall RT was dramatically reduced with externally specified goals compared with the condition where the movement was instructed with regard to the body. The authors concluded: "When external goals are available, the two hands seem to be able to produce non-homologous trajectories without difficulty" (Diedrichsen et al., 2001, p. 498). In other words, explicit, detailed, and complete parameterization of the body movements seems not always to be a necessity in movement control.

Additional support for this claim could be inferred from an experiment by Mechsner et al. (2001). They showed that participants could easily perform bimanual circling movements at a frequency ratio of 4:3 when they controlled, by way of this movement, a simple symmetrical movement, supervised by vision. Bimanual movements at a 4:3 ratio are virtually impossible to perform when tried as such. Thus, it seems plausible to assume that in the mentioned experiment, the 4:3 frequency ratio was not controlled explicitly by the body, by way of organizing the hand movements according to a 4:3 frequency ratio. Instead this bimanual frequency ratio seems only implicitly tuned by way of controlling the much simpler visual movement effect.

In the reported experiment by Mechsner et al. (2001), participants certainly had to purposefully plan and control the bimanual circling pattern of the flags. In consequence, it does not come as a surprise that there was bimanual interference at this level, resulting in a symmetry tendency. Rosenbaum (2002) went a step further and asked whether participants would be able to move the hands in full independence if they only had to track a guided movement and thus would not have to plan and control the movement pattern by themselves. Rosenbaum showed that this seems indeed to be the case. Participants were well able to perform otherwise impossible, and thereby virtually independent, bimanual movements in a haptic pursuit task. Participants pushed with their two middle fingers against buttons mounted under vertically oriented shafts that were displaced rapidly, continuously, and quasi-randomly in a horizontal plane either by one or two experimenters. One person is usually not able to actually move the hands independently. However, participants did equally well in the one- and two-experimenter conditions, which is remarkable in view of the fact that the shafts were moved essentially independently in the two-experimenter case. It seems that those processes in movement organization, which usually lead to bimanual interference, can be bypassed if the movement pattern is specified by guidance and does not have to be purposefully specified by the actor him- or herself.

These results indicate that there is no necessity for a complete and detailed parameterization of body movements. In service of specified perceptual goals, movements can be performed without complete parameterization, which allows greater movement flexibly, reduced informational cost, and reduced interference. Accordingly, it might well be the case that there is not much sense in functionally distinguishing a body-parameterization level from an external goal-specification level. A unifying perspective might be possible in simply claiming that movement coordination is concerned with perceptual effects, be they connected to the body or to external goals. In this view, distal and proximal perceptual effects are categorically similar and can replace each other.

In conclusion, the present experiments demonstrated that homology of active fingers, muscular portions, and thus motor commands plays virtually no role in defining preferred coordination patterns, in particular the symmetry tendency, in bimanual four-finger tapping. We propose that the symmetry advantage does not originate at the level of motor commands or specification of muscular activity but originates at a more abstract level, in connection with planning processes involving perceptual anticipations. This holds independent of whether the hands are visible, which points to a possibly dominant role of the proprioceptive modality in mediating the symmetry tendency. A somewhat unexpected additional result is that the symmetry tendency, though probably perceptual in nature, is not defined in an external frame of reference but in an intrinsic, hand-centered frame of reference.

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