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RESEARCH ARTICLE

Transfer of learning between unimanual and bimanual rhythmic movement coordination: transfer is a function of the task dynamic

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Abstract Under certain conditions, learning can transfer from a trained task to an untrained version of that same task. However, it is as yet unclear what those certain conditions are or why learning transfers when it does. Coordinated rhythmic movement is a valuable model system for investigating transfer because we have a model of the underlying task dynamic that includes perceptual coupling between the limbs being coordinated. The model predicts that (1) coordinated rhythmic movements, both bimanual and unimanual, are organised with respect to relative motion information for relative phase in the coupling function, (2) unimanual is less stable than bimanual coordination because the coupling is unidirectional rather than bidirectional, and (3) learning a new coordination is primarily about learning to perceive and use the relevant information which, with equal perceptual improvement due to training, yields equal transfer of learning from bimanual to unimanual coordination and vice versa [but, given prediction (2), the resulting performance is also conditioned by the intrinsic stability of each task]. In the present study, two groups were trained to produce 90° either unimanually or bimanually, respectively, and tested in respect to learning (namely improved performance in the trained 90° coordination task and improved visual discrimination of 90°) and transfer of learning (to the other, untrained 90° coordination task). Both groups improved in the task condition in which they were trained and in their ability to visually discriminate 90°, and this learning transferred to the untrained condition. When scaled by the relative intrinsic stability of each task, transfer levels were found to be equal. The results are discussed in the context of the perception–action approach to learning and performance.

Keywords Bimanual coordination · Motor learning · Transfer of learning

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Introduction

The acquisition of skilled performance generally depends on practice; more practice leads to better performance. Also, there seems to be a high level of specificity in that performance is usually best when tested under the same conditions that were present during learning (e.g. Newell et al. 1979; Proteau et al. 1992). At the same time, there is abundant evidence that the perception/action system is flexibly organised so that many actions can be skilfully executed despite changes in test conditions or modifications of the task. A good example of this comes from handwriting. Merton (1972) showed that the shape and form of a person's signature is largely preserved across changes in the effector system used to produce the signature, an extension of the original use of handwriting by Bernstein (1967) to demonstrate "motor equivalence". In line with this, one of the most prominent theories concerning human motor control, schema theory (Schmidt 1975), used generality as its basis.

This apparent discrepancy between specificity and generality is vexing. How can learning be both specific and general? A number of solutions have been proposed (as seen in Keetch et al. 2005) dating back to Thorndike

(1913) who theorised that it is the number of "identical elements" between two tasks that dictate the degree of transfer. According to this, learning is specific if the number of elements is low and, learning is general (i.e. learning transfers) if the number is high. The difficulty lies in the ability to predict specificity or generality, i.e. how can one know (in advance) whether learning will transfer to another task? Part of the problem comes from finding a suitable definition of a *task*. In their review of the topic, Schmidt and Young (1987) noted the lack of a principled way to identify whether two movements are examples of different tasks or class of actions. The problem is generally solved post hoc; when (positive) transfer of learning occurs, the two movements are characterised as examples of the same task, while no transfer is interpreted to mean that they were different tasks. Solving this problem for prediction, rather than retrodiction, requires a way to formally define the structure of the perception–action system assembled to perform a given action. Task dynamics was formulated as a means for doing this (e.g. Beek and Bingham 1991; Bingham 1988, 1995; Bingham et al. 1991; Kugler and Turvey 1987; Saltzman and Kelso 1987; Simko and Cummins 2010; Warren 2006). When the task dynamic is well specified, then it is possible to make and test predictions derived from the hypothesised mechanism about how learning should transfer.

Coordinated rhythmic movement is a standard model perception–action task for studying performance and learning, and the task dynamic has been modelled explicitly as a perception–action system with terms in the equations representing the perceptual information and action control variables involved (Bingham 2001, 2004a, b, Snapp-Childs et al. 2011). The model predicted results both from movement studies (e.g. Kay et al. 1987, 1991; Kelso 1984; Schmidt et al. 1990) and from perceptual judgment studies that had investigated both vision (Bingham et al. 1999, 2001; Zaal et al. 2000) and proprioception (Wilson et al. 2003). It is this model that motivated the current study because it generates predictions about how learning one version of this task should generalise to another version.

The basic phenomena of the rhythmic movement coordination task are well known: people can typically only produce two coordination patterns stably, 0° mean relative phase (in which the limbs oscillate so as to do the same thing at the same time) and 180° (in which the limbs alternate). In addition, 180° is less stable than 0°; when the required movement frequency is increased to make the task harder, people transited from 180° to 0° at around 3 Hz (for bimanual coordination) but not vice versa. Without training, other coordination patterns (such as the intermediate 90° phase) are unstable with a reliable tendency to transition to 0° (Kelso 1984; Kelso et al. 1986, 1987). However, people can learn to produce initially unstable patterns either with feedback-driven training (e.g. Wilson et al. 2010b) or with transformed feedback displays which simplify the task (e.g. Kovacs et al. 2009a, b; Zanone and Kelso 1992a, b, 1997). Studies on the learning of novel coordination patterns also found transfer. Learning transfers to untrained and previously unstable coordination patterns (e.g. Kelso and Zanone 2002) that are highly specific to the trained pattern. Improvement only transfers to the symmetry partners of the trained pattern. For example, improvement at 90° only transfers to 270° and improvement at 135° only transfers to 225° (Zanone and Kelso 1997). Furthermore, the stability of the intrinsically stable coordination patterns (that is, 0° and 180°) or other novel patterns is not affected.

The original Bingham model (2001, 2004a, b) was not explicitly set up to handle learning. However, the perception–action theory it instantiates can explain the pattern of transfer to symmetry partners. The model is based on the premise that information guides the assembly of the movement patterns and the execution of actions. The model predicts that the system producing coordinated rhythmic movements is organised with respect to the information for relative phase, rather than relative phase per se. Learning a novel coordinated rhythmic movement is therefore primarily about learning to use appropriate perceptual information (Wilson et al. 2010a), and the consequences of learning are constrained by the nature of this information. Wilson and Bingham (2008) demonstrated that learning to visually perceive 90° entails learning to use new information, either position or position plus velocity. That work also demonstrated that the information used to produce 0° or 180° coordination is relative direction, not position (or position plus velocity). The information used to produce a learned 90° coordination and (for example) a 180° coordination is different, and so learning fails to transfer between these relative phases (Wilson et al. 2010a).

As far as relative direction is concerned, however, a coordinated rhythmic movement pattern and its symmetry partner are identical states with the only difference being which oscillator is leading the other. The same is true for moving at 90° with one trained arm–leg combination versus another untrained combination. In each of these cases, the information is the same, and thus, to a large extent, learning one of these actions *is* learning the other. Training thus "transfers". Information is thus the key factor that shapes learning and transfer of learning, and transfer only occurs when the information that was learned is the same in both the trained and the transfer task. A similar idea was described by Langley and Zelaznik (1984) in terms of learning essential versus non-essential variables. However, they did not specify a way to identify which were which ahead of time, and our analysis points specifically to information as the essential variable.

An intuition of how information might shape transfer comes from Wilson et al. (2010a) who trained participants to become expert perceivers of 90° mean relative phase. This improved visual discrimination of 90° then allowed stable movement at 90°, without any training on the movement task. We did not interpret these results as reflecting "transfer between a perceptual and a motor task". Instead, we argued that both the perceptual judgment and movement tasks required access to the same information and that the training provided this common access. Nevertheless, the result following the perceptual learning reflected a type of transfer between tasks, from judgments to performance of actions. The latter entails additional dynamics that contribute to a determination of the stability of performance as seen, for example, in the case of unimanual versus bimanual rhythmic coordination tasks. The information is the same, but the action dynamics are different and thus the stability.

In sum, learning to produce stable coordination patterns is largely about learning to detect the relevant information. There are multiple ways to facilitate the learning process. Wilson et al. (2010b) demonstrated that (augmented or extrinsic) feedback is required to learn 90°. The feedback was a visual "hot/cold" signal which activated when the participant was producing 90° within a certain range of accuracy. There are, of course, other ways to provide feedback. Auditory feedback about the relative positions of the hands or joints has been shown to be effective in enabling learning of 90° (de Boer et al. 2013). Another way to provide feedback is by using Lissajous figures (for example, see Swinnen et al. 1991). Lissajous figures are a very powerful tool to enable performance of otherwise difficult tasks (for example, see Kovacs et al. 2009a). However, they do not actually enable learning of 90° (again, see Kovacs et al. 2009a) unless the presence of the Lissajous figure is faded during the learning process (Kovacs and Shea 2011). Without this fading, people become dependent on the augmented feedback, failing to develop perceptual sensitivity to the naturally occurring information that can specify a 90° coordination, and thus, are unable to produce the trained movements without the Lissajous figure. Our previous work (Wilson et al. 2010a) showed that people do not become dependent on the hot/cold feedback signal. Instead, the evidence shows that what the feedback does is signal when information specifying 90° coordination (in contrast to 0° or 180°) is available, and thus, it allows participants to learn to detect the new information.

Another variation in coordinated rhythmic movements is whether the required movement is unimanual or bimanual. Many studies have investigated bimanual coordinated rhythmic movements (a single person moving and coordinating two limbs), but it is well known that the pattern of key stability characteristics are preserved when the coordination is between two people (e.g. de Rugy et al. 2006; Schmidt et al. 1990; Temprado et al. 2003; Temprado and Laurent 2004), or between a person and a computer display (e.g. Wimmers et al. 1992; Buekers et al. 2000; Wilson et al. 2005a, b, 2010a, b). These latter cases are called *visual coordination.* A single actor is responsible for controlling only one of the oscillators, and the two oscillators interact or are coupled visually. In the human–computer case, the coupling between the two oscillators is unidirectional because the computer does not perceive or react to the human. However, the pattern of stabilities and instabilities (that is, the transition phenomena) of the bimanual task remain essentially the same. Accordingly, the visual (unimanual) and bimanual versions are essentially the same task. However, unimanual coordination with unidirectional coupling exhibits weaker stability while preserving the overall patterns of stability.

Snapp-Childs et al. (2011) modified the Bingham model of bimanual coordination to make the coupling unidirectional and then tested the effects of this change. The primary consequence was that coordination stability in the model was diminished. Simulations of the bimanual model, for example, show that 180° movements remain stable with increases in frequency up to ≈3 Hz (matching empirical data, e.g. Kelso 1984; Kelso et al. 1986, 1987). Simulations of the unimanual model showed that 180° movements only remained stable up to ≈1.5 Hz, again matching the empirical data (Snapp-Childs et al. 2011). Other than this, the unimanual model produces all the same coordination phenomena as the bimanual model. The coupling function is of the same form and entails the same information (the relative direction of motion).

As shown by Wilson and Bingham (2008) and Wilson et al. (2010a), learning to perform 90° coordination entails the acquisition of the ability to discriminate new and different perceptual information used to produce stable 90° movement. The original Bingham model, in both its bimanual and unimanual versions, successfully simulated coordinative movement at 0° and 180° and transitions between them. However, the information represented in the coupling function of the model has to be changed to model 90° coordination. Bingham and Snapp-Childs (in preparation) extended the original Bingham model to account for patterns of performance in the learning of 90° coordination. The driver in the original model was a normed velocity. The driver in the new model is a normed position.[1] The models include hypotheses about perceptual information variables, and the hypothesis in the extended model is that participants learn to perform 90° coordination, in part, by learning to perceive the positions of the oscillators, whereas the original model hypothesised that the velocities were

[1] The normed forms of these state variables in the dynamics are those appropriate to model visual event perception (Bingham 2004a, b).

perceived. Just as in the original model, bimanual and unimanual versions entail the same information variables and differ only in whether the coupling is bidirectional or unidirectional.

The current experiment

Coordinated rhythmic movements exhibit a pattern of stability that emerges from a perception–action task dynamic in which the information for relative phase provides much of the structure. Learning a novel coordination pattern entails perceptual learning of new information that specifies the coordination, and the learning only transfers to a symmetry partner or a novel limb combination because the relevant information is the same. In the unimanual and bimanual versions of the tasks, the information remains the same (even though the coupling functions are uni- and bidirectional, respectively) so these are, therefore, treated as examples of nearly (but obviously not entirely) the same task dynamic (Snapp-Childs et al. 2011). Our previous work (Wilson et al. 2005a, b, 2010a, b) has assumed this to be this case, but we have never tested it empirically. Therefore, in the current study, we trained two groups of participants to move at 90° either unimanually or bimanually, respectively. Participants used either one or two joysticks to control either one or two dots on a computer screen so as to move them at 90° to one another (in the unimanual case one dot was controlled by the computer as a simple harmonic oscillator). We measured learning and also transfer of learning between unimanual and bimanual versions. We predicted that learning should indeed transfer between the two versions because the information learned is the same. To confirm that it was the perceptual information that was learned and that this is what supports the predicted transfer, we also tested the visual perception of mean relative phase at 90° (Wilson and Bingham 2008; Wilson et al. 2010a). Participants were asked to identify displays showing 90° in a two-alternative forced choice (2AFC) paradigm, and we measured thresholds for the required difference in displays. We predicted that practice of the action tasks should be associated with lower perceptual thresholds for the trained relative phase.

Finally, Snapp-Childs et al. (2011) showed in model simulations and confirmed with data that performance in the unimanual tasks is inherently less stable than in the bimanual tasks because the coupling is unidirectional instead of bidirectional. Thus, we must expect the level of improvement in performance, after equivalent amounts of training, to be less in the unimanual task than in the bimanual task. The same must be expected in tests of transfer. Thus, measured amounts of transfer from unimanual to bimanual and vice versa must be adjusted by the decrement in performance to be expected for the unimanual as compared to the bimanual task. We will measure the difference in performance (as expected due to the inherent difference in stability) as the proportion of the respective amounts of improvement in trained performance (post-test minus baseline) in the unimanual and bimanual tasks. This proportion will be used to adjust portions between transfer and trained performance. The prediction is that the adjusted transfer levels should be equal.

Methods

Participants

Fourteen adults (18–35 years old) participated in this study. All were right-handed, had normal or corrected-to-normal vision and were free from any known neurological defects or motor disabilities. All participants were naïve to the experimental questions, and their 90° relative phase production was worse than their 0° and 180° relative phase production prior to training. Ethical approval was granted by the Institutional Review Board at Indiana University, Bloomington.

Procedure

Participants performed seven separate sessions (see Table 1). Participants performed all sessions on a 20″ iMac which was located 70 cm from the participants and was connected to one or two Logitech Force 3D Pro joysticks; the joysticks' force feedback feature was disabled. The computer presented a display[2] of two white dots, one above the other, moving horizontally across a black background (screen refresh rate 60 Hz, resolution 1024 × 768). The vertical position of both dots was fixed, but the horizontal position of either one or both dots, depending on condition, was controlled by the horizontal position of the joystick(s). The mapping of joystick(s) to screen amplitude was set so that required amplitude on the screen did not entail hitting limits of the joystick range of movement.

During the baseline and post-training assessment sessions, participants performed three different tasks in the order described. In the unimanual task, participants were shown an 8-s demonstration of 0° relative phase (two dots moving in the same direction at the same time). Participants then performed one block of five 20-s trials in which the computer controlled the motion of the top dot [0.75 Hz

[2] All displays were presented and controlled by a custom MATLAB toolbox written by ADW and incorporating the Psychtoolbox (Brainard 1997; Kleiner et al. 2007; Pelli 1997, http://psychtoolbox.org). This software also recorded and analysed the data.

Table 1 Experimental design

Session	Unimanual group	Bimanual group
Baseline	5 trials each of unimanual 0°, 180°, 90°	5 trials each of unimanual 0°, 180°, 90°
	5 trials each of bimanual 90°	5 trials each of bimanual 90°
	2AFC judgment task (90°)	2AFC judgment task (90°)
Training 1	12× trials unimanual 90° w/feedback (±30°)	12× trials bimanual 90° w/feedback (±30°)
Training 2	12× trials unimanual 90° w/feedback (±25°)	12× trials bimanual 90° w/feedback (±25°)
Training 3	12× trials unimanual 90° w/feedback (±20°)	12× trials bimanual 90° w/feedback (±20°)
Training 4	12× trials unimanual 90° w/feedback (±15°)	12× trials bimanual 90° w/feedback (±15°)
Training 5	12× trials unimanual 90° w/feedback (±10°)	12× trials bimanual 90° w/feedback (±10°)
Post-training	5 trials each of unimanual 0°, 180°, 90°	5 trials each of unimanual 0°, 180°, 90°
	5 trials each of bimanual 90°	5 trials each of bimanual 90°
	2AFC judgment task (90°)	2AFC judgment task (90°)

All participants worked through these tasks in the order noted. The feedback bandwidth (e.g. ±30°) indicates over what range from the target relative phase the colour feedback was triggered; this is faded over time to drive learning (Wilson et al. 2010a, b)

frequency, 300 pixels (~11.5 cm) amplitude], while they controlled the motion of the bottom dot with their dominant hand. Participants were instructed to move the joystick in a smooth, side-to-side, movement to produce 0°. The first trial in the block was practice and was not analysed. This procedure was then repeated for 180° and 90° relative phase. These data were used to be sure that none of the participants could already perform 90° at a level equivalent to 0° or 180° and could take part in the learning study.

Next, in the bimanual task, participants were shown another 8-s demonstration of 90° relative phase and then performed one block of five, 20-s duration, trials in which they controlled the horizontal motion of both dots (bottom dot controlled by the participants' dominant hand). Participants were instructed to move the joysticks in a smooth, side-to-side, movement to produce 90°, while an external metronome played at 45 beats per minute (0.75 Hz).

Bimanual movements introduce an additional aspect: muscle homology. Movements which use homologous muscle groups at the same time (e.g. mirror symmetric movements in the fronto-parallel plane) are typically referred to as in-phase and are more stable than those which entail using non-homologous muscle groups at the same time (anti-phase). In the case of these two coordinations, that is, in-phase or 0° and anti-phase or 180°, the *egocentric* constraint interacts with the *allocentric* constraint of whether the motion is in the same direction or not to affect overall coordination stability (Swinnen et al. 1997, 1998). However, a 90° coordination does not entail this interaction. Producing 90° bimanual movements produces 90° or 270° visually where 270° is the symmetry partner of 90°, and thus, these are identical states with respect to the perceiver–actor. For the current study, we were only interested in learning and transfer of learning at 90°, where egocentric and allocentric constraints are not pitted against one another directly. We did, therefore, not assess changes in bimanual performance at 0°/anti-phase or 180°/in-phase and focused only on 90° where the interaction of these constraints does not affect the data. We did nevertheless test 0° and 180° at baseline, so we could use them to establish the relative lack of ability to produce 90° coordination before training.

Finally, in the judgment task, participants performed a series of two-alternative forced choice (2AFC) judgments about 90°. 2AFC is a standard psychophysical method for determining perceptual thresholds that we have used with this task before (Wilson et al. 2010a; Wilson and Bingham, 2008). Each trial consisted of a 4-s demonstration trial of 90° and a pair of successively presented stimuli (two dots moving harmonically on the screen at some mean relative phase, for 4 s at 0.75 Hz). The motion of both dots was cantered at the screen centre, with an amplitude of 300 pixels (~11.5 cm). One of each pair showed two dots moving at the target relative phase (90°), and the other was "different" from 90°; the participants' goal was to choose which one of the displays, first or second, was 90°. The magnitude of the "different" displays was determined using a transformed 1-up/2-down staircase procedure, using a step size "up" of 10° and a stop rule of 8 reversals. Step size "down" was fixed according to Table 5.1 of Kingdom and Prins (2009). The staircase makes the judgments easier or more difficult as a function of whether or not the last choice was correct or incorrect, and so the number of trials that each participant experiences varies as the pattern of responses varies. No feedback about performance was given.

After the baseline session, participants were trained to produce 90° either unimanually or bimanually. The first group of seven participants was trained to produce 90° unimanually. In this case, the computer controlled the motion of the top dot, while the participant controlled the (horizontal) motion of the bottom dot. The second group of seven participants was trained to produce 90° bimanually. These participants controlled the (horizontal) motion of both the top and bottom dots; unlike during the baseline and post-training sessions, there was no external metronome. During each of the five training sessions, participants performed twelve different (20-s duration) trials where their goal was to produce 90°. Participants received coordination feedback for all trials except for every fourth trial in each session; feedback was removed for every fourth trial to encourage participants not to become dependent on it (as it would not be present during post-test) (see Kovacs et al. 2009b). The dot(s) which were under their control changed colour from white to green when performance was within a given error bandwidth of the target relative phase. This error bandwidth was reduced in each successive training session; the bandwidth during the first training session was 30° and decreased 5° (to 25°, 20°, 15° and 10°) during each subsequent training session (as per Wilson et al. 2010a, b).

A note on terminology

All of the action tasks included a display of two dots at all times. There was therefore visual *information* about the coordination being performed available at all times. Prior to training, this information (for 90°) was not reliably detected, while after training it was, and being able to detect this information about the coordination being performed is what allowed participants to maintain the coordination (Wilson et al. 2010a). During training only, we provided visual *feedback* about the success of the coordination being performed. This feedback is in the form of a colour change that acts as a "hot/cold" signal to the participant and has been shown to drive learning successfully (Wilson et al. 2010b). We are therefore using *feedback* (present only during training) to improve the detection of coordination *information* (present throughout but not reliably detected at the beginning), and it is this latter learning that we expect to transfer between unimanual and bimanual movements.

Data analysis

For the action tasks, a 60 Hz position time series for both the computer- and person-controlled dots was recorded. The time series data were filtered using a low-pass Butterworth filter with a 10 Hz cut-off frequency and numerically differentiated using a central difference method to produce a velocity time series. For each trial, a continuous relative phase time series was computed as the difference between the arctangent of each dot's velocity divided by position with requisite corrections for the quadrants of the phase plane. From each relative phase time series (trial), we computed *proportion of time-on-task*. Proportion of time-on-task is the proportion of each continuous relative phase time series (trial) that fell within the range of the target phase ± a tolerance (set to 20° for all sessions, and, in addition, to the error bandwidth in the training sessions). It is a valid measure of performance at the required relative phase, i.e. how well the participant was able to move as requested (Wilson et al. 2010a, b). We then averaged proportion of time-on-task, for each participant, over the trials performed in a given condition.[3]

For the judgment tasks, the computer recorded the responses ("correct" or "incorrect") in relation to the relative phase of the "different" displays that were shown. We separately averaged the difference from 90° of relative phases at which reversals in the staircase procedure occurred for the "different" phases that were greater than 90° and those less than 90°, excluding the first reversal, for each participant. We then averaged those thresholds for perceiving 90° for each participant.

Results

Baseline performance

First, we verified that the groups were similar before training with respect to their 90° performances (Fig. 1a shows the group means at baseline for unimanual 90° and bimanual 90°). To do this, we first performed a repeated-measures ANOVA with the following factors and levels: group (unimanual training, bimanual training) as a between-subject factor and condition (unimanual 90°, bimanual 90°) as a within-subject factor. The ANOVA yielded no significant factors (group × condition: $F_{(1,12)} = 0.40$, $p = 0.54$, group: $F_{(1,12)} = 0.19$, $p = 0.67$, condition: $F_{(1,12)} = 0.09$, $p = 0.77$).

Next, we used the confidence interval approach to the two one-sided test procedures to infer equivalence. In this procedure, equivalence is established if the designated confidence interval (for $\alpha = 0.05$, the CI $= (1 - 2\alpha) \times 100 = 90$ %) for the mean difference between groups is contained within the equivalence margin or $(-\delta, \delta)$ interval (Walker and Nowacki 2011). For this experiment, the mean difference between groups was

[3] Other coordination researchers rely on measures of mean error and variability. However, the hallmark of human coordinated rhythmic movement is that these are not independent. A common problem at unstable phases (e.g. 90°) is that people produce large errors (e.g. moving at 0° instead) but with low variability. You therefore cannot interpret variability without the error and vice versa. We use and advocate for the proportion measure because it addresses these problems; it succinctly and validly measures performance at the required relative phase (Wilson et al. 2010a, b).

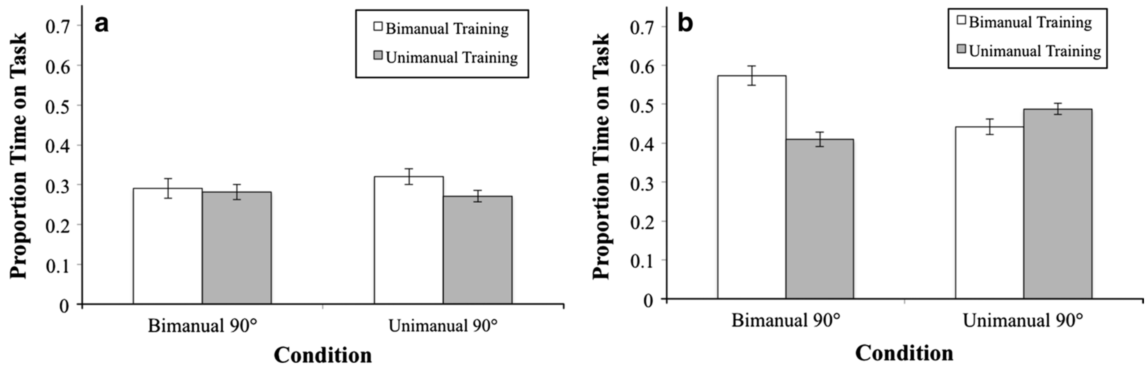

Fig. 1 Unimanual 90° and bimanual 90° performance for both training groups **a)** before training and **b)** after training. *Error bars* represent the standard error of the mean

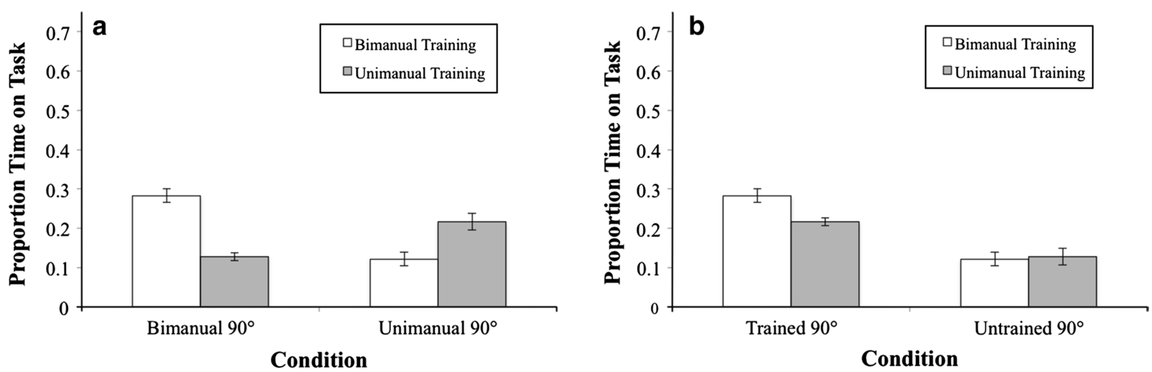

Fig. 2 Difference scores (post-training–baseline) for performance at 90° by **a)** condition: unimanual 90° versus bimanual 90° and **b)** training condition: trained versus untrained condition. *Error bars* represent the standard error of the mean

obtained by subtracting the unimanual training group's performance from the bimanual training group's performance (so negative numbers reflect the unimanual group being superior to the bimanual group). The (−δ, δ) interval was set at (−0.125, 0.125). We chose this (−δ, δ) because this approximately reflects the difference between 0° and 180°; again, 0° is well established to be more stable than 180° and, usually between 0.10 and 0.15, for the total proportion measure. For both the unimanual 90° and bimanual 90° conditions, we report the mean difference between groups and the confidence intervals as follows: 0.049 ± 0.075 (−0.026, 0.124) and 0.009 ± 0.074 (−0.065, 0.083), respectively. Therefore, performance levels were equivalent between the training groups at baseline in both unimanual 90° and bimanual 90° conditions.

Learning and transfer

Next, to examine how training mode influenced performance of 90°, we analysed average time-on-task using a three-way mixed-design ANOVA with the following factors and levels: group (unimanual training, bimanual training) as a between-subject factor and condition (unimanual 90°, bimanual 90°) and session (baseline, post-training) as within-subject factors. Figure 1a shows proportion of time-on-task at baseline for unimanual 90° and bimanual 90° for each of the training groups, while Fig. 1b shows the same measure after training. There was a significant three-way (condition by session by group) interaction ($F_{(1,12)} = 7.03$, $p < 0.05$) as well as a main effect of session ($F_{(1,12)} = 77.3$, $p < 0.01$). No other main effects or interactions were significant (all p's > .05). The three-way interaction indicates that the groups changed unequally, from before to after training, for the unimanual 90° and bimanual 90° conditions.

To illustrate the source of this interaction, we plotted improvement in performance by performance condition (Fig. 2a) and training condition (Fig. 2b). The trained data entail post-testing using the task in which participants trained. So, trained data are the difference scores (post-test minus baseline) for unimanual 90° performed by the unimanual training group and for bimanual 90° performed by the bimanual training group. The untrained data entail post-testing using the transfer task in each case. The untrained data are the difference scores for unimanual 90° performed by the bimanual training group and for bimanual 90° performed by the unimanual training group. As expected given the difference in stability intrinsic to the respective tasks, the bimanual training group improved more at bimanual 90° than the unimanual group did at unimanual 90° (the trained conditions). On the other hand, the mean difference scores were the same for the two groups in the untrained 90° conditions. To confirm this, we tested for equivalence using the two one-sided test procedures. The mean difference between groups and 90 % confidence intervals for the trained 90° and untrained 90° were as follows: 0.066 ± 0.078 (−0.012, 0.144) and −0.006 ± 0.077 (−0.083, 0.071), respectively. Thus, equivalence for the trained 90° condition was not established, but equivalence for the untrained 90° was established.

However, the latter scores (that is, the difference scores for untrained) do not provide a measure of transfer. This requires the relevant proportions of untrained and trained difference scores, namely untrained unimanual to trained bimanual (transfer for the bimanual training group) and untrained bimanual to trained unimanual (transfer for the unimanual training group), respectively, yielding 0.45 and 0.56. However, to control for the known difference in inherent stability of unimanual and bimanual performance, these proportions must be adjusted by the proportion of unimanually trained to bimanually trained difference scores, which was 0.77. (That is, unimanual only does 77 % as well as bimanual.) So, 0.77 × 0.56 = 0.43. So, the two transfer amounts were 45 and 43 %. Thus, as predicted, the measures of transfer, adjusted for the inherent difference in stability of the two tasks, reveal equal transfer in the two cases, that is, from unimanual to bimanual and from bimanual to unimanual. This is the main result of the study.

Judgment thresholds

The perception–action approach to coordination predicts that learning primarily entails learning to perceive the target novel relative phase, which then allows stable coordinated actions (Wilson et al. 2010a). We hypothesised that this perceptual learning underpins the observed transfer of learning between the training conditions. To test this, we measured 90° visual judgment thresholds at baseline and post-training (note that there was no training on the judgment task). These data are shown in Fig. 3. We ran a two-way mixed-design ANOVA with group (unimanual training, bimanual training) as a between-subjects factor and session (baseline, post-training) as repeated measures. As shown in Fig. 4, there were no group differences in ability to perceive 90°, but judgment thresholds improved from before to after training. This was confirmed by a main

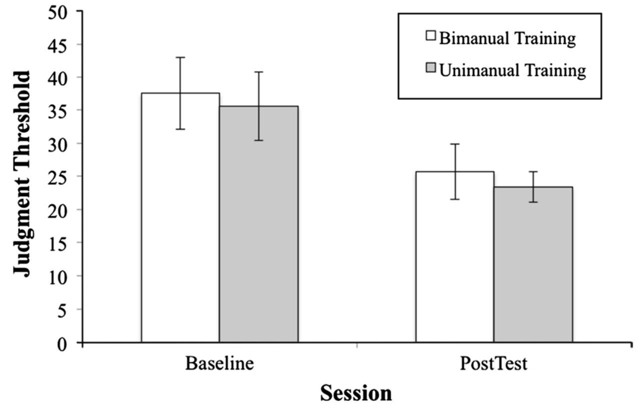

Fig. 3 Thresholds for judging 90° before and after training for the two training groups. Thresholds were high at baseline but reduced equally with training. *Error bars* represent the standard error of the mean

effect of session ($F_{(1,12)} = 18.09$, $p < 0.01$), but no effect of group nor any group × session interaction (all p's > 0.05). To confirm that the groups were equivalent in their ability to visually perceive 90° after training, we tested for equivalence using the two one-sided test procedures. The (−δ, δ) interval was set at (−10°, 10°). The mean difference between groups and 90 % confidence intervals for the 90° judgment threshold at post-test was as follows: −2.315° ± 5.663° (−7.978°, 3.348°). Thus, equivalence was established for 90° judgment thresholds at post-test.

Relating perceptual judgments and coordination performance

Initially, we hypothesised (1) that after equivalent amounts of training, the level of improvement in performance would be less in the unimanual task than in the bimanual task (due to differences in intrinsic stability) and (2) that perceptual learning underpins the transfer of learning. We found equal perceptual improvement and unequal improvement in coordination performance as expected. Performance of the unimanual task is less stable not because of any difference in information or perceptual ability, but because the coupling in the task dynamic is unidirectional rather than bidirectional as it is for the bimanual task. Accordingly, we also expected that there would be a stronger relationship between performance at 90° and judgment thresholds for the bimanual task than for the unimanual task, although on average, there should be no difference between trained and untrained because the information and perceptual ability are the same. To examine these possibilities, we performed Pearson correlations of performance at 90° and the 90° judgment thresholds separately for each training group and task. (The tasks in the context of training groups become trained and untrained.) Here, we also expected all

Table 2 Pearson correlations by training group and trained and untrained (transfer) tasks

	Trained 90°	Untrained 90°
Bimanually trained	−0.83	−0.62
Unimanually trained	−0.55	−0.73
Overall	−0.69	−0.68

r's for the combined trained tasks (and thus training groups) and combined untrained tasks (and training groups) are shown as overall

correlations to be negative because the coordination performance measure goes up with training, while the perceptual threshold measure goes down.

The resulting Pearson r's are shown in Table 2. As expected, the r's for the bimanual task ($r = -0.83$, $t(12) = -5.1$, $p < 0.001$; $r = -0.73$, $t(12) = -2.8$, $p < 0.02$) were greater than those for the unimanual task (– = −0.55, $t(12) = -2.3$, $p < 0.04$; $r = -0.62$, $t(12) = -3.7$, $p < 0.005$). Also, (once the different tasks were factored out by averaging over them) there was no difference in the overall r's for trained and untrained, respectively. All tests revealed significant relations between the judgments and the coordination performance levels accounting for about 40–70 % of the variance.

Discussion

We suggest that a task dynamic model can be used to predict the extent to which learning will transfer among tasks with related task dynamics (for task dynamics, see Beek and Bingham 1991; Bingham 1988; Feldman et al. 1990; Kugler and Turvey 1987; Saltzman and Kelso 1987). We tested this idea in the context of an extensively studied type of task, namely rhythmic movement coordination (e.g. Kelso 1984). Both bimanual and unimanual versions of this general type of task have been modelled using a perception–action task dynamic in which the movements are perceptually coupled (e.g. Snapp-Childs et al. 2011). In addition, previous studies have shown that novel patterns of coordination, i.e. 90° relative phase, must be learned (Wilson et al. 2010b; Zanone and Kelso 1992a, b). And, in this context, it has been shown that the learning of a new coordination pattern is largely a matter of learning to perceive that coordination (Wilson et al. 2010a). So, the task dynamic for a to-be-learned coordination pattern is different in respect to perceptual information in the coupling function that specifies the relevant coordinative mode: for instance, 90° in contrast to 0° or 180° (Snapp-Childs and Bingham in preparation; Wilson and Bingham 2008). In other words, learning the new coordination entails learning to discriminate the new information variable. Once this has been accomplished, learning is predicted to transfer to other versions of the coordination task that include the same information variable in the respective task dynamics. Thus, the learning of a 90° bimanual coordination task is predicted to transfer to the performance of a 90° unimanual coordination task and vice versa.

Bimanual coordination and unimanual coordination are different tasks as shown by the fact that they exhibit differences in their respective intrinsic stability (Snapp-Childs et al. 2011). The task dynamic for unimanual coordination entails a unidirectional coupling function, whereas that for bimanual coordination entails a bidirectional coupling. The former is weaker, and thus, the coordinative modes exhibited in a unimanual coordination task are less stable than those exhibited in bimanual tasks. Of course, these differences must be taken into account when evaluating the amount of transfer between these tasks when a new coordinative mode has been learned. For a given amount of training, less improvement in performance can be expected for the less stable task, namely unimanual coordination as compared to bimanual coordination. Likewise, when learning transfers between these tasks, the respective level of performance should be expected to be lower for unimanual coordination.

We set out in the current study to test these predictions. Over multiple sessions, we trained two groups of participants to produce 90° coordination, one group in a unimanual task and the other in a bimanual task. Then, we measured both learning and transfer of learning. For learning, we measured performance in the trained task and judgment thresholds for the visual discrimination of 90°. For transfer, we measured performance in the other, untrained task. Both groups improved in their ability to produce 90° in their trained task, although bimanual more so than unimanual as expected because of the difference in the intrinsic stability of the tasks. Both groups also improved in their visual discrimination of 90°, but this time equally so. Finally, we derived measures of transfer of learning and found that the groups exhibited equal amounts of transfer. This derivation required that the differences in the intrinsic stability of the tasks be taken into account.

When we evaluated the learning that had occurred as a result of the multi-session training, we found equal improvements in perceptual thresholds for both training groups, but unequal improvements in coordination performance levels. The improvement was greater for the bimanual training group performing the bimanual coordination task than for the unimanual training group performing the unimanual task. Direct comparison of improvements in perceptual judgments and in coordination performance yielded stronger correlations for the bimanual group and task than for the unimanual group and task. This pattern of results had been expected. Equal improvements in ability to discriminate 90° perceptually were not expected to yield equal improvements in performance of 90° in the two tasks, unimanual and bimanual. The respective task dynamics did entail the same information variable but different coupling functions that yield differences in performance level. The unidirectional coupling in unimanual coordination is weaker and results in less stable and thus poorer performance than that produced by the stronger bidirectional coupling in bimanual coordination.

Thus, the different correlational results were expected to reflect the tasks (and the differences in coupling functions) and not the training groups as such, because the training groups entailed equivalent learning of the same information variable. To test this, we performed the correlational analyses on the untrained data with the expectation that stronger correlations would be found for the bimanual as compared to the unimanual task. In the untrained data, the bimanual task was performed by the unimanual training group and the unimanual task was performed by the bimanual training group. Indeed, the results were as predicted. Finally, to confirm that the differences in these correlations between improvements in perceptual thresholds and improvements in coordination performance reflected differences in the stability of the tasks (and thus the nature of the coupling functions in the task dynamics), we performed the correlations on the combined data of the two training groups but separately in the case of the trained data and the untrained data. This controlled for the difference in tasks but preserved the commonality of the information. The prediction was that the correlations would be of equal strength. This was indeed the result. In all cases, the correlations were significant and showed that the perceptual learning underwrote the improvements in performance of the new coordination.

Thus, we were successful in predicting the relative levels of transfer of learning in the context of these two rhythmic coordination tasks using the task dynamics underlying the two tasks to make the predictions. The task dynamics conditioned the levels of transfer in two ways. First, transfer was conditioned by the perceptual information variables incorporated into the coupling functions in the task dynamics for both tasks. Both the information used to perform skilled coordination at 0° and 180° and new information used to perform learned coordination at 90° were common to both unimanual and bimanual tasks. Progressively learning to discriminate and perceive new information enabled participants to progressively improve in their performance of 90° coordination in both unimanual and bimanual tasks. The performance of coordination tasks cannot, however, be reduced to the ability to perceive (contra Mechsner et al. 2001) because actions entail task dynamics that include, but are more complex than, mere perceptual information. So, second, transfer performance was conditioned by the intrinsic stability of each task and this is determined, in part, by the nature of the coupling. In these cases, the coupling in the two tasks was different, unidirectional versus bidirectional. Because the former is weaker, the respective transfer performance was bound to be less good. This difference in stability must be taken into account when evaluating the amount of transfer of learning.

So, transfer of learning occurs when the composition of the underlying task dynamic does not change, and in the case of coordinated rhythmic movement this dynamic critically involves perceptual information. When the information is different, the composition of the dynamic is changed, and the two instances are then different tasks and learning does not transfer. When the information remains the same and there are not major alterations to the organisation of the dynamic, as in the current experiment, then the task remains the largely the same and transfer can occur (although as always the relative level of performance reflects the relative levels of stability exhibited by the respective task dynamics). The details of learning itself depend on the alteration to the task dynamic, and here, a change in the perceptual information. As shown in earlier studies, learning to perform 90° coordination entailed perceptual learning, learning to detect the information required to perceive and control 90° coordination. The model shows that this entailed a change from detecting velocity of movement to detecting the evolving position of each oscillator as well as a change from detecting consistently same or opposite directions of movement to detecting a balance of both. The details of transfer depend on these changes to perception. Improved visual discrimination of 90° allowed transfer to occur, but the magnitude of transfer was incomplete, equal to about 40–50 %. This may have reflected the relatively modest magnitudes of improvement exhibited by the perceptual learning. Post-training visual perceptual thresholds in the current study averaged between 22° and 26°. Wilson et al. (2010a) found final thresholds at 90° averaged ~13° after much more extensive training. So, in the current study, there was room for further improvement in visual discrimination. These modest levels of improvement may well contribute, when combined with the difference in stability of the bimanual and unimanual tasks, to the magnitudes of transfer.

Finally, the understanding developed in the current study of what occurs during learning to promote transfer required theoretically motivated models of the task at hand such as the various versions of the Bingham model (bimanual 0°/180°: Bingham 2001, 2004a, b; unimanual 0°/180°: Snapp-Childs et al. 2011; bimanual and unimanual 90°: Bingham and Snapp-Childs in preparation). These models contain specific hypotheses about mechanism that, in turn, enables us to use them to make successful predictions about learning and transfer. The perception–action task dynamic models (and the theory-driven research programme that generated them) stand as examples of the explanatory power to be gained by studying the actual composition and organisation of the perception–action mechanism responsible for observed behaviour in a task.

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Appendix: Additional measures of coordination performance

Measures of mean error and variability have been used in some studies to evaluate coordination performance and learning. We report these measures and show that they are difficult to interpret in the current context in contrast to the proportion of time-on-task (PTT) measure that we have used. Similar to Maslovat et al. (2010), we computed the relative phase distributions windowed at intervals of 20° ranging from 0° to 180° and produced a histogram showing where participants were spending time when trying to move at 90° both before and after training (see Fig. 4a, b). We used this graph to interpret the mean error and variability.

The problem for the measures is as follows. As participants begin to try to perform 90° coordination, they often fail to remain in the neighbourhood of 90° and transition to spend significant time at either 0° or 180°. As they learn and improve in performance, they succeed better in staying near or at 90° (as shown directly by the PTT measure) although they may still occasionally transition to 0° or 180°. There are individual differences in whether a performer tends to transition either to 0° or to 180° or to both. If it is both rather than just 0° or 180°, for instance, then the resultant overall variability can be increased. However, this is not relevant to the level of success in performing the task, which is to stay at or near 90°. It is all the same if the movement is at 0° or 180° instead of 90°. Also, if the performer spends similar amounts of time at 0° and at 180°, then the mean can be 90°, whereas if the performer transitions more reliably to 0°, then the mean can biased towards 0°. Again, these differences are not of direct relevance to the success in performing the task. For these reasons, measures of mean error and variability are problematic for evaluating performance in this learning task.

First, we describe the relevant measures of mean error and variability.

Data analysis

Relative phase is a circular variable (the distribution of possible values lies on a circle) that creates a problem for computing standard means and standard deviations. Circular statistics provide trigonometric solutions to these problems by treating each data point in a relative phase time series as a vector of unit length and an orientation that matches the relative phase at that time point. *Mean direction* is effectively the result of concatenating these vectors and computing the orientation of the vector between the origin and the tip of the final data point vector. The *mean vector length* or *uniformity* (U) (Fisher 1993) measures the variability as the length of the resultant vector divided by the number of data points (and which therefore ranges from 0 to 1). This latter was transformed into a linear variable (SDψ) that varies between 0 and infinity using the following transformation:

$$\mathrm{SD}\psi = \left(-2\log_e U\right)^{1/2}$$

Results

First, to examine performance before and after training, we computed relative phase distributions (that is, the proportion of time spent at relative phases between 0° and 180°

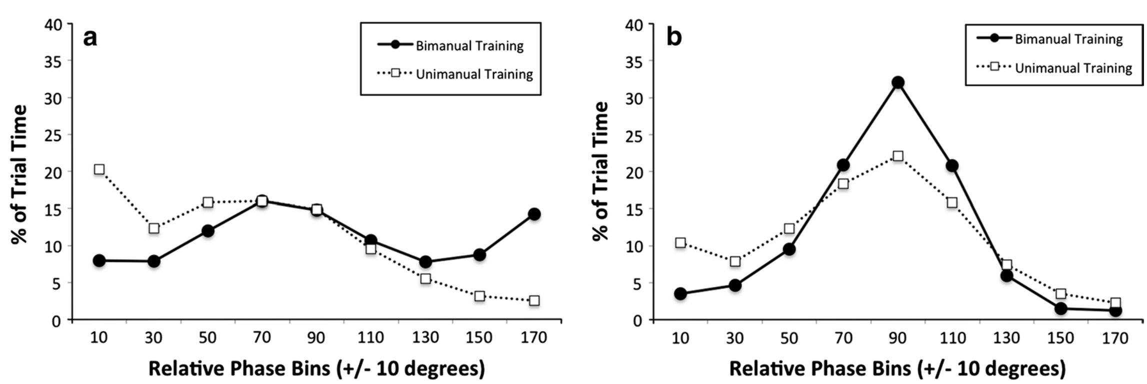

Fig. 4 Relative phase distributions for baseline and post-training for bimanual 90° separated by group: **a**) baseline; **b**) post-training

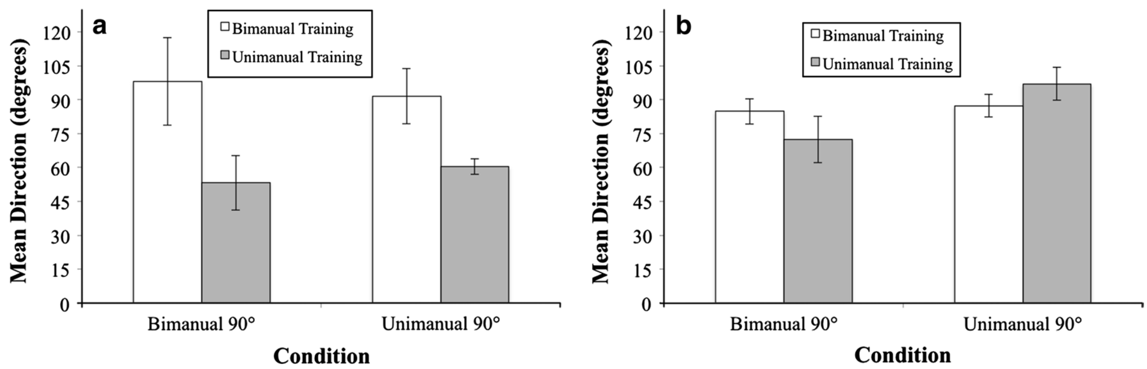

Fig. 5 Mean vector direction (in degrees) at baseline and post-training separated by condition and group: **a)** baseline, bimanual versus unimanual 90°; **b)** post-training, bimanual versus unimanual 90°

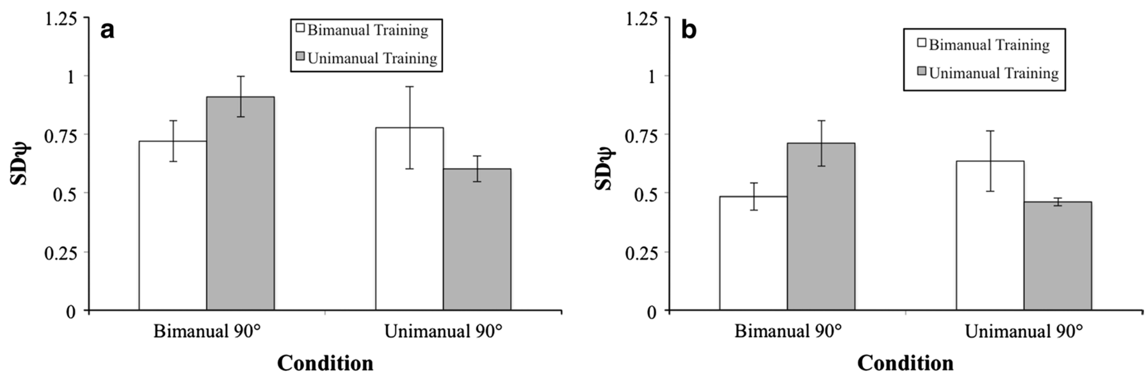

Fig. 6 SDψ at baseline and post-training separated by condition and group: **a)** baseline, bimanual versus unimanual 90°; **b)** post-training, bimanual versus unimanual 90°

using 20° bins) by condition (unimanual 90°, bimanual 90°) and separated by group. We illustrate the resulting individual differences in Fig. 4. When performing the bimanual task at baseline, as expected, neither training group consistently produced a relative phase at or near 90°. As shown in Fig. 4a, the group that would subsequently be trained at the bimanual task tended to transition to and spend time at 180°, while the group that would be trained at the unimanual task tended to transition to and spend time at 0°. This was merely an individual difference between the groups that was, however, reflected in the pattern of results for the mean direction at baseline. (Note that individual differences also appeared in results at baseline for the unimanual task.) As shown in Fig. 5a, the training groups exhibited significant differences in mean direction that reflected the individual differences. To analyse the mean direction, we used a two-way mixed-design analysis of variance (ANOVA) with group (unimanual training, bimanual training) as a between-subjects factor and condition (unimanual 90°, bimanual 90°) as a within-subject factor. The result was a significant main effect of group ($F_{(1,12)} = 4.98$, $p < .05$). However, this difference was not relevant to the level of success in performing the task to be learned. Accordingly, we had found no differences when performance was evaluated using the PTT measure of success in performing the 90° task.

We used the same ANOVA design to analyse SDψ and found no significant main effects or interactions. This indicated that there was no difference in consistency between the groups at baseline as shown Fig. 6a. (Note that there could have been a difference if participants in one of the groups had tended to transition equally often both to 0° and to 180°, but this difference, if significant, also would not have been relevant to the evaluation of success in performing the task to be learned.)

Next, we analysed mean direction and SDψ at post-test. For mean direction, as shown in Fig. 5b, there were no significant main effects or interactions. However, as shown in Fig. 4b, the unimanually trained group still spent more time at 0° (in the bimanual task), while the bimanually trained group spent more time at 90°. This yielded a result in the analysis of SDψ where there was a significant group by condition interaction ($F_{(1, 12)} = 7.82$, $p < 0.02$) as shown in Fig. 6b. A comparison of baseline and post-test yielded a main effect of session for SDψ ($F_{(1,12)} = 13.50$, $p < 0.05$), but not for mean direction. Nevertheless, both measures must be taken into account when evaluating success in learning this task. The reason is that stable but highly inaccurate performance can result from spending time only at 0° or only at 180° and that apparently accurate but highly unstable performance can result from spending equal time at 0° and at 180°.

So finally, using the two measures (mean direction and SDψ), it remained unclear how to evaluate the relative transfer of training, appropriately scaled by intrinsic differences in stability between the tasks. PTT measures the goal of the learning task directly, providing a single measure of success in performing the 90° task. It also yielded good measures of transfer. Thus, this was the preferable measure to use.

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