When kinesthetic information is neglected in learning a Novel bimanual rhythmic coordination

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Abstract Many studies have shown that rhythmic interlimb coordination involves perception of the coupled limb movements, and different sensory modalities can be used. Using visual displays to inform the coupled bimanual movement, novel bimanual coordination patterns can be learned with practice. A recent study showed that similar learning occurred without vision when a coach provided manual guidance during practice. The information provided via the two different modalities may be same (amodal) or different (modality specific). If it is different, then learning with both is a dual task, and one source of information might be used in preference to the other in performing the task when both are available. In the current study, participants learned a novel 90° bimanual coordination pattern without or with visual information in addition to kinesthesia. In posttest, all participants were tested without and with visual information in addition to kinesthesia. When tested with visual information, all participants exhibited performance that was significantly improved by practice. When tested without visual information, participants who practiced using only kinesthetic information showed improvement, but those who practiced with visual information in addition showed remarkably less improvement. The results indicate that (1) the information is not amodal, (2) use of a single type of information was preferred, and (3) the preferred information was visual. We also hypothesized that older participants might be more likely to acquire dual task performance given

their greater experience of the two sensory modes in combination, but results were replicated with both 20- and 50-year-olds.

Keywords Kinesthesia · Visual perception · Multisensory processing

In the original studies of rhythmic coordination (Kelso, 1984; Kelso, Scholz, & Schoner, 1986), a participant rhythmically moved two joints, each in a separate limb, to perform one of two coordinative modes: in phase and antiphase coordination (also described as 0° or 180° relative phase, respectively). Spontaneous mode switching occurred when participants performed 180° at preferred rates and then gradually increased the frequency of oscillation. As the frequency increased, the stability of the 180° coordination decreased until, finally, coordination switched to stable movement at 0°. Subsequently, this and other associated phenomena were reproduced in rhythmic coordination performed between people (Schmidt, Carello, & Turvey, 1990) where each person performed rhythmic joint oscillations while watching the other person's movements to produce and maintain the coordination. In this case, the coupling between the movements was strictly visual, whereas in the original studies it had also been kinesthetic (Serrien, Li, Steyvers, Debaere, & Swinnen, 2001).

The between-person coordination results inspired perceptual judgment studies (Bingham, 2004a, 2004b; Bingham, Schmidt, & Zaal, 1999; Bingham, Zaal, Shull, & Collins, 2001; Zaal, Bingham, & Schmidt, 2000) in which observers judged the stability of the coordination when viewing computer displays of two dots oscillating at different relative phases and frequencies. The results were consistent with the previous mode switching results—0° coordination was judged to be the most stable and equally stable at all frequencies, while 180° was judged to be less stable and increasingly less

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stable as frequency increased until it was judged to be as unstable as 90° relative phase; 90° coordination was judged to be maximally unstable and equally so at all frequencies.

This visual judgment paradigm was replicated in a kinesthetic judgment task (Wilson, Bingham, & Craig, 2003). Participants used their fingers to track two manipulanda that exhibited the same movements as in the visual judgment study and judged the stability of coordinative movement in the same way. The pattern of results was nearly identical to those in the visual judgment studies, leading the researchers to hypothesize that the information used in the two tasks, visual and kinesthetic, was amodal. Gibson (1950, 1966, 1979) had advocated that perception might be largely amodal, meaning that the information detected using different perceptual modalities, like vision and kinesthesia, would be the same (see also Epstein, 1985, for review). Amodal information would allow the synchronous perceptual control and guidance of limb movements using both kinesthesia and vision and presumably stabilize motor control, given the redundantly available information.

However, kinesthesia would seem to be different from vision in being intrinsically integrated with motor control. On the one hand, kinesthesia has been shown to function best in the context of active movement. Studies of kinesthetic sensitivity and ability have shown that active touch (or haptics) yields significantly more effective kinesthetic performance (e.g., Clark & Horch, 1986; Goodwin, 1976; McCloskey, 1978, 1980; Paillard & Brouchon, 1968, 1974). On the other hand, leading models of the generation and control of movements describe kinesthesia as intrinsic to the organization of the fundamental units of control in limb movements (e.g., Feldman, 1966, 1986, 2010; Feldman, Adamovich, Ostry, & Flanagan, 1990; Hogan, Bizzi, Mussa-Ivaldi, & Flash, 1987; Latash, 1993, 2012). Indeed, when kinesthesia is removed, the ability for coordinated and functionally effective limb movements is lost (Cole, 1995; Sainburg, Ghilardi, Poizner, & Ghez, 1995), although—with sufficient experience, practice, and training—vision can be substituted for kinesthesia to once again enable performance of coordinated actions.

Furthermore, kinesthesia as integrated with the control of muscles, joints, and limb movements is bound to be related to, but not identical to, kinesthetic information about coordination used to generate and maintain such coordination. Wilson et al. (2003) found that participants were able to perform a haptic tracking task that enabled them to produce coordinated movements (that is, 90° relative phase) that they would otherwise not be able to perform freely (that is, without tracking the manipulanda or, alternatively, without significant training and practice). When they were asked to perceive and judge the coordinations as such, despite the fact that they were stably producing the 90° coordination by tracking the manipulanda, they judged it as maximally unstable in contrast to 0° which was judged as maximally stable. So, kinesthetic/haptic control of movement is not the same as

kinesthetic perception of coordinative modes. On the other hand, kinesthetic perception of coordination can be essential to the generation, control, and learning of freely coordinated movements (e.g., Wilson, Snapp-Childs & Bingham, 2010; Kovacs & Shea, 2011).

Fundamental differences between kinesthetic and visual control of coordinated limb movements have been suggested in the context of the mode-switching results that were attributed in the original studies (Kelso, 1984) to muscle homologies. This would entail a uniquely different frame of reference for the kinesthetic coupling as compared to visual coupling of rhythmic coordination because the spatial frame of reference for visual coupling would not entail the asymmetry in muscle homologies. Pairing homologous muscles to perform 0° coordination yields stable performance in contrast to the pairing of heterologous muscle in performance of 180° coordination. Nevertheless, studies have shown that the instability of movement in a 180° coordination at higher frequency performed by a single person using two different limbs can be overcome when participants were instructed to perceive and control the movement visually as a 0° coordination (Mechsner, Kerzel, Knoblich, & Prinz, 2001; Mechsner & Knoblich, 2004). This implies that kinesthetic perception of a coordination is not required for its production and performance.

When untrained participants attempt to perform a 90° coordination, they often crash. It is indeed maximally unstable. However, participants have been shown to be able to learn to perform stable and coordinated rhythmic movements at 90° relative phase (Zanone & Kelso, 1992). Normally, significant training and practice is required before a 90° coordination can be performed stably. Kovacs, Buchanan, and Shea (2009) found that this coordinative mode could be performed almost immediately if participants were moving to draw a circle in a Lissajous plot. In a Lissajous figure, the position of one moving limb is plotted against the position of the other moving limb. When the limbs are moved to produce a 0° coordination, a line of positive slope is drawn in the plot. When the limbs are moved to produce a 180° coordination, a line of negative slope is drawn. A 90° coordination yields a circle. Guiding the coordinated movements visually to produce a circle eliminates the need for perceptual learning to become sensitive to the natural form of the movement (that is, the visual information) normally used to generate the coordination. Kovacs et al. did find that their participants were dependent on the availability of the Lissajous plot to be able to perform the coordination, presumably because they had not acquired sensitivity to the information otherwise available and normally used. Consequently, Kovacs and Shea (2011) used a “faded” practice regime in which the Lissajous plots were only intermittently available to participants to enable them to perform 90° when the Lissajous plot was no longer available.

Clearly, use of Lissajous plots for visual guidance in performance of rhythmic coordination entails kinesthetic and

visual information that is modality specific, that is, explicitly not amodal. Participants who attempt to perform the task using both sources of information necessarily must perform a dual task, which is more difficult than simply using the single and more accessible information provided by the Lissajous plot. Thus, the result obtained by Kovacs et al. (2009) is not surprising in respect to the participants having failed to gain ability to perform the task using the available kinesthetic information. By implication, participants in Kovacs and Shea (2011) worked to perform the dual task to gain the ability to perform the coordination either using the visual Lissajous information or using the naturally available kinesthetic information.

The Lissajous paradigm introduces a possible means to investigate the relation between visual and kinesthetic information used in rhythmic coordination, that is, whether the information in the two modalities is effectively the same (that is, amodal) or not (that is, modality specific). Wilson and colleagues have shown that learning to perform 90° coordination in a unimanual visual coordination task entails perceptual learning to acquire sensitivity to a new information variable used to perform the skilled task (Wilson, Collins, & Bingham, 2005a, 2005b; Wilson, Snapp-Childs, & Bingham, 2010; Wilson, Snapp-Childs, Coats, & Bingham, 2010). If such information is modality specific (thus, different in vision and kinesthesia), then one might expect a result similar to that in the Lissajous studies, that is, a preference to use only the effective information available in a single modality with a concurrent failure to acquire use of the information in the other modality.

Ren et al. (2015) investigated the learning of 90° bimanual rhythmic coordination using either only kinesthetic information or both visual and kinesthetic information. They tested participants of two different ages, 20-year-olds and 50-year-olds. Participants oscillated joysticks held in the left and right hands to produce and control the movements of two corresponding dots on a computer screen. Half of the participants in each age group trained only using kinesthesia, and the other half trained using both kinesthesia and vision. During training, all participants received feedback indicating at each moment whether they were successfully performing the 90° task. After multiple sessions of training, all participants were tested without the feedback in two conditions, namely, with only kinesthesia and with both kinesthesia and vision. The participants that had trained using only kinesthesia performed equally well in both information conditions (that is, with or without vision in addition). They exhibited performance levels significantly improved by training. In contrast, participants that trained with vision in addition to kinesthesia performed less well when only kinesthesia was available, without vision. They exhibited improved performance as a function of training but more so when the visual information they had trained with was available. The decrement in posttraining

performance without vision was smaller in older 50-year-old participants. They were less affected by the loss of the visual information with which they had trained.

If it is the case that performance of rhythmic coordination using both kinesthetic and visual information about the coordinative mode is effectively a dual task because the information is modality specific, then, logically, older participants should be expected to perform better in this dual-task situation simply because they have had decades of more experience performing tasks using both kinesthesia and vision together. This may well account for the pattern of results in the Ren et al.'s (2015) study.

If participants in the Ren et al.'s (2015) study preferred to use a single modality because the information was modality specific and preferred the visual information when it was available, then it might be expected that extended training would yield a complete dependence on the visual information. On the other hand, if older participants are better able to handle the dual-task nature of the modality-specific visual and kinesthetic information, then one might expect less dependence on visual information to develop in that case. Given the intrinsic involvement of kinesthesia in the control of limb movements, it would be remarkable to find participants unable to use kinesthetic information in skilled performance of a coordination task, despite the reliable availability of that kinesthetic information during extended training. To pursue this question in this study, we doubled the amount of training and practice used in the Ren et al.'s (2015) study, and again tested participants that were in their 20s and in their 50s.

Method

Apparatus

A custom-built shelf was set on a table with a 15-in. PC laptop sitting on top of the shelf and two joysticks hidden underneath by a tablecloth covering the shelf. A stool was provided to the participant so that he or she could adjust its height to see the laptop screen at eye-height level and grasp the joysticks underneath the shelf without seeing them. Two Logitech Force 3D joysticks were connected via USB to the PC laptop, one joystick opposite the left shoulder of the participant and the other opposite the right shoulder. The display resolution was 1024 × 768 with a refresh rate of 60 Hz. In the visual conditions, the PC laptop displayed two white dots on a black background, one dot above the other. The top dot was controlled by the left joystick and the bottom dot by the right joystick (see Fig. 1 for illustration). The amplitude of movement of each dot was 300 pixels, and each dot was 60 pixels in diameter at the viewing distance of 70 cm (yielding a movement that spanned ~7.5° visual angle). In the kinesthetic conditions, only a single unmoving dot appeared in the display.

Fig. 1 Illustration of experimental apparatus. In the visual condition, two moving dots were seen. In the kinesthetic condition, one static dot was seen. In both cases, the dot(s) will change color (white to green) when the required coordination pattern is produced accurately. Note that the

joysticks were covered by the tablecloth when the participants were moving them so that the participants could not see their hands or joysticks when producing the required coordination patterns

Stimulus presentation, data recording, and all data analyses were handled by a custom MATLAB toolbox written by Andrew D. Wilson, incorporating the Psychtoolbox (Wilson, Tresilian, & Schlaghecken, 2011).

Participants

A total of 40 adults were recruited on and off the campus of the University of Wyoming (UW) through a flyer. Informed consents were obtained according to the UW institutional review board protocol. Participants were recruited in two age groups: half were younger adults (10 males and 10 females; mean age = 22.1 years), and half were older adults (10 males and 10 females; mean age = 53.6 years). All participants were naïve to the experimental questions, had normal or corrected-to-normal vision, had good upper limb functioning (Upper Extremity Functional Scale score $\geq 80\%$), and could not produce 90° prior to training.

Procedure

Participants in each age group were randomly divided into two groups of 10 participants each. One group, called “visual+,” received both visual and kinesthetic information about relative phase while learning 90° , and the other group, called “kinesthetic,” received only kinesthetic information about the movements while learning 90° . The visual information about the movements was provided by two moving dots in a display, which mirrored the movements of the two hands. The kinesthetic information came from the hands moving the joysticks. Participants in the kinesthetic group saw only a single static dot displayed on the screen while they moved joysticks (see Fig. 1 for illustration). The visual+ and kinesthetic conditions were also tested during assessment sessions.

Participants performed the coordination tasks in three assessment sessions (baseline, posttest, and retention) and five training sessions, each occurring on a different day, following the timeline: baseline $\rightarrow$ 5 days of training $\rightarrow$ posttest $\rightarrow$ retention.

Assessment sessions

The visual+ and kinesthetic groups were tested in the same ways during assessment sessions. They were asked to produce bimanual coordination in 90° relative phase. First, an 8-second-long demonstration of the 90° relative phase was provided to the participants either in a visual or kinesthetic format. Then, participants were given a practice trial (data not recorded) in which they grasped and moved joysticks attempting to reproduce the pattern of the movement they had just experienced. In the visual demonstration, participants viewed a display of two dots moving at 90° relative phase at the frequency of 0.75 Hz. In the kinesthetic demonstration, participants closed their eyes and experienced a coach moving their hands to produce 90° relative phase at the frequency of ≈ 0.75 Hz (the coach has been trained previously using the same visual demonstration). During the practice trial, participants were provided with feedback indicating the accuracy of their movement performance. When bimanual coordination was performed with vision, the moving dots turned from white to green when the relative phase being produced was within a bandwidth $\pm 20^\circ$ of the target relative phase. When bimanual coordination was performed with only kinesthesia, a static dot on the screen turned from white to green when the relative phase being produced was within a bandwidth $\pm 20^\circ$ of the target relative phase. After the demonstration and the practice trial, participants were tested in producing the 90° relative phase for five trials without any feedback; that is, the dot(s) simply remained white in both moving and static conditions. Each trial lasted 20 seconds.

To investigate whether the visual and kinesthetic information were different (that is, modality specific), we had to isolate the coordination information available in the respective modalities. This information was available during both training and posttraining tests. Previous research (Wilson et al., 2010) had shown the necessity of providing feedback information during training to isolate the information. The feedback was provided in the form of a discrete binary (hot/cold) visual signal that was, of necessity, exactly the same in both

the kinesthetic only and kinesthetic plus vision conditions, so that only the modality specific information from movements would be different. This feedback was available during training but not during posttraining tests.

Training sessions

The training phase consists of 5 days of performing the target relative phase of 90° with two sessions of 12 trials each day, so a total of 120 trials. In each session, participants performed four blocks of three trials. An 8-second-long demonstration was provided at the beginning of each trial block. For the visual+ group, the demonstration was a display of two dots moving at a relative phase of 90° . Following this demonstration, three training trials were performed with visual information and concurrent feedback; that is, when the participant moved at 90° within an error bandwidth, the moving dots turned from white to green. Participants were encouraged to move to keep the dots green as long as possible during a trial. For the kinesthetic group, the demonstration involved manual guidance in which a coach passively moved the participant's hands on the joysticks to produce 90° while the participant's eyes were closed. The concurrent feedback provided in the following three training trials was a single static dot in the center of screen that changed color from white to green when the participant actively moved the joysticks at 90° within an error bandwidth. Similarly, participants were encouraged to move to keep the static dot in green as long as possible in a trial. The error bandwidth for the target-relative phase was set to fade across sessions: $\pm 30^\circ$ in the first training session, $\pm 25^\circ$ in the second, $\pm 20^\circ$ in the third, $\pm 15^\circ$ in the fourth, and $\pm 10^\circ$ in the last.

Posttraining assessment

The posttraining assessment consisted of a posttest and a retention test separated by a day; both were the same as the baseline assessment, with motor performance of 90° being tested both visually and kinesthetically.

Data analysis

The two position time series from each trial were filtered using a low-pass Butterworth filter with a cutoff frequency of 10 Hz and numerically differentiated to yield a velocity time series. These were used to compute a time series of relative phase, the key measure of coordination between the two joysticks.

Primary analysis

To assess coordination performance over the course of a trial, we used a measure of proportion of time on task (PTT), which is the proportion of time during a trial that the performed

relative phase falls within a $\pm 20^\circ$ window of the target relative phase (e.g., 90°). We chose PTT as the primary measure because stability is not independent of mean relative phase in human movement, and measures that simply assess overall movement variability (e.g., the standard deviation of mean relative phase or mean vector length) are confounded with the actual relative phase produced. For instance, coordination stability at 90° can be artificially elevated if participants spend time at other locations back and forth (e.g., 0° or 180°), which they do, as these locations are natural attractors, being more stable (see Wilson et al., 2010a, b, for an extended analysis of this problem). PTT allows us to assess within-trial stability. It is simply the proportion of the relative phase time series that falls within the range of the target phase $\pm$ a tolerance (e.g., of 20°), thus summarizing the data of interest (consistency and accuracy). This measure ranges from 0% to 100% and validly measures stability of coordination at the required relative phase in a single trial. We averaged PTT, for each participant, over the trials performed in a given condition. Due to the similar performance demonstrated by participants in posttest and retention (paired t-test showed no difference, $p > .05$), we report the averaged PTT of the posttest and retention sessions as “posttest.” We then performed a mixed-design ANOVA on subjects' mean PTTs with session (baseline and posttest) as within-subjects factors, and age (20s and 50s) and training modality (visual+ and kinesthetic) as between-subjects factors. Significance levels were set at $\alpha = .05$, and a measure of generalized effect size (η) were reported.

Secondary analysis

Previous studies examining coordination performance and learning have used measures related to the relative phase such as mean vector length and mean direction error. Snapp-Childs et al. (2015) demonstrated that these measures could be difficult to interpret because these types of measures cannot be used in isolation. The basic problem is that variability measures alone do not give any indication that participants are performing the “correct” coordination pattern (i.e., 90°), while mean error measures alone do not provide any information about the consistency of performance. For instance, if the performer spends similar amounts of time at 0° and at 180° , then the mean can be 90° (which is not at all reflective of what the performer is actually doing). However, to confirm the findings from our primary measure (PTT), we performed secondary data analysis on the variables related to the relative phase. For each participant, we first computed relative phase distributions between 0° and 180° using 20° bins. Next, we computed the mean direction error, which was simply the absolute value of the mean direction subtracted from the target phase (90°). We also computed the mean vector length or uniformity (U ; Fisher, 1993), which was then linearly

transformed to be $SD\psi$ to quantify the variability of coordination performance: $SD\psi = (-2\log_e U)^{1/2}$.

Results

Primary analysis

Baseline performance

First, we verified that the training groups were similar before training with respect to their 90° performance. We found that the performance of younger participants was better. Otherwise, the training groups were the same in both conditions. We performed a repeated-measures ANOVA with the following factors and levels: age (20s vs. 50s) and training modality (visual+ vs. kinesthetic) as between-subjects factors, and testing modality (visual+ vs. kinesthetic) as a within-subjects factor. The ANOVA yielded only a main effect of age, $F(1, 36) = 4.67$, $p = .04$, $\eta = .09$.

Learning and improvement

Next, we examined the performance change that occurred over training. The age difference found at baseline was preserved over training. Performance improved over sessions, so participants of both ages learned to perform the new coordination. Participants trained with vision improved more than participants trained only with kinesthesia. The changed PTT in each session from baseline ($PTT_{\text{session}(i)} - PTT_{\text{baseline}}$) were calculated for each participant. As revealed by the ANOVA performed on those changed PTTs (treating age and training modality as the between-subjects factors, and session as the within-subjects factor), the two groups trained with vision improved more than the two groups trained without, $F(1, 18) = 4.54$, $p = .04$, $\eta = .20$, and there was no age difference in such improvement ($p > .05$).

To evaluate the amount of learning that occurred as a result of training, we calculated improvement of performance from baseline to posttest ($\Delta PTT = PTT_{\text{posttest}} - PTT_{\text{baseline}}$ or learning scores), and examined them by testing modality and training modality as well as age (see Fig. 2). The retention condition are the ΔPTT s for the visual+ training group tested in visual+ condition and the kinesthetic training group tested in kinesthetic condition. The transfer condition are the ΔPTT s for the kinesthetic training group tested in visual+ condition and the visual+ training group tested in kinesthetic condition. All participants exhibited greater learning when tested posttraining in the retention condition. This result replicated the previous Ren et al. (2015) study. However, there was an interaction that reflected the fact that only the visual+ training group exhibited a large drop in improvement of performance

Fig. 2 Improvements (posttest – baseline) in proportion of time on task for older (50-year-olds) and younger (20-year-olds) adults in retention and transfer tests. **a** Participants trained to produce kinesthetic 90°. **b** Participants trained to produce visual 90°

when tested in the transfer condition, namely, kinesthetic condition. The kinesthetic training group did not exhibit this drop in the transfer condition.

We performed a three-way mixed-design ANOVA on ΔPTT s with the following factors and levels: age (20s vs. 50s) and training modality (visual+ vs. kinesthetic) as the between-subjects factors, and testing condition (retention vs. transfer) as a within-subjects factor. There was a main effect of testing condition, $F(1, 36) = 5.66$, $p = .03$, $\eta = .06$, and a significant two-way interaction (training modality by testing condition: $F(1, 36) = 11.43$, $p = .002$, $\eta = .11$). No other main effects or interactions were significant (all $ps > .05$). When we investigated the interaction further, we found that there was no evidence of significant improvement for participants who had trained with vision when tested without it (see Fig. 2b).

To test the level of learning, we performed a series of paired-samples t tests on ΔPTT s to examine the difference of improvement between the testing conditions separately for each age group and training condition. (We tested the age groups separately to be sure that this result was replicated by those groups.) As revealed by the results, the groups trained with vision exhibited significantly dropped learning when tested without than with vision, $t(1, 8) = 2.37$, $p = .04$ for young; $t(1, 8) = 2.63$, $p = .03$ for old, which was not seen in

groups trained with kinesthetic information, $t(1, 8) = -.59, p = .57$ for young; $t(1, 8) = -1.17, p = .28$ for old. The kinesthetic training yielded equivalent improvement for both ages in both testing conditions.

Effect of prolonged practice

Finally, we tested the possible learning benefits from the prolonged training in this study compared to the previous one (Ren et al., 2015). We had hypothesized that the additional training might enable younger participants, in particular, to master the dual task, that is, to learn to perform the task using both visual and kinesthetic information. The results failed to support this hypothesis. To the contrary, the additional training yielded a remarkable drop in the posttraining performance for the visual+ training group when tested in the kinesthetic condition (the transfer condition). The improved performance by training dropped approximately from 20% to 5%, which we found to be the case for both age groups (20- and 50-year-olds).

We performed a four-way mixed-design ANOVA on learning scores with the following factors and levels: study (original training vs. double training), age (20s vs. 50s), and training modality (visual+ vs. kinesthetic) as the between-subjects factors, and testing condition (retention vs. transfer) as a within-subjects factor. There were main effects of age, $F(1, 80) = 4.8, p = .04$, testing condition, $F(1, 80) = 12.0, p < .001$, a significant two-way interaction (training modality by testing condition: $F(1, 80) = 15.2, p < .001$, and a significant three-way interaction (study by training modality by testing condition: $F(1, 80) = 5.4, p < .03$). No other main effects or interactions were significant (all $ps > .05$). To further examine the effect of prolonged training, we pooled data for young (20s) and older (50s) adults, and performed independent-samples t tests on their improved performance between the previous (Ren et al., 2015) and current studies for each training groups (visual+ vs. kinesthetic) separated by testing conditions (retention vs. transfer). As seen in Table 1, the only difference detected was for the groups trained with visual information. There was a significant drop of improvement in the current study compared to the previous one, $t(1, 42) = 2.51, p = .02$. Thus, the current study demonstrated that prolonged training with visual information resulted in a complete reliance on the visual information to produce the trained coordination pattern.

Additionally, the lack of a main effect for study indicated that doubling the number of training trials failed to yield any additional improvement in overall performance. In fact, most participants in the current study reached an asymptote near the end of training that was not seen in the previous study. However, we did notice that both young and older participants improved performance similarly during practice with extra training, and those who trained with visual information improved more.

Secondary analysis

To examine performance before and after training, we computed relative phase distributions (relative phases between 0° and 180° using 20° bins) by condition (kinesthetic 90° , visual 90°), age (20-year-olds, 50-year-olds), and separated by training group. As illustrated in Fig. 3 (younger adults) and Fig. 4 (older adults), when performing the kinesthetic 90° task at baseline, as expected, a relative phase at or near 90° was not consistently produced (see Figs. 3a and 4a). As shown in Fig. 4a, the group of older adults that would subsequently be trained using kinesthetic information only tended to spend time at 0° , while the group of older adults that would be trained using kinesthetic plus visual information tended to spend time at 180° . This was merely an individual difference between the groups that was, however, reflected in the pattern of results for the mean direction at baseline. The groups of younger adults exhibited a fairly similar pattern of results at baseline. At posttest, however, the groups performed much more similarly (see Figs. 3d and 4d) with the exception of the visually trained participants, who failed to produce 90° frequently in the kinesthetic 90° task (see Figs. 3c and 4c).

Next, we analyzed $SD\psi$ and mean direction error separately. To do this, we performed four-way mixed-design analysis of variance (ANOVA) with group (kinesthetic vs. visual+ training), and age (20-year-olds, 50-year-olds) as a between-subjects factors, and condition (visual 90° , kinesthetic 90°) and session (baseline, posttest) as within-subjects factors. For $SD\psi$ at posttest, the analyses revealed only an effect of age, $F(1, 36) = 7.38, p = .01, \eta = .08$, and session, $F(1, 36) = 20.38, p < .001, \eta = .10$. That is, younger adults outperformed older adults and training improved performance (these results are depicted in Fig. 5). These results alone would make it seem that training modality had a general effect on learning, however, this is not a fair representation of the results.

Again, measures of consistency and accuracy must be taken into account when evaluating success in learning 90° ¹; stable but inaccurate performance can result from spending time only at 0° (or 180°), while seemingly accurate but unstable performance can result from spending equal time at 0° and 180° . For mean direction error, the result was significant main effects of age, $F(1, 36) = 5.91, p = .02, \eta = .10$, and session, $F(1, 36) = 22.84, p < .001, \eta = .07$, as well as a Condition $\times$ Session interaction, $F(1, 36) = 8.28, p = .006, \eta = .02$, and a Group $\times$ Condition $\times$ Session interaction, $F(1, 36) = 4.35, p = .04, \eta = .01$. These results are pictured in Figs. 6a and b and reflect that (1) younger adults outperform older adults, and (2) for those trained with vision, at posttest, there was a negative impact of removing vision, whereas there was minimal impact for adding vision for those trained kinesthetically.

¹ Or one could use a single, unambiguous measure, such as PTT, which takes into account consistency and accuracy components of performance.

Table 1 Independent samples *t* test on the improved performance between OLD (Ren et al., 2015) and NEW (current) studies for each training groups (visual vs. kinesthetic) separated by testing conditions (retention vs. transfer)

Comparison	Group	Condition	Means	<i>t</i> value	<i>p</i> value
OLD vs NEW	Visual	Retention	0.15 ± 0.08 vs. 0.19 ± 0.15	$t(1, 42) = -0.93$	$p = 0.36$
	Kinesthetic	Retention	0.16 ± 0.15 vs. 0.13 ± 0.11	$t(1, 42) = 0.74$	$p = 0.46$
	Visual	Transfer	0.12 ± 0.07 vs. 0.05 ± 0.11	$t(1, 42) = 2.51$	$p = 0.02$
	Kinesthetic	Transfer	0.12 ± 0.15 vs. 0.16 ± 0.15	$t(1, 42) = -0.78$	$p = 0.44$

Data were pooled for young and old subjects

Discussion

The goals of the current study were twofold. First, we investigated whether extended training would yield complete dependence on use of visual information in skilled performance of a learned 90° rhythmic coordination. If so, then this would yield evidence that visual and kinesthetic information about the coordination is modality specific, making simultaneous use of both sources of information a more difficult dual task and yielding a preference for using the single visual modality to generate and control the coordinated movements. Second, if we did indeed find such dependence, we investigated whether older participants might be less dependent on the visual information as a result of extended practice because they are more

experienced in performing the dual task entailed by the combined visual and kinesthetic modality specific information.

We found that dependence of on vision to produce the trained coordination did indeed become substantial, and this occurred for both younger and older participants. When our participants trained using only kinesthesia to learn to produce the new bimanual coordination, then they learned to perform it as well as participants who trained with the availability of vision, and they performed equally well with the availability of either kinesthesia alone or kinesthesia plus vision. However, participants who trained using both vision and kinesthesia failed to demonstrate the improved ability to produce the trained coordination when vision was made unavailable and they were required to use only kinesthesia. Apparently,

Fig. 3 Relative phase distributions for younger adults (20-year-olds) at baseline and posttraining for the kinesthetic 90° and visual 90° tasks separated by group: **a** kinesthetic 90° at baseline; **b** visual 90° at baseline; **c** kinesthetic 90° at posttest; **d** visual 90° at posttest

Fig. 4 Relative phase distributions for older adults (50-year-olds) at baseline and posttraining for the kinesthetic 90° and visual 90° tasks separated by group: **a** kinesthetic 90° at baseline; **b** visual 90° at baseline; **c** kinesthetic 90° at posttest; **d** visual 90° at posttest

during the extended training, attention was increasingly directed to visual information so that the available kinesthetic information was not learned.

The implication of these results is that the visual information and the kinesthetic information used to perform rhythmic coordinated movements are not the same. The information is modality specific. This makes performance using both sources

of information a variety of dual task, something that is rather difficult. The simultaneous availability of both forms of information does not provide redundancy that would make performance more stable. The result is that our participants, whether young or old, prefer to use only the information available in a single modality and the modality that is preferred in this case is vision, presumably because the information is more salient.

The fact that kinesthetic information was not used when available might be counterintuitive. There is a deep-seated intuition that coordination involving two limbs (i.e., bimanual coordination) is intrinsically body centric (kinesthetic). That is, coordination is stable because it is rooted in the body sense. An example of this comes from descriptions of bimanual coordination in terms of homologous muscle groups rather than spatially or visually. The spatial or visual orientations of the oscillators can be altered without altering coordination stability in a meaningful way. For example, if the two index fingers are oscillating together at 0°, reversing the direction of one of the limbs so that the spatially defined coordination becomes 180° does not affect coordination stability. Thus, it is kinesthesia and the motor commands to homologous or heterologous muscles that appears to determine the stable modes. A notable example of how important effective kinesthesia is

Fig. 5 $SD\psi$ by age and testing condition at baseline and post-training

Fig. 6 Mean direction error at baseline and posttraining: **a** by age and testing condition; **b** by training modality and testing condition

generally in the control of movement is described by Cole (1995), a neurologist who provides an account of a patient who lost kinesthesia from the neck down through loss of the large fiber afferents. With this loss, the patient lost the ability to coordinate and control all of his limb and trunk movements. However, what is notable about this case is that Cole's patient regained motor skills by substituting vision for kinesthesia to perceive and thus control and coordinate the ongoing evolution of his own movements. Unfortunately, when he subsequently experienced temporary loss of vision, he also lost the ability to control and coordinate his movements.

Similarly, although less dramatically, providing visually salient information has been shown to override coordination dynamics based on intrinsic kinesthetic components of the dynamics. Specifically, a number of studies have demonstrated that using Lissajous figures enables very rapid acquisition of the ability to perform relative phase patterns (90°) that are extremely difficult to produce otherwise (Kovacs et al., 2010; Kovacs & Shea, 2011; Wang, Kennedy, Boyle, & Shea, 2013).

The problem with using transformed visual information in the form of Lissajous figures is that once it is removed, producing the relative phase pattern of interest is no longer

possible (Kovacs et al., 2009). This result is similar to the results of the current study except that the acquisition of the ability to perform the 90° coordination using visual information in the Lissajous figure is much more rapid. Presumably, this is because that information is much more salient and easy to discriminate, namely, drawing a circle. This is in contrast to learning to discriminate the spatial-temporal syncopated patterning of the 90° coordination. Wilson et al. (2010) found that the ability to discriminate the latter well can be learned, but this takes time and numerous training sessions. During the perceptual training, participants performed a two-alternative forced-choice task, namely, to discriminate which of two successively viewed displays was 90° and which was not. Feedback was provided informing participants whether each of their judgments was correct. Once the perceptual pattern was learned, the participants were able to motorically produce the stable coordination. Learning to perform the coordination by practicing the movements also required feedback informing participants at each moment during performance whether they were correctly producing 90° (Wilson et al., 2010). Learning to perform the movements was found to also yield learned ability to perceptually discriminate the coordination pattern. Kovacs and Shea (2011) found that they could employ a “faded” training regime in which the more salient Lissajous information was only intermittently available, thus strongly encouraging participants to attend to the normally available syncopated kinesthetic pattern while producing it successfully using, and thus co-attending to, the Lissajous information. This is a dual task involving two forms of modality-specific information: visual and kinesthetic. It is indeed rather surprising to find that a form of the dual task is actually the naturally occurring and thus representative circumstance when both kinesthetic and visual information is used to perform and learn bimanual rhythmic coordination.

Compliance with ethical standards

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Conflict of interest All authors declare that they have no conflicts of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. This article does not contain any studies with animals performed by any of the authors.

Informed consent Informed consent was obtained from all individual participants included in the study.

References

- Bingham, G. P. (2004a). Another timing variable composed of state variables: Phase perception and phase driven oscillators. *Advances in Psychology*, 135, 421–442.
- Bingham, G. P. (2004b). A perceptually driven dynamical model of bimanual rhythmic movement (and phase perception). *Ecological Psychology*, 16(1), 45–53.
- Bingham, G. P., Schmidt, R. C., & Zaal, F. T. (1999). Visual perception of the relative phasing of human limb movements. *Perception & Psychophysics*, 61(2), 246–258.
- Bingham, G. P., Zaal, F. T., Shull, J. A., & Collins, D. R. (2001). The effect of frequency on the visual perception of relative phase and phase variability of two oscillating objects. *Experimental Brain Research*, 136(4), 543–552.
- Clark, F. J., & Horch, K. W. (1986). Kinesthesia. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance*, vol. 1: *Sensory processes and perception* (pp. 13–113–61). New York: Wiley.
- Cole, J. (1995). *Pride and a daily marathon*. Cambridge: MIT Press.
- Epstein, W. (1985). Amodal information and transmodal perception. In D. H. Warren & E. R. Strelow (Eds.), *Electronic spatial sensing for the blind: Contributions from perception, rehabilitation, and computer vision* (pp. 421–430). Dordrecht: Springer.
- Feldman, A. G. (1966). Functional tuning of the nervous system with control of movement or maintenance of a steady posture: II. Controllable parameters of the muscle. *Biophysics*, 11, 565–578.
- Feldman, A. G. (1986). Once more on the equilibrium-point hypothesis (lambda model) for motor control. *Journal of Motor Behavior*, 18, 17–54.
- Feldman, A. G. (2010). New insights into action-perception coupling. *Experimental Brain Research*, 194, 39–58.
- Feldman, A. G., Adamovich, S. V., Ostry, D. J., & Flanagan, J. R. (1990). The origin of electromyograms: Explanation based on the equilibrium point hypothesis. In J. M. Winters & S. L. Y. Woo (Eds.), *Multiple muscle systems: Biomechanics and movement organization* (pp. 195–213). New York: Springer.
- Fisher, N. I. (1993). *Statistical analysis of circular data*. Cambridge: Cambridge, UP.
- Gibson, J. J. (1950). *The perception of the visual world*. Westport: Greenwood Press.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Goodwin, G. M. (1976). The sense of limb position and movement. *Exercise and Sport Science Review*, 4, 87–124.
- Hogan, N., Bizzi, E., Mussa-Ivaldi, F. A., & Flash, T. (1987). Controlling multijoint motor behavior. In K. B. Pandolf (Ed.), *Exercise and sport sciences reviews* (Vol. 15, pp. 153–190). New York: MacMillan.
- Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative & Comparative Physiology*, 15, R1000–R1004.
- Kelso, J. A. S., Scholz, J. P., & Schoner, G. (1986). Non-equilibrium phase transition in coordinated biological motion: Critical fluctuations. *Physics Letters A*, 118, 279–284.
- Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2009). Bimanual 1:1 with 90° continuous phase: Difficult or easy? *Experimental Brain Research*, 193, 129–136.
- Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2010). Impossible is nothing: 5:3 and 4:3 multi-frequency bimanual coordination. *Experimental Brain Research*, 201(2), 249–259.
- Kovacs, A. J., & Shea, C. H. (2011). The learning of 90 continuous relative phase with and without Lissajous feedback: External and internally generated bimanual coordination. *Acta Psychologica*, 136(3), 311–320.
- Latash, M. L. (1993). *Control of human movement*. Champaign: Human Kinetics.
- Latash, M. L. (2012). *Fundamentals of motor control*. San Diego: Academic Press.
- McCloskey, D. I. (1978). Kinesthetic sensibility. *Psychological Review*, 58, 763–820.
- McCloskey, D. I. (1980). Kinaesthetic sensations and motor commands in man. In J. E. Desmedt (Ed.), *Spinal and supraspinal mechanisms of voluntary motor control and locomotion*. Basel: Karger.
- Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, 414, 69–73.
- Mechsner, F., & Knoblich, G. (2004). Do muscles matter for coordinated action? *Journal of Experimental Psychology: Human Perception and Performance*, 30, 490–503.
- Paillard, J., & Brouchon, M. (1968). Active and passive movements in the calibration of position sense. In S. J. Freeman (Ed.), *The neuropsychology of spatially oriented behavior* (pp. 37–55). Homewood: Dorsey Press.
- Paillard, J., & Brouchon, M. (1974). A proprioceptive contribution to the spatial encoding of position cues for ballistic movements. *Brain Research*, 71, 273–284.
- Ren, J., Huang, S., Zhang, J., Zhu, Q., Wilson, A. D., Snapp-Childs, W., & Bingham, G. P. (2015). The 50s cliff: A decline in perceptuo-motor learning, not a deficit in visual motion perception. *PLoS ONE*, 10(4), e0121708.
- Sainburg, R. L., Ghilardi, M. F., Poizner, H., & Ghez, C. (1995). Control of limb dynamics in normal subjects and patients without proprioception. *Journal of Neurophysiology*, 73, 820–835.
- Schmidt, R. C., Carello, C., & Turvey, M. T. (1990). Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 227–247.
- Serrien, D. J., Li, Y., Steyvers, M., Debaere, F., & Swinnen, S. P. (2001). Proprioceptive regulation of interlimb behavior: Interference between passive movement and active coordination dynamics. *Experimental Brain Research*, 140, 411–419.
- Wang, C., Kennedy, D. M., Boyle, J. B., & Shea, C. H. (2013). A guide to performing difficult bimanual coordination tasks: Just follow the yellow brick road. *Experimental Brain Research*, 230(1), 31–40.
- Wilson, A. D., Bingham, G. P., & Craig, J. C. (2003). Proprioceptive perception of phase variability. *Journal of Experimental Psychology: Human Perception and Performance*, 29(6), 1179.
- Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005a). Human movement coordination implicates relative direction as the information for relative phase. *Experimental Brain Research*, 165(3), 351–361.
- Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005b). Perceptual coupling in rhythmic movement coordination: Stable perception leads to stable action. *Experimental Brain Research*, 164(4), 517–528.
- Wilson, A. D., Snapp-Childs, W., & Bingham, G. P. (2010). Perceptual learning immediately yields new stable motor coordination. *Journal of Experimental Psychology: Human Perception and Performance*, 36(6), 1508.
- Wilson, A. D., Snapp-Childs, W., Coats, R., & Bingham, G. P. (2010). Learning a coordinated rhythmic movement with task-appropriate coordination feedback. *Experimental Brain Research*, 205(4), 513–520.
- Wilson, A. D., Tresilian, J., & Schlaghecken, F. (2011). The masked priming toolbox: An open-source MATLAB toolbox for masked priming researchers. *Behavior Research Methods*, 43(1), 210–214.
- Zaal, F. T., Bingham, G. P., & Schmidt, R. C. (2000). Visual perception of mean relative phase and phase variability. *Journal of Experimental Psychology: Human Perception and Performance*, 26(3), 1209.
- Zanone, P. G., & Kelso, J. (1992). Evolution of behavioral attractors with learning: Nonequilibrium phase transitions. *Journal of Experimental Psychology: Human Perception and Performance*, 18(2), 403–421.