RESEARCH ARTICLE

Gesture imitation in musicians and non-musicians

Michael J. Spilka · Christopher J. Steele · Virginia B. Penhune

Received: 14 January 2010/Accepted: 30 May 2010/Published online: 24 June 2010 © Springer-Verlag 2010

Abstract Imitation plays a crucial role in the learning of many complex motor skills. Recent behavioral and neuroimaging evidence suggests that the ability to imitate is influenced by past experience, such as musical training. To investigate the impact of musical training on motor imitation, musicians and non-musicians were tested on their ability to imitate videoclips of simple and complex twohanded gestures taken from American Sign Language. Participants viewed a set of 30 gestures, one at a time, and imitated them immediately after presentation. Participants' imitations were videotaped and scored off-line by raters blind to participant group. Imitation performance was assessed by a rating of performance accuracy, where the arm, hand, and finger components of the gestures were rated separately on a 5-point scale (1 = unrecognizable;)5 = exact imitation). A global accuracy score (PAglobal) was calculated by summing the three components. Response duration compared to the model (%MTdiff), and reaction time (RT) were also assessed. Results indicated that musicians were able to imitate more accurately than non-musicians, reflected by significantly higher PAglobal and lower %MTdiff scores. Furthermore, the greatest difference in performance was for the fine-motor (finger) gesture component. These findings support the view that the ability to imitate is influenced by experience. This is consistent with generalist theories of motor imitation, which explain imitation in terms of links between perceptual and motor action representations that become strengthened through experience. It is also likely that musical training contributed to the ability to imitate manual gestures by influencing the personal action repertoire of musicians.

Keywords Action-imitation · Mirror neuron system · Observational learning · Musical training

Introduction

Humans learn many skills through the process of imitation. For example, in musical training, a common method through which beginners learn is by attempting to reproduce their instructors' demonstrations. In addition to the learning of complex motor skills, it has been hypothesized that imitation plays an important developmental role in the acquisition of language and the process of socialization (Brass and Heyes 2005; Bekkering and Wohlschläger 2002). However, little is known about what influences the development of the ability to imitate. It may be that, as is the case with other types of motor learning, learning through imitation relies on practice and past experience. Looking at imitation in the context of musical training may provide a novel opportunity for studying the influence of prior experience on imitation. In the present study, we compared the imitation performance of musicians and nonmusicians in order to look at what kind of experience is important for the development of the ability to imitate.

Also known as observational learning or modeling, imitation is the ability to learn to perform an action by seeing it done (Thorndike 1898). Imitation has been a major topic of interest in psychology because the ability to imitate is often viewed as crucial for human development. For example, Piaget (1952) saw the ability to imitate as a developmental milestone that was necessary before further aspects of cognitive development in children could take

M. J. Spilka (⊠) · C. J. Steele · V. B. Penhune Department of Psychology, Concordia University, 7141 Sherbrooke St. W., Montreal, QC H4B 1R6, Canada e-mail: michael.j.spilka@gmail.com

place. Furthermore, Bandura (1977) emphasized the importance of observational learning in his social learning theory, in which he postulated the role of observation and imitation in the development of social behavior. It has also been suggested that the ability to imitate is most common and complex in humans (see Heyes 2001 for a review). Recent studies from neuroscience have identified brain regions forming an "action-imitation" or "mirror neuron" system, containing neurons that fire for both action observation and action execution (Buccino et al. 2004a). Most studies have shown engagement of the mirror neuron system for the imitation of well-known actions [see Vogt and Thomaschke 2007 for a review]. However, several recent studies have shown that it can also be engaged by the observation of novel actions, suggesting that this system may be important for imitation learning (Vogt et al. 2007).

The fact that many complex motor skills, such as throwing a baseball or riding a bicycle, can be learned through observation raises a crucial question known as the correspondence problem (Brass and Heyes 2005): Given that imitation learning involves observing a model's overt actions, how can an observer learn the covert muscle activations that are necessary to reproduce the model's actions? An implication of the correspondence problem is that there are two types of processes involved in imitation, perceptual and motor, and that they may exert an influence on each other (Bekkering 2002). At the behavioral level, a variety of studies have used interference paradigms to investigate the link between perception and action in imitation (Prinz 2002; Stürmer et al. 2000). In these studies, participants are required to perform simple actions at the same time as observing either congruent or incongruent actions. When the observed and performed actions are incongruent, a Stroop-like effect is found such that reaction times are slower than when the observed and performed gestures are congruent. These findings have been interpreted as demonstrating an interference effect at the level of motor execution, such that the observed incongruent gesture activated an internal motor representation that interfered with the motor execution of the response gesture.

In a recent study of learning through observation, Mattar and Gribble (2005) showed that information at the level of motor execution can be acquired during observation. In this experiment, participants used a robotic arm to track a cursor across a screen. The arm was programmed to systematically disrupt the trajectory of movement, creating a novel mechanical environment. It was found that viewing a video of a person learning to use the robotic arm facilitated participants' performance on the same task. The results imply that through observation, participants were able to extract information at the level of motor execution, such as the specific muscle forces required to guide the robotic arm through the mechanical environment. In support of the above findings, neuroimaging studies using techniques such as fMRI and PET have provided clear neurophysiological evidence that motor regions are involved in action perception. These studies have demonstrated that even the passive observation of an action leads to the activation of cortical regions involved in movement execution, including the action-imitation system (Buccino et al. 2004b; Decety and Grèzes 1999).

The findings from the above studies illustrate the close link between action perception and action execution involved in imitation. Yet, they do not account for the mechanism through which visual information about observed body movements is translated into a matching motor output during imitation. The most widely accepted theories of imitation, such as the ideomotor (IM) theory and associative sequence learning (ASL) model, are termed "generalist" because they suggest that the mechanism for perceptual-motor translation is mediated by general processes of motor control (Brass and Heyes 2005; Heyes 2001). For example, according to the ASL model, the ability to imitate an action depends on the extent to which a link has been formed between the perceptual representation (visual information for what the action looks like) and motor representation (how it is initiated and what it feels like) of the action. These links may be formed through a variety of experiences, such as observing our own actions, being imitated, or synchronizing our actions with those of others. Repeated experiences subsequently strengthen these perceptual-motor links through a process similar to Hebbian learning. Generalist theories suggest that the mechanism for perceptual-motor translation is highly experience-dependent; therefore, a person's ability to imitate will depend on his or her past experience (Heyes 2001). A common approach for studying the role of experience in imitation is to look at acquired motor skills and learned expertise. In an fMRI study, Calvo-Merino et al. (2005) compared the brain activity of expert ballet and capoiera dancers while viewing closely matched video footage of either dance style. It was found that the activation of motor areas in the action-imitation system was stronger when viewing footage of one's own dance style, demonstrating the influence of expertise on the activation of cortical areas involved in imitation. A follow-up study comparing male and female ballet dancers while viewing gender-specific ballet moves confirmed that the pattern of brain activity was mediated, specifically, by the learned motor capabilities of the observer (Calvo-Merino et al. 2006). In a similar study looking at musical training, it was found that the simple observation of piano chords led to stronger activation of motor regions in expert piano players than in non-musician controls (Haslinger et al. 2005). The results of these studies indicate that the important first step of imitationacquiring motor information from action observation depends on the observer's past experience. However, the tasks in these studies involved observation only; therefore, they do not speak directly to the role of past experience in imitation performance.

Providing more direct evidence for the theory that imitation learning is experience-dependent, a recent metaanalysis by Ashford et al. (2007) reported an influence of age on the ability to benefit from learning by observation. The meta-analysis surveyed the motor learning literature in order to ascertain the effect of observational learning on motor skill acquisition. The results showed that the effect of observational learning on skill acquisition was larger for adults than for children. These findings have been interpreted as showing that adults, through their additional years of experience, have acquired a larger personal action repertoire for both perception and execution (Ashford et al. 2007).

The neuroimaging and behavioral evidence described above offers support for the influence of experience, such as motor expertise, on the ability to imitate. However, key questions remain as to what kind of experience contributes to this ability, and how this experience will influence novel imitation performance. Experiences such as observing our own actions or synchronizing our actions with those of others may help to "get imitation off the ground" by initially establishing a link between the perceptual and motor representations of a given action. An additional possibility is that all experiences of learning through observation may contribute to a general imitative ability. An experiencedependent account of imitation would predict that learning through observation strengthens the perceptual-motor action links necessary to reproduce an observed action. The strengthening of these perceptual-motor links in one's personal action repertoire may provide an advantage for future imitation learning.

A potential way to test this prediction is to look at the relationship between observational learning experience and performance on a novel imitation task. As previously mentioned, learning through observation and imitation are common aspects of musical training. Haslinger et al. (2005) have called attention to the anecdotal evidence for the important role of observational learning in musical training by reporting that "learning by listening, observation, and imitation of a teacher's actions are crucial steps in musical skill acquisition that are widely applied in music pedagogics" (p. 282). Furthermore, most musicians will have gained additional experience by synchronizing their actions with other musicians and/or following cues from a conductor. These experiences may help musicians establish a link between perceptual and motor action representations necessary for imitation. In addition, repeated experiences of imitating other musicians during their training would strengthen the perceptual-motor action links, facilitating future imitation performance for similar actions. Musicians, therefore, are a suitable population for studying the influence of past observational learning experience on the ability to imitate.

The present study compared musicians and non-musicians on the ability to imitate unfamiliar and complex manual gestures, in order to identify the influence of prior experience on imitation performance. Neither musicians nor non-musicians were familiar with the gestures to be imitated, making it possible to study the effect of past experience by using the same stimuli for both groups. We hypothesized that musical training would influence the ability to imitate, such that musicians would outperform non-musicians. Based on musicians' particular expertise in observing, performing, and practicing complex hand and figure movements, we predicted that the greatest performance differences between musicians and non-musicians would be for imitating the hand and finger components of the gestures.

Method

Participants

Thirty participants between 18 and 35 years of age were recruited from Concordia University, McGill University and the Montreal area (Quebec, Canada) through advertisements, in-class recruitment, and word of mouth. All participants were right-handed and free from visual, motor, and neurological impairments that would interfere with the imitation task. Musicians (6 men and 9 women, M = 23.20 years, SD = 3.32) had over three years of musical experience (M = 12.93 years, SD = 5.03) and were currently practicing/playing their instrument at least two times per week. Non-musician participants (4 men and 11 women, M = 23.93 years, SD = 4.06) had less than three years total musical experience (M = 0.60 years), SD = 0.99) and were not currently playing/practicing an instrument. The musician participants were predominantly piano and guitar players. None of the participants reported being familiar with sign language when asked at the end of testing. All participants gave written informed consent before participating and were compensated for their time. The study protocol was approved by the Concordia University Psychology Departmental Ethics Committee.

Questionnaires

A questionnaire package was administered during screening to determine participant eligibility and included a Handedness Questionnaire adapted from Crovitz and Zener (1962), a General Health Questionnaire, and a Musical Experience Questionnaire (Watanabe et al. 2007).

Stimuli

In order to compare the ability to imitate manual gestures between musicians and non-musicians, we designed a task in which participants imitated a series of complex arm and hand gestures presented on a computer screen. Participants' imitations of each gesture were recorded with a video camera for offline coding.

Thirty-eight gestures were selected from American Sign Language to be performed by a model fluent in American Sign Language. All gestures required the use of both hands and were divided a priori into two categories according to their complexity: simple and complex. Simple gestures involved a small number of movements where the movement of both limbs was often symmetrical. Complex gestures required the performance of a larger sequence of movements where both limbs followed different trajectories. The model was videotaped (with a Sony DCR-PC1 camera) performing each gesture in front of a dark background. The gestures began with the model's hands clasped and resting in a relaxed manner at lower torso level and ended with the model holding the final position of the gesture. Each gesture was edited into individual videoclips of approximately 3 s in length using iMovie software (Apple Inc., CA, USA). The perspective of the recording was such that the model was visible from the neck to the waist with 30 cm of free space on either side of the shoulders to ensure full visibility of the gestures. The 38 gesture videoclips were presented on a computer screen (Dell SE 198WFP, $720 \times 1,110$ pixels, 75 Hz refresh rate) connected to a desktop computer (AMD Athlon 2.80 GHz, Windows Vista). Presentation software (Neurobehavioral Systems, CA, USA) controlled the sequence and presentation of each clip. Participants observed each clip and imitated each one after the sounding of a tone. A video camera (Sony DCR-PC1) mounted on a tripod recorded participant responses (hands and arms only, retaining approximately the same field of view as the model gestures) on MiniDV tapes that were later transferred to computer for coding.

The stimuli were divided into familiarization (8 gestures) and test (30 gestures) trials. The familiarization trials were presented in order of increasing complexity (from simple to complex gestures) and served to familiarize participants with the imitation task. The test trials were presented in a randomized order. Figure 1 illustrates the chronological structure of the trials. For each trial, a black prompt screen with the text "Get Ready to Imitate" preceded each gesture videoclip and served as an indicator for the participant to be prepared to observe the clip. A mouse-click initiated the presentation of the gesture clip and was followed immediately by a black screen and a 500 ms tone acting as a cue for the participant to begin the imitation response.

Procedure

At the beginning of each testing session, participants were shown the computer screen and the video camera located directly behind the computer screen. Participants were instructed to stand on a marked area of the floor 1.5 m away from the computer screen so that they would be centered in front of the screen and camera during the trials. The experimenter then ensured that the camera properly framed the participants, such that they would be filmed between the neck and waist with 30 cm of space on either side of the shoulders. Participants were assured that only their arms and hands would be recorded, not their face.

During the familiarization trials, participants were walked through the trial structure and given instructions about the task. They were shown the "Get Ready to Imitate" prompt instructing them to put their hands in the "Ready Position" (hands clasped comfortably in the front), and instructed when they should be prepared to observe the next videoclip. After viewing a single familiarization trial and hearing the auditory cue, participants were instructed to imitate the gesture they observed after hearing the cue. The experimenter emphasized that participants should begin their imitation "as soon as you can after you hear the tone". It was also emphasized that participants should



attempt to accurately reproduce not only the movements they saw, but the timing and speed of those movements as well. Lastly, participants were instructed to hold the gesture for 1 or 2 s at the end of the imitation. The experimenter provided feedback between performances on the remaining familiarization trials to ensure that participants were familiar with the task. After the last familiarization trial, the video camera began to record and the test trials commenced. No feedback was given during the test trials; however, the experimenter remained present to initiate each new trial and ensure that participants were adhering to the instructions. Upon completion of the last trial, participants were asked about their sign language experience. This was to ensure that the data for participants with sign language experience could be excluded from the analyses.

Performance measures

Imitation performance was assessed through three distinct measures: the performance accuracy of the response, the reaction time to initiate a response (RT), and the discrepancy between the duration of the response and the duration of the model gesture (%MTdiff).

Performance accuracy

The measure of performance accuracy rated how kinematically similar an imitation response was to its model gesture. To do so, each participant response was assessed on three gesture parameters: Arms (the position and motion of the arms), Hands (the hand angle relative to the wrist and the hand motion), and Fingers (the arrangement and motion of the fingers). In this way, the Arms parameter represented the overall shape of the response, while Hands and Fingers accounted for the more fine-motor kinematics of the response. These parameters were derived from a rating system commonly used to rate sign language performance in motor learning experiments (Weeks et al. 1996; Fawcett and Clibbens 1983). A 5-point scale was used to rate the performance accuracy for each parameter (1 = unrecognizable,5 = exact imitation), producing three accuracy scores for each participant response: PAarms, PAhands, and PAfingers. A global accuracy score (PAglobal) (3 = lowest, 15 =highest) was created by summing the three parameters.

Reaction time

RT measured the elapsed time for participants to begin their imitation following the onset of the tone cue. This measure was included to assess the planning and mental preparation time required to generate an imitation response to the observed gesture videoclip. First, the extracted audio waveform of the participant footage was used to record the precise onset time of the 500 ms tone cue. A rater then noted the time that participants began their gesture, defined as the time that both hands began pulling apart from the "Ready Position". RT was then calculated as the difference of the two times.

Response duration compared to the model

%MTdiff was calculated as the percentage discrepancy between the participant's response duration and the duration of the model gesture. This is a measure of how well the temporal quality of the model gesture is preserved in the response. For example, a %MTdiff score of 50% indicates that the duration of the response is 1.5 times the duration of the model gesture from the videoclip. Therefore, when comparing two %MTdiff scores, the closest score to 0% indicates the better imitation performance. This measure was calculated by first having a rater calculate the end time of participant responses, defined as the time at which participants ended the motions involved in performing the gesture and began to hold the end position. Small movements, such as a slight wavering of the hands, were not considered to be part of the gesture motion. The end time was then subtracted from the gesture imitation start time (previously identified during the RT calculation) to calculate the movement time for each response (MTresponse). This same procedure was used to calculate the movement time for the model gesture (MTmodel). %MTdiff was then calculated according to the following formula: %MTdiff = [(MTresponse - MTmodel)/ MTmodel] \times 100.

Scoring procedure

The video footage of participant responses was viewed with iMovie software (Apple Inc., CA, USA) for scoring. Each imitation performance measure was rated blind to the participant group. In order to obtain a measure of the reliability of the scoring procedure, 11 participants (7 musicians, 4 non-musicians) were rated by at least two independent raters. Inter-rater reliability for PAglobal was then calculated through two-tailed Pearson correlations, by correlating raters' scores for each individual item (gesture trial) across all the participants. The Pearson correlation coefficients for PAglobal for each rater pair were above r(11) = 0.75. Thus, each rater pair had good inter-rater reliability. For the 11 participants rated by more than one rater, the PAglobal, RT, and %MTdiff scores of each rater were averaged and only the resulting scores were used for the analyses.

Results

In order to measure the effect of musical training on imitation performance, musicians and non-musicians were compared on the following performance measures: PAglobal, PAarms, PAhands, PAfingers, RT, and %MTdiff. The measures of PAglobal, RT, and %MTdiff were each analyzed using a separate 2×2 mixed analysis of variance (ANOVA), with musical training (musicians, non-musicians) as the between-groups variable and gesture complexity (simple, complex) as the within-groups variable. In addition. a $2 \times 2 \times 3$ mixed ANOVA, with gesture parameter as a within-groups variable, was conducted to assess performance accuracy at the parameter level (PAarms, PAhands, and PAfingers). Significant interactions were analyzed using pairwise comparisons Bonferroni corrected for multiple comparisons. Lastly, the association between years of musical training and imitation performance (PAglobal, %MTdiff, RT) was assessed with Pearson correlations. All effect sizes were calculated as partial eta-squared (η_p^2) , and statistical power is denoted by phi (ϕ). Confidence intervals of the mean difference (musiciansnon-musicians; simple gestures-complex gestures) were reported at the 95% level (CI.95).

Performance accuracy

The scores for PAglobal are plotted in Fig. 2. A 2 × 2 mixed ANOVA found a significant main effect of musical training on PAglobal ($F_{(1,28)} = 5.44$, p < 0.05, $\eta_p^2 = 0.16$, $\phi = 0.62$, CI_{.95} = 0.06 to 0.90). On average, musicians (M = 12.20, SD = 0.52) were more accurate at gesture imitation than non-musicians (M = 11.72, SD = 0.61). In the case of gesture complexity, a significant main effect was observed ($F_{(1,28)} = 252.32$, p < 0.001, $\eta_p^2 = 0.90$, ϕ = 1.00, CI_{.95} = 1.6 to 2.02), such that performance was worse on the complex gestures (M = 11.06, SD = 0.81) than on the simple gestures (M = 12.85, SD = 0.51). Thus, the complex gestures were more challenging to



Fig. 2 Mean global performance accuracy (PAglobal) (\pm SEM) for musicians and non-musicians according to gesture complexity. ****p < 0.001; *p < 0.05

accurately reproduce than the simple gestures. Finally, no significant interaction was found between musical training and gesture complexity ($F_{(1,28)} = 0.01$, p > 0.05, $\eta_p^2 = 0.00$, $\phi = 0.05$).

Whereas the previous ANOVA assessed performance accuracy at the global level, a subsequent $2 \times 2 \times 3$ mixed ANOVA took into account each of the three parameters (PAarms, PAhands, PAfingers). A significant main effect of gesture complexity was observed, such that scores at each parameter were lower for complex than for simple gestures $(F_{(1,56)} = 252.32, p < 0.001, \eta_p^2 = 0.90, \phi = 1.00, CI_{.95} =$ 0.52 to 0.67). Furthermore, there was a significant complexity × parameter interaction ($F_{(2.56)} = 26.92, p <$ 0.001, $\eta_p^2 = 0.49$, $\phi = 1.00$). Post hoc pairwise comparisons revealed that the greatest differences in performance accuracy between simple and complex gestures were for the parameters of the hands (p < 0.001, CI₉₅ = 0.64 to 0.83) and fingers (p < 0.001, CI_{.95} = 0.60 to 0.80), compared to the arms $(p < 0.001, CI_{.95} = 0.24$ to 0.47). No musical training \times parameter interaction was found ($F_{(2.56)} = 0.85$, $p > 0.05, \eta_p^2 = 0.03, \phi = 0.17$). However, planned post hoc comparisons revealed that, although the PAarms and PAhands scores were similar between musicians (PAarms: M = 4.07, SD = 0.24; PAhands: M = 4.03, SD = 0.22) and non-musicians (PAarms: M = 3.97, SD = 0.37; PAhands: M = 3.93, SD = 0.20), the PAfingers scores were significantly greater for musicians (M = 4.09,SD = 0.13) than for non-musicians (M = 3.87, SD = 0.22) $(p < 0.005, CI_{.95} = 0.09$ to 0.36) (see Fig. 3). In other words, the greatest difference in performance accuracy between musicians and non-musicians was for the parameter of the fingers, such that musicians were more accurate than non-musicians. Lastly, no significant complexity \times parameter × musical training interaction was observed $(F_{(2,56)} = 0.46, p > 0.05, \eta_p^2 = 0.02, \phi = 0.12).$



Fig. 3 Mean performance accuracy (PA) (\pm SEM) for musicians and non-musicians according to gesture parameter. ***p < 0.005



Fig. 4 Mean reaction time (RT) (\pm SEM) according to gesture complexity. ***p < 0.005

Reaction time

Results for RT are plotted in Fig. 4. A 2 × 2 mixed ANOVA found no significant main effect of musical training ($F_{(1,28)} = 0.94$, p > 0.05, $\eta_p^2 = 0.03$, $\phi = 0.15$, CI_{.95} = -231 to 82 ms), indicating that the reaction time to initiate a response did not differ significantly between musicians and non-musicians. A significant main effect of gesture complexity was observed ($F_{(1,28)} = 11.82$, p < 0.005, $\eta_p^2 = 0.30$, $\phi = 0.91$, CI_{.95} = 21 to 82 ms), such that the time to initiate a response was greater for the simple gestures (M = 630 ms, SD = 206) than for the complex gestures (M = 579 ms, SD = 222). Lastly, there was no significant musical training × complexity interaction ($F_{(1,28)} = 0.36$, p > 0.05, $\eta_p^2 = 0.01$, $\phi = 0.09$).

Response duration compared to the model

For % MTdiff, a 2 × 2 mixed ANOVA revealed a significant main effect of musical training ($F_{(1,28)} = 7.75$, p < 0.01, $\eta_p^2 = 0.22$, $\phi = 0.77$, CI_{.95} = -29.90 to -4.56%) such that, compared to the scores of non-musicians (M =44.09%, SD = 18.66), musicians (M = 26.87%, SD =



Fig. 5 Mean percentage of the movement time difference (%MTdiff) (\pm SEM) for musicians and non-musicians according to gesture complexity. ***p < 0.005; **p < 0.01

15.03) had significantly less discrepancy between the duration of their responses and the duration of the model gestures (see Fig. 5). Thus, musicians were better than non-musicians at preserving the duration of the model gestures during their imitations. A significant main effect of gesture complexity was also found ($F_{(1,28)} = 7.97$, p < 0.005, $\eta_p^2 = 0.22$, $\phi =$ 0.78, CI_{.95} = 1.66 to 10.41%), such that participants were less accurate at reproducing the duration of the simple gestures (M = 38.50%, SD = 20.06) than the complex gestures (M = 32.45%, SD = 19.33). Finally, no significant musical training × complexity interaction ($F_{(1,28)} = 0.79$, p > 0.05, $\eta_p^2 = 0.03$, $\phi = 0.14$) was found.

Correlations

When analyzed across groups, there was a significant moderate correlation between years of musical training and PAglobal (r (30) = 0.41, p < 0.05), such that greater musical training was correlated with greater performance accuracy. However, the large number of non-musicians with zero years of experience and the already established mean difference between the groups may have skewed this result. When analyzed for the musician group alone, there was no significant correlation (r (15) = 0.20, p > 0.05), indicating that for the musician group, years of musical training did not influence imitation performance in a systematic way. A similar pattern of results was found for %MTdiff, such that there was a significant negative correlation between musical training and %MTdiff across groups (r (30) = -0.42, p < 0.05), but not within the musician group alone (r (15) = 0.01, p > 0.05). No significant correlation was found between musical training and RT (r (30) = -0.09, p < 0.05).

Discussion

In the present experiment, we investigated the influence of musical training on the ability to imitate unfamiliar, complex manual gestures. Musicians performed more accurately than non-musicians at the global level (PAglobal) and were more successful at matching the duration of their responses to the duration of the model gestures (%MTdiff). Furthermore, the greatest difference in performance accuracy between musicians and non-musicians was at the level of the fingers (PAfingers), and this pattern of results was similar for both simple and complex gestures. This suggests that musicians' imitation advantage over non-musicians stemmed, at least in part, from the ability to reproduce the fine-motor components of the model gestures. The results also show that musical training was positively correlated with imitation performance. On the other hand, within the musician group, musicians with a

greater number of years of musical training were not at an advantage over less experienced musicians. Taken together, these findings support the idea that prior experience, in this case musical training, influences the ability to imitate.

The view of imitation as shaped by experience is the one espoused by the leading cognitive theories of imitation. For example, the ASL model predicts that the successful imitation of an action depends on the link between the perceptual and motor representations of that action that was previously established through experience. When a person imitates an observed action, the resulting motor feedback becomes linked to the perceptual representation of that action (Brass and Heyes 2005). This view of imitation can account for the performance differences between musicians and non-musicians on our imitation task. Musical training involves several components that would strengthen the perceptual-motor links necessary for the imitation of manual gestures. First, there is anecdotal evidence that learning through observation and imitation, such as when reproducing the demonstrations of an instructor, are important elements of early musical training (Haslinger et al. 2005). Second, musical practice and performance regularly involves self-monitoring and sensory feedback, for example looking at where one is placing one's fingers on the neck of a guitar while playing. These two processes may lead to the strengthening of links between the perceptual and motor representations of actions observed and performed by musicians, leading to improvements in future imitation performance.

Experience-dependent theories of imitation support another explanation for the performance differences observed between musicians and non-musicians. It is possible that musical training contributes to the ability to imitate manual gestures by influencing the personal action repertoire of musicians. Playing musical instruments requires the learning and extensive practice of complex hand and finger arrangements, resulting in stored representations of both the sensory and motor aspects of these movements. It may be that musician participants possess a greater personal action repertoire of hand and finger arrangements that are necessary to accurately imitate gestures. This view may account for the finding that the greatest difference in performance accuracy between musicians and non-musicians was for the fingers parameter (PAfingers). The role of one's personal action repertoire in imitation learning has been suggested by Ashford et al. (2007) in support of their finding that acquiring motor skills through imitation was more effective for adults than for children. They proposed that adults, with their greater years of motor experience than children, were more likely to have acquired the action repertoire necessary to imitate the observed tasks. Therefore, it may be that the ability to imitate an action depends on the similarity between the action to be imitated and the actions previously acquired by the observer.

The idea that the ability to imitate is influenced by one's personal action repertoire is also supported by findings from studies of the action-imitation system, often referred to as the mirror neuron system (MNS). As described in the Introduction, fMRI studies of dancers and pianists have shown that the observation of well-learned actions results in greater MNS activity than the observation of unfamiliar actions (Calvo-Merino et al. 2005, 2006; Haslinger et al. 2005). Two recent fMRI studies have demonstrated the involvement of the MNS in imitation learning, as well as confirming the role of personal action repertoire in this process. First, Buccino et al. (2004a) looked at MNS activity during the imitation of unfamiliar guitar chords in non-guitarists. Strong MNS activation was found during all stages of imitation: observation of guitar chords, motor preparation to imitate, and action execution. This study provided direct evidence that the MNS is indeed involved in all aspects of imitation learning. The researchers went on to propose a model of imitation postulating that through the MNS, an observed novel action is broken down into the basic motor elements present in one's personal action repertoire, and that these elements are subsequently recombined into the action to be imitated. To test this hypothesis, a follow-up study compared MNS activation during the imitation of both novel and practiced guitar chords. The results showed that MNS activation was greater for the imitation of novel than of practiced chords (Vogt et al. 2007), suggesting that greater demands were placed on "action selection and recombination" in the MNS for novel imitation than for imitating familiar actions.

The findings described above demonstrate the involvement of the MNS in learning novel movements through imitation, as well as the impact of an individual's personal action repertoire on learning. Our results, while purely behavioral, are consistent with these findings. Furthermore, the present study complements the above studies on imitation learning by making the link between past experience and imitation performance. While it is possible that other forms of training could affect performance on this task, musical training may have particularly influential effects on the MNS (and the ability to imitate) because of the sensorimotor quality of musical training. It has been found that sensorimotor learning, rather than purely visual or motor learning, has the greatest influence on the MNS system (Catmur et al. 2008). Therefore, musical training, which includes sensory feedback from multiple modalities (visual, proprioceptive, and auditory), may have an important influence on the ability to imitate the manual gestures used in the present study.

The present study also suggests that musical training can transfer to other non-musical motor learning domains. The majority of studies have shown the impact of musical training on musically relevant tasks, such as rhythm synchronization (Chen et al. 2008). Although there was some overlap between the demands of the imitation task and certain aspects of musical training (the practice of complex hand and finger arrangements), the sign language gestures used in this experiment were not musically relevant actions. Furthermore, the imitation task was purely visual, without an auditory feedback component. This suggests that musical experience modifies more basic sensorimotor functions that are relevant for other motor tasks.

Given that musicians were found to be more accurate than non-musicians at the fine-motor parameter of the fingers, and seeing as the parameters of the hands (PAhands) and fingers (PAfingers) showed the greatest declines in performance accuracy between the gesture complexity categories, it is surprising that no musical training \times gesture complexity interaction was found. Rather, musicians were more accurate than non-musicians for both simple and complex gestures, suggesting that it is not merely the complexity manipulation that led to performance differences between musicians and non-musicians. The lack of interaction also suggests that musicians' advantage over non-musicians was not due to the influence of musical training on working memory. Compared to the simple gestures, the complex gestures contained a larger and more varied sequence of movements within each gesture, creating a greater working memory load. The current results suggest that both musicians' and non-musicians' performances suffered equally from the increased working memory demands presented by the complex gestures. However, it should be noted that a correlation between musical training and verbal working memory abilities has been observed (Schellenberg 2006), and it cannot be ruled out that imitation performance might be linked to working memory ability, independent of musical training.

Another interesting finding was that musicians were better able to imitate the duration of the gestures (%MTdiff) compared to non-musicians. This difference may reflect a greater ability in musicians for reproducing the temporal organization of the gestures. Although the present study cannot account for the mechanism involved in this difference, several explanations can be suggested. It is possible that this difference in performance resided at the level of motor control and execution, such that musicians were better able to control the speed of their movements. On the other hand, the difference may stem from differences at the level of information processing during the observation of the gestures to be imitated. There is evidence that the action-imitation system is involved in encoding the temporal structure of observed movements (Gangitano et al. 2001). The influence of musical training on the action-imitation system may thus also affect the temporal encoding properties of this system. However, the difference in %MTdiff scores between musicians and nonmusicians may instead be a consequence of other differences in imitation performance. For example, poorer imitation accuracy in non-musicians may have led to less smooth performances, also affecting response duration.

The results also show that across the entire sample, years of musical training was positively correlated with imitation performance. This result may have been skewed, however, by the large number of non-musicians with zero years of musical experience and the already established mean performance difference between the groups. Within the musician group, musicians with a greater number of years of musical training were not at an advantage over less experienced musicians. However, it should be noted that the present study was not correlational in design and therefore, cannot reasonably look at the relationship between musical experience and imitation performance in this manner. In order to do so, the sample would need to include a greater range of years of musical training.

Although the results of the present study support the view that musical experience influences imitation performance, an obvious alternative explanation is that musicians had pre-existing differences in the ability to imitate that were not related to their training. As previously mentioned, learning through observation is an important component of musical training; therefore, individuals who are good at imitating may be more motivated to pursue and continue musical training. This interpretation is partially supported by the lack of a correlation between years of musical experience and imitation performance with the musician group. However, this hypothesis could only be addressed by future longitudinal studies examining the relationship between imitation performance and aptitude for musical training. A limitation of the current study is that our imitation task cannot identify the exact nature of the contributions of musical training to imitation performance. There may be potential contributions that are unrelated to past observational learning experience or personal action repertoire. Several previously reported differences between musicians and non-musicians that may have influenced gesture imitation include sensorimotor integration abilities (Watanabe et al. 2007), fine-motor control (Costa-Giomi 2005), and visuospatial skills (Brochard et al. 2004).

In conclusion, the present study found that musicians outperformed non-musicians on the imitation of complex manual gestures. Specifically, musicians were better able to accurately reproduce the fine-motor components of the gestures, as well as match the duration of their responses to the duration of the model gestures. Taken together, these imitation performance differences between musicians and non-musicians add support to the view that imitation learning is influenced by past experience, such as musical training. This view suggests that one's acquired personal action repertoire, represented in the action-imitation system in the form of sensory-motor links, is crucial for the ability to imitate. An important step for future research is to look at how past experience influences the relationship between activation in the action-imitation system and imitation performance during novel imitation learning.

Acknowledgments The authors wish to thank Robert Carver for his sign language expertise, and all those who participated in this study. We also thank Magali Keil, Amanda Daly, Annie Dubé, and Olga Ganova for their assistance with data collection and scoring. This research was supported by the National Sciences and Engineering Research Council of Canada (NSERC-238670) and the Fonds de la recherche en santé du Québec (V.P.); and the NSERC- CREATE Auditory Cognitive Neuroscience Training Grant (M.S.).

References

- Ashford D, Davids K, Bennett SJ (2007) Developmental effects influencing observational modelling: a meta-analysis. J Sports Sci 25:547–558
- Bandura A (1977) Social learning theory. Prentice-Hall, Oxford England
- Bekkering H (2002) Imitation: common mechanisms in the observation and execution of finger and mouth movements. In: Meltzoff AN, Prinz W (eds) The imitative mind: development evolution and brain bases. Cambridge University Press, New York, pp 163–182
- Bekkering H, Wohlschläger AM (2002) Action perception and imitation: a tutorial. In: Prinz W, Hommel B (eds) The imitative mind: development evolution and brain bases. Oxford University Press, New York, pp 294–314
- Brass M, Heyes C (2005) Imitation: is cognitive neuroscience solving the correspondence problem? Trends Cogn Sci 9:489–495
- Brochard R, Dufour A, Després O (2004) Effect of musical expertise on visuospatial abilities: evidence from reaction times and mental imagery. Brain Cogn 54:103–109
- Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G (2004a) Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. Neuron 42:323–334
- Buccino G, Lui F, Canessa N, Pastteri I, Lagravinese G, Benuzzi F, Porro CA, Rizzolatti G (2004b) Neural circuits involved in the recognition of actions performed by nonconspecifics: an fMRI study. J Cogn Neurosci 16:114–126
- Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P (2005) Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb Cortex 15:1243–1249
- Calvo-Merino B, Grezes J, Glaser DE, Passingham RE, Haggard P (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. Curr Biol 16:1905–1910

- Catmur C, Gillmeister H, Bird G, Liepelt R, Brass M, Heyes C (2008) Through the looking glass: counter-mirror activation following incompatible sensorimotor learning. Eur J Neurosci 28:1208– 1215
- Chen JL, Penhune VB, Zatorre RJ (2008) Moving on time: brain network for auditory-motor synchronization is modulated by rhythm complexity and musical training. J Cogn Neurosci 20:226–239
- Costa-Giomi E (2005) Does music instruction improve fine motor abilities? Ann N Y Acad Sci 1060:262–264
- Crovitz HF, Zener K (1962) A group-test for assessing hand- and eyedominance. Am J Psychol 75:271–276
- Decety J, Grèzes J (1999) Neural mechanisms subserving the perception of human actions. Trends Cogn Sci 3:172–178
- Fawcett GF, Clibbens JS (1983) The acquisition of signs by the mentally handicapped: measurement criteria. Br J Disord Commun 18:13–21
- Gangitano M, Mottaghy FM, Pascual-Leone A (2001) Phase-specific modulation of cortical motor output during movement observation. Neuroreport 12:1489–1492
- Haslinger B, Erhard P, Altenmüller E, Schroeder U, Boecker H, Ceballos-Baumann A (2005) Transmodal sensorimotor networks during action observation in professional pianists. J Cogn Neurosci 17:282–293
- Heyes C (2001) Causes and consequences of imitation. Trends Cogn Sci 5:253–261
- Mattar AA, Gribble PL (2005) Motor learning by observing. Neuron 46:153–160
- Piaget J (1952) Play. dreams and imitation in childhood, W W Norton & Co, New York
- Prinz W (2002) Experimental approaches to imitation. In: Meltzoff AN, Prinz W (eds) The imitative mind: Development. evolution, and brain bases. Cambridge University Press, New York, pp 143–162
- Schellenberg EG (2006) Long-term positive associations between music lessons and IQ. J Educ Psychology 98:457–468
- Stürmer B, Aschersleben G, Prinz W (2000) Correspondence effects with manual gestures and postures: a study of imitation. J Exp Psychol Hum Percept Perform 26:1746–1759
- Thorndike EL (1898) Animal intelligence: an experimental study of the associative processes in animals. Psychol Rev Monogr 2:551–553
- Vogt S, Thomaschke R (2007) From visuo-motor interactions to imitation learning: behavioural and brain imaging studies. J Sports Sci 25:497–517
- Vogt S, Buccino G, Wohlschlager AM, Canessa N, Shah NJ, Zilles K, Eickhoff SB, Freund HJ, Rizzolatti G, Fink GR (2007) Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage 37:1371–1383
- Watanabe D, Savion-Lemieux T, Penhune VB (2007) The effect of early musical training on adult motor performance: evidence for a sensitive period in motor learning. Exp Brain Res 176:332–340
- Weeks DL, Hall AK, Anderson LP (1996) A comparison of imitation strategies in observational learning of action patterns. J Mot Behav 28:348–358