



Have I grooved to this before? Discriminating practised and observed actions in a novel context



Dilini K. Sumanapala^a, Laurel A. Fish^a, Alex L. Jones^{a,b}, Emily S. Cross^{a,*}

^a *Social Brain in Action Laboratory, School of Psychology, Bangor University, Bangor, Gwynedd, LL57 2AS Wales, United Kingdom*

^b *Department of Psychology, Swansea University, Swansea, SA1 8EN Wales, United Kingdom*

ARTICLE INFO

Keywords:

Action memory
Motor learning
Observational learning
Dance
Motion tracking

ABSTRACT

Learning a new motor skill typically requires converting actions observed from a third-person perspective into fluid motor commands executed from a first-person perspective. In the present study, we test the hypothesis that during motor learning, the ability to discriminate between actions that have been observed and actions that have been executed is associated with learning aptitude, as assessed by a general measure of physical performance. Using a multi-day dance-training paradigm with a group of dance-naïve participants, we investigated whether actions that had been regularly observed could be discriminated from similar actions that had been physically practised over the course of three days, or a further set of similar actions that remained untrained. Training gains and performance scores at test were correlated with participants' ability to discriminate between observed and practised actions, suggesting that an individual's ability to differentiate between visual versus visuomotor action encoding is associated with general motor learning.

1. Introduction

When learning a new motor skill, observing a model can facilitate the acquisition of complex new movement patterns, such as those required for sport, dance, or playing a musical instrument. Although numerous studies directly attribute gains in motor performance to physical practice (Lee, Swinnen, & Serrien, 1994; Savion-Lemieux & Penhune, 2004; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Wulf & Schmidt, 1997), other studies indicate that some aspects of motor information can be learnt by observing a model before any physical attempts have been made (Blandin, Lhuisset, & Proteau, 1999; Carroll & Bandura, 1985, 1987; Hodges, Williams, Hayes, & Breslin, 2007; Horn, Williams, & Scott, 2002). However, few studies have addressed whether an increased ability to retain the visual profile of observed movements is associated with a similarly increased ability to perform these movements following physical or observational experience. For instance, individuals who retain detailed visuospatial information regarding observed movements (e.g., placement of limbs in time and space, the physical relationship between different limbs, the timing and rhythm of movements) may be better able to access this information during subsequent attempts to perform these actions, thus leading to superior performance abilities. Alternatively, the level of detail with which a visually experienced action is encoded in long term memory may be unrelated to motor learning and performance ability if an

individual is unable to adapt this information into corresponding motor commands. If the former scenario is supported by empirical evidence, measures addressing an individual's ability to retain movement information acquired through observation might provide a vital index of how well this individual could learn to perform complex new movements in new learning scenarios. In addition, if this relationship between action memory and performance aptitude is borne out, tests of action memory could be used to differentiate between individuals who learn actions best through observational experience, physical experience, or a combination of both in order to cater to individual learning needs.

Leading theoretical accounts of how we make sense of other people moving around us in a social world suggest that action understanding is achieved by a sensorimotor resonance process whereby observed actions are mapped onto corresponding components of an observer's existing motor repertoire (Gallese, 2003; Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti, Fogassi, & Gallese, 2001). In general, this correspondence between perception and action has been linked to action understanding as well as action learning (Buccino et al., 2004; Catmur, Walsh, & Heyes, 2007). Meta-analyses of action observation studies using neuroimaging document common regions of premotor and parietal cortices that are active during action observation as well as action execution (Caspers, Zilles, Laird, & Eickhoff, 2010; Grèzes & Decety, 2001). These overlapping regions may contribute to the

* Corresponding author.

E-mail address: e.cross@bangor.ac.uk (E.S. Cross).

<http://dx.doi.org/10.1016/j.actpsy.2017.02.008>

Received 2 June 2016; Received in revised form 6 January 2017; Accepted 28 February 2017

Available online 08 March 2017

0001-6918/© 2017 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

formation of action memories by integrating kinematic and visuospatial information learnt through observation as well as execution.

Studies that report observational learning of novel movement patterns in the absence of concurrent physical practice demonstrate that sensory feedback is not essential for learning certain aspects of new movement profiles (Black & Wright, 2000; Kohl & Shea, 1992; Maslovat, Hodges, Krigolson, & Handy, 2010). In a task requiring participants to trace dynamic patterns using a computer mouse, observing another learner led to improvements in a subject's own movement trajectories, even without prior or concurrent physical practice (Hayes, Elliott, & Bennett, 2013). Specifically, using a between-subjects design, these authors demonstrated that the observation group improved between pre- and post-test when these participants were yoked to participants in a physical practice group, indicating that motor information regarding the intended tracing motions could be acquired through observation alone. The value of observational experience on subsequent motor performance has also been demonstrated using paradigms that require participants to perform immediately following observation as well. Mattar and Gribble (2005) found that participants who observed videos of individuals learning to manipulate a robotic arm were themselves able to immediately manipulate the arm better than control participants who had no prior observational experience. Additionally, performance accuracy was improved if the direction of force generated by the robotic arm (clockwise or counter-clockwise) in the execution condition matched the force-field seen during observation. In contrast, observing manipulations of the robotic arm in an opposite direction to the field encountered during execution led to poorer execution compared to receiving no observational experience, indicating that observational experience inconsistent with what is expected during physical performance can also *reduce* subsequent performance. Collectively, these studies suggest that observational experience can engage the motor system in a manner that can either facilitate or attenuate performance gains across a variety of physical tasks, depending on the contextual congruency between observation and execution.

Evidence for the neurophysiological substrates that could support physical performance gains stemming from observational experience come from studies demonstrating common regions of cortical activity engaged when participants view actions that have been previously observed or executed (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009). In a study that investigated the effects of a week-long dance-training intervention on action performance and perception, Cross et al. (2009) found that activity in premotor and parietal regions while observing dance movements was linked to the prior training context of each movement. Specifically, both physically practised and passively observed movements evoked premotor and parietal cortices to a greater degree than untrained movements during action observation. Since engagement of premotor and parietal cortices is frequently associated with visuomotor learning (Binkofski et al., 1999; Jonides et al., 1993), Cross et al. (2009) suggest that engagement of these regions when viewing actions that had been passively observed reflects their involvement in learning, even when no concurrent motor practice was present. In contrast to the findings reported by Cross et al. (2009), Calvo-Merino et al. (2006) demonstrated that after years of formal training, classical ballet dancers showed much greater engagement of parietal and premotor regions when observing movements learnt through extensive physical practice compared to similar movements that had only been visually experienced. Although action understanding can be achieved by visual means, both studies demonstrate the possibility of selective and specific action encoding within sensorimotor brain regions as a function of an individual's prior experience. The overall novelty of actions featured in the paradigm by Cross et al. (2009) may have given rise to similar cortical engagement for physically practised and observed actions during an early stage of motor learning. In contrast, Calvo-Merino et al.'s (2006) paradigm addressed action perception following years of formal dance training, possibly tapping into greater

differentiation of visuomotor compared to visual experience at the neural level. Together, the work by Cross et al. (2009) and Calvo-Merino et al. (2006) raises important questions concerning the impact of differentiated sensorimotor experience on neurocognitive engagement during action observation.

Findings from a recent dance-training paradigm similar to that used by Cross et al. (2009) add weight to the notion that the manner in which actions are experienced shapes their subsequent perception. In this study, auditory experience alone (i.e., listening to the soundtrack that could be paired with a dance sequence) was associated with weak engagement of premotor and parietal brain regions following training, while additional layering of visual and physical experience led to marked increases in activation within the same cortical regions (Kirsch & Cross, 2015). The increased neural response for each additional sensory modality was interpreted as evidence for increasing action embodiment as a consequence of multi-modal action experience during learning. The fact that physical experience was associated with the strongest engagement of parietal and premotor brain regions may be unsurprising, given that physical experience is consistently linked to greater performance gains relative to observational experience alone (Black & Wright, 2000; Cross et al., 2009; Maslovat, Hodges, Krigolson, & Handy, 2010). These results may be due to the fact that direct, physical engagement of the motor system facilitates detailed learning of temporal and kinematic features of a task in a manner that is unmatched by observational experience (Ellenburger, Boutin, Blandin, Shea, & Panzer, 2012; Gruetzmacher, Panzer, Blandin, & Shea, 2011; although see Hayes, Roberts, Elliott, & Bennett, 2014, for compelling evidence of complex kinematic information being learned from observation in the absence of motor signals).

In support of this notion, other studies have demonstrated the aspects of performance that are least served through observational practice compared to physical practice. In a study involving a serial reaction time task, observational practice of key sequences led to poorer intermanual transfer, since an intermanual version of a sequence bears limited visual similarity to the observed model (Osman, Bird, & Heyes, 2005). In a separate study, Bird and Heyes (2005) found that observational practice of a tapped finger sequence was effector dependent, given that sequence production with untrained digits led to poorer performance. All together, these findings suggest that in order to benefit most from observational training, a model must demonstrate the task in a manner that is visually compatible with how the observer might reproduce the movement.

In order to accurately translate observed movements into motor commands, an observer must differentiate between his or her own physically executed movements and those executed by a model. One's ability to discriminate differences between observed and performed actions on the basis of differences in sensorimotor engagement could be intricately linked with overall performance ability - a relationship that, to our knowledge, has not yet been empirically examined. We hypothesised that dance-naïve participants who showed the best performance ability after a week of observational and physical practice with previously novel dance movements would also be better at discriminating between observed, practised, and untrained dance actions within a training-modality categorisation task. Such a pattern of findings would suggest that aptitude with learning to physically execute coordinated, whole-body movements is also associated with heightened abilities to encode and recall visuomotor experience specific to individual movements. The establishment of such a relationship could lead to the development of metrics that assess individual skill in sensorimotor differentiation, which could in turn be useful in classifying individual movement learning aptitudes.

2. Method

2.1. Participants

Thirty participants with no prior history of dance training or

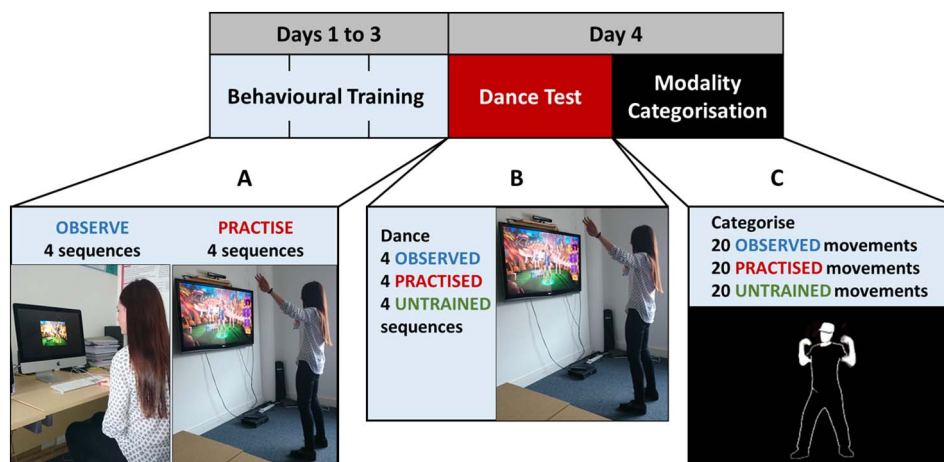


Fig. 1. Training setup. A) Overview of behavioural training, involving three consecutive days of observing one set of sequences, and physically practising a different set. B) Performance test for four observed sequences, four practised sequences and four untrained sequences on Day 4. C) Modality categorisation task depicting a still frame of the silhouette dancer from an example movement clip.

experience with dance-based video games took part in this study. All protocols were approved by the Bangor University School of Psychology Research Ethics committee. All participants taking part in the study provided written informed consent before beginning any experimental procedures and were reimbursed for their participation. The final sample comprised 16 females and 14 males, with a mean age of 20.93 years ($SD = 2.80$ years).

2.2. Stimuli and apparatus

Twelve dance sequences were selected from Dance Central 2 (Harmonix Music Systems, 2011), a motion-capture based video game available on Microsoft's Xbox Kinect™ 360 console (see Fig. 1). These sequences were selected on the basis of gender-neutral choreography and minimal background graphics, after which they were randomly assigned to three separate groups. Game choreography was set to popular dance music, with an average song length of 2 min and 19 s ($SD: 12$ s), and an average tempo of 115 beats per minute ($SD: 10.24$ bpm). For each participant, these sequence groups were counter-balanced across three training conditions: physically practised, observed, and untrained sequences. Each sequence group did not significantly differ in difficulty rating, duration, or beats per minute. All participants experienced all sequences from the three training groups.

2.3. Behavioural training procedure

During physical practice, participants performed four dance sequences approximately 2 m in front of a wall-mounted Sharp 52-inch flat-screen TV. The Kinect™ motion capture system was calibrated so that 3D full body motion for each participant was captured. The set-up and calibration procedures followed for each participant were those set out by the accompanying instruction manual for the Dance Central 2 Xbox 360 Kinect™ video game (see also Karpati, Giacosa, Foster, Penhune, & Hyde, 2017; Kirsch, Drommelschmidt, & Cross, 2013; Kirsch & Cross, 2015; and Kirsch, Dawson, & Cross, 2015 for the use and reporting of similar procedures). For each sequence, participants were instructed to mirror the choreography of a computer-generated avatar featured in the Dance Central 2 video game. Performance was scored online using the videogame's Kinect motion-capture hardware, which matches the overall silhouette of the performer with the silhouette of the computer avatar. During the execution of a movement, a performer's silhouette must closely mirror the movements performed by the avatar in order to obtain a high score. The game generates a total performance score based on mirroring accuracy after each sequence is completed, whereby higher scores indicate better mirroring of the

avatar's moves. Scores obtained for each sequence were averaged to reflect overall performance ability on each training day. Importantly, in the native gameplay context, real-time feedback appears on the right side of the screen as participants perform each dance movement. This feedback includes a dynamic silhouette of the participant dancing, as well as written verbal feedback letting them know how well they were matching their movements to the avatar on screen (terms such as 'flawless!!' or 'almost!!' appear) and numeric feedback (a participant's overall score tally grows depending on performance). In order to keep the physical training condition as similar as possible to the observational condition, the side of the screen where most real-time feedback was displayed was covered with card so that participants could not see how well they were doing as they performed, and this part of the screen was cropped out of the stimuli videos created for the observation condition. Participants could, however, catch a glimpse of their final dance score as it was briefly flashed up in the centre of the screen after each performance, as well as see occasional written feedback under the avatar's feet as they performed (such as 'flawless!!'), as there was no way to hide this feedback or disable this feature in the game.

For the observation condition, participants were seated in front of a computer running Psychophysics Toolbox 3 in MATLAB R2013a (Mathworks, Inc.) and observed four dance sequences recorded from the video game (see Fig. 1B). After watching each sequence, participants were shown 8 movement clips and asked to state whether each movement had been featured in the preceding sequence ("Did you see this movement in the video you just watched?"). Participants responded "yes" or "no" using the computer's cursor to select the respective option. Half of the displayed movements were extracted from the preceding sequence, while the other half were extracted from sequences not used during training. Total accuracy for each day was calculated as the number of movements correctly identified from the observed sequences.

For three consecutive days, participants experienced both physical practise and observation conditions. On the fourth day (test), participants physically performed all sequences featured in physical and observational training, in addition to four untrained sequences. To limit the impact of instructional differences between physical practice and observational experience on test performance, participants were only made aware of the test phase on the last day of participation. In addition, they were never explicitly instructed to try to learn or memorise the sequences they experienced during physical or observational training conditions (see Grèzes, Costes, and Decety (1999) and Badets, Blandin, and Shea (2006) for further discussion of the impact of instructions on learning). The four scores generated for each condition were averaged to reflect a global measure of performance ability for

each training condition at test.

2.4. Training modality categorisation task

After completing the dance task on the fourth (test) day of the study, participants then completed a brief computer task requiring them to categorise movements into physically practised, observed, and untrained movement conditions (see Fig. 1C). The stimuli for this task featured moving body silhouettes performing the individual choreographed moves that composed the longer movement sequences used in the game. Critically, these stimuli were devoid of the complex and dynamic background graphics and associated music present during training, which could be used to recognise actions from their respective training contexts using visual and auditory cues specific to the videogame. For a comparison of movements as presented during training compared to their presentation during scanning and categorisation, see Fig. 2.

Each move performed by the silhouetted dancer was approximately 2 s long, and was presented once followed by the question “In what context did you see this movement?”. Participants were required to select the appropriate training condition (“physical”, “observed”, or “untrained”) using the computer's cursor. Total accuracy was calculated as a percentage of all correctly categorised movements. Accuracy scores for each training condition were also generated for the purposes of analysis.

2.5. Design

To assess whether performance ability for physically practised movements improved across training, a repeated-measures ANOVA was used to compare performance scores for physically practised movements across all three days of physical training. A repeated-measures, within-subjects ANOVA was similarly conducted to determine whether accuracy on the observation task also improved across training prior to test. Modality-specific performance at test was examined using a one-way, within subjects ANOVA by comparing average differences in performance between physically practised, observed, and untrained movement sequences. Differences in categorisation ability between the three groups of movements were also examined using a one-way, within subjects ANOVA. Post hoc pairwise comparisons were conducted using Tukey's HSD. Performance scores were then correlated with modality categorisation to examine the association between specific sensorimotor action memory and performance ability.



Fig. 2. Movement stimuli. Left panel depicts movements as encountered during training. Right panel depicts movement silhouettes encountered during the training modality categorisation task.

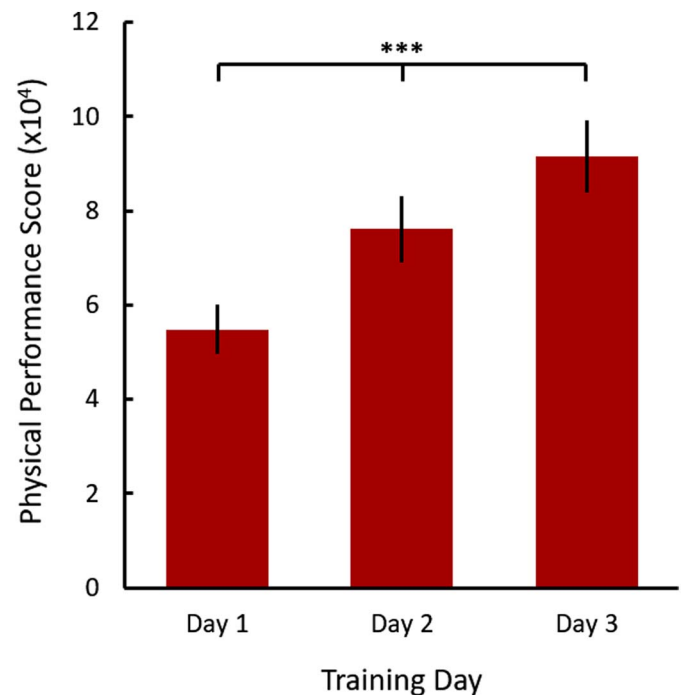


Fig. 3. Physical training performance. Scores recorded from XBOX based videogame (Dance Central 2). Error bars indicate standard error of the mean. ***significant at $p < 0.001$.

3. Results

3.1. Training performance

Results from the within-subjects, repeated measures ANOVA indicates a main effect of day across four days of training, including test, $F(2, 58) = 62.61$, $p < 0.001$, $\eta_p^2 = 0.68$, whereby average performance improved over time. Pairwise comparisons indicate that significant differences were observed between *all* possible pairs of days (see Fig. 3). The overall difference in scores across the three days of training can be described as a linear trend, $F(1, 29) = 104.12$, $p < 0.001$, $\eta_p^2 = 0.78$.

Results from the within-subjects, repeated measures ANOVA indicate a main effect of day (see Fig. 4), $F(2, 58) = 3.73$, $p = 0.03$, $\eta_p^2 = 0.11$, indicating that participants became increasingly accurate at identifying whether or not specific movements were present in the observed sequences. Pairwise comparisons revealed that performance accuracy was significantly higher on Day 3 than Day 1. Overall

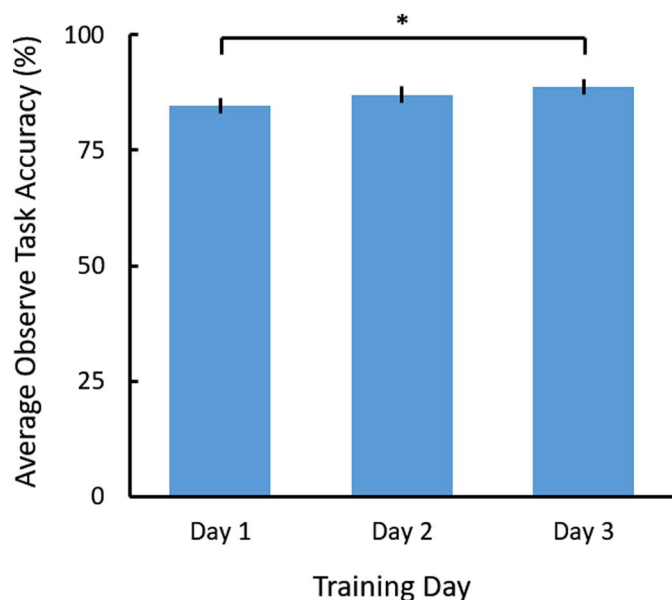


Fig. 4. Observation task accuracy. Scores depict average accuracy for selecting seen versus unseen movements during observational training across each training day. Error bars indicate standard error of the mean. *significant at $p < 0.05$.

differences in scores across the three days of training can be described as a linear trend, $F(1, 29) = 6.43, p = 0.02, \eta_p^2 = 0.18$.

A main effect of training modality was observed for performance scores during the test session on day 4, $F(2, 87) = 3.92, p < 0.05$. Post hoc comparisons (Tukey's HSD) revealed that physically practised sequences were performed significantly better than untrained sequences (see Fig. 5). Pairwise comparisons revealed that performance on observed sequences did not significantly differ from physically practised or untrained sequences.

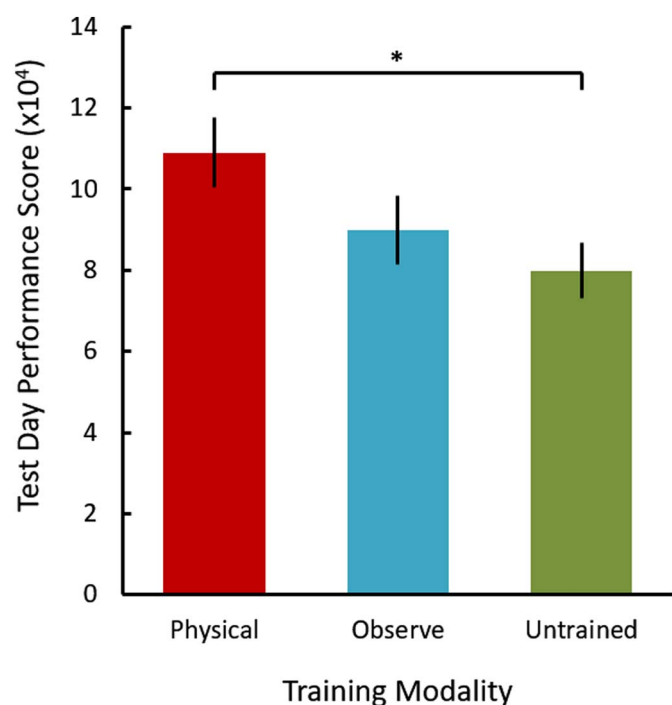


Fig. 5. Test day performance scores for all sequences. Error bars indicate standard error of the mean. *significant at $p < 0.05$.

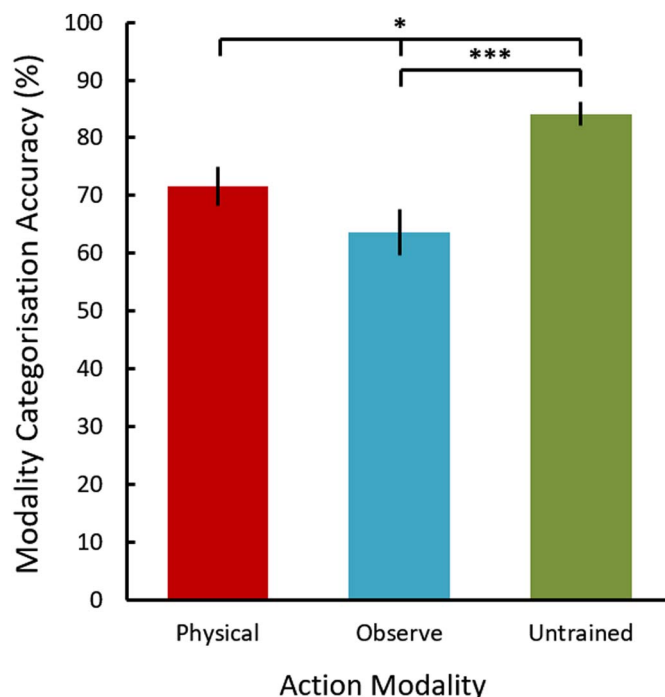


Fig. 6. Test day modality categorisation accuracy. Error bars indicate standard error of the mean. *significant at $p < 0.05$; ***significant at $p < 0.001$.

3.2. Training modality categorisation task

At test, participants were able to recall the correct training modality for viewed action silhouettes at a rate well above chance (mean recall rate = 73.17%; chance rate = 33.33% - see Fig. 6).

Given that the assumption of homogeneity of variance was violated, the Brown-Forsythe F-ratio is reported. A main effect of modality was observed, whereby untrained movements were categorised more accurately compared to physically practised or observed movements, $F(2, 71.05) = 10.09, p < 0.001$. The rate of categorisation was highest for untrained movements (84.17%), followed by physically practised (71.67%) and observed actions (63.67%). Pairwise comparisons indicate that accuracy for untrained movements was significantly higher than accuracy for physically practised movements and accuracy for observed movements. Accuracy for physically practised movements and observed movements did not reliably differ (see Fig. 6).

As predicted, overall accuracy rates for modality categorisation correlated with global performance scores on test day, $r(30) = 0.60, p < 0.001$, indicating that participants who overall performed dance sequences better at test also scored higher on modality categorisation ability (see Fig. 7).

Accuracy for categorising physically practised as well as observed movements was respectively associated with performance ability for physically practised, $r(30) = 0.43, p = 0.02$, and observed sequences, $r(30) = 0.40, p = 0.03$, indicating that performance in the modality categorisation task was associated with performance ability for observed and practised sequences, but not for untrained sequences (see Fig. 8).

4. Discussion

The primary aim of this study was to investigate the extent to which an individual's ability to learn novel, whole-body actions is associated with his or her ability to discriminate the learning context of these actions following training. A second question we explored was whether an individual with a heightened ability to recognise learning modality-based differences in action sequences might also be capable of

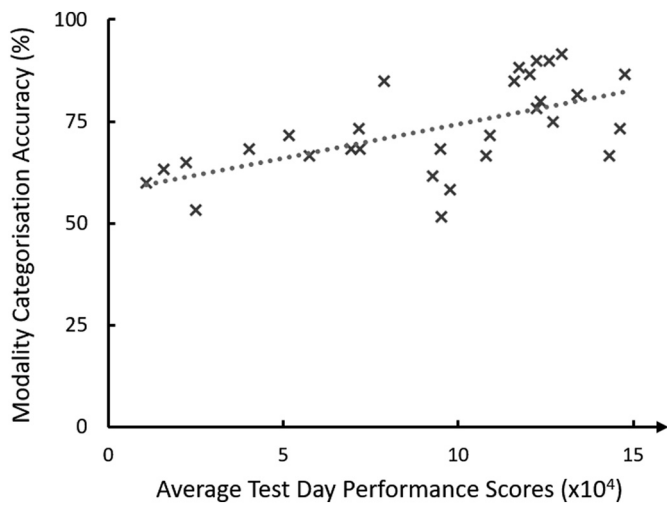


Fig. 7. Categorisation versus performance. Test day modality categorisation accuracy correlated with test day average performance scores.

reproducing these movements with greater accuracy following training. As hypothesised, our findings demonstrate a positive association between participants' ability to accurately classify learning modality and their post-training dance performance, indicating that increased performance aptitude does indeed track with the ability to recall the sensory modality through which an action was originally learned.

In order to probe action learning, participants in this experiment were asked to identify the training context in which each action was originally learned using novel versions of the action stimuli, stripped of the rich visual and auditory cues that might make linking specific actions to their original training contexts easier. These stimuli were used so that participants had to rely more on prior sensorimotor experience to identify training contexts, rather than the rich visual and auditory cues specific to the immersive videogame context that they experienced during physical and observational training (see Fig. 2). Across all training contexts (physically practised, observed and untrained), accurate categorisation of these actions was significantly above chance, indicating that the type of sensorimotor experience associated with an action (or lack thereof) was reliably recalled. Within this task, response accuracy did not significantly differ between physically practised and observed actions, although higher categorisa-

tion accuracy for both forms of experience was associated with an increased ability to perform these trained actions. These results suggest that participants' learning was also associated with their ability to discriminate between visually encoded versus physically experienced actions.

In contrast, categorisation of untrained actions was not associated with performance aptitude for untrained actions, despite categorisation accuracy being highest for movements from this set. It is plausible that high categorisation accuracy for movements from this training category is due to the novelty of these previously unseen/undanced actions. In essence, since participants completed the categorisation task promptly after performing all three sets of dance sequences (physically practised, observed, and untrained), the novelty and recency of the visuomotor experience associated with performing untrained dances sequences may have selectively facilitated categorisation accuracy for untrained actions. In contrast, physically practised and observed movements were encountered for an equivalent period of time over several days prior to test performance, which may have affected the ease with which they could be discriminated from each other. The equivalence in training duration across physically practised and observed movements could potentially explain the similarity in categorisation accuracy between these two conditions, whereas the novelty and recency of the untrained sequences appears to have led to a non-specific, general boost in recognition accuracy (c.f. McLaren, Leavers, & Mackintosh, 1994), unrelated to participants' ability to physically reproduce these movements. When revisiting the categorisation data as a whole, however, we see that participants' overall physical aptitude with performing dance sequences across all training conditions positively correlates with overall modality categorisation accuracy.

Although physically practised sequences were performed better than untrained and observed sequences, performance scores for observed sequences did not significantly differ from untrained sequences. While this finding stands in contrast with some prior studies that demonstrate increased performance ability for action sequences that have been observed compared to untrained actions (Black & Wright, 2000; Kirsch & Cross, 2015), others have reported a similar pattern of findings to those found in the present study, where observational experience alone does not lead to significant performance gains for observed compared to untrained sequences (Cross et al., 2009). It is less surprising that participants' performance of the physically practised sequences is superior to the observed sequences, as this finding is frequently reported in studies that examine physical and observational

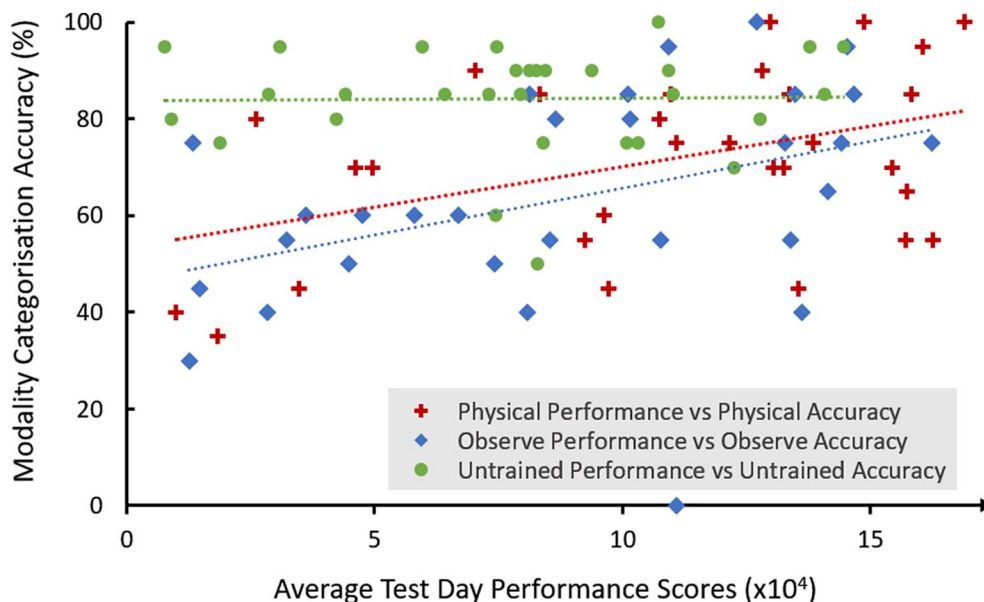


Fig. 8. Training-specific performance and categorisation. Modality categorisation accuracy at test correlated with test day performance scores, depicted according to training type.

learning within the same participants (Hodges et al., 2007; Maslovat, Hayes, Horn & Hodges, 2010). In the present study, it is possible that participants' statistically indistinguishable performance on the observed and untrained sequences was due to lowered performance difficulty settings within the videogame (compared to, for example, the more difficult settings used in the same game by Kirsch & Cross, 2015), which might have consequently reduced sensitivity to differences in performance gains associated with the less intensively practised conditions. Another explanation for this pattern of findings concerns our lack of explicit instructions to participants to try to learn the dance sequences encountered during the observational training condition. As a number of prior studies have demonstrated (e.g., Badets et al., 2006; Grèzes et al., 1999), and indeed, as our team demonstrated in a recent study using the same dance video game set up as that used in the present study (Kirsch & Cross, 2015), explicitly requesting participants to observe with the intention to learn increases observational learning compared to passive learning alone, and relative to untrained actions. It is thus perhaps all the more striking that participants' classification accuracy for physically practised and observed sequences is statistically indistinguishable, and tracks with their ability to perform these sequences. A challenge for future work will be to more closely examine *how* the accuracy with which an action is executed relates to the accuracy with which an individual encodes visuospatial and kinematic features during action experience, as well as to examine how the varying instructions about learning intentions further shapes this relationship.

In general, evidence suggests people are proficient at differentiating previously observed action profiles. In a study by Urgolites and Wood (2013) that investigated visual action memory, participants observed a series of computer-animated actions performed by an avatar (such as jumps, arm raises, and crouches) and were then presented with pairs of actions featuring a previously seen and an unseen action. For actions observed between one and five times, accuracy for selecting seen over unseen actions ranged between 76% and 81%, suggesting that visual properties of observed actions can be accurately recalled from long-term memory. The authors conclude that acquisition of new actions may critically depend on integrating new sensorimotor information with pre-existing action templates held within long-term memory. The increased engagement of sensorimotor brain regions documented while dancers observed previously practised actions in Calvo-Merino and colleagues' study (2006) could reflect this type of long-term action memory facilitated by physical experience. For actions that have only been observed for a similar period of time, lesser engagement of sensorimotor regions when observing these actions may be indicative of reduced sensorimotor integration. In essence, frequently observed actions that are never accompanied by physical practice may be encoded primarily using visual information, while actions that are observed as well as practised benefit from both visual and motor encoding (Calvo-Merino et al., 2006). The additive impact of these two forms of encoding could promote the retention of physically practised actions in long term memory, given that performers are able to recall and perform routines trained many years ago (Stevens, Ginsborg, & Lester, 2011). In contrast, extensive visual experience with actions in the absence of physical practice may not facilitate gains in performance to an equal degree, despite facilitating detailed visual encoding (c.f. Cross et al., 2009).

The present study demonstrates that the ability to recognise observed and physically practised actions is linked to behavioural performance aptitude. As such, an area of interest for future work could be to examine the degree to which visuomotor representations are separable at a neural level. If individuals who are poor at recalling the original training context of actions nevertheless show distinctions in neural engagement when observing these movements, this discrepancy would suggest that neural differentiation between observed and physically practised movements does not necessarily translate into direct awareness or memory of training context. However, if neural

differentiation between learning modalities is predictive of later performance gains, this activation could provide an index of how much an individual might learn through an observational training paradigm, even if he or she has difficulties accessing modality information at an explicit level of awareness. Such metrics could then be used to devise appropriate training interventions depending on individual learning profiles. In addition, stimuli used to probe differences in movement encoding could be further reduced to minimal motion cues (such as those provided by point-light figures), in order to gauge whether practice-related information can be conveyed in the absence of cues to human form. If participants were able to classify training related differences using simplified movement stimuli, this would point to action encoding mechanisms that are not necessarily reliant on detailed human models, widening the scope of visual instructions that could be used for new action training. More broadly, the approach and findings of the present study hold potential value for specific motor-training paradigms by demonstrating how individual differences in movement encoding might be linked to motor learning and performance.

Conflict of interest

The authors report no conflict of interest with respect to the content featured in this article.

Acknowledgements

The authors would like to thank David Carey for helpful comments on a previous version of this manuscript, and Guillaume Thierry for use of his wide screen television. This research was supported by a Future Research Leaders Award from the ESRC (ES/K001892/1), a VENI award from the Netherlands Organisation for Scientific Research (451-11-002) and a Marie Curie Career Integration grant (CIG11-2012-322256) to E.S.C.

References

- Badets, A., Blandin, Y., & Shea, C. H. (2006). Intention in motor learning through observation. *The Quarterly Journal of Experimental Psychology*, 59(2), 377–386.
- Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research*, 128(2), 210–213. <http://dx.doi.org/10.1007/s002210050838>.
- Bird, G., & Heyes, C. (2005). Effector-dependent learning by observation of a finger movement sequence. *Journal of Experimental Psychology: Human Perception and Performance*, 31(2), 262–275. <http://dx.doi.org/10.1037/0096-1523.31.2.262>.
- Black, C. B., & Wright, D. L. (2000). Can observational practice facilitate error recognition and movement production? *Research Quarterly for Exercise and Sport*, 71(4), 331–339. <http://dx.doi.org/10.1080/02701367.2000.10608916>.
- Blandin, Y., Lhuisset, L., & Proteau, L. (1999). Cognitive processes underlying observational learning of motor skills. *The Quarterly Journal of Experimental Psychology*, 52A(4), 957–979. <http://dx.doi.org/10.1080/027249899390882>.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*, 42(2), 323–334. [http://dx.doi.org/10.1016/S0896-6273\(04\)00181-3](http://dx.doi.org/10.1016/S0896-6273(04)00181-3).
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, 16(19), 1905–1910. <http://dx.doi.org/10.1016/j.cub.2006.07.065>.
- Carroll, W. R., & Bandura, A. (1985). Role of timing of visual monitoring and motor rehearsal in observational learning of action patterns. *Journal of Motor Behavior*, 17(3), 269–281.
- Carroll, W. R., & Bandura, A. (1987). Translating cognition into action: The role of visual guidance in observational learning. *Journal of Motor Behavior*, 19(3), 385–398.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, 50(3), 1148–1167. <http://dx.doi.org/10.1016/j.neuroimage.2009.12.112>.
- Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human mirror system. *Current Biology*, 17(17), 1527–1531. <http://dx.doi.org/10.1016/j.cub.2007.08.006>.
- Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. D. C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex*, 19(2), 315–326. <http://dx.doi.org/10.1093/cercor/bhn083>.
- Ellenberger, T., Boutin, A., Blandin, Y., Shea, C. H., & Panzer, S. (2012). Scheduling observational and physical practice: Influence on the coding of simple motor sequences. *The Quarterly Journal of Experimental Psychology*. <http://dx.doi.org/10.1080/17470218.2012.700000>.

- 1080/17470218.2011.654126.
- Gallese, V. (2003). The manifold nature of interpersonal relations: The quest for a common mechanism. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 358(1431), 517–528. <http://dx.doi.org/10.1098/rstb.2002.1234>.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, 8(9), 396–403. <http://dx.doi.org/10.1016/j.tics.2004.07.002>.
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, 12(1), 1–19. [http://dx.doi.org/10.1002/1097-0193\(200101\)12:1<1::AID-HBM10>3.0.CO;2-V](http://dx.doi.org/10.1002/1097-0193(200101)12:1<1::AID-HBM10>3.0.CO;2-V).
- Grèzes, J., Costes, N., & Decety, J. (1999). The effects of learning and intention on the neural network involved in the perception of meaningless action. *Brain*, 122, 1875–1887.
- Gruetzmacher, N., Panzer, S., Blandin, Y., & Shea, C. H. (2011). Observation and physical practice: Coding of simple motor sequences. *Quarterly Journal of Experimental Psychology* (2006), 64(6), 1111–1123. <http://dx.doi.org/10.1080/17470218.2010.543286>.
- Hayes, S. J., Elliott, D., & Bennett, S. J. (2013). Visual online control processes are acquired during observational practice. *Acta Psychologica*, 143(3), 298–302. <http://dx.doi.org/10.1016/j.actpsy.2013.04.012>.
- Hayes, S. J., Roberts, J. W., Elliott, D., & Bennett, S. J. (2014). Top-down attentional processes modulate the coding of atypical biological motion kinematics in the absence of motor signals. *Journal of Experimental Psychology: Human Perception & Performance*, 40(4), 1641–1653.
- Hodges, N. J., Williams, A. M., Hayes, S. J., & Breslin, G. (2007). What is modelled during observational learning? *Journal of Sports Sciences*, 25(5), 531–545. <http://dx.doi.org/10.1080/02640410600946860>.
- Horn, R. R., Williams, A. M., & Scott, M. A. (2002). Learning from demonstrations: The role of visual search during observational learning from video and point-light models. *Journal of Sports Sciences*, 20(3), 253–269. <http://dx.doi.org/10.1080/026404102317284808>.
- Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working-memory in humans as revealed by pet. *Nature*, 363(6430), 623–625. <http://dx.doi.org/10.1038/363623a0>.
- Karpati, F. J., Giacosa, C., Foster, N. E., Penhune, V. B., & Hyde, K. L. (2017). Dance and music share gray matter structural correlates. *Brain Research*, 1657, 62–73.
- Kirsch, L. P., & Cross, E. S. (2015). Additive routes to action learning: Layering experience shapes engagement of the action observation network. *Cerebral Cortex*. <http://dx.doi.org/10.1093/cercor/bhv167>.
- Kirsch, L., Drommelschmidt, K. A., & Cross, E. S. (2013). The impact of sensorimotor experience on affective evaluation of dance. *Frontiers in Human Neuroscience*, 7, 521. <http://dx.doi.org/10.3389/fnhum.2013.00521>.
- Kirsch, L. P., Dawson, K., & Cross, E. S. (2015). Dance experience sculpts aesthetic perception and related brain circuits. *Annals of the New York Academy of Sciences*, 1337, 130–139.
- Kohl, R. M., & Shea, C. H. (1992). Pew (1966) revisited: Acquisition of hierarchical control as a function of observational practice. *Journal of Motor Behavior*. <http://dx.doi.org/10.1080/00222895.1992.9941620>.
- Lee, T. D., Swinnen, S. P., & Serrien, D. J. (1994). Cognitive effort and motor learning. *Quest*, 46(3), 328–344. <http://dx.doi.org/10.1080/00336297.1994.10484130>.
- Maslovat, D., Hodges, N. J., Krigolson, O. E., & Handy, T. C. (2010a). Observational practice benefits are limited to perceptual improvements in the acquisition of a novel coordination skill. *Experimental Brain Research*, 204(1), 119–130. <http://dx.doi.org/10.1007/s00221-010-2302-7>.
- Maslovat, D., Hayes, S. J., Horn, R., & Hodges, N. J. (2010b). Motor learning through observation. In D. Elliott, & M. A. Kahn (Eds.), *Vision and goal-directed movement: Neurobehavioural perspectives* (pp. 315–340). Champagne, IL: Human Kinetics.
- Mattar, A. G., & Gribble, P. L. (2005). Motor learning by observing. *Neuron*, 46(1), 153–160. <http://dx.doi.org/10.1016/j.neuron.2005.02.009>.
- McLaren, I. P. L., Leavers, H. J., & Mackintosh, N. J. (1994). Recognition, categorisation and perceptual learning. In C. Umlita, & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 889–909). Cambridge, MA: MIT Press.
- Osman, M., Bird, G., & Heyes, C. (2005). Action observation supports effector-dependent learning of finger movement sequences. *Experimental Brain Research*, 165(1), 19–27. <https://doi.org/10.1007/s00221-005-2275-0>.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews. Neuroscience*, 2(9), 661–670. <http://dx.doi.org/10.1038/35090060>.
- Savion-Lemieux, T., & Penhune, V. B. (2004). The effects of practice and delay on motor skill learning and retention. *Experimental Brain Research*, 161(4), 423–431. <http://dx.doi.org/10.1007/s00221-004-2085-9>.
- Stevens, C., Ginsborg, J., & Lester, G. (2011). Backwards and forwards in space and time: Recalling dance movement from long-term memory. *Memory Studies*, 4, 234–250. <http://dx.doi.org/10.1177/175069801038701>.
- Urgolites, Z. J., & Wood, J. N. (2013). Binding actions and scenes in visual long-term memory. *Psychonomic Bulletin & Review*, 20(6), 1246–1252. <http://dx.doi.org/10.3758/s13423-013-0440-1>.
- Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002). Practice with sleep makes perfect. *Neuron*, 35(1), 205–211. [http://dx.doi.org/10.1016/s0896-6273\(02\)00746-8](http://dx.doi.org/10.1016/s0896-6273(02)00746-8).
- Wulf, G., & Schmidt, R. A. (1997). Variability of practice and implicit motor learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23(4), 987–1006. <http://dx.doi.org/10.1037/0278-7393.23.4.987>.