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RESEARCH ARTICLE

The effects of acute exercise on visuomotor adaptation, learning, and inter-limb transfer

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Abstract
Pairing an acute bout of lower-limb cycling exercise with skilled motor practice enhances acquisition and learning. However, it is not known whether an acute bout of exercise enhances a specific form of motor learning, namely motor adaptation, and if subsequent inter-limb transfer of this adaptation is enhanced. Seventeen young healthy participants performed a bout of cycling exercise and rest, on separate days, prior to right-arm reaching movements to visual targets under 45° rotated feedback of arm position (acquisition), followed by an immediate test of inter-limb transfer with the untrained left arm. After a 24-h delay, participants returned for a no-exercise retention test using the right and left arm with the same rotated visual feedback as acquisition. Results demonstrated that exercise enhanced right-arm adaptation during the acquisition and retention phases, and transiently enhanced aspects of inter-limb transfer, irrespective of usual levels of physical activity. Specifically, exercise enhanced movement accuracy, decreased reaction and movement time during acquisition, and increased accuracy during retention. Exercise shortened reaction time during the inter-limb transfer test immediately after right-arm acquisition but did not influence left-arm performance assessed at retention. These results indicate that an acute bout of exercise before practice enhances right-arm visuomotor adaptation (acquisition) and learning, and decreases reaction time during untrained left arm performance. The current results may have implications for the prescription of exercise protocols to enhance motor adaptation for healthy individuals and in clinical populations.

Keywords Exercise · Visuomotor adaptation · Inter-limb transfer · Motor adaptation · Retention

New and Noteworthy

An acute bout of cycling exercise enhances visuomotor adaptation and learning, with a transient effect to inter-limb transfer. Specifically, exercise enhances movement accuracy, decreases reaction and movement time during visuomotor adaptation (acquisition), and movement accuracy 24-h later. Acute exercise decreased untrained left arm reaction time immediately after right-arm training.

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Introduction

Acute leg cycling exercise has been shown to influence skilled sensorimotor control and learning using the non-exercised, upper limbs. In healthy young adults, a bout of exercise prior to practicing visuomotor tracking and sequence tasks enhances skill acquisition (Mang et al. 2014; Statton et al. 2015) and promotes learning shown at retention tests 5 h (Stavrinos and Coxon 2017), 24 h (Roig et al. 2012; Skriver et al. 2014; Mang et al. 2014; Thomas et al. 2016), and 7 days after practice (Roig et al. 2012; Skriver et al. 2014; Thomas et al. 2016). Additionally, one recent study showed a bout of intense shuttle running performed prior to practicing a visual rotation task using a joystick enhances early consolidation (1 h after practice; Ferrer-Uris et al. 2017). A growing body of literature suggests that acute exercise may enhance both motor sequence learning and visuomotor tracking tasks. Yet, little work has investigated the effects of acute exercise on motor adaptation during reaching movements. Although motor adaptation and sequence learning share some similarities, there is evidence that they rely on different brain networks (Doyon et al. 1996, 1997, 2003, 2011; Ungerleider et al. 2002; Doyon and Benali 2005; Spampinato and Celnik 2018). Further, motor adaptation generally involves the formation of a novel sensorimotor map (i.e., a new internal model) and motor sequence learning relies on repetition and reinforcement of successful actions during motor practice (Shadmehr and Brashers-Krug 1997; Wolpert et al. 1998; Krakauer et al. 1999; Haith and Krakauer 2013). Thus, motor adaptation of arm reaching movements may be uniquely impacted by acute exercise. Specifically, no work has investigated the effects of acute leg cycling exercise on visuomotor adaptation (a method to study motor adaptation) of non-exercised upper-limb movements.

The effects of acute exercise on sensorimotor learning tasks have typically been examined using fine motor skills with digit (Mang et al. 2014; Statton et al. 2015; Stavrinos and Coxon 2017), hand, and 2-dimensional wrist movements (Roig et al. 2012; Singh et al. 2015; Ferrer-Uris et al. 2017). Although fine motor tasks provide sound control over the muscles and joints involved in the task, examining multi-joint reaching movements allows for the investigation of how exercise benefits arm-reaching movements that are practiced in sport, everyday life, and rehabilitation. Using an arm-reaching task, Mang et al. (2016b) showed enhancement in a discrete sequence-learning task when practice was preceded by a bout of exercise (Mang et al. 2016b). However, no work to date has investigated the effects of acute exercise on visuomotor adaptation and learning of an arm-reaching task or considered potential transfer to the untrained arm.

Practicing a novel task with one arm can improve performance of the opposite untrained arm, which is known as inter-limb transfer (Laszlo et al. 1970; Elliott and Roy 1981; Morton et al. 2001). Inter-limb transfer with visuomotor adaptation tasks can be enhanced by providing visual feedback of a reversed image of the trained hand/arm (Dionne and Henriques 2008) or by pairing intermittent passive movements of the opposite arm following the same movement as the trained arm (Bao et al. 2017; Lei et al. 2017). Studies reporting imaging and neurophysiological findings suggest an acute bout of exercise (Rajab et al. 2014; Mang et al. 2016a; Neva et al. 2017) may influence the neural mechanisms potentially underlying inter-limb transfer (Schmidt et al. 1979; Dizio and Lackner 1995; Swinnen 2002; Cardoso de Oliveira 2002; Criscimagna-Hemminger et al. 2003; Malfait and Ostry 2004; Shadmehr 2004; Wang and Sainburg 2004). Specifically, resting-state functional magnetic resonance imaging shows that acute cycling exercise modulates co-activation of homologous sensorimotor regions (e.g., pre and postcentral gyri; Rajab et al. 2014). Moreover, transcranial magnetic stimulation studies demonstrate that a bout of cycling exercise decreases transcallosal inhibition of the homologous non-exercised upper-limb muscles (Neva et al. 2017) and inhibition between the cerebellum and primary motor cortex (Mang et al. 2016a).

In the current study, we aimed to determine the effects of an acute bout of cycling exercise on: (1) acquisition of a visuomotor rotation task with the trained (right) arm, (2) initial inter-limb transfer to the untrained (left) arm, and (3) performance at a 24-h retention test of both arms as our measure of motor learning. We hypothesized that an acute bout of leg cycling exercise would enhance visuomotor adaptation (acquisition), inter-limb transfer, and retention performance with both arms.

Methods

Participants

Seventeen healthy individuals aged 20–30 years participated in the study (mean ± SD: 24 ± 3 years, 9 F). All participants scored ≥ 40 on the Edinburgh Handedness Inventory (Oldfield 1971) indicating right-hand dominance. Participants were free from neurological disorders. Informed consent was obtained from all participants prior to undergoing the experimental protocol and they were screened for any contraindications to exercise using the Physical Activity Readiness Questionnaire for Everyone (PAR-Q+). The Clinical Research Ethics Board at the University of British Columbia approved all experimental procedures and all participants provided written informed consent in accordance with the Declaration of Helsinki.

Experimental design

Each individual participated in 4 experimental days in a within-subjects design to compare the effects of 25 min of rest and a 25-min bout of moderate-intensity cycling exercise (65–70% of age-predicted maximal heart rate) on acquisition, inter-limb transfer, and retention performance of adaptation to a visuomotor rotation task with both arms (Fig. 1). Participants were instructed to refrain from exercising on testing days outside of that required by the study. The study was completed over 4 separate days: (Day 1) 25-min bout of rest prior to dominant arm (right arm) motor practice under the visuomotor rotation (acquisition), immediately followed by a non-dominant (left arm) inter-limb transfer test; (Day 2) to assess learning, a no-exercise 24-h retention test with the dominant and non-dominant arms was performed; (Day 3) at a minimum of 2 weeks later, participants returned to perform

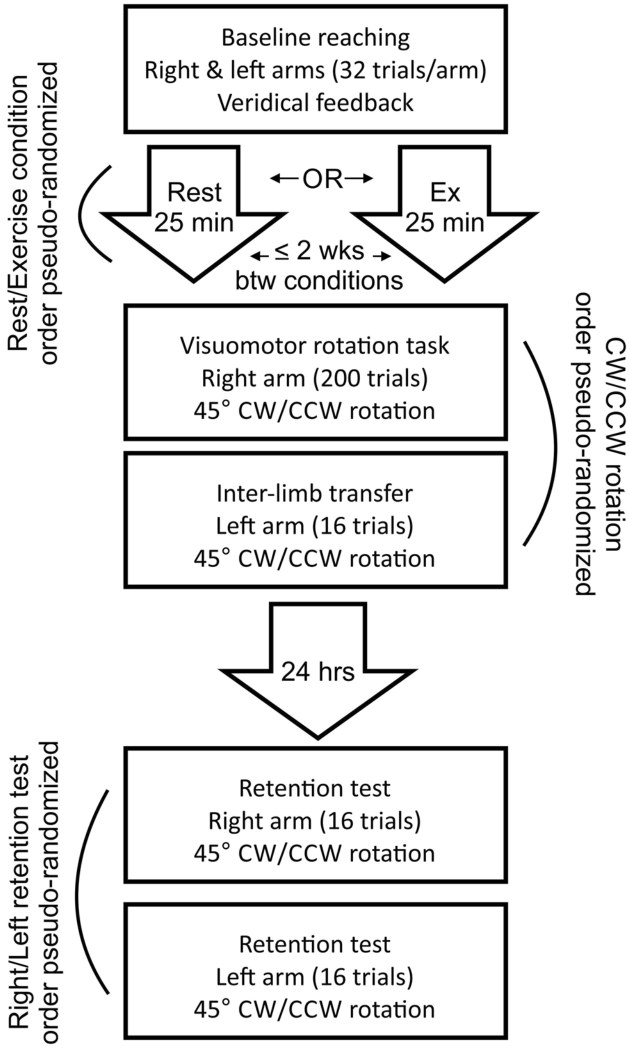


Fig. 1 Overview of experimental procedures. Participants performed two experimental sessions separated by a minimum of 2 weeks. Each experimental session involved reaching to visual targets with veridical visual feedback with both arms for 32 trials. This was followed by a period of quiet rest or moderate-intensity cycling exercise on a cycle ergometer for 25 min. Immediately after rest or exercise, participants performed 200 trials reaching to visual targets with rotation cursor feedback of hand position (45° CW/CCW) with the right (dominant) hand. Inter-limb transfer was tested with the left arm under the same rotated cursor feedback for 16 trials. Participants returned 24 h later (±2 h) to perform a retention test for both the right and left arms (order pseudo-randomized) under the same visuomotor rotation as the previous day. *Ex* exercise, *Wks* weeks. *Btw* between, *CW* clockwise, *CCW* counter-clockwise

a 25-min acute bout of cycling exercise prior to dominant arm motor practice under the visuomotor rotation (acquisition), immediately followed by a non-dominant inter-limb transfer test; and (Day 4) to assess learning, a no-exercise 24-h retention test with the dominant and non-dominant arms was performed (Fig. 1). There was a minimum washout period of 14 days between visuomotor adaptation under the different experimental conditions (i.e., rest or exercise). On each experimental session, participants experienced a 45° clockwise (CW) or counter-clockwise (CCW) visual rotation throughout the acquisition, inter-limb transfer and retention tests of that particular condition. Participants were pseudo-randomly assigned to either experimental condition (exercise or rest) order, such that half of the participants experienced either condition first. Additionally, on the 24-h no-exercise retention test, the order in which participants performed the right or left arm test was pseudo-random.

Assessment of usual levels of physical activity

Usual levels of physical activity were assessed using the International Physical Activity Questionnaire (IPAQ; Booth 2000), which assesses physical activity undertook during leisure time, domestic and gardening activities, and work-related and transport-related activities. The specific types of activity are classified into three categories: (1) walking, (2) moderate-intensity activities, and (3) vigorous-intensity activities. Frequency (days per week) and duration (time per day) are collected separately for each specific activity category. The total score used to describe physical activity was computed as the weighted sum of the duration (in min) and frequency (in days) of walking, moderate-intensity, and vigorous-intensity activity. Each type of activity was weighted by its energy requirements defined in Metabolic Equivalent of Task (MET): 3.3 METs for walking, 4.0 METs for moderate physical activity, and 8.0 METs for vigorous physical activity (Ainsworth et al. 2000). The total score of the IPAQ correlates with objective measures of physical activity, such as maximal treadmill time (Papathanasiou et al. 2010), accelerometer data (Craig et al. 2003; Mäder et al. 2006), pedometer data (Deng et al. 2008), and actimeter data (Scheeres et al. 2009). Further, as usual level of physical activity as measured by the IPAQ has been associated with motor skills (Boisgontier et al. 2017), we collected these data as a control variable in the current study.

Exercise protocol

The 25-min exercise bout was conducted on a cycle ergometer (Ergoselect 200; Ergoline, Bitz, Germany) and heart rate was visually monitored using a wrist-mounted monitor (Polar Electro; Oy, Kempele, Finland). Participants performed a 5-min warm-up (50 W, self-selected cadence) followed by 20 min of continuous stationary biking at 65–70% of their age-predicted maximal heart rate (average range = 129–139 beats per min [bpm]) while maintaining a cadence between 70 and 90 rotations per min. Throughout the exercise session, Borg's 6–20 scale of rating of perceived exertion (RPE) (Borg 1998) was verbally reported by the participant, and heart rate was continuously monitored and recorded by the experimenters, every 5 min. Participants kept their hands relaxed (not gripping the handlebars) with their arms resting on top of the handlebars during the session to avoid any contraction and/or fatigue of the non-exercised upper limbs involved in the visuomotor rotation task. We have consistently shown that the moderate-intensity bout of leg cycling exercise used in the current study does not produce significant muscle activity in the arm (Singh et al. 2014a) and hand muscles (Singh et al. 2014b; Neva et al. 2017).

Visuomotor rotation task

Participants made out-and-back reaching movements using the End-Point KINARM robotic manipulandum (Fig. 2a) by moving a cursor from a central target to a peripheral target and then reaching back to the central target after it reappeared. During all reaching tasks, participants were unable to see their arms or hands. Real-time hand feedback was displayed as a white circular cursor on a reflective horizontal surface along with all visual targets (Fig. 2b). Cursor feedback of hand position was provided during the reach out to peripheral targets, and not provided on the reach back to center until the hand was within a 2-cm radius of the central target. For all reaching tasks, participants were instructed to reach as quickly and accurately as possible. With further clarification that 'as quickly as possible' meant to begin, quickly reaching to the presented target as soon as it appeared, and as 'accurately as possible' meant to perform reaching movements that made the

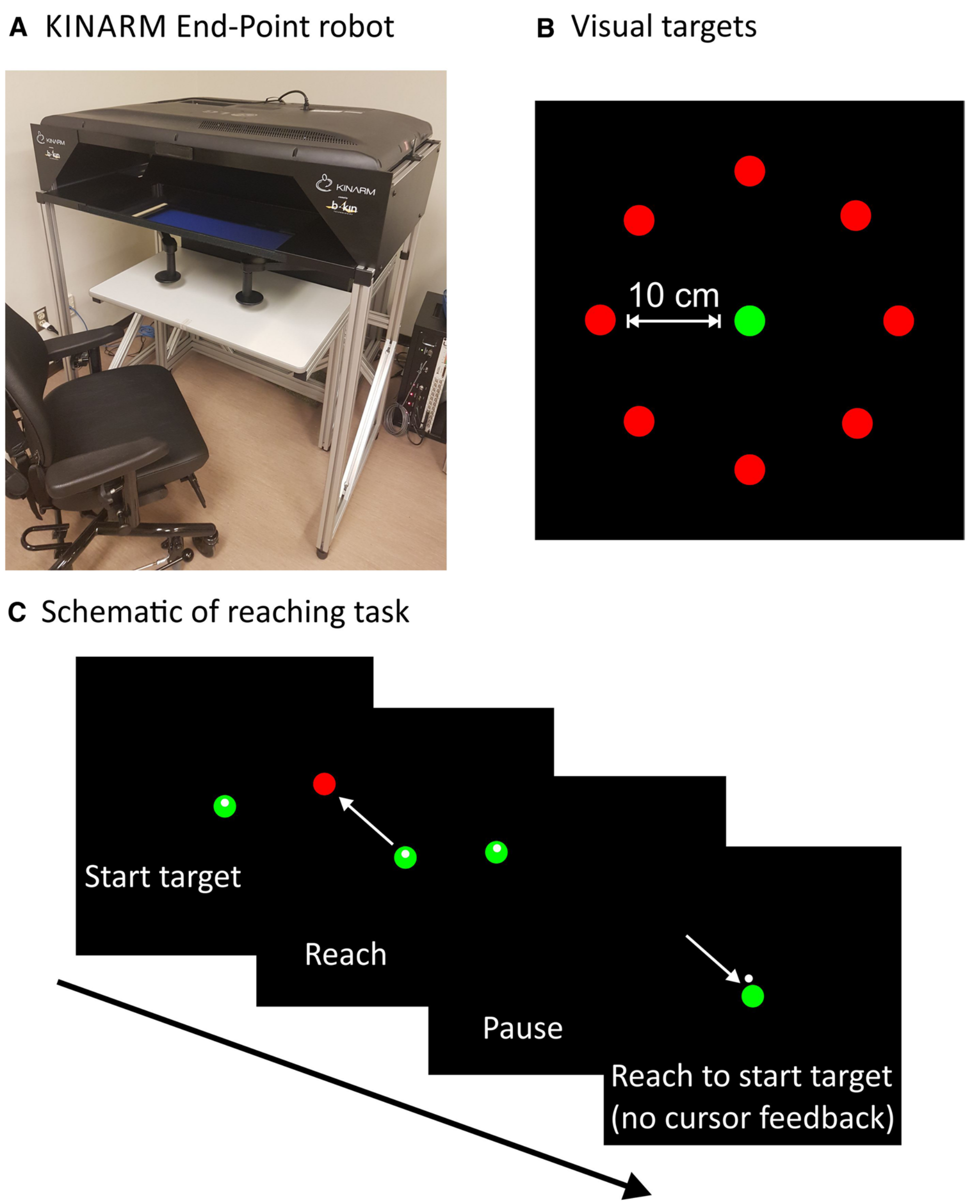


Fig. 2 Apparatus and visuomotor rotation task. **a** KINARM End-Point bilateral robot manipulandum. **b** Visual targets. Despite all targets displayed in this image, only the central target followed by one peripheral target was displayed during each trial. Central start target is shown in green and peripheral targets are shown in red. All trials began with a reach to the central start target, which then was followed by the appearance of one of the 8 peripheral targets. Targets are displayed in red and once the participant reaches the target (by placing the white cursor representing veridical or rotated hand position) it turns green. **c** Schematic of reaching task. Participants began by reaching to the start target. A peripheral target appeared, which signaled to participants to reach the target as quickly and accurately as possible. Participants pause for a brief moment before the central start target reappeared, then participants reached back to the start target without cursor feedback (until within a 2 cm radius of the start target). White circular cursor represents hand position

white cursor (representing hand position) move in an ideal (straight) path to the target.

All 8 peripheral targets were radially spaced 45° apart, with all visual targets 10 cm away from the central target (Fig. 2b). The workspaces for the right and left arm were horizontally spaced 44 cm apart based on the location of the central start target with symmetrical spacing of peripheral visual targets. This ensured that the right and left arm reaching tasks, and presented visual targets, were in separate workspaces. Participants reached the presented central target location, which was the first go-cue. Once participants reached the central start location, the next go-cue was the presentation of the peripheral target location. Participants held the peripheral target location for 500 ms until the central target reappeared and a movement was made back to it. No time constraints were placed on the return to the central start location. A successful trial involved a movement from the centre to a peripheral target, which appeared red and turned green once the participant moved the cursor representing hand position into the target. An unsuccessful trial occurred if participants did not reach the peripheral target within 5 s; however, this did not occur with any of our participants. The visual targets were 1 cm in diameter displayed in red, while the cursor feedback of hand/robot arm position was 0.5 cm in diameter and displayed in white. The movements made by the participants were congruent with the projected image of the cursor in a 1:1 fashion, such that a movement of 5 cm with the robot arm produced a 5 cm movement of the cursor on the screen (Fig. 2c).

Participants performed 4 reaching tasks to visual targets in the following order: (1) reaching with veridical feedback with both the dominant (right) and non-dominant (left) arms for 32 trials each, which served as familiarization trials (Krakauer et al. 2000; Taylor et al. 2014), (2) dominant (right) arm reaching with 45° CW or CCW rotated cursor feedback about the central target for 200 trials, (3) non-dominant (left) arm reaching with the same rotated cursor feedback as experienced in (2) for 16 trials, and (4) 24 h later both dominant (right arm) and non-dominant (left arm) reaching with the same rotated cursor feedback as experienced in (2) and (3) for 16 trials each. The CW/CCW rotation was applied for reaching movements to peripheral visual targets as well as for the return to the central start location, although visual feedback of cursor position was not provided for the reach back until the cursor was within a 2-cm radius of the central start location. For all reaching tasks, the order of targets was pseudo-randomized, such that, within each block of 8 trials, all 8 peripheral target locations were presented once in random order. In total, the session on Day 1 took ~ 1.5 h including the 25-min exercise or rest condition, and the session on Day 2 took approximately ~ 10 min. The second condition, which occurred at a minimum of 14 days after the first session, involved participants performing the visuomotor rotation task under the equal and opposite rotation (45° CW vs. 45° CCW) as the previous session, such that half of the participants experienced the 45° CW (or 45° CCW) rotation for the exercise condition and the other half experienced the 45° CCW (or 45° CW) in the rest condition first. Previous work showed that a 24-h interval between experiencing equal and opposite visuomotor rotations ensures that there is no interference or carry-over effects from the previous session; therefore, a 14-day time period between equal and opposite visuomotor rotation training likely prevented potential inference (Tong and Flanagan 2003).

Data processing and analysis

Data processing

Hand position data were collected on a KINARM, sampled at a rate of 1 kHz and digitally smoothed using a fourth-order, low-pass Butterworth filter with a cutoff frequency of 14 Hz. All trials for all reaching tasks were screened with respect to their velocity profile, movement trajectory, and end-point position using custom MATLAB scripts (MATLAB R2016a, MathWorks, Natick, MA, USA). Trials with reaction time, movement time, peak lateral displacement and angle at peak velocity greater than 3 standard deviations from the mean were discarded (accounting for 0.5% of the total trials). The outward reach was analyzed from the central to peripheral targets with respect to the cursor position. The return back to center was not analyzed. The kinematic accuracy measures (peak lateral displacement and angle at peak velocity) for the CW and CCW rotations were rectified so that errors could be quantified in the same direction for each condition (exercise vs. rest) to allow statistical comparisons. This approach has also been used in previous research (Wang and Sainburg 2003, 2004). The kinematic measure of interest was the peak lateral displacement, indicating the point in cursor path trajectory at the furthest perpendicular distance from the ideal straight path to the peripheral target from the central start location (in cm). This type of metric has been shown to yield similar results as other kinematic measures such as angular error and path length (Shadmehr and Brashers-Krug 1997; Thoroughman and Shadmehr 1999; Mattar and Gribble 2005; Shabbott and Sainburg 2009; Huang and Ahmed 2014). As a secondary measure, we analyzed angle at peak velocity, which measures the angular error of cursor position relative to an ideal straight path to the peripheral target at the fastest point in movement. Lastly, we analyzed reaction time and movement time as tertiary measures of performance for comparison to other similar studies investigating the effects of acute exercise on acquisition and learning (Roig et al. 2012; Skriver et al. 2014; Mang et al. 2014; Statton et al.

2015). Reaction time was defined as the time (in seconds) between target appearance and initial cursor movement off of the center target, and movement time was defined as the time (in seconds) when the cursor reached the peripheral visual target.

Statistical analysis

The extent to which condition (exercise vs. rest) and reaching across trials (trial number) explained performance on the visuomotor rotation task and how the factors interacted were analyzed using linear mixed models. These models provide a better framework than traditional regression analyses (Boisgontier and Cheval 2016). Unlike traditional analysis of variance, linear mixed models take into account both the nested and crossed structure of the data, thereby providing results with lower type I error rates, i.e., stronger reliability (Baayen et al. 2008). Linear mixed models also avoid information loss due to averaging over trials (Judd et al. 2012). Moreover, treating both participants and target directions (Fig. 2) as random effects allows generalizing the results not only to the population of participants but also to the population of target directions (Barr et al. 2013). We built a dataset with repeated nested measurements crossed with each condition to create linear mixed models with crossed random factors. Four linear mixed models were built for visuomotor adaptation of the right arm, transfer to the untrained left arm, and retention performance of the right and left arm for each dependent measure (peak lateral displacement, angle at peak velocity, reaction time, and movement time) using R (Core Team 2017) and the lme4 package, version 1.1–14 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) package, version 2.0–36 (http://www.r-project.org/). As the usual level of physical activity as measured by the IPAQ has been associated with motor skills (Boisgontier et al. 2017), this variable was standardized and included in the models as a control variable. Whether the effect of performance at the visuomotor rotation task across trials was modulated by prior exercise was also tested by including an interaction term in the equation. P values were calculated based on Satterthwaite's approximations for degrees of freedom. As target deviation scores were skewed, this variable was normalized using the Box–Cox transformation (Box and Cox 1964). The Box–Cox transformation represents a family of power transformations that incorporates and extends the traditional methods (e.g., square root, log, inverse) to find the optimal normalizing transformation for each variable. As such, Box–Cox represents a potential best practice to normalize the data (Osborne 2010). An estimate of the effect size was reported using the conditional pseudo-R^2, which was computed using the MuMin package, version 1.40.4 of the R software (Nakagawa and Schielzeth 2013).

Results

Descriptive results

During the 20 min moderate-intensity exercise bout, average heart rate was 137.5 ± 4.3 bpm and average RPE was 12.6 ± 0.95, which corresponds to between 'light' and 'somewhat hard' perceived exertion. All participants demonstrate moderate to high levels of physical activity according to the IPAQ (Craig et al. 2003), with a mean (± SEM) metabolic equivalents-min/week of 3461 ± 1848. Figure 3 displays the arm-reaching data for each dependent measure for all participants, conditions and days, with each data point representing a mean of a block of 8 trials.

Reaching with veridical cursor feedback

Figure 3 displays average baseline reaching errors for the left and right arms when reaching visual targets with veridical feedback (see Fig. 3, dotted horizontal lines displaying aligned cursor feedback performance). The mean baseline performance for the *exercise* condition for the *left* arm (peak lateral displacement, mean = 0.88 cm, SD = 0.47; angle at peak velocity, mean = 5.7°, SD = 4.7; reaction time, mean = 354 ms, SD = 58; movement time, mean = 285 ms, SD = 135) and *right* arm (peak lateral displacement, mean = 0.88 cm, SD = 0.46; angle at peak velocity, mean = 5.6°, SD = 4.6; reaction time, mean = 354 ms, SD = 68; movement time, mean = 279 ms, SD = 132), and for the *rest* condition for the *left* arm (peak lateral displacement, mean = 0.87 cm, SD = 0.43; angle at peak velocity, mean = 5.4°, SD = 4.1; reaction time, mean = 364 ms, SD = 57; movement time, mean = 290 ms, SD = 124) and *right* arm (peak lateral displacement, mean = 0.83 cm, SD = 0.45; angle at peak velocity, mean = 5.2°, SD = 3.9; reaction time, mean = 367 ms, SD = 56; movement time, mean = 295 ms, SD = 129) were similar to each other and are comparable to that previously reported (Krakauer et al. 1999, 2000; Wang and Sainburg 2003, 2004; Neva and Henriques 2013). To ensure baseline reaching performance that is similar in both conditions (exercise or rest), we tested each dependent measure (peak lateral displacement, angle at peak velocity, reaction time and movement time) and found no difference between conditions (all ps < 0.14) or arms (all ps < 0.54). Since baseline reaching errors were not different between conditions (exercise and rest) or between arms (left and right) we are confident that baseline reaching performance did not influence adaptation to the visuomotor rotation task.

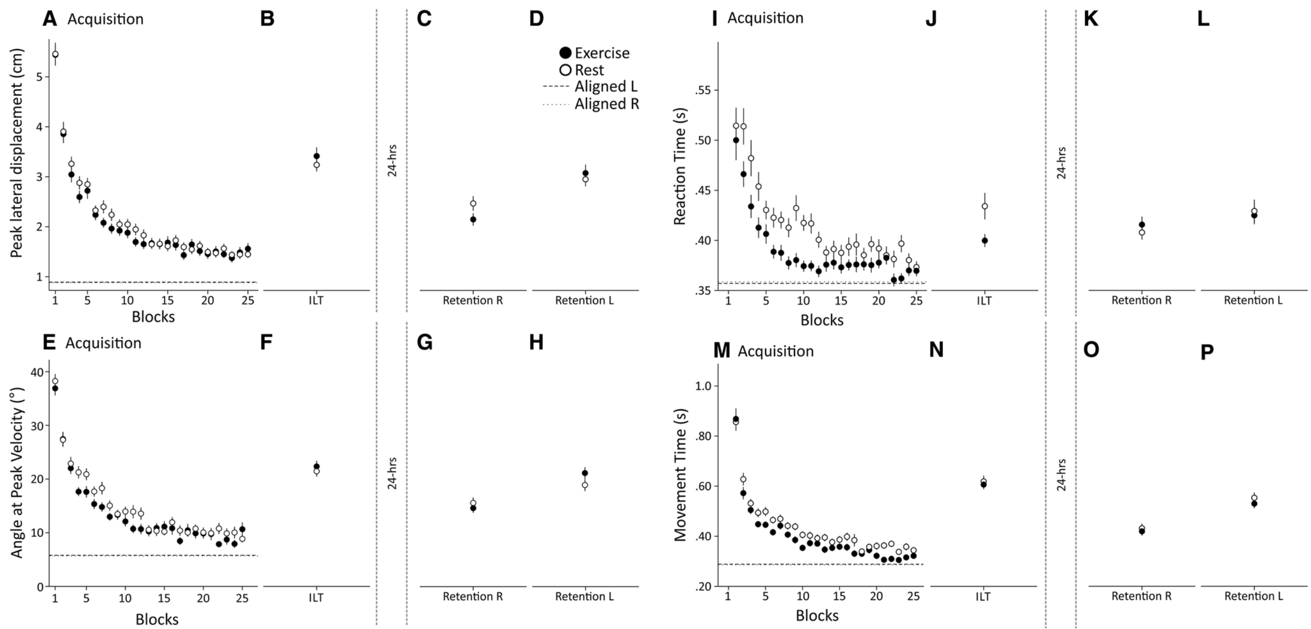


Fig. 3 Average results of peak lateral displacement (top left panel), angle at peak velocity (bottom left panel), reaction time (middle panel) and movement time (bottom panel). **a–d** Average peak lateral displacement results for both exercise (black circles) and rest (white circles) conditions for acquisition (**a**), inter-limb transfer (**b**), and 24-h retention of right (**c**) and left (**d**) arm reaching. **e–h** Average angle at peak velocity results for both exercise (black circles) and rest (white circles) conditions for acquisition (**e**), inter-limb transfer (**f**), and 24-h retention of right (**g**) and left (**h**) arm reaching. **i–l** Average reaction time results for both exercise (black circles) and rest (white circles) conditions for acquisition (**i**), inter-limb transfer (**j**), and 24-h retention of right (**k**) and left (**l**) arm reaching. **m–p** Average movement time results for both exercise (black circles) and rest (white circles) conditions for acquisition (**m**), inter-limb transfer (**n**), and 24-h retention of right (**o**) and left (**p**) arm reaching. Black dotted horizontal lines represent left-arm and grey dotted horizontal lines represent right-arm aligned visual feedback reaching before exercise/rest. Each data point represents a block of 8 trials. Error bars represent standard error of the mean (±). *ILT* inter-limb transfer, *R* right arm, *L* left arm

Reaching with rotated cursor feedback

Peak lateral displacement

As acquisition of the visuomotor rotation task using the right arm was not linear across trials, a quadratic term was included in the models to account for this non-linearity of the distribution. The model testing the acquisition with the right arm immediately after exercise or rest (Table 1) showed significant fixed effects of condition ($b = -0.059$, $p < 3\times10^{-5}$; Table 1; Fig. 4a, top left panel) and trial^2 ($b = 0.156$, $p < 2\times10^{-16}$; Table 1) but no interaction between these effects ($b = -0.016$, $p = 0.200$). Importantly, although there appears to be a faster decrease in peak lateral displacement in the exercise condition compared to rest, this is not reflected statistically by an interaction between condition and trial. Further, we demonstrate that exercise and rest adapted to a similar extent by the end of acquisition with no difference in peak lateral displacement during the last bock of acquisition ($p = 0.76$). Therefore, this indicates that overall peak lateral displacement was lower following exercise compared to rest during acquisition of the visuomotor rotation task. The model testing the initial inter-limb transfer to the left arm (Table 1) showed a significant effect of trial ($b = -0.005$, $p < 9\times10^{-6}$) but no significant effect of condition ($b = 0.058$, $p = 0.473$) and no interaction between these terms ($b = 0.012$, $p = 0.435$). An additional model indicated significantly lower peak lateral displacement during the inter-limb transfer test compared to the initial (first block) performance during acquisition regardless of condition ($b = 0.403$, $p < 2\times10^{-16}$), demonstrating transfer of performance of the trained right arm adaptation to the untrained left arm as previous work has shown (Dionne and Henriques 2008). The model testing the retention of the visuomotor rotation task with the right arm (Table 1) showed a significant effect of condition ($b = -0.205$, $p = 0.033$; Fig. 4b) and trial ($b = -0.060$, $p < 1\times10^{-7}$), with no interaction between these terms ($b = -0.029$, $p = 0.132$). This indicates that peak lateral displacement was lower in the exercise condition compared to rest when tested at 24 h. An additional model indicated that peak lateral displacement was lower at the right arm retention test compared to the initial (first block) performance in acquisition ($b = -0.751$, $p < 2\times10^{-16}$), demonstrating recall of visuomotor adaptation with the right arm regardless of condition ($b = -0.0057$, $p = 0.898$). Finally, the model testing left arm

Table 1 Results of the linear mixed models testing the effect of trial and exercise on the peak lateral displacement while controlling for levels of physical activity (IPAQ)

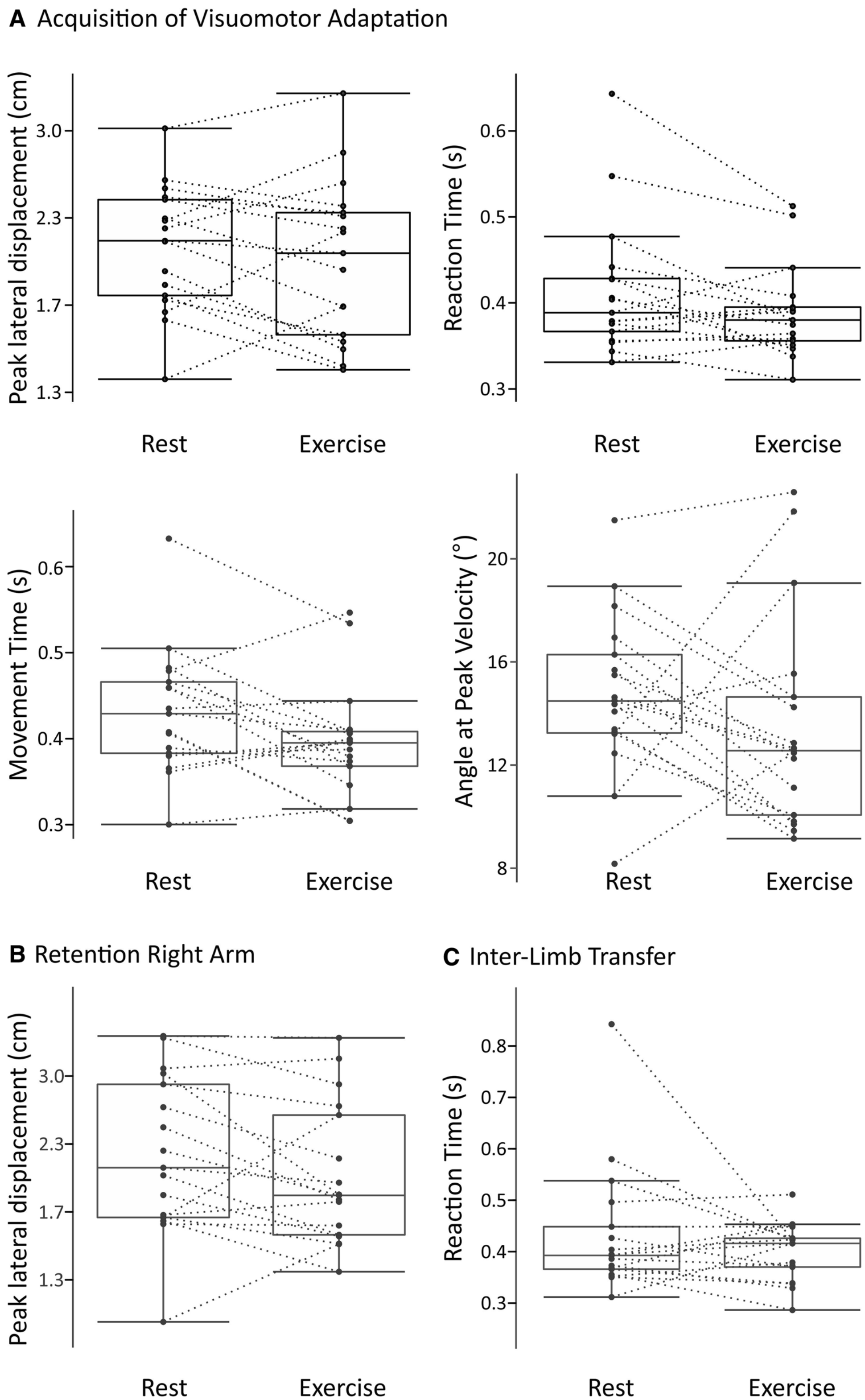
Fixed effects	Day 1								Day 2							
	Acquisition				Inter-limb transfer				Retention right				Retention left			
	b	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*
Intercept	−3.495	0.059	22	$<2\times10^{-16}$***	−2.782	0.079	63	$<2\times10^{-16}$***	−3.096	0.090	71	$<2\times10^{-16}$***	−2.777	0.083	71	$<2\times10^{-16}$***
Physical activity	0.028	0.054	17	0.614	−0.015	0.054	17	0.781	0.052	0.060	17	0.398	0.021	0.057	17	0.716
Trial	−0.329	0.009	6776	$<2\times10^{-16}$***	−0.005	0.011	252	$<9\times10^{-6}$***	−0.060	0.013	251	$<1\times10^{-7}$***	−0.075	0.013	255	$<2\times10^{-8}$***
Trial^2	0.156	0.009	6776	$<2\times10^{-16}$***												
Exercise (vs. rest)	−0.059	0.014	6776	$<2\times10^{-5}$***	0.058	0.080	251	0.473	−0.205	0.096	252	0.033*	0.066	0.091	255	0.466
Trial × exercise	−0.001	0.012	6776	0.923	0.012	0.016	252	0.453	−0.029	0.019	253	0.132	0.016	0.018	255	0.360
Trial^2 × exercise	−0.016	0.013	6776	0.200												
Random effects			σ^2			σ^2				σ^2				σ^2		
Participant																
Intercept			0.049			0.045				0.053				0.048		
Direction																
Intercept			0.004			0.003				0.003				< 0.001		
Residual			0.149			0.090				0.127				0.116		
Effect size R_c^2			0.439			0.396				0.416				0.387		

The sample of participants and directions are treated as random effects, thereby generalizing the results to the entire population of participants and targets

SE standard error, *df* degrees of freedom

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Fig. 4 Significant results shown with boxplots during acquisition (**a**), 24-h retention (**b**) and **c** inter-limb transfer. **a** Top Left panel shows the effect of condition (rest vs. exercise) on the peak lateral displacement during acquisition. Top right panel shows the effect of condition (rest vs. exercise) on reaction time. Bottom left panel shows the effect of condition (rest vs. exercise) on movement time. Bottom right panel shows the effect of condition (rest vs. exercise) on angle at peak velocity. **b** Shows the effect of condition (rest vs. exercise) on peak lateral displacement of right retention. **c** Shows the effect of condition (rest vs. exercise) on reaction time of inter-limb transfer. The middle line of the boxplot = median, lower hinge = 25% quantile, upper hinge = 75% quantile, lower whisker = smallest observation greater than or equal to lower hinge − 1.5 × interquartile range, upper whisker = largest observation less than or equal to upper hinge + 1.5 × interquartile range. The dots represent the averaged data for each participant per condition across all trials



retention performance (Table 1) showed a significant effect of trial ($b = -0.075$, $p < 1 \times 10^{-8}$) but no effect of condition ($b = 0.066$, $p = 0.466$) and no interaction between these terms ($b = 0.016$, $p = 0.360$).

Angle at peak velocity

We employed a quadratic term to account for non-linearity of the distribution in the angle of peak velocity during acquisition. The model testing the acquisition with the right arm immediately after exercise or rest (Table 2) showed significant fixed effects of condition ($b = -0.230$, $p < 2 \times 10^{-4}$; Table 2; Fig. 4a, bottom right panel) and trial^2 ($b = 0.576$, $p < 2 \times 10^{-16}$; Table 2) but no interaction between these effects ($b = -0.026$, $p = 0.655$). While visually there appears to be a faster decrease in angle at peak velocity in the exercise condition compared to rest, this is not reflected by an interaction between condition and trial. Further, we demonstrate that exercise and rest adapted to a similar extent by the end of acquisition with no difference in angle at peak velocity during the last bock of acquisition ($p = 0.38$). This indicates that overall angle at peak velocity was lower following exercise compared to rest during acquisition of the visuomotor rotation task. The model testing the initial inter-limb transfer to the left arm (Table 2) showed a significant effect of trial ($b = -1.68$, $p < 2 \times 10^{-5}$) but no significant effect of condition ($b = 1.433$, $p = 0.606$) and no interaction between these terms ($b = 0.119$, $p = 0.829$). An additional model indicated significantly lower angle at peak velocity during the inter-limb transfer test compared to the initial (first block) performance during acquisition regardless of condition ($b = 15.1$, $p < 2 \times 10^{-16}$), demonstrating transfer of the trained right arm adaptation to the untrained left arm as previous work showed (Dionne and Henriques 2008).The model testing the retention of the visuomotor rotation task with the right arm (Table 2) showed a significant effect of trial ($b = -1.59$, $p < 6 \times 10^{-6}$), with no effect of condition ($b = -3.73$, $p = 0.130$) and no interaction between these terms ($b = -0.613$, $p = 0.209$). Finally, the model testing left arm retention performance (Table 2) showed a significant effect of trial ($b = -1.87$, $p < 4 \times 10^{-6}$) but no effect of condition ($b = -1.91$, $p = 0.501$) and no interaction between these terms ($b = -0.071$, $p = 0.900$).

Reaction time

Acquisition of the visuomotor rotation task of the right arm was not linear across trials for reaction time and, thus, a quadratic term was included in the models to account for this non-linearity of the distribution. The model testing the acquisition with the right arm immediately after exercise or rest (Table 3) showed a significant fixed effect of condition ($b = -0.036$, $p < 2 \times 10^{-16}$; Table 3; Fig. 4a, top right panel) and trial^2 ($b = 0.016$, $p < 9.8 \times 10^{-14}$; Table 3) but no interaction between these effects ($b = -0.0035$, $p = 0.238$). Without a significant interaction, this indicates an overall decreased reaction time following exercise compared to rest during acquisition of the visuomotor rotation task. Importantly, we demonstrate that the exercise and rest conditions decreased reaction time to a similar extent by the end of acquisition with no performance difference during the last bock of acquisition ($p = 0.73$). The model testing the initial inter-limb transfer to the left arm (Table 3) showed a significant effect of condition ($b = -0.052$, $p = 0.045$; Fig. 4c), but no significant effect across trials ($b = -0.002$, $p = 0.627$) and no interaction between these terms ($b = -0.004$, $p = 0.443$). This indicates a decreased reaction time during the inter-limb transfer test following exercise compared to rest immediately after acquisition. An additional model indicated significantly decreased reaction time during the inter-limb transfer test compared to the initial (first block) performance during acquisition regardless of condition ($b = 0.105$, $p < 2.4 \times 10^{-7}$), demonstrating transfer of the trained right arm performance to the untrained left arm. The model testing the retention of the visuomotor rotation task with the right arm (Table 3) did not show a significant effect of condition ($b = -0.024$, $p = 0.194$), with a significant effect of trial ($b = 0.011$, $p < 6 \times 10^{-5}$; Table 3) and no interaction between these terms ($b = 0.004$, $p = 0.324$). The model testing left arm retention performance (Table 3) showed no significant effect of trial ($b = -0.004$, $p = 0.332$), condition ($b = -0.002$, $p = 0.949$) and no interaction between these terms ($b = 0.001$, $p = 0.803$).

Movement time

Again a quadratic term was included in the models to account for non-linearity of the distribution of the data during acquisition. The model testing acquisition of the visuomotor rotation task with the right arm immediately after exercise or rest (Table 4) showed a significant fixed effect of condition ($b = -0.032$, $p = 0.0005$; Table 4; Fig. 4a, bottom left panel) and trial^2 ($b = 0.042$, $p < 2 \times 10^{-16}$; Table 4) but no interaction between these effects ($b = -0.0009$, $p = 0.889$). Without a significant interaction, these data show an overall decreased movement time following exercise compared to rest during acquisition of the visuomotor rotation task. However, we demonstrate that the exercise and rest conditions decreased movement time to a similar extent by the end of acquisition with no performance difference during the last bock of acquisition ($p = 0.24$). The model testing the initial inter-limb transfer to the left arm (Table 4) showed no significant effect of condition ($b = -0.035$, $p = 0.542$), a significant effect of across trials ($b = -0.029$, $p = 0.0004$) and no interaction between these terms ($b = -0.005$, $p = 0.663$). An additional model indicated significantly decreased movement time during the inter-limb transfer test compared to the initial (first block) performance during acquisition regardless of condition ($b = 0.273$, $p < 1.01 \times 10^{-10}$), demonstrating transfer of the trained right arm performance to the untrained left arm. The model testing the retention of the visuomotor rotation task with the right arm (Table 4) did not show a significant effect of condition ($b = 0.062$, $p = 0.166$), with a significant effect across trials ($b = 0.023$, $p = 0.0003$; Table 3), and no interaction between these terms

Table 2 Results of the linear mixed models testing the effect of trial and exercise on angle at peak velocity while controlling for levels of physical activity (IPAQ)

Fixed effects	Day 1								Day 2							
	Acquisition				Inter-limb transfer				Retention right				Retention left			
	b	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*
Intercept	3.202	0.176	22	$<2\times10^{-12}$***	2.259	0.079	63	$<2\times10^{-16}$***	2.072	0.02	71	$<2\times10^{-16}$***	2.33	0.33	71	$<2\times10^{-16}$***
Physical activity	0.114	0.099	17	0.268	0.988	1.2	17	0.424	1.35	0.99	17	0.190	1.76	1.35	17	0.209
Trial	−1.28	0.040	6776	$<2\times10^{-16}$***	−1.68	0.389	252	$<2\times10^{-5}$***	−1.59	0.343	251	$<1\times10^{-6}$***	−1.87	0.398	255	$<4\times10^{-6}$***
Trial^2	0.576	0.040	6776	$<2\times10^{-16}$***												
Exercise (vs. rest)	−0.230	0.062	6776	$<2\times10^{-4}$***	−1.434	2.78	252	0.606	3.73	2.45	252	0.130	−1.91	2.84	255	0.501
Trial × exercise	−0.016	0.057	6776	0.778	0.119	0.550	252	0.829	−0.613	0.487	253	0.209	−0.071	0.563	255	0.900
Trial^2 × exercise	−0.026	0.057	6776	0.655												
Random effects	σ^2				σ^2				σ^2				σ^2			
Participant																
Intercept	0.159				4.245				3.391				4.89			
Direction																
Intercept	0.158				1.223				2.236				<0.001			
Residual	3.07				10.36				9.116				10.64			
Effect size R^2_c	0.290				0.243				0.313				0.296			

The sample of participants and directions are treated as random effects, thereby generalizing the results to the entire population of participants and targets

SE standard error, *df* degrees of freedom

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 3 Results of the linear mixed models testing the effect of trial and exercise on reaction time while controlling for levels of physical activity (IPAQ)

Fixed effects	Day 1								Day 2							
	Acquisition				Inter-limb transfer				Retention right				Retention left			
	b	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*
Intercept	0.421	0.015	20	$<2\times10^{-16}$***	0.392	0.025	85	$<2\times10^{-16}$***	0.463	0.018	74	$<2\times10^{-16}$***	0.442	0.024	80	$<2\times10^{-16}$***
Physical activity	0.003	0.015	17	0.819	0.001	0.018	17	0.938	−0.009	0.012	17	0.470	−0.009	0.017	17	0.564
Trial	−0.0005	0.0003	6776	$<2\times10^{-16}$***	−0.002	0.004	252	0.627	−0.011	0.003	251	$<6\times10^{-5}$***	−0.004	0.004	253	0.332
Trial^2	0.016	0.002	6776	$<9\times10^{-14}$***												
Exercise (vs. rest)	−0.04	0.004	6776	$<2\times10^{-16}$***	−0.052	0.004	251	0.045*	−0.024	0.018	252	0.194	−0.002	0.027	252	0.949
Trial × exercise	−0.0007	0.0004	6776	0.109	−0.004	0.005	252	0.443	0.004	0.004	252	0. 324	0.001	0.005	253	0.803
Trial^2 × exercise	−0.004	0.037	6776	0.238												

Random effects	σ^2	σ^2	σ^2	σ^2
Participant				
Intercept	0.004	0.005	0.002	0.004
Direction				
Intercept	< 0.001	< 0.01	0.0002	< 0.01
Residual	0.008	0.009	0.005	0.010
Effect size R_c^2	0.330	0.370	0.386	0.272

The sample of participants and directions are treated as random effects, thereby generalizing the results to the entire population of participants and targets

SE standard error, *df* degrees of freedom

*$p<0.05$, **$p<0.01$, ***$p<0.001$

Table 4 Results of the linear mixed models testing the effect of trial and exercise on movement time while controlling for levels of physical activity (IPAQ)

Fixed effects	Day 1								Day 2							
	Acquisition				Inter-limb transfer				Retention right				Retention left			
	b	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*	*b*	SE	*df*	*p*
Intercept	0.517	0.017	20	$<2\times10^{-16}$***	0.731	0.047	85	$<2\times10^{-16}$***	0.521	0.040	74	$<2\times10^{-16}$***	0.672	0.044	114	$<2\times10^{-16}$***
Physical activity	0.016	0.014	17	0.271	−0.013	0.024	17	0.603	−0.004	0.024	17	0.885	−0.0002	0.021	17	0.992
Trial	−0.002	<0.001	6776	$<2\times10^{-16}$***	−0.029	0.008	252	0.0004**	−0.023	0.006	251	$<3\times10^{-4}$***	−0.032	0.008	253	$<3\times10^{-5}$***
Trial^2	0.042	0.004	6776	$<2\times10^{-16}$***												
Exercise (vs. rest)	−0.032	0.009	6776	$<5\times10^{-4}$***	−0.035	0.057	251	0.542	−0.062	0.045	252	0.167	−0.006	0.054	252	0.904
Trial × exercise	<0.001	0.0001	6776	0.551	−0.005	0.011	252	0.663	−0.011	0.009	252	0.210	0.004	0.011	253	0.729
Trial^2 × exercise	−0.0008	0.006	6776	0.890												

Random effects	σ^2	σ^2	σ^2	σ^2
Participant				
Intercept	0.003	0.007	0.008	0.005
Direction				
Intercept	<0.001	0.002	<0.001	0.001
Residual	0.039	0.044	0.028	0.040
Effect size R_c^2	0.202	0.238	0.325	0.221

The sample of participants and directions are treated as random effects, thereby generalizing the results to the entire population of participants and targets

SE standard error, *df* degrees of freedom

*$p<0.05$, **$p<0.01$, ***$p<0.001$

($b = -0.011$, $p = 0.210$). The model testing left arm retention performance (Table 4) showed a significant effect of trial ($b = -0.032$, $p < 3 \times 10^{-5}$), no effect of condition ($b = -0.0065$, $p = 0.904$) and no interaction between these terms ($b = 0.0037$, $p = 0.729$).

Discussion

To the best of our knowledge, this is the first study to demonstrate acute exercise-induced enhancement of motor adaptation, involving sensorimotor remapping (i.e., formation of a novel internal model), using kinematic and time-based measures of reaching movements. We showed that a single bout of leg cycling exercise, compared to rest, enhanced acquisition and learning of a visuomotor rotation task using arm-reaching movements. Additionally, a bout of exercise transiently decreased reaction time during inter-limb transfer of visuomotor adaptation but did not influence left-arm performance at retention. We discovered overall lower peak lateral displacement and angle at peak velocity during acquisition (but by a similar extent at the end of acquisition) for the exercise condition compared to rest. Further, the exercise condition demonstrated shorter reaction and movement times during acquisition, shorter reaction times during initial inter-limb transfer, and lower peak lateral displacement at the retention test compared to rest.

Exercise enhances skill acquisition of a visuomotor rotation task

Participants showed enhanced acquisition during the visuomotor rotation task when practice was preceded by a bout of moderate-intensity cycling exercise compared to rest. Specifically, both the kinematic measures of reaching accuracy (peak lateral displacement, angle at peak velocity) and time-based measures (reaction time and movement time) were enhanced following exercise. The current study extends previous work showing acute exercise enhances sequence motor learning (Mang et al. 2014; Statton et al. 2015), to demonstrate a single bout of exercise enhances the formation of a new internal model (sensorimotor mapping) for reaching movements (e.g., motor adaptation).

The visuomotor rotation task is widely used to measure motor adaptation, generalization, and longer term consolidation of reaching movements (Krakauer et al. 2000; Sainburg and Wang 2002; Wang and Sainburg 2003, 2005; Neva and Henriques 2013; Lei and Wang 2014), yet no previous study investigated whether acute exercise impacts visuomotor adaptation of arm-reaching movements. Most studies investigating the effects of exercise on enhanced motor sequence learning and visuomotor tracking focus on response time or spatial accuracy, usually involving the timing of movements (Roig et al. 2012; Skriver et al. 2014; Mang et al. 2014, 2016b; Statton et al. 2015; Thomas et al. 2016). However, a recent study included measures of kinematic accuracy of isolated wrist movements measured with a joystick visuomotor rotational task (Ferrer-Uris et al. 2017). Ferrer-Uris et al. (2017) showed that a bout of intense shuttle running performed prior to practicing a visual rotation task with wrist movements using a joystick enhanced early consolidation (1 h after practice), but not acquisition or learning (tested 24-h and 7 days later) (Ferrer-Uris et al. 2017). These results are inconsistent with previous results showing exercise-induced enhancements of motor sequence learning and visuomotor tracking studies (Roig et al. 2012; Skriver et al. 2014; Mang et al. 2014, 2016b; Statton et al. 2015; Thomas et al. 2016). This inconsistency may stem from differences in the type of exercise (shuttle run vs. cycling), the intensity of exercise (moderate, higher intensity), and the specific design of the visuomotor task (Ferrer-Uris et al. 2017). First, previous work showed that attentional resources devoted to cognitively demanding tasks, as well as task performance decreases after higher-intensity exercise, whereas it is optimally increased after moderate-intensity exercise (Kamijo et al. 2004, 2007). This notion is further supported by other recent work showing that high-intensity interval exercise does not enhance initial acquisition of motor skill practice (Roig et al. 2012; Mang et al. 2016b), whereas moderate-intensity exercise improves skill acquisition (Statton et al. 2015). The intense shuttle running (Ferrer-Uris et al. 2017) may have taxed cognitive resources to a greater extent than other studies involving seated cycling (Roig et al. 2012; Skriver et al. 2014; Mang et al. 2014, 2016b; Ostadan et al. 2016; Thomas et al. 2016) or moderate-intensity treadmill running (Statton et al. 2015), which could have impaired skill acquisition. Second, the nature of isolated wrist movements during the visuomotor rotational task may have influenced the lack of enhanced acquisition following exercise (Ferrer-Uris et al. 2017), as the majority of research with visuomotor rotation tasks involve some form of arm reaching movements (Krakauer et al. 2000; Mazzoni and Krakauer 2006; Galea et al. 2011; Neva and Henriques 2013; Taylor et al. 2014). In the current study, we addressed these potential confounders.

We found exercise-induced improvements in movement accuracy (peak lateral displacement, angle at peak velocity) along with decreased movement time and reaction time, which may be indicative of enhanced movement planning and cognitive strategy. However, previous work suggested that increases in reaction time during visuomotor adaptation tasks suggest heightened movement planning and an improved cognitive strategy (Saijo and Gomi 2010; Fernandez-Ruiz et al. 2011; Haith et al. 2015). In the current study, we showed a decreased reaction time with a concurrent increase in movement accuracy when individuals performed a bout of exercise before practicing the visuomotor rotation task. Taken together, our results suggest that a bout of exercise enhanced the efficiency in movement planning and reaching accuracy, which may be associated with previous work demonstrating higher levels of arousal and attention-related processes following exercise (Kamijo et al. 2004, 2007; Masley et al. 2009; Yanagisawa et al. 2010; Byun et al. 2014). Further, motor adaptation has been shown to involve cerebellar-to-motor communication as a unique form of model-based learning (Shadmehr and Brashers-Krug 1997; Wolpert et al. 1998; Krakauer et al. 1999; Haith and Krakauer 2013; Spampinato et al. 2017; Spampinato and Celnik 2018). Our previous work showed that acute cycling exercise decreases inhibition from the cerebellum to the non-exercised hand area of the motor cortex (Mang et al. 2016a), which may represent a network that supports acquisition of visuomotor rotation tasks. However, as we did not measure brain activity or cortical excitability this interpretation is speculative and beyond the scope of the current study. Future work could delineate the potential neural underpinnings of the exercise-induced enhancements of visuomotor adaptation.

Exercise enhances retention performance of trained arm visuomotor adaptation

We showed that a bout of cycling exercise performed prior to practicing reaching movements under a visuomotor rotation enhances retention performance compared to rest. Specifically, we discovered that exercise improved peak lateral displacement of reaching under the visual rotation, whereas reaction and movement time, and angle at peak velocity were unchanged. The current results extend previous knowledge that exercise enhances retention performance of motor sequence learning and other visuomotor skills (Roig et al. 2012; Mang et al. 2014, 2016b; Stavrinos and Coxon 2017) showing that learning a new internal model of reaching movements (i.e., visuomotor adaptation) is enhanced at a 24-h retention test. There are several potential explanations for our findings of exercise-induced enhancements in adaptation learning using the trained upper-limb.

Our specific findings of decreased peak lateral displacement with a lack of change in angle at peak velocity may indicate that the exercise condition enhanced processes of error correction after the time of peak velocity. This is the time when online correction of movement errors may be integrated. In contrast, the feedforward processes involved in changes of angle at peak velocity (Krakauer et al. 2000; Huang and Ahmed 2014) may have been unaffected by exercise 24-h later. However, this is speculative and future research could more comprehensively delineate online correction vs. feedforward processes that may be enhanced by exercise at a 24-h retention test. Further, we cannot discount the possibility that the exercise-induced enhancement in retention performance was influenced by the specific degree of rotation used in the current study (45°), which may lead to awareness of the rotation as compared to a smaller degree of rotation (e.g., 30°) (Taylor et al. 2014; Huberdeau et al. 2015).

It is possible that exercise modulated arousal and attention-related cortical areas as well as cerebellar regions (Yanagisawa et al. 2010; Macintosh et al. 2014; Rajab et al. 2014; Mang et al. 2016a). This may translate into enhanced skill acquisition and improved retention performance of the visuomotor rotation task with the trained arm. Additionally, modulations in intracortical neuronal circuits immediately after exercise (Singh et al. 2014a; Smith et al. 2014; Mooney et al. 2016; Lulic et al. 2017; Neva et al. 2017; Stavrinos and Coxon 2017) may contribute to enhanced acquisition of the skill at retention (Stavrinos and Coxon 2017). Therefore, it is possible that a bout of exercise paired with motor skill learning can create a neural environment for enhanced plasticity in motor-related areas, which may underlie retention of visuomotor adaptation in the current study. Future work could include neurophysiological measures to test these ideas directly.

Enhancement of visuomotor adaptation regardless of usual levels of physical activity

To the best of our knowledge, we are the first to find enhanced acquisition and retention of visuomotor adaptation regardless of levels of usual physical activity (as measured by the IPAQ). These findings are corroborated by recent work showing that regardless of scoring as sedentary or active on the IPAQ, a bout of cycling exercise decreases intracortical inhibition (Lulic et al. 2017). However, most individuals in the current study were moderately to highly physically active. Previous work has shown that physical activity levels may predict skilled motor performance of an unpracticed upper-limb task (Boisgontier et al. 2017); therefore, we cannot discount the possibility that our particular group of physically active individuals may benefit more than less active individuals from acute exercise on motor adaptation. Future work could consider investigating the influence of levels of physical activity and fitness on exercise-induced enhancement of motor adaptation.

The effect of exercise on inter-limb transfer

We found that adaptation to the visuomotor rotation task with the right arm transferred to the left arm regardless of prior exercise or rest. Interestingly, we discovered a subtle and transient enhancement of inter-limb transfer following right-arm visuomotor adaptation preceded by acute exercise compared to rest. Specifically, reaction time was faster in the exercise condition during inter-limb transfer, with no effect on movement time, peak lateral displacement or angle at peak velocity. Further, this effect was not present at the 24-h test of left arm performance for any dependent measure. Similar to our interpretation of enhanced retention performance, arousal and attention-related processes (Kamijo et al. 2004, 2007; Masley et al. 2009; Yanagisawa et al. 2010; Byun et al. 2014) enhanced by exercise during acquisition may have carried over to the inter-limb transfer test. However, with no enhancement in our accuracy measure or decreased movement time, this result should be interpreted with caution.

A potential explanation as to why we did not find an exercise-induced enhancement in our accuracy measures (peak lateral displacement, angle at peak velocity) is evidence suggesting that adaptation to a visuomotor rotation task with the trained arm depends more on developing an internal model of a novel sensorimotor map (model-based learning). In contrast, transfer of adaptation to the opposite limb depends more on a type of use-dependent and reinforcement learning (model-free learning) (Shadmehr and Mussa-Ivaldi 1994; Kagerer et al. 1997; Haith and Krakauer 2013; Wang et al. 2015; Wang and Lei 2015). Therefore, our results suggest that acute exercise facilitated the development of an internal model for the trained limb but did not impact use-dependent and reinforcement learning during the inter-limb transfer test. It is possible that we missed a more robust effect of exercise-enhanced inter-limb transfer due to very few practice trials with the untrained (left) limb. It is also possible that our lack of robust exercise-induced enhancement of inter-limb transfer was due to adaptation of the visuomotor rotation task in subject-specific coordinates and extra-personal coordinate frames (Krakauer et al. 2000; Carroll et al. 2014; Poh et al. 2017). This may be because inter-limb transfer could be driven by explicit processes rather than use-dependent or reinforcement learning (Poh et al. 2016). Exercise may have differentially influenced adaptation and inter-limb transfer based on intrinsic and extrinsic coordinates and may have modulated explicit and implicit learning processes uniquely. However, we did not intend to answer these specific questions as they are beyond the scope of the current study.

Limitations

There are limitations to this study. First, due to the design of our task we were not able to assess end-point (or final position) errors as in previous studies assessing inter-limb transfer of the visuomotor rotation task (Sainburg and Wang 2002; Wang and Sainburg 2004). Future work could consider altering the visuomotor rotation task to assess the effects of end-point errors in inter-limb transfer following exercise. Second, our findings of an exercise effect on inter-limb transfer may be influenced by the bout of acute exercise performed before visuomotor adaptation with the trained arm (right arm). Since we found an increased adaptation of the trained arm following exercise, we cannot discount the fact that this influenced our inter-limb transfer findings. Future work could consider performing exercise following visuomotor adaptation of the trained arm (where presumably all individuals would adapt to the same extent since there is no prior intervention like in the current study) to control for the extent of trained limb adaptation transferred to the untrained limb. Third, due to the within-subjects design, participants experienced the visuomotor rotation task on two separate occasions using both arms, which might have influenced visuomotor adaptation, inter-limb transfer, or retention. However, we controlled for this factor by having participants experience the equal and opposite degree of rotation (45° CW vs. 45° CCW) on the second session in a counter-balanced order. We also included a minimum washout period of 14 days, which is far beyond the 24-h intervening period showing no interference between equal and opposite rotations previously (Tong and Flanagan 2003). We also demonstrate little influence on visuomotor adaptation from the previous session as shown by the lack of difference in initial performance (first block of 8 trials) during acquisition of the visuomotor rotation task for all dependent measures (see Fig. 3a, e, i, m). Lastly, assessing the influence of acute exercise on rotation direction was out of the scope of the current study. However, future work could consider investigating this question as recent work has shown differential re-adaptation following practice with opposing rotations with both arms (Kumar et al. 2018).

Conclusions

Our data demonstrate that an acute bout of cycling exercise enhances acquisition and learning of a visuomotor adaptation skill with the trained arm, with a transient and subtle influence on reaction time during inter-limb transfer. These results contribute to a growing body of literature to demonstrate an acute bout of exercise can enhance motor adaptation of non-exercised arm reaching movements. These findings may have implications when prescribing exercise protocols to enhance the effects of motor adaptation tasks in clinical rehabilitation settings.

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Author contributions JLN conceived the study, primarily collected, processed and interpreted the data, wrote and edited the manuscript and contributed to data analysis. JAM contributed to data collection, processing, and edited the manuscript. DO contributed to data analysis and edited the manuscript. MPB primarily analyzed the data, contributed to interpretation of the results, and to writing and editing the manuscript. LAB contributed to the interpretation of data, and to writing and editing the manuscript.

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