










Fine motor control improves in older adults after 1 year of piano lessons: Analysis of individual development and its coupling with cognition and brain structure

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Abstract

Musical training can improve fine motor skills and cognitive abilities and induce macrostructural brain changes. However, it is not clear whether the changes in motor skills occur simultaneously with changes in cognitive and neurophysiological parameters. In this study, 156 healthy, musically naïve and right-handed older adults were recruited and randomly assigned to a piano training or a music listening group. Before, after 6 and 12 months, participants were scanned using MRI and assessed for fine motor skills, auditory working memory and processing speed. A Bayesian multilevel modelling approach was used to examine behavioural and neurophysiological group differences. The relationships between motor and cognitive and between motor and neurophysiological parameters were determined using latent change score models. Compared with music listening, practicing piano resulted in greater improvement in fine motor skills and probably working memory. Only in the piano group, unimanual fine motor skills and grey matter volume of the contralateral M1 changed together during the 6–12-month period. Additionally, M1 co-developed with ipsilateral putamen and thalamus. Playing piano induced more prevalent coupling between the motor and cognitive domains. However, there is little evidence that fine motor control develops concurrently with cognitive functions. Playing an instrument promotes motor, cognitive and neural development into older age. During the learning process, the consolidation of piano skills appears to take place in sensorimotor networks, enabling musicians to perform untrained motor tasks with higher acuity. Relationships between the

Abbreviations: BMLM, Bayesian multilevel modelling; C₀I, confidence interval; C_rI, credible interval; DCSM, dual change score modelling; DSB, Digit Span Backward test; DSY, Digit Symbol test; M1, primary motor cortex; MuCu, musical culture group; PiPl, piano playing group; PP, Purdue Pegboard test; Put, putamen; RCT, randomized controlled trial; ROI, regions of interest; Tha, thalamus; TIV, total intracranial volume.

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development of motor acuity and cognition were bidirectional and can be explained by a common cause as well as by shared resources with compensatory mechanisms.

KEYWORDS

brain plasticity, healthy aging, motor learning, music intervention, working memory

1 | GENERAL INTRODUCTION

Learning to play the piano is a complex form of motor skill acquisition—a process, by which movements or movement sequences become progressively optimized through repetitive practice. Ultimately, the skill becomes automated, that is, it can be performed effortlessly and is characterized by considerable stability over time, even without intermediate performance (Doyon & Benali, 2005). Two complementary, highly influential models of motor sequence learning are presented in Doyon et al. (2003, 2009, 2018) and Penhune and Steele (2012). In these models, motor sequence learning is assumed to occur in distinct stages and includes parallel and interacting processes (Ackerman, 1988; Doyon et al., 2009; Hikosaka et al., 2002; Penhune & Steele, 2012). Although a rapid improvement of performance is observed in the first fast learning phase, the subsequent slow learning phase is characterized by an asymptotic function evolving towards optimal individual performance (Doyon et al., 2003). During early learning, explicit information processed in the striatum (consisting of the putamen [Put] and caudate nucleus), for example, sequence order, is thought to play a crucial role. Additionally, this stage is impacted by the recruitment of sensorimotor regions (e.g., the primary motor cortex [M1] and supplementary motor area), prefrontal regions, limbic structures (e.g., hippocampus) and contributions of the cerebellum to error correction (Doyon et al., 2009). Consequently, the movements become consolidated, highly optimized and increasingly automated. During the slow learning phase, implicit processes dominate, and performance is mainly determined by the involvement of the striatum and cerebellum in chunking movements and developing internal models, respectively (Penhune & Steele, 2012). During this phase, the acquired skill is believed to be coded for the long term within a distributed network including motor and parietal cortical regions and possibly the striatum (Doyon et al., 2009; Penhune & Steele, 2012).

Unfortunately, despite cognitive and sensorimotor abilities being closely related (Li & Lindenberger, 2002), neither model reveals much about the role of cognitive processes during motor learning. It has been suggested,

however, that the fast learning phase is associated with an individual's general intelligence and broad task-appropriate content abilities (Ackerman, 1988; Ackerman & Cianciolo, 2000), as well as working memory capacity and attention (Hikosaka et al., 2002; Seidler et al., 2012). The above-mentioned variables may become less important when movement sequences are consolidated and automatized (e.g., slow learning phase), with performance influenced by processing and psychomotor speed (Ackerman, 1988; Ackerman & Cianciolo, 2000). To our knowledge, no study to date has thoroughly examined the longitudinal coupling between motor and cognitive functions during musical instrument learning.

The potential influence of individual traits to predict the change in task performance is an important consideration, previously addressed by Edward Thorndike (1908) and Lee Cronbach (1957); for a historic review of the study of individual differences in motor learning, see Anderson et al. (2021). Two opposing explanations have generally been proposed to explain individual differences in intervention-related adaptations. The *compensation account* predicts that individuals with lower baseline levels of task-relevant resources will benefit more from training, while the *magnification account* predicts the opposite (Lövdén et al., 2012). Despite a long tradition of research, understanding of variables likely to predict individual learning success remains sparse, as does the knowledge regarding the precise mechanisms of motor skill acquisition. We agree with Anderson et al. (2021) that the limited understanding may be due, at least in part, to statistical issues, such as the traditional focus on group-level effects through repeated-measures analyses of variance (ANOVA). In the present randomized-controlled trial (RCT), we used dual change score models (DCSMs) shown to be particularly suitable for analysing multiple groups (i.e., piano group and music listening group), multiple time points (i.e., baseline, 6 and 12 months of intervention), individual differences (e.g., low vs. high baseline performance), the influence of baseline performance on change scores (i.e., compensation vs. magnification account) and the coupling of two or more parameters (e.g., motor and cognitive variables). The present analysis was based on the data of the long-term study ‘Train the brain with music’

(TBM). The overarching goal of the TBM project was to investigate brain plasticity, well-being and cognitive and sensorimotor benefits induced by musical training, comparing two different musical interventions (see Methods).

The central question of this research paper was whether piano lessons improve fine motor control and how this relates to cognitive and neurophysiological changes. Intact motor functions provide the basis for autonomous living. In daily life, many activities require adequate upper limb function and especially hand and finger control, such as dressing, eating and writing. Because aging has degenerative effects on hand function (Ranganathan et al., 2001), it would be an important finding if piano playing can slow or even reverse this negative age-related development. Motor function was tested using the Purdue Pegboard (Tiffin & Asher, 1948), a finger dexterity task that is music-independent. Hence, the present RCT is also a study of (far) transfer (Barnett & Ceci, 2002), that is, an experiment determining the generalizability of piano training on motor acuity in piano-unrelated novel tasks.

This manuscript has been split into two parts, organized around distinct research questions:

Part 1: Do fine motor control and cognitive functioning improve during 1 year of musical instruction? Do both variables co-develop and is baseline performance associated with changes within and across domains?

Part 2: Do grey matter volumes of M1, Put and thalamus (Tha), defined as motor-related regions of interest (ROIs) as they are part of the cortico-basal ganglia-thalamo-cortical loop, increase after 12 months of piano practice? Is fine motor control dynamically associated with the volume of M1 during the intervention? And finally, do grey matter volumes of the ROI co-develop?

2 | PART 1

2.1 | Introduction

As a special form of ‘simultaneous motor–cognitive training’ (Herold et al., 2018), playing a musical instrument might harbour a particular potential to enhance motor and cognitive functions. Accordingly, it could interrupt negative developmental cascades and promote a positive course of life in aging people. In fact, numerous experiments showed enhancement in attention, processing speed and working memory (Bugos, 2010; Bugos, 2019; Bugos et al., 2007; Degé & Kerkovius, 2018; Frischen et al., 2021; Roden, Könen, et al., 2014; Schellenberg, 2004), as well as improvements in children (Costa-Giomi, 2005; Forgeard et al., 2008; Hyde et al., 2009; James, Zuber, et al., 2020; Martins

et al., 2018) and older adults’ fine motor abilities following musical training (Bugos, 2019). But in general, research in this area has yielded conflicting results (e.g., Seinfeld et al., 2013; Steele, 2005), including meta-analyses examining music-related far transfer effects on non-musical cognitive functions with unconvincing results (Sala & Gobet, 2017, 2020). However, most of these studies analysed only group-level effects, that is, they examined the effects of music on ‘the average person’. One of the few studies considering potential individual predictors was conducted by Burgoyne et al. (2019). Using structural equation modelling, the researchers identified that subjects’ general intelligence measured prior the intervention accounted for 21.4% of the variance in piano-related skill acquisition (playing ‘Happy birthday’). Although the study only examined a single session of piano playing, limiting conclusions to a very short period of time, this study confirmed a motor–cognitive relationship during piano training, with measures of working memory and processing speed correlating with the rate of learning.

There is growing evidence that motor and cognitive skills are interrelated (for a review, see Li & Lindenberger, 2002). The two domains appear to develop contiguously in childhood (Bart et al., 2007; Grissmer et al., 2010; Murray et al., 2006; Murray et al., 2007; Rigoli et al., 2013), and from middle adulthood onwards, they are subject to a fairly large age-related decline (Finkel et al., 2016; van der Willik et al., 2021). Many cross-sectional studies have shown that dexterity and other ‘motor fitness’ indices are associated with cognitive functions, for example, processing speed and working memory, in old age (Curreri et al., 2018; Kobayashi-Cuya, Sakurai, Sakuma, et al., 2018; Kobayashi-Cuya, Sakurai, Suzuki, et al., 2018; Voelcker-Rehage et al., 2010). Additionally, some longitudinal studies including older adults revealed a positive relationship between motor and cognitive functions. For example, walking speed, finger tapping speed and manual dexterity predicted global cognitive states and the likelihood of mild-cognitive impairment at a later time point (Camicioli et al., 1998; Curreri et al., 2018; Marquis et al., 2002). Although the nature of the associations between motor and cognitive domains is yet not understood, an increasing number of long-term studies are questioning a unidirectional relationship between the two domains (Finkel et al., 2016; McGrath et al., 2020). Based on the results of a Swedish population study covering a 19-year follow-up period, Finkel et al. (2016) suggested a potential bidirectional relationship between fine motor control and processing speed, in which changes in one variable precede and therefore may cause subsequent changes in the other. Because of these findings of longitudinal coupling

between sensorimotor and cognitive parameters, which seems to intensify with increasing age (Li & Lindenberger, 2002), authors assumed an underlying ‘common cause’ (Lindenberger & Baltes, 1994), representing a common biological factor that accounts for much of the variance in sensorimotor and cognitive functioning. An alternative hypothesis that accounts for the sensorimotor–cognitive link refers to the shared resources model (Li & Lindenberger, 2002). It explains the interdependence of both domains by sharing limited resources, which leads to competition for resources but also allows for compensatory trade-offs (Li & Lindenberger, 2002). For example, it has been shown that age-related hearing loss may be compensated by recruiting general cognitive brain areas and deploying mental resources such as attention and working memory for processing speech (Wong et al., 2009). Similar compensatory mechanisms have been found in the motor–cognitive relationship. For example, in a study with elderly people examining balance control during walking while performing memory tasks, maintaining balance was prioritized at the expense of memory performance (Li et al., 2001). Although some studies have shown beneficial music-related effects on motor and cognitive abilities, to our knowledge, there is no study that has thoroughly investigated the longitudinal coupling between motor and cognitive functions during the learning of a musical instrument. Despite Bugos (2019) found improvements in some measures of motor and cognitive skills in a 16-week music training program, some of which correlated before and/or after the intervention, we cannot infer whether changes in one variable are related to changes in the other. Yet, understanding the dynamical coupling of motor and cognitive changes can provide more insight into the mechanisms of experience-related adaptations. Accordingly, positively correlated changes of motor and cognitive outcomes during the intervention period could indicate a ‘common cause’ or possibly even a causal relationship between the two variables. On the other hand, negative covariances would rather indicate the shared resources perspective including compensatory mechanisms and resource reorganization. Lastly, absent associations would point to different causes.

In the present work, we examined two cognitive functions, processing speed and working memory. Processing speed is considered a general marker of cognitive aging. It has a major impact on all cognitive functions (Salthouse, 1996) but also on motor control and musical skills, such as performance on the Purdue Pegboard (Kobayashi-Cuya, Sakurai, Sakuma, et al., 2018; Kobayashi-Cuya, Sakurai, Suzuki, et al., 2018) and sight-reading while playing music (Kopiez & in Lee, 2008), respectively. The concept of working memory proposes

that a system with limited capacity maintains and stores information in the short term, supporting human thought processes (Baddeley, 2003). The commonly used multi-component working memory model (Baddeley, 2000) assumes that this limited capacity system (the so-called *central executive*) is in turn assisted by two distinct subsystems—the visuospatial sketchpad and the phonological loop, which are crucial for encoding and processing visual and acoustic information, respectively. The phonological loop is thought to facilitate language acquisition (Baddeley et al., 1998) and to be substantially involved in playing music (Chan et al., 1998; Roden, Grube, et al., 2014). Processing speed and working memory have been found to be involved in motor learning (Ackerman, 1988; Hikosaka et al., 2002) and may improve during musical training, as mentioned above.

The questions investigated in the following analysis are as follows: (1) Do fine motor control, processing speed and working memory improve on a group level during 1 year of musical instruction? (2) Do motor and cognitive variables co-develop? In line with former experiments, we hypothesize general beneficial effects in motor as well as cognitive outcomes after 12 months of piano playing. We assume that the changes in both variables are bidirectionally related and probably derive from a ‘common cause’ and shared resources; however, we do not expect them to change simultaneously and therefore consider a causal effect between the two unlikely.

2.2 | Methods

2.2.1 | Participants and intervention

The present analysis was conducted on data from a two-site RCT including 156 healthy older adults (mean age = 69.7, standard deviation [SD] = 3.5) from Hanover (Germany; $N = 92$; women = 42) and Geneva (Switzerland; $N = 64$; women = 50). All participants were right-handed with a laterality quotient of ≥ 50 according to the Edinburgh Handedness Inventory (Oldfield, 1971) and demonstrated acceptable levels of global cognitive functioning (COGTEL; Ihle et al., 2017; Kliegel et al., 2007). All subjects reported that they had less than 6 months of regular musical practice during their lives. Both groups had similar degrees of handedness (PiPl: mean = 93.8, SD = 11.3; MuCu: mean = 95, SD = 11.4; $p = 0.53$) and musical sophistication levels (PiPl: mean = 49.51, SD = 12.03; MuCu: mean = 50.03, SD = 10.99, $p = 0.784$) as measured by the Goldsmiths Musical Sophistication Index (Müllensiefen et al., 2014). In short, participants were either assigned to piano playing (PiPl; $N = 82$) or music listening/musical culture

groups (MuCu; $N = 74$) and received weekly 60 min sessions in small groups of 2 (PiPl) or 4–7 subjects (MuCu), excluding the teacher. All participants agreed to the study contract to attend at least 20 sessions within 6 months and to do their assigned homework for ~30 min/day. Furthermore, they were asked not to attend any other music course during the experiment. For teaching, we recruited music students with prior experience from local music universities, which were supervised by university professors of music education and piano pedagogy throughout the study.

The PiPl sessions included non-piano sensory-motor exercises, such as clapping and walking to a beat, as well as traditional listen-and-repeat exercises and improvisations on the instrument. Note that reading was introduced using an approach specifically designed for older people, based on Schlichting's Piano Prima Vista (Inter-Note GmbH Musikverlag 2013) and the Hall Leonard Piano Method for Adults (ISBN 9789043134378). PiPl participants learned simple pieces of music using various textbooks, for example, 'A Dozen a Day' Vol. 1 (ISBN 9780711954311) or 'Youth Album for Piano' by Schmitz (ISBN 9783932587412). The MuCu sessions included analytical listening and experiencing as well as some music theory. The goal of this group was to understand and appreciate music by discussing various musical aspects such as musical genres, instrument groups, music history and famous composers. However, active music making (e.g., singing and clapping) was not permitted. A more detailed 6-month curriculum can be found in the Supporting Information of Worscher et al. (2021).

The participants were assigned to an experimental group according to a matched-pairs design. First, all subjects were divided into pairs of two that were as identical as possible with respect to age, sex, education and COGTEL. For this purpose, Mahalanobis distances were considered, using the R package *nbpMatching* (Beck et al., 2016). Then, within each pair, participants were randomly assigned to either PiPl or MuCu. The equality of these factors in both groups was confirmed using chi-squared and two-sample independent *t*-tests (see Jünemann et al., 2022). The second half of the intervention period (i.e., months 6–12) was impacted by the COVID-19 pandemic. Because our participants belonged to the risk group, no face-to-face classes could be held for several weeks. However, the intervention continued in an online format with the highest possible intensity and the least possible interruption. At baseline, 6 months and 12 months after the intervention, participants underwent a battery of behavioural tests as well as MRI sessions. More information regarding the design of the RCT can be obtained from the study protocol (James, Altmüller, et al., 2020).

2.2.2 | Fine motor control

The Purdue Pegboard test (Tiffin & Asher, 1948) was used to measure fine motor control. This test consists of two unimanual and two bimanual conditions. During the first three conditions, participants were asked to put as many pegs as possible in a vertical row within 30 s. This was done with the right (PP_R) and left hand (PP_L) as well as with both hands (PP_B) simultaneously. In the final condition (PP_A), participants had to use both hands to assemble as many 'towers' as possible in 60 s; each tower consisted of a pin, a washer, a collar and another washer. Each condition was performed twice, with the better score used for analysis. Before the first measurement of each condition, the task was demonstrated and a short practice time was allowed.

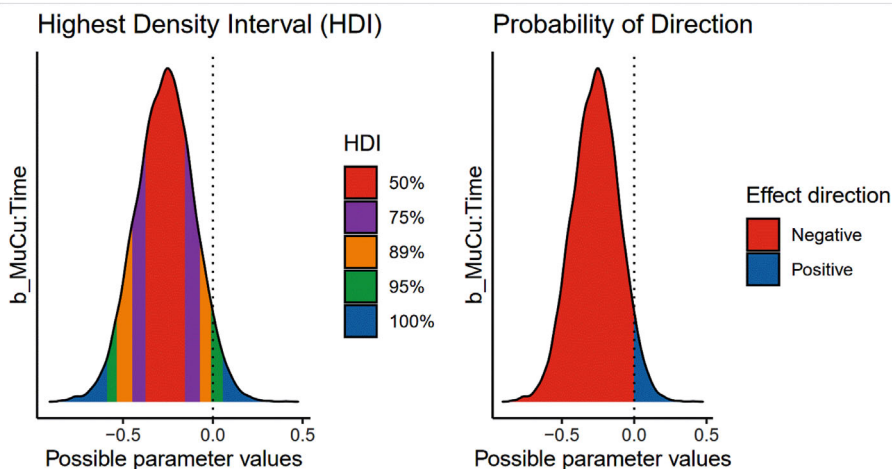
The Purdue Pegboard is commonly used as a laboratory task to measure the quality of action execution. Although speed, accuracy, and precision are critical components of this test, explicit knowledge can be largely neglected because of the simple and previously practiced sequence (Krakauer et al., 2019). Purdue Pegboard results have already been analysed on a subsample ($N = 109$) of this RCT. Using ANOVA, Jünemann et al. (submitted) found significant Time*Group interactions after 12 months of the PP_R, PP_L and PP_A but not PP_B condition. Although we included 47 more participants in the present analysis and used a different statistical approach, we did not expect major differences from these results.

2.2.3 | Cognitive outcomes

Two cognitive tests from the Wechsler Adult Intelligence Scale-IV (WAIS-IV; Wechsler, 2011) were included in the analysis. As a measure of processing speed and attention, we used the Digit Symbol test (DSY; also called Coding). The DSY involves numbers from 1 to 9, each paired with a unique, easy-to-draw symbol. In this test, participants were asked to draw as many symbols as possible below the corresponding number in a row within 120 s.

Additionally, auditory working memory was measured using the Digit Span Backward test (DSB; Wechsler, 2011). In this test, subjects were asked to repeat an orally presented series of numbers (e.g., 5-3-1) in reverse order (1-3-5). The span continuously increased from two to eight numbers. Each level of difficulty (i.e., length of the series) was repeated twice, and each correct answer was scored with one point. If the participant made two consecutive errors of the same difficulty level, the task was terminated.

FIGURE 1 Posterior distribution represented with its highest density intervals (left) and probability of direction (right). The effect estimate was -0.26 $[-0.56, 0.04]$. Both plots were created using the R package *bayestestR* (Makowski et al., 2019).



2.2.4 | Statistics

Before the analysis, the variables sex and group were dummy coded as *Male* (female [0] |male [1]) and *MuCu* (PiPl [0]|MuCu [1]), respectively. Each dependent variable except group was centered at its mean and standardized (e.g., Male $[-0.5, 0.5]$) such that a one-unit change refers to a change in one SD (z -score). By including an interaction term, all predictor variables are held constant at zero. Thus, the population-level effects relate to the ‘neutral’ sex (Male = 0 $[-0.5 = \text{men}, 0.5 = \text{women}]$) and the piano group (Group = 0 [0 = PiPl, 1 = MuCu]) at baseline (Time = 0 [0 = baseline, 1 = 6 months]), and the coefficients of Male and MuCu represent the contrasts between men and women and PiPl and MuCu, respectively.

We applied two different statistical approaches to answer two different research questions. (1) To test whether fine motor control and cognitive functioning improved on a group level after 1 year of musical instruction, we applied Bayesian multilevel modelling (BMLM) using the package *brms* (Bürkner, 2017) in R (R Core Team, 2020). We estimated the following regression:

$$\text{Outcome} \sim \text{MuCu} * \text{Time} + \text{Male} * \text{Time} + (1 + \text{Time} | \text{ID})$$

In this analysis, *Time* was dummy coded (pre [0]|post [1]) and represents baseline and 12-month scores. MuCu, Male and Time*MuCu and Time*Male interactions were included as predictors. In contrast to frequentist approaches, Bayesian statistics provide a posterior distribution that contains all probable effect values. The credible interval (C_RI) defines the central part of the posterior distribution that contains a certain percentage of the effect values. Which C_RI is chosen is an arbitrary decision by the researcher, and in Bayesian statistics, C_RIs of 89 and 90% are not uncommon choices. In this article,

95% C_RIs are given, which means that there is a 95% probability that the effect falls within this range. Suppose our BMLM yields a time*group interaction effect with a C_RI of $[-0.56, 0.04]$. According to Figure 1 (left), the C_RI would include the green but not the blue part of the posterior distribution. For comparison, a C_RI of 89% would not enclose the infamous zero point. Given the posterior distribution of this time*group interaction effect, 94.8% of all probable effect values are strictly positive. We interpret the result to mean that it is likely that group 1 deteriorates over time relative to group 0.

For better model fit, we allowed intercepts and slopes for each participant to vary; however, we did not report varying effects, as they are also captured and reported in the subsequent analysis.

In this form, BMLMs did not provide information regarding changes after 6 months of musical intervention. To better temporally resolve developmental trajectories across groups and evaluate longitudinal coupling between motor/cognitive variable pairs, we developed (2) multiple-group DCSMs (Figure 2; for a tutorial, see Kievit et al., 2018) with the R package *lavaan* (Rosseel, 2012). Because regressing baseline values on its change score may result in biased model outcomes (i.e., regression to the mean; Sorjonen et al., 2021; Sorjonen et al., 2022), we calculated covariances instead. By doing so, we evaluated whether the performance measured prior the intervention (X_0, Y_0 [Figure 2]) was related to the 6-month change in the same (g/G) or the other variable (h/H). This allows the parameters g/G to quantify potential compensation or magnification effects. It was also examined whether the change from 6 to 12 months of intervention ($\Delta X_2, \Delta Y_2$ [Figure 2]) was related to the first change (i/I), and whether the two variables changed simultaneously (K/N) or with a time lag (L/M). As it is known from literature that men show worse Purdue Pegboard performance than women

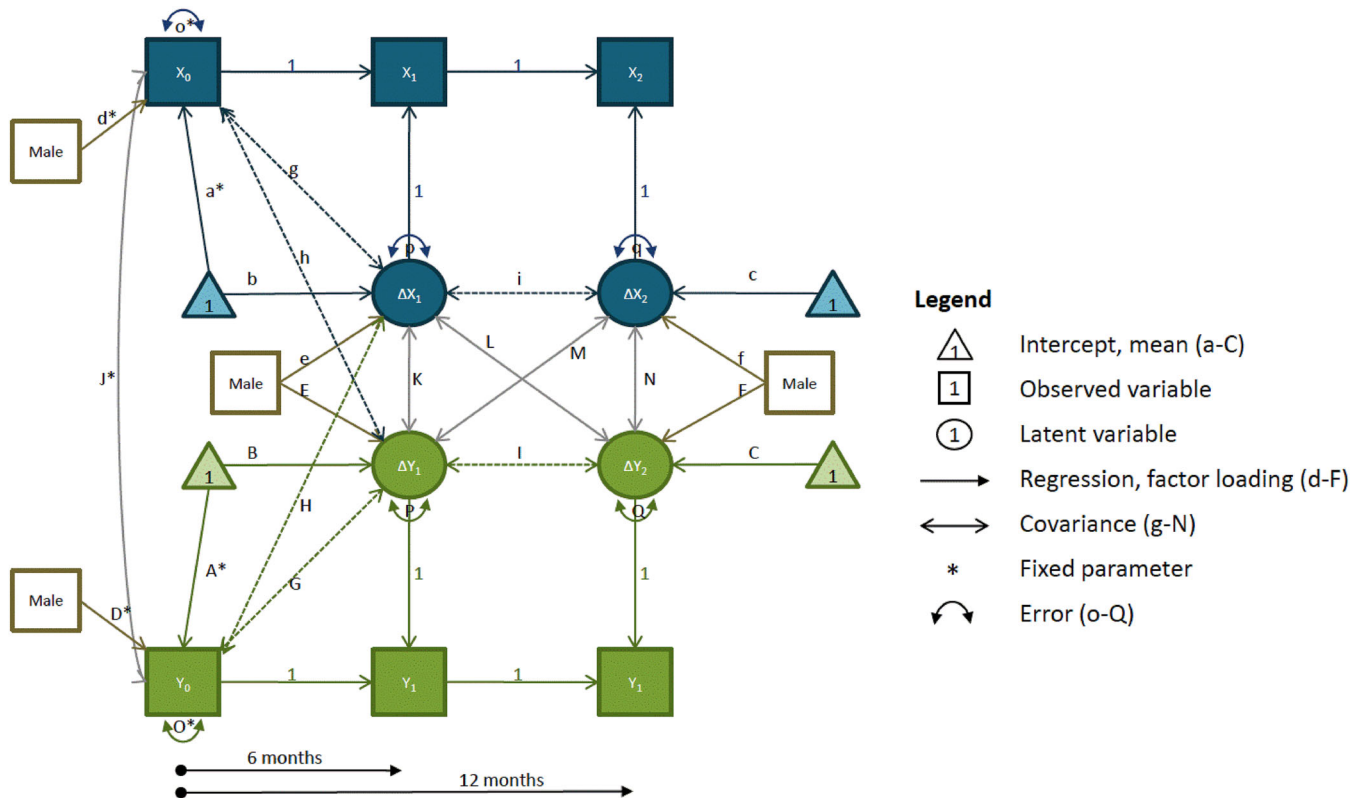


FIGURE 2 Dual change score model (DCSM). Analysis of two variables coded X (blue; top) and Y (brown; bottom) and their coupling over time. Δ_1 and Δ_2 represent changes during the first and second 6 months of intervention, respectively.

(Agnew et al., 1988; Peters et al., 1990; Peters & Campagnaro, 1996; Schmidt et al., 2000), we modelled the effect of sex (i.e., being male) on baseline (d/D) and change scores ($e/E, f/F$).

The complete model is represented in Figure 2. Because the two groups, PiPI and MuCu, were carefully matched for age, sex, education and cognitive performance, we assumed the baseline performances (a/A [Figure 2]) and their variance (o/O), as well as the correlation between the baseline performances (J) and the effect of sex on the baseline performances (d/D) to be the same in both groups and fixed their parameters (*).

In total eight models were computed, in which each condition of the Purdue Pegboard was related to DSY and DSB. We provided standardized estimates based on the variances of the latent variables, which allows comparing effects within and across models. Effects with $p < 0.05$ are reported with a 95% confidence interval (C_{oI}). In line with the statement on statistical significance by the American Statistical Association (ASA), we did not interpret the p -value as a probability of a hypothesis being true. Instead, we consider the p -value as the probability that a statistical summary of data is equal to or more extreme than its observed value under a particular statistical model (Wasserstein & Lazar, 2016). Because

scientific conclusions should not be based solely on whether or not a p -value exceeds a certain threshold (Andrade, 2019; Wasserstein & Lazar, 2016), we also considered effects with $0.05 < p < 0.08$ and discussed them with their C_{oI} and the exact p -value given.

Model fit was estimated using Chi-square (X^2), whose p -value should be >0.05 . Additionally, we computed Root Mean Square Error Approximation (RMSEA) with its C_{oI} and Standardized Root Mean Square Residual (SRMR). Means of RMSEA and SRMR <0.08 indicate adequate model fit (Ben-Shachar et al., 2020).

2.3 | Results

$N = 10$ participants (2 PiPI, 8 MuCu) left the study during months 0–6, and another 12 participants during months 6–12 (2 PiPI, 10 MuCu) yielded a dropout rate of 14.1%. All BMLMs converged (no divergent transitions, R_{hat} values < 1.1) and yielded well-mixed chains upon visual inspection. Posterior predictive checks suggested adequate model fit. BMLMs did not yield meaningful group differences at baseline (Table 1). DCSMs also converged without any problems and, depending on the fit index, achieved good-to-acceptable model fit (see

TABLE 1 Behavioural group-level effects after 12 months of intervention.

	PP _R	PP _L	PP _B	PP _A	DSY	DSB
Intercept	-0.23 [-0.42, -0.04]	-0.10 [-0.30, 0.10]	-0.03 [-0.21, 0.16]	-0.16 [-0.35, 0.04]	-0.28 [-0.47, -0.08]	-0.20 [-0.42, 0.02]
Time	0.49 [0.29, 0.69]	0.39 [0.18, 0.59]	0.25 [0.05, 0.46]	0.30 [0.09, 0.50]	0.33 [0.18, 0.49]	0.24 [0.04, 0.45]
MuCu	0.04 [-0.23, 0.31]	-0.04 [-0.32, 0.23]	0.04 [-0.21, 0.29]	0.16 [-0.11, 0.44]	0.10 [-0.16, 0.37]	0.17 [-0.13, 0.47]
Male	-0.71 [-0.97, -0.43]	-0.38 [-0.65, -0.10]	-0.20 [-0.45, 0.06]	-0.73 [-1.00, -0.46]	-0.08 [-0.36, 0.19]	0.06 [-0.25, 0.37]
MuCu*Time	-0.42 [-0.72, -0.12]	-0.30 [-0.59, -0.01]	-0.29 [-0.58, 0.00]	-0.37 [-0.56, -0.07]	-0.03 [-0.25, 0.19]	-0.26 [-0.56, 0.04]
Male*Time	0.21 [-0.08, 0.51]	0.34 [0.04, 0.64]	-0.25 [-0.55, 0.05]	0.12 [-0.18, 0.43]	-0.17 [-0.40, 0.06]	-0.11 [-0.41, 0.20]

Note: Effects are estimated by BMLMs (mean [95% CrI]). Meaningful effects are represented in bold. At the bottom, Time*Group interactions are plotted.

Abbreviations: PP_{R/L/B/A}, Purdue Pegboard_(condition); DSY, Digit Symbol; DSB, Digit Span Backward; PiPI, Piano Playing; MuCu, Musical Culture. [Correction added on 01 June 2023, after first online publication: Abbreviations have been updated in this version.]

Table S1). The raw data were visualized as violin plots and can be retrieved from the supplement.

2.3.1 | Fine motor control

After 12 months, PiPI improved in all pegboard conditions (effect of Time) and yielded stronger improvements when compared with MuCu (Time*Group interaction; Table 1). Further, DCSMs showed that piano-related improvements in PP_R and PP_A occurred mainly in the first 6 months (PP_R: 0.54 [0.31, 0.77], $p < 0.001$; PP_A: 0.27 [0.04, 0.49], $p = 0.019$; parameter b [Figure 2]). PP_L and PP_B showed greater improvements from months 6 to 12 (PP_L: 0.29 [0.05, 0.53], $p = 0.016$; PP_B: 0.30 [0.06, 0.54], $p = 0.013$; parameter c [Figure 2]), although PP_L also appeared to improve in the first half of the intervention (0.20 [-0.01, 0.52], $p = 0.067$). MuCu showed an initial improvement in PP_R (0.33 [0.11, 0.54], $p = 0.003$), which subsequently appeared to worsen again (-0.23 [-0.46, 0.01]; $p = 0.057$).

In all Pegboard conditions, men had lower baseline performance than women (Table 1) and showed less 12-month improvement in PP_B condition (-0.25 [-0.55, 0.05]). In the left and probably also in the right-hand condition, however, men showed stronger improvement than women (PP_R: 0.21 [-0.08, 0.51], PP_L: 0.34 [0.04, 0.64]). DCSM revealed that men in the PiPI group improved less during the first-half year in comparison with women

(PP_B: -0.52 [-0.94, -0.10]; parameter e [Figure 2]), whereas men in MuCu improved more during the second half-year of intervention compared with women (PP_R: 0.56 [0.12, 1.00]; PP_L: 0.49 [0.04, 0.94]; f [Figure 2]).

Regardless of group and condition, we observed a compensation account: Lower baseline performance was associated with higher change in the same variable during the first half-year of intervention (g [Figure 2]), and lower initial change was associated with higher change 6 months later (i [Figure 2]).

2.3.2 | Cognition

BMLMs revealed an improvement in DSY in PiPI after 12 months of intervention (0.33 [0.18, 0.49]). This effect was not substantially different in comparison to MuCu (-0.03 [-0.25, 0.19]), that is, both groups improved similarly over time. According to the DCSMs, the change was mainly driven by a strong 6-month improvement (B [Figure 2]) in both groups (MuCu: 0.58 [0.34, 0.83], $p < 0.001$; PiPI: 0.69 [0.44, 0.94], $p < 0.001$).

Compared with MuCu, a stronger 12-month improvement was found for DSB in PiPI (-0.26 [-0.56, 0.04]). The posterior distribution of the MuCu*Time interaction effect is depicted in Figure 1. DCSMs showed that after initial improvement in MuCu at 6 months (0.26 [0.04, 0.48], $p = 0.02$), this improvement faded at 12 months (-0.22 [-0.46, 0.02], $p = 0.074$), whereas PiPI showed a

probable improvement after 6 months (0.20 [−0.02, 0.42], $p = 0.074$) with subsequent stabilization (0.03 [−0.20, 0.26], $p = 0.793$).

No sex effects were found on baseline performance or change scores.

As with fine motor skills, a compensatory account was observed for DSB: Lower baseline performance was associated with greater 6-month changes (g [Figure 2]), which in turn were negatively associated with 12-month changes (i [Figure 2]). Similarly, in DSY, a lower increase in the first 6 months was associated with a higher later change (I [Figure 2]). However, lower baseline performance was only associated with a higher 6-month change in the PiPl group (G [Figure 2]).

2.3.3 | Motor–cognitive coupling

Baseline performances of DSY correlated positively with all Purdue Pegboard conditions (J [Figure 2]) from 0.20 ([0.07, 0.33], $p = 0.002$) for PP_B up to 0.31 ([0.16, 0.45], $p < 0.001$) for PP_A . Additional significant coupling parameters (h, H, K, L, M, N [Figure 2]) are depicted in Figure 3.

For MuCu, two significant coupling parameters including DSY were found: Higher PP_B baseline performance is linked to lower DSY change after 6 months (−0.16 [−0.31, −0.01], $p = 0.035$; h [Figure 2]); DSY and PP_A changed together during the first 6 months (0.22 [0.02, 0.43], $p = 0.034$; K [Figure 2]). In the PiPl group, DSY and PP_A seemed to be negatively coupled from months 6–12 (−0.21 [−0.43, 0.02], $p = 0.072$; N [Figure 2]), DSY and PP_L showed positive and negative time-lagged coupling with a higher 6-month gain in PP_L

linked to higher 12-month gains in DSY (0.22 [0.02, 0.42], $p = 0.033$; L [Figure 2]) and higher 6-month gains in DSY were linked to lower 12-month PP_L gains (−0.26 [−0.47, −0.04], $p = 0.019$; M [Figure 2]). Baseline performance of DSB only correlated with PP_A (0.23 [0.08; 0.38], $p = 0.002$; J [Figure 2]). In MuCu, we found only one significant additional coupling parameter (H [Figure 2])—better DSB measured prior the intervention was associated with stronger PP_B improvement after 6 months (0.21 [0.06, 0.35], $p = 0.007$). In PiPl, high DSB at baseline was related to reduced PP_R 6-month improvement (−0.28 [−0.48, −0.07], $p = 0.009$; H [Figure 2]). Additionally, higher early improvement in PP_A seemed to be related to a lower early increase in DSB (−0.20 [−0.42, 0.02], $p = 0.074$; K [Figure 2]). Further, two positive time-lagged associations were found: Higher early left-hand improvement predicted a stronger DSB improvement 6 months later 0.24 ([0.05, 0.43], $p = 0.012$; L [Figure 2]), and vice versa, higher early DSB improvement was associated with higher PPL change from 6 to 12 months (0.19 [0.00, 0.39], $p = 0.049$; M [Figure 2]).

2.4 | Discussion

2.4.1 | Changes at a group level

Compared with MuCu, PiPl improved in unimanual and bimanual fine motor control after 12 months of intervention. This finding indicates that adaptations to motor demands during piano practice generalize to piano-independent motor domains (i.e., transfer of skill). The greatest piano-related improvements were observed in the right hand, an adaptation that is likely to be highly

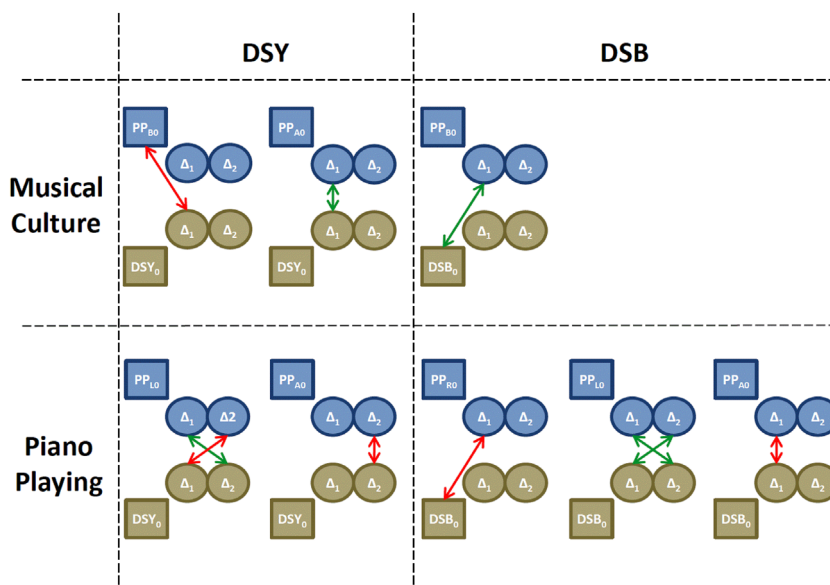


FIGURE 3 Longitudinal coupling between motor and cognitive adaptation. Only meaningful cross-domain effects (h, H, K, L, M, N) with $p < 0.08$ are depicted. The red and green arrows represent negative and positive covariances, respectively. DSY_0 , baseline Digit Symbol test; DSB_0 , baseline Digit Span Backward test; $PP_{R/L/B/A0}$, baseline Purdue Pegboard_(condition) test; Purdue Pegboard conditions, R (right hand only), L (left hand only), B (both hands), A (assembly); Δ_1 , change from 0 to 6 months; Δ_2 , 6–12 months.

functional; the right, dominant hand is used for more complex tasks in everyday life and is particularly relied upon for dexterity in old age (Bonilha et al., 2009). Additionally, it appeared that different motor aspects developed at different times: from dominant (PP_R) to non-dominant hand (PP_L) and from asynchronous (PP_A) to synchronous (PP_B) movements. On the one hand, this can be explained by the composition of the curriculum, with an initial emphasis on the right hand and increasing left-hand involvement. On the other hand, an explanation can be found by the model of Penhune and Steele (2012), in which motor synchronization (i.e., in bimanual tasks like PP_B) develops rather late and increasingly determines motor performance over time.

Consistent with literature, we found that Purdue Pegboard baseline scores were lower in men (Agnew et al., 1988; Schmidt et al., 2000), probably because of anatomical differences such as greater finger diameter (Peters et al., 1990; Peters & Campagnaro, 1996). However, the performance of men seemed to catch up to the women's, especially during the second half-year of the intervention.

Furthermore, in both groups, we found a strong improvement in processing speed during the first 6 months and a small but sustaining increase in working memory capacity in PiPl.

2.4.2 | Individual changes and coupling parameters

With respect to both motor and cognitive development, we predominantly found compensation but not magnification accounts (Lövdén et al., 2012). In other words, people with low baseline performance are those who benefited most from the musical intervention. Thus, although people with higher cognitive abilities are more likely to take music lessons (Schellenberg, 2006; Swaminathan & Schellenberg, 2019), it is worthwhile to motivate people with lower cognitive abilities to engage in musical activity.

Regardless of group, baseline performances of all Pegboard conditions correlated positively with processing speed (see also Fauth et al., 2017; Kobayashi-Cuya, Sakurai, Sakuma, et al., 2018), but only PP_A scores were related to working memory capacity. As the PP_A condition involves the most complex sequence of the Purdue Pegboard test, it is likely that, despite practicing in order to familiarize with the test, the motor sequences were not fully automated. Accordingly, this finding confirms previous suggestions that working memory might be more involved in the early stages of learning (Seidler et al., 2012), when motor sequences are not yet automated and need to be kept in mind during execution (Figure 4).

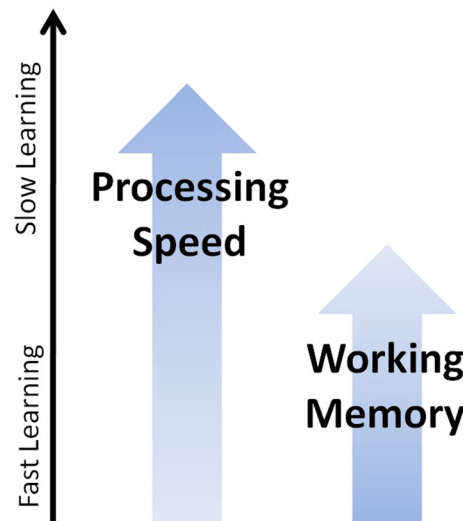


FIGURE 4 Different motor learning stages may be supported by different cognitive processes.

Significant cross-domain couplings present a rather unsystematic picture with positive and negative covariances (Figure 3). What we could clearly observe is that playing the piano induced more prevalent bidirectional coupling between motor and cognitive domains compared with MuCu (seven meaningful coupling parameters in PiPl versus only three in MuCu). Although the performances of some variables were correlated at baseline (e.g., PP_A and DSY are correlated at 0.31 ([0.16, 0.45])) and improved during the intervention (e.g., in PiPl after 6 months, PP_A (0.27 [0.04, 0.49]) and DSY (0.69 [0.44, 0.94])), changes in one variable were not necessarily associated with changes in the other variable. Moreover, positive covariances with a lag of 6 months also tend to argue against one variable directly *causing* the other; rather, they are consistent with the ‘common cause’ hypothesis that learning to play the piano can initiate a developmental cascade that ultimately affects a wide range of motor and cognitive parameters. For example, those individuals who initially showed a high piano-related increase in PP_L are more likely to also show a greater increase in DSY (0.22 [0.02, 0.42]) and DSB (0.24 [0.05, 0.43]) later on.

We also found opposite patterns, where higher working memory capacity at baseline or greater initial processing speed improvement was associated with *less* subsequent PP_R (−0.28 [−0.48, −0.07]) and PP_L (−0.26 [−0.47, −0.04]) improvement, respectively. These negative and unidirectional time-lagged associations confirm the shared resource perspective and suggest possible compensatory relationships between cognitive and motor adaptation. Potentially, they are mediated by individual processing styles, cognitive flexibility and a complex

interplay of environmental demand, cognitive-motor resources and coping strategies (person-environment fit, see Caplan & Harrison, 1993; Swinnen & Gooijers, 2015). For example, it is conceivable that individuals with greater cognitive abilities might not 'need' to make motor adaptations to meet the demands of piano instruction. Instead, they might rely on processing speed and working memory to cope with challenging situations during lessons. The opposite phenomenon could also be explained by similar compensatory mechanisms: Participants who improved their fine motor skills may have automated their piano playing. This allows for effortless and less cognitively demanding piano playing that does not require adjustment of cognitive functions.

There are several potential explanations for the lack of positive correlations between change scores during the *same* time period. First and most likely, the findings suggest a non-causative development of fine motor acuity and cognitive variables. This would confirm previous assumptions that cognitive processes are generally more important for early explicit learning (e.g., sequence ordering) and not for the execution of automated movements as we have tested with the Purdue Pegboard (Doyon et al., 2009). The finding that only PP_A changes along with DSY performance in the first 6 months in MuCu (0.22 [0.02, 0.43]) supports this explanation, as PP_A was the condition with the most complex sequence and therefore may not have been fully automated. A second explanation could be that only a basic capacity of certain cognitive functions, especially processing speed, is required for the execution of (automated) motor tasks, but any further cognitive enhancement does not additionally contribute to movement execution. Working memory might be important for the acquisition of motor sequences and the execution of sophisticated bimanual movements, including complex sequences, but not for the execution of simple and automated movements. A third explanation that could account for the lack of longitudinal coupling between motor and cognitive development is the chosen measurement period. Accordingly, fine motor control and processing speed or working memory might have developed together, but at an earlier stage, and the long 6-month inter-test interval might have masked this cross-domain coupling. The last point will be taken up again in the general discussion.

3 | PART 2

3.1 | Introduction

M1 plays a crucial role in manual skill learning and is thought to harbour representations of specific motor skills (Karni et al., 1998; Penhune & Steele, 2012).

Although the evidence in animal research is much clearer, M1 is considered a key area responsible for movement execution in humans (Hardwick et al., 2013; Krakauer et al., 2019; Meister et al., 2005; Schieber, 2000; Shmuelof et al., 2014). There is a consensus that M1 is well-lateralized in its function, that is, movements of the left hand are mainly controlled by the right M1, and vice versa (Hardwick et al., 2013; Jäncke et al., 2000; Ogawa et al., 2019; Scholz et al., 2000). In a cross-sectional study including 217 healthy older individuals, Koppelmans et al. (2015) demonstrated that the volume of the right M1 correlated positively with the performance in PP_L. Interestingly, a similar link between the left M1 and PP_R performance was not found. Landi et al. (2011) showed that motor adaptation training with the right hand led to an increase in grey matter concentration of the contralateral M1 after only 1 week. Moreover, grey matter volume after training was predictive of improvements in the speed of learning during re-adaptation 1 year later.

There is ample literature showing macrostructural adaptations of M1 in musicians (Amunts et al., 1997; Gaser & Schlaug, 2003; Han et al., 2009; Hyde et al., 2009; Schlaug et al., 2005). In a longitudinal experiment, Hyde et al. (2009) measured a volumetric increase of grey matter in the right M1 in children after 15 months of keyboard lessons. They showed that the increase was associated with an improvement in a left-hand four-finger motor sequence test. However, additional longitudinal studies are needed to understand the relationships between fine motor control and the volume of M1. We are aware that single brain areas like M1 alone are hardly capable of eliciting complex and fine-tuned motor behaviour. Instead, they are embedded in distributed networks (Altenmüller & Furuya, 2017). For example, in a separate analysis of the present study, we found increased resting state functional connectivity after 12 months between the right-hand area of M1, defined as seed region, and bilateral sensorimotor regions. Additionally, the strength of connectivity correlated positively with the performance in PP_A (Jünemann et al., *submitted*).

Typically, brain connectivity is derived from structural (i.e., measuring white matter tracts), functional (i.e., analysing synchronous neuronal activity) or effective parameters (i.e., modelling influences of one region's activity on other regions; for a review, see Friston, 2011). Another, less commonly applied approach to inferring brain connectivity is the analysis of structural covariances. This assumes that functionally or structurally connected brain regions also covary in their morphology and that environmental factors influence their coordinated development and thus covariance (for a review, see Alexander-Bloch & Giedd, 2013). For example, in patients with stroke, alterations in structural covariance

were found in a network including the cortico-striato-thalamical loop and diverse sensorimotor cortices (Abela et al., 2015) and between the ipsilesional M1 and motor as well as non-motor brain regions (Chen et al., 2022).

As the cortico-basal ganglia-thalamo-cortical loop is critically involved in motor learning (Doyon et al., 2003; Hardwick et al., 2013; Jin & Costa, 2015; Krakauer et al., 2019), we sought to analyse the dynamical coupling of grey matter volume changes of three ipsilateral brain ROIs: M1, thalamus (Tha) and putamen (Put). All three ROIs are part of the cortico-basal ganglia-thalamo-cortical loop.

Thus, the questions investigated in this part of the analysis are: (1) Does the grey matter volume of the motor-related ROI increase after 12 months of musical intervention, and do unimanual fine motor control and the volume of the contralateral M1 develop together during piano training? (2) Do motor-related ROI show coordinated experience-related development? Consistent with previous experiments, we hypothesize that PiPl in comparison with MuCu would provoke both positive covariance between changes in fine motor control and grey matter volume of M1 and more coordinated growth (or shrinkage) between M1, Tha and Put.

3.2 | Methods

3.2.1 | Participants

Because MRI could not be performed for all subjects this analysis is based on a subsample of Part A with $N = 136$ participants (women = 80, men = 56; mean age = 69.7, SD = 3.6) from Hanover ($N = 81$) and Geneva ($N = 55$).

3.2.2 | Fine motor control

For measuring fine motor control, the Purdue Pegboard test (Tiffin & Asher, 1948) was used (see Part A).

3.2.3 | Structural MRI

At each measurement time point, participants were scanned with 3 Tesla MRI systems (Siemens TIM Trio and Siemens MAGNETOM Skyra, Erlangen, Germany). The settings for obtaining T1-weighted images were described in Worschech et al. (2022): MP2RAGE sequence; voxel size: 1 mm isotropic; 176 slices; field of view: $256 \times 240 \times 176$ mm; repetition/echo time: 5000/2.98 ms; inversion time 1/inversion time 2: 700/2500 ms; flip angle 1/2: 4/5 degrees. Both scanners

were equipped with Siemens 32-channel head coils. Regional and total intracranial volume (TIV) was automatically computed. The longitudinal pipeline of the Computational Anatomy Toolbox (CAT12) of the Statistical Parametric Mapping Software (SPM12) was used for this purpose. Individual volumes of three bilateral ROIs (M1, Put and Tha), as defined by the Neuromorphometrics Brain Atlas (Neuromorphometrics, Inc.), and the TIV were exported to R for statistical analysis.

3.2.4 | Statistics

To test macrostructural changes at the group level after 1 year of music instruction, we applied BMLM (see Part A). We added TIV as a control variable and removed the variable sex to avoid multicollinearity. Therefore, the equation is as follows:

$$Outcome \sim PiPl * Time + TIV + (1 + Time|ID)$$

For evaluating longitudinal coupling between fine motor control and brain regional volume we used DCSMs as described in the methods section of Part A. In addition to the effect of sex, we also controlled baseline as well as change scores for TIV. To measure the structural covariances of ipsilateral M1, Tha and Put, we extended the DCSM (Figure 2) by a third variable. To reduce model complexity and because brain networks are characterized by synchronous activity and development (Alexander-Bloch et al., 2013), we removed parameters modelling time-lagged covariances of change scores (L and M [Figure 2]).

3.3 | Results

BMLMs as well as DLCMs converged satisfactorily and yielded good model fit. BMLMs did not yield meaningful group differences at baseline (Table 1). All parameters of the DCSMs can be found in the supplement (Table 2).

3.3.1 | Macrostructural changes

BMLMs revealed shrinkage after 12 months of musical intervention in all ROI, with the exception of the bilateral Tha (Table 2). In all ROIs, neither group effects at baseline nor Group*Time interactions were found. For a whole-brain voxel-based morphometry (VBM) analysis after 6 months, see Marie et al. (2023).

DCSMs revealed that in MuCu, bilateral M1 shrank during the first 6 months ($M1_L$ and $M1_R$: -0.39 [-0.63 ,

TABLE 2 Effects on grey matter volume at the group level after 12 months of intervention.

	M1 _L	M1 _R	Tha _L	Tha _R	Put _L	Put _R
Intercept	0.07 [−0.08, 0.22]	0.03 [−0.12, 0.18]	0.13 [−0.04, 0.31]	0.12 [−0.06, 0.31]	0.03 [−0.14, 0.19]	−0.03 [0.19, 0.14]
Time	−0.08 [−0.15, −0.01]	−0.06 [−0.13, 0.00]	−0.05 [−0.15, 0.04]	−0.03 [−0.12, 0.06]	−0.07 [−0.11, −0.02]	−0.06 [−0.10, −0.02]
MuCu	−0.05 [−0.27, 0.16]	0.01 [−0.20, 0.22]	−0.16 [−0.40, 0.08]	−0.15 [−0.41, 0.10]	−0.01 [−0.24, 0.23]	0.08 [−0.15, 0.30]
MuCu*Time	−0.01 [−0.11, 0.08]	−0.03 [−0.13, 0.06]	−0.07 [−0.21, 0.08]	−0.06 [−0.19, 0.07]	−0.02 [−0.09, 0.05]	0.02 [−0.03, 0.07]

Note: Effects are estimated by BMLMs (mean [95% C_RI]). Meaningful effects are represented in bold. M1, primary motor cortex; Tha, thalamus; Put, putamen; L/R, left/right hemisphere.

−0.14], $p = 0.002$; *B* [Figure 2]). In PiPl, shrinkage occurred during the second 6 months of intervention (M1_L: −0.37 [−0.62, −0.12], $p = 0.004$; M1_R: −0.32 [−0.56, −0.07], $p = 0.012$; *C* [Figure 2]), and men appeared to have a smaller volumetric decrease in left M1 as compared with women (0.56 [−0.04, 1.16], $p = 0.069$; *E* [Figure 2]). In MuCu, Put_L (−0.36 [−0.61, −0.12], $p = 0.002$) and Tha_L (−0.25 [−0.49, −0.01], $p = 0.045$) decreased after 6 months, whereas in PiPl, there was shrinkage of bilateral Put after 6 months (Put_R: −0.25 [−0.49, −0.01], $p = 0.039$; Put_L: −0.23 [−0.46, 0.01], $p = 0.065$). Further, in PiPl, men experienced much more shrinkage than women in bilateral Tha after 12 months (Tha_R: −0.79 [−1.36, −0.22], $p = 0.012$; Tha_L: −0.63 [−1.22, −0.04], $p = 0.033$).

3.3.2 | Motor-M1 coupling

Bilateral M1 volume did not correlate with pegboard performance before intervention. However, in PiPl, we found a positive coupling between volumetric changes of bilateral M1 and fine motor control of the contralateral hand during the second half-year of intervention (PP_R-M1_L: 0.26 [0.03, 0.50], $p = 0.027$; PP_L-M1_R: 0.27 [0.04, 0.49], $p = 0.02$; *N* [Figure 2]; Figure 5). Longitudinal coupling between grey matter volume changes of M1 and motor as well as neuroanatomical changes are depicted in Figure 5.

3.3.3 | Cortico-basal ganglia-thalamo-cortical coupling

Both statistical models aiming to estimate cortico-basal ganglia-thalamo-cortical coupling yielded a good fit for the right ($\chi^2_{50} = 51.11$, $p = 0.43$; RMSEA 0.02 [0.00, 0.08];

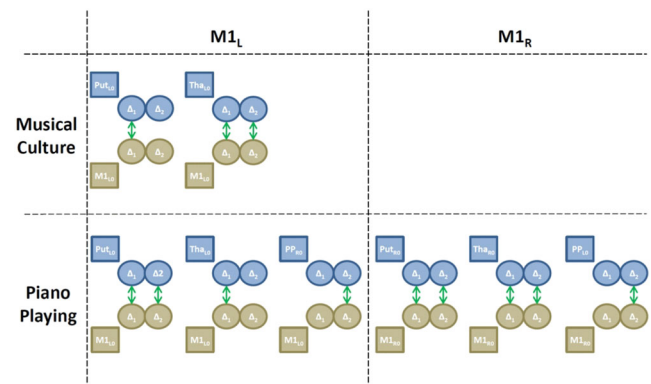


FIGURE 5 Longitudinal coupling between grey matter volume changes of M1 and motor as well as neuroanatomical adaptations. Only meaningful cross-domain effects (*h*, *H*, *K*, *L*, *M*, *N*) with $p < 0.08$ are depicted. Green arrows represent positive covariances. Put₀, baseline Digit Symbol test; DSB₀, baseline Digit Span Backward test; PP_{R/L/B/A0}, baseline Purdue Pegboard_(condition) test; Purdue Pegboard conditions, R (right hand only), L (left hand only), B (both hands), A (assembly); Δ_1 , change from 0 to 6 months; Δ_2 , 6–12 months.

SRMR 0.07) and acceptable fit for the left hemisphere ($\chi^2_{50} = 66.92$, $p = 0.06$; RMSEA 0.07 [0.00, 0.11]; SRMR 0.08).

In the right hemisphere, baseline volume of Tha_R correlated weakly with M1_R (0.11 [0.01, 0.21], $p = 0.039$) and Put_R (0.10 [−0.01, 0.21], $p = 0.063$) in both groups. No other coupling parameters were found for MuCu in the right hemisphere. In PiPl, M1_R changed together with Put_R and Tha_R during the first (Put_R: 0.19 [0.02, 0.36], $p = 0.038$; Tha_R: 0.32 [0.11, 0.52], $p = 0.007$) and second 6 months (Put_R: 0.17 [0.00, 0.35], $p = 0.056$; Tha_R: 0.35 [0.15, 0.55], $p = 0.004$). Furthermore, during months 6–12, Put_R and Tha_R also changed together (0.34 [0.18, 0.50], $p = 0.001$).

In the left hemisphere, baseline volume of Tha_L correlated weakly with M1_L (0.23 [0.07, 0.39], $p = 0.004$) and Put_L (0.19 [0.03, 0.35], $p = 0.02$) in both groups. In MuCu, during the first 6 months, Put_L changed together with M1_L (0.20 [0.02, 0.39], $p = 0.04$) and Tha_L (0.22 [-0.02, 0.45]; $p = 0.068$). During the second 6 months of intervention, changes of Put_L were associated with changes in Tha_L (0.43 [0.22, 0.65], $p = 0.002$). In PiPl, during the first 6 months, M1_L changed together with Put_L (0.25 [0.04, 0.45], $p = 0.03$) and Tha_L (0.35 [0.16, 0.55], $p = 0.003$), as well as Put_L with Tha_L (0.26 [0.04, 0.48], $p = 0.021$). During months 6–12, M1_L changes were linked to changes in Put_L (0.26 [0.05, 0.47], $p = 0.027$).

Irrespective of group, 6-month changes were negatively correlated with 12-month changes. Only baseline volume of Tha was negatively associated with 6-month changes (compensation account). Neither model showed negative cross-coupling between different ROIs.

3.4 | Discussion

3.4.1 | Changes at a group level

Although bilateral Tha shrank only insignificantly after 1 year of music training, there was a reduction in grey matter volume in bilateral M1 and Put. When considering 6-month measurement periods, group-related macrostructural adaptations seemed to occur on different time scales during the intervention: Although MuCu showed volume decreases in bilateral M1 and Put_L during months 0–6 and subsequent stabilization, PiPl experienced first shrinkage of subcortical (bilateral Put) and later of cortical structures (bilateral M1; Figure 6). Non-linear volume changes in response to practicing fine motor tasks were also reported in a longitudinal MRI experiment by Wenger et al. (2017). The authors measured the expansion of bilateral M1 after 4 weeks, which afterwards partially returned to pre-intervention volume. Functional non-linear brain responses have also been observed during 4-week practice of finger movement sequence tasks (Ma et al., 2010): From pretraining to week 2, regional activity in M1 and supplementary motor area increased and then decreased from week 2 to week 4. The phenomenon of shifting execution-related activity from cortical to striatal regions was considered an indicator of automaticity (Lövdén et al., 2020). In general, research on the appropriate analysis of non-linear brain changes is still in its infancy. However, previous findings have been incorporated into the ‘Exploration-Selection-Refinement Model’, proposed by Lindenberger and Lövdén (2019). According to this theory, neural microcircuits

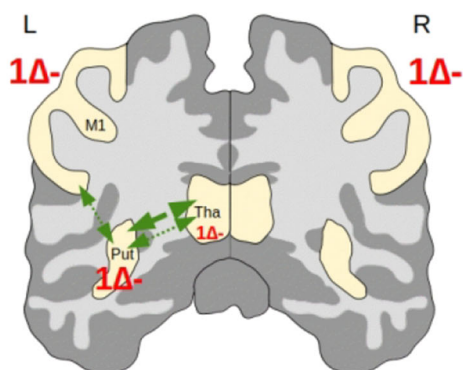
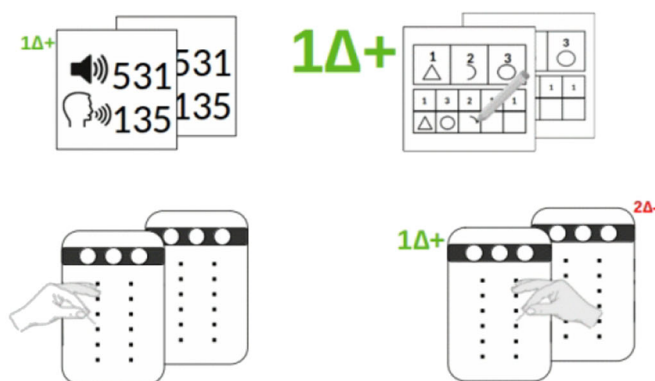
are extensively probed during the early, exploratory stages of learning. This may lead to macrostructural expansions associated with an increase in skill representation. Subsequently, ‘successful’ microcircuits are selected and reinforced, again leading to macrostructural shrinkage but *without* loss of representational stability. This model fits very well to our results. It suggests a piano-related deceleration of age-related atrophy in bilateral M1 during the first half-year of intervention. During this period, piano skills may become consolidated. With increasing automation, bilateral Put becomes more involved and stops shrinking, whereas M1 becomes less important. Associations between subsequent volume decreases in bilateral M1 and reduced manual dexterity of the contralateral hand suggest that successful transfer of trained skills (i.e., piano) to untrained domains (i.e., pegboard) may depend on the stage of learning, that is, on the phase of structural and functional experience-related adaptation. With increasing time and thus specialization, skill transfer to distant domains becomes less likely. This prediction should be tested in future experiments.

3.4.2 | Individual changes and coupling parameters

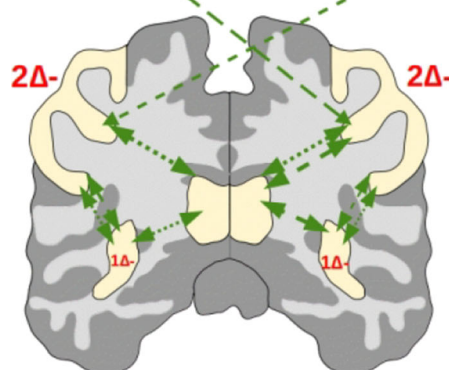
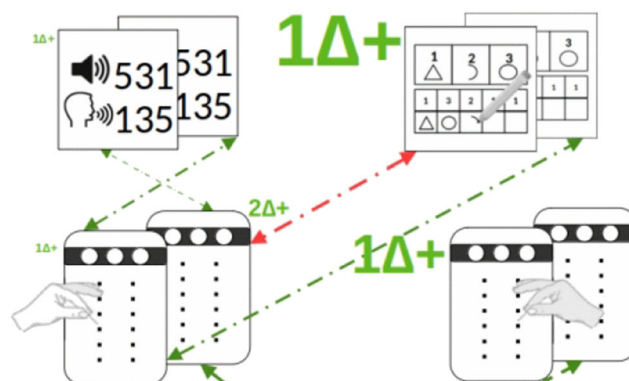
Similar to behavioural outcomes, compensation but not magnification accounts were found for changes in grey matter volume. In other words, participants with large increases in ROI grey matter volume at 6 months showed relatively smaller further increases in volume over the 6- to 12-month period. However, the association between baseline volume and 6-month change was less clear. Here, only the baseline volume of Tha was negatively associated with the 6-month changes.

As reported in the first part of the paper, unimanual fine motor control especially evolved during the first half-year of intervention. However, the 6-month improvement was independent of M1 and is therefore likely to have other neuronal causes, probably not in single brain regions but instead in distributed neuronal networks (Bangert et al., 2006; Doyon et al., 2009), as we also have shown in Jünemann et al. (submitted). As expected, M1 did not change alone in the PiPl group, but in concert with Put and Tha (and most certainly other neural structures) forming an effective and well-connected network. These longitudinal couplings suggest a coordinated music-induced development of neural structures within the cortico-basal ganglia-thalamo-cortical-loop, which in its entirety may support motor execution. In PiPl, M1 showed the most coupling parameters ($N = 7$) among ROIs, which may indicate strong

Musical Culture



Piano Playing



Legend

← ····· → time-lagged covariance



← ····· → strong positive covariance 0-6 months
 ← ····· → weak negative covariance 6-12 months

1Δ+ small increase 0-6 months
 2Δ- large decrease 6-12 months

FIGURE 6 Piano-related improvement in fine motor control is coupled with cognitive and neural parameters. Symbols of the upper two rows represent 6- and 12-month change scores. Green symbols represent positive effects/covariances; red symbols represent negative effects/covariances. The size of the symbols scales with the magnitude of the effect/covariance. Dotted arrows represent covariances during 0–6 months; dashed arrows during 6–12 months. Dotted and dashed arrows show time-lagged covariances. 1Δ/2Δ, change scores (0–6/6–12 months); DSB, Digit Span Backward test; DSY, Digit Symbol test; PP_L/PP_R, Purdue Pegboard test (left/right hand only).

integration and connectivity of M1. Of these parameters, the strongest were those involving Tha. Therewith we can corroborate the findings of sleep studies, which highlighted the importance of thalamo-cortical coupling in offline consolidation of sequential finger movements (Boutin et al., 2018; Morin et al., 2008).

Interestingly, left-lateralized coupling was also present in the MuCu group. This could reflect the natural dynamic network characteristics in aging or be explained by the recruitment of the motor system during music listening (see also Action Simulation for Auditory Prediction [ASAP] hypothesis by Patel and Iversen [2014]). A recent activation likelihood estimation (ALE) meta-analysis of fMRI data found auditory activation, among others in bilateral M1 (Gordon et al., 2018). This finding suggests that motor-related brain areas are not only

recruited for motor planning and execution but also for music perception. However, the overall coupling was weaker and less prevalent in MuCu ($N = 3$) than in PiPl ($N = 9$; see Figure 6).

Finally, it should be mentioned that the ability to positively alter motor circuits could offer valuable therapeutic potential for neurological motor disorders such as Parkinson's and Huntington's disease (Devlin et al., 2019), stuttering (Alm, 2004) or stroke (Altenmüller et al., 2009; Villeneuve et al., 2014).

3.5 | General discussion

Piano training involves motor sequence learning, which includes explicit (sequence order) and implicit

(optimization) learning stages. Skill consolidation may occur, among others, in well-connected bilateral motor circuits (e.g., cortico-basal ganglia-thalamo-cortical loops) with a strong integration of M1. By reactivating these circuits, novel motor tasks in untrained domains (e.g., Purdue Pegboard) can be executed with higher acuity (i.e., transfer). Furthermore, stronger macrostructural expansions of bilateral M1 seem to beneficially impact the success of skill transfer.

Different motor learning stages may be supported by different cognitive processes (Figure 4). Working memory may be important for the acquisition of motor sequences and the execution of challenging bimanual movements, including complex sequences. Processing speed, on the other hand, may generally promote movement execution, particularly in later, implicit stages (i.e., optimization). However, there may be a saturation point beyond which higher cognitive capacity does not provide additional support for motor execution.

Macrostructural and cognitive changes at a group level, as well as individual changes in unimanual dexterity and their coupling with neural and cognitive changes, are summarized graphically in Figure 6. The development of motor acuity and cognition exhibit bidirectional relationships, but they do not necessarily change together during motor learning and thus may not be causative. Rather, motor and cognitive adaptations are related to both common causes (e.g., through a developmental cascade triggered by piano playing that affects a variety of sensorimotor and cognitive parameters) and shared resources with reallocation and reorganization of limited resources as compensatory trade-offs (Li & Lindenberger, 2002).

One limitation of the study is its focus on M1 and the cortico-striatal circuit. The cortico-cerebellar system, cortico-motoneuronal connections and other brain regions (e.g., somatosensory cortex; see Elbert et al., 1995) have also been shown to contribute meaningfully to the acquisition and/or execution of motor sequences (Doyon et al., 2009; Doyon et al., 2018; Krakauer et al., 2019; Penhune & Steele, 2012).

Furthermore, by using the Purdue Pegboard test, our conclusions are limited to motor acuity. Processes involved in earlier learning stages (e.g., during goal selection and action selection) were not considered in this study.

When evaluating correlated changes, it should be noted that the interval between measurement time points is very critical. On the one hand, the time period must be long enough for the effects of interest to become manifested; on the other hand, longer periods may obscure correlated changes. Therefore, fine motor control and cognitive (e.g., processing speed) or neural parameters (e.g., grey matter volume of M1) may change

simultaneously during the first weeks of intervention but diverge thereafter.

Although we could show that piano practice in older adults leads to a coordinated development of neural structures within the cortico-basal ganglia-thalamo-cortical-loop, we cannot link structural covariance between brain regions to inter-individual differences or behavioural development. It is reasonable to assume, however, that individuals with stronger covariance may also show stronger behavioural improvement.

Finally, in the second half of the study, the Corona crisis had a detrimental effect on the intervention. Although the highest effort was made to continue the intervention online as intensively as possible without interruption, it is doubtful that the online format was as effective as face-to-face instruction given the feedback from teachers and participants. Training effects are expected to diminish with decreasing intensity, yet in this study, significant effects were found in the second half of the intervention—this only further emphasizes the potential of musical activity to promote neuroplasticity and offline learning during rest (Schlichting & Preston, 2014).

AUTHOR CONTRIBUTIONS

Florian Worschech wrote the first draft of this manuscript. Damien Marie, Florian Worschech and Kristin Jünemann collected the data. Florian Worschech performed the statistical analysis. Clara E. James and Eckart Altenmüller wrote the proposal submitted to the DFG (German Research Foundation) and the SNSF (Swiss National Science Foundation). Matthias Kliegel and Tillmann H. C. Krüger made a detailed contribution to the grant application. All authors critically reviewed and revised the article and approved the submitted manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article are openly available at <https://osf.io/k9b7d/>.

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