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Prediction processes in the acquisition of sequence representations

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ABSTRACT

Action-Imagery-Practice describes the repetitive imagination and Action-Observation-Practice the repetitive observation of an action. Both Action-Imagery-Practice and Action-Observation-Practice are assumed to involve similar motor mechanisms as Action-Execution-Practice, resulting in motor learning. To investigate whether these practice styles differ in the acquired representation types, we compared performance of the practice and transfer hand for same, mirrored, and random sequences in pre- and post-tests. All participants practiced a serial reaction time task to auditory stimuli in ten practice sessions. Five separate groups either physically executed the responses (Action-Execution-Practice), imagined the responses (Action-Imagery-Practice), observed keypresses with an animated hand (Action-Observation-Practice), observed animated keys (Observation-Without-Action), or completed a control condition in which they listened to the stimuli (Auditory-Control). Evidence for effector-dependent representations was obtained after Action-Execution-Practice and Action-Imagery-Practice, but not after Action-Observation-Practice and Observation-Without-Action. Although all groups acquired partial sequence knowledge, sequence recognition was more strongly related to kinesthesis than to the tones alone after Action-Execution-Practice and Action-Imagery-Practice. It is concluded that effector-dependent representations can be acquired via Action-Imagery-Practice even though actual feedback is not available. Conceivably, effector-dependent learning might have been provoked by forward models that predict the action consequences in Action-Imagery-Practice, but not in Action-Observation-Practice, where the action consequences were externally presented on screen.

1. Introduction

Action-Imagery and Action-Observation are two cognitive processes that play fundamental roles in motor learning, skill acquisition, and performance optimization (Moran et al., 2012; Mulder, 2007). Action-Imagery involves mentally rehearsing or visualizing specific motor actions without physically executing them (Jeannerod, 1995). Individuals create internal representations of actions, engaging sensorimotor networks (Lorey et al., 2013) to simulate sequences of movements and anticipate outcomes. In contrast, Action-Observation entails watching another individual perform a motor action (Vogt, 1995). In non-human primates, Action-Observation has been demonstrated to activate “mirror neurons” in premotor and parietal areas (di Pellegrino et al., 1992; Gallese, 2005), and a similar system for Action-Observation has been identified in humans (Caspers et al., 2010). This Action-Observation system overlaps with sensorimotor networks in imagery and execution (Lorey et al., 2013), which enables individuals to map observed actions onto their own motor representations to understand the intentions behind the actions (Baldwin and Baird, 2001) and imitate them (Caspers et al., 2010). By examining the underlying representations and behavioral outcomes, we seek to enhance our understanding of how Action-Imagery and Action-Observation contribute to motor learning and skill acquisition. We aim to delineate whether there are unique contributions of Action-Imagery and Action-Observation to performance optimization, ultimately informing the development of effective interventions for enhancing motor skills (Ladda et al., 2021; Lindsay et al., 2023; Simonsmeier et al., 2021) and rehabilitation strategies for motor impairments (Braun et al., 2013; Mulder, 2007).

1.1. Representation types

Action-Imagery Practice (also called motor imagery practice or mental practice) and Action-Observation Practice can both contribute to motor learning and skill acquisition (Gatti et al., 2013; Gonzalez-Rosa

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et al., 2015). Action-Imagery Practice and Action-Observation Practice serve as alternative forms of practice when Action-Execution Practice is not possible due to injury, location, or lack of material. The present study investigated whether Action-Observation Practice and Action-Imagery Practice result in the acquisition of different action representation types (Dahm et al., 2022), namely effector-independent visual-spatial representations, effector-independent intrinsic representations, or effector-dependent representations.

Effector-dependent representations are specific to the motor system and are closely tied to the characteristics and capabilities of specific effectors of the body, (e.g., the right hand). These representations encode motor commands and kinematic parameters tailored to a specific effector involved in the action (Imamizu and Shimojo, 1995; Panzer et al., 2009). Effector-dependent representations contribute to performance improvements that are stronger in a practiced effector compared to an unpracticed effector (e.g., Practice Hand vs. Transfer Hand).

Effector-independent visual-spatial representations, by contrast, are detached from specific effectors and instead focus on the spatial relationships and visual features of the environment, e.g., moving to the left side, regardless of the hand used (Imamizu and Shimojo, 1995; Remillard, 2003; Soetens et al., 2004; Verwey and Clegg, 2005; Willingham et al., 2000). These representations allow individuals to mentally manipulate objects and navigate spatial layouts irrespective of the effector used to interact with them. Effector-independent visual-spatial representations contribute to performance improvements in both hands, whenever the same stimuli or response locations are involved.

Lastly, *effector-independent intrinsic representations* encompass the intrinsic properties of actions, such as the involved muscles, without relying on specific effectors or visual-spatial cues, e.g., responding by pressing a key with the index finger of either hand (Criscimagna-Hemminger et al., 2003). Although the contralateral activity is inhibited under normal circumstances (Cohen et al., 1991), mirror actions of the opposite limb can be facilitated (Gordon et al., 1994). As a result, effector-independent intrinsic representations can contribute to performance improvements, for instance in mirror movements with the transfer hand.

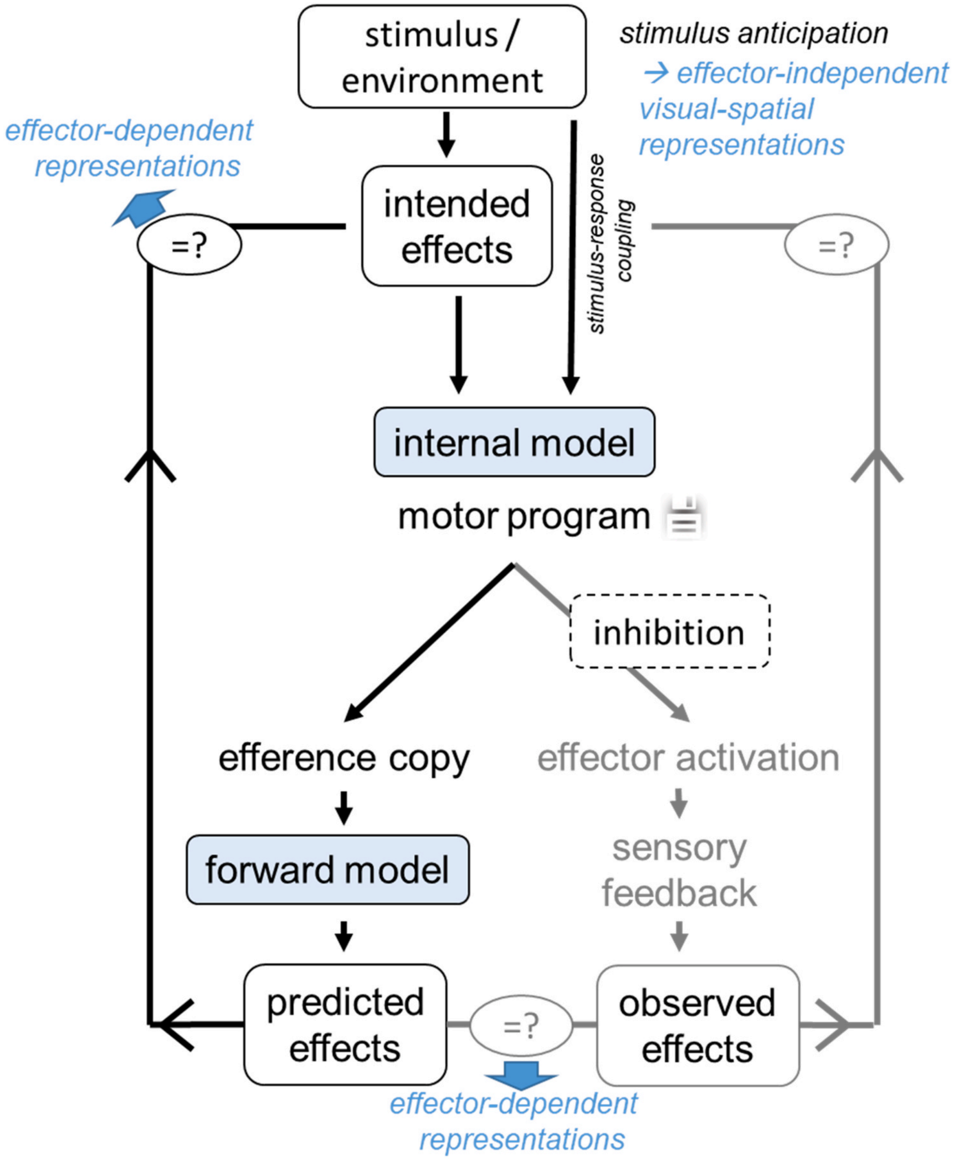

Fig. 1. Theoretical framework of motor control. Marked in grey are the mechanisms that are available in Action Execution, but not in Action Imagery. Effector-independent visual-spatial representations are expected to evolve due to stimulus anticipation. Effector-dependent representations are expected to evolve from comparisons of the predicted and observed effects as well as the predicted and intended effects.

1.2. Mechanisms in Action-Imagery Practice and Action-Observation Practice

The simulation theory (Jeannerod, 2001) states that Action-Imagery and Action-Observation draw on similar mechanisms that are involved in action initialization. This theoretical approach has been dominant in the literature and has received relatively little challenge for almost two decades (see Glover and Baran, 2017 for an exception). However, notably, the simulation theory does not specify precise mechanisms, and neglects the involvement of action realization processes in Action-Imagery. More recent work has proposed that internal and forward models developed during Action-Imagery play a pivotal role in enhancing subsequent execution performance (Rieger et al., 2023). Internal models draw on motor commands that encapsulate the dynamics and characteristics of motor actions, thereby provoking a stimulation of the effectors (Miall and Wolpert, 1996). In Action-Imagery, the stimulation of the effectors is inhibited (Guillot et al., 2012; Rieger et al., 2017). Nevertheless, internal models allow individuals to predict and anticipate the consequences of their movements even in Action-Imagery (Dahm and Rieger, 2019a, 2019b; See Fig. 1). Based on efference copies of the motor commands, forward models (Wolpert et al., 2001, 2011) can generate predictions of the sensory outcomes of a planned action. By comparing these predicted outcomes (based on internal and external information) and the intended outcomes, deviations can be detected which leads to optimization processes and learning (Rannaud Monany et al., 2022). Therefore, by simulating the anticipated outcomes of motor actions, forward models enable individuals to mentally rehearse and visualize movements in advance, aiding in motor planning (Kawato, 1999; Simon and Daw, 2011), coordination (Miall, 2007; Miall and Reckess, 2002), and error correction (Shadmehr et al., 2010). Such updating of internal forward models is located in the cerebellum (Cengiz and Boran, 2016; Rannaud Monany et al., 2022) which facilitates excitability in the primary motor cortex during imagery (Tanaka et al., 2018).

Similar mechanisms involving internal and forward models have also been proposed in Action-Observation (Miall, 2003), though direct evidence of the involvement of forward models is more limited in sequence learning. However, forward prediction processes have been shown to occur in grasping and flick movements (Urgesi et al., 2010), basketball (Aglioti et al., 2008), and volleyball (Urgesi et al., 2012). In line with this, it has been argued that forward simulation in action observation occurs automatically even when watching a static picture of a person in action (Ianì et al., 2021, 2023).

While observing another person's actions is a common method used in Action-Observation Practice, it is not the only approach. Action-Observation can involve various stimuli, including videos, animations, or virtual simulations depicting human or non-human actions. These stimuli can be presented in a controlled environment, allowing individuals to observe and study the actions without direct human involvement (Biswas et al., 2024; Yoshimura et al., 2020). When individuals observe someone else performing a motor action, they activate internal representations of that action, which are proposed to be akin to internal models. These internal representations encompass the dynamics and characteristics of the observed action (Schenke et al., 2016). Additionally, forward models have been proposed to be engaged during Action-Observation to predict the sensory consequences of the observed action based on the observer's motor knowledge and previous experiences (Miall, 2003; Steenbergen et al., 2020). These predictions would enable individuals to anticipate the outcomes of the observed actions and understand the intentions behind them. Through the activation of internal and forward models during Action-Observation (Pickering and Clark, 2014), individuals could vicariously experience the observed actions (Bach and Schenke, 2017), predict the aimed action consequences (Baldwin and Baird, 2001), and incorporate observed skills into their own motor repertoire (Sarasso et al., 2015). Neurophysiological data, however, provides contradictory evidence regarding the recruitment of forward models during action observation. In particular, meta-analytic evidence indicates that the cerebellum, which is widely regarded as the physiological location of forward models (for a review see Ishikawa et al., 2016) is consistently recruited during movement execution and action imagery, but was not consistently recruited during action observation (Hardwick et al., 2018; though c.f., Abdelgabar et al., 2019; Calvo-Merino et al., 2006; Errante and Fogassi, 2020; Frey and Gerry, 2006; Molenberghs et al., 2012). Therefore, it remains unresolved whether forward models are involved in the internal representations of movements generated during action observation.

Besides similarities, there are also notable differences between Action-Imagery and Action-Observation (Gatti et al., 2013; Hardwick et al., 2018). Action-Imagery primarily relies on internally generated representations, whereas Action-Observation involves externally observed stimuli. Hence, in the absence of external perceptual input, Action-Imagery relies on internal simulations that are fed primarily with information from long-term memory (Helm et al., 2015; Kim et al., 2017) which is then processed in working-memory. In contrast, Action-Observation is driven by the perception of externally provided visual information that is processed in working memory (Kim et al., 2017; Wright et al., 2015) which may include experiences from long-term memory (Bouazzaoui et al., 2025; Calvo-Merino et al., 2005). Furthermore, while Action-Imagery allows individuals to mentally rehearse one's own actions (Holmes and Collins, 2001; Moreno-Verdú et al., 2024; Roberts et al., 2008), Action-Observation provides opportunities to learn from the actions of others and incorporate observed strategies into one's own motor repertoire (Mizuguchi and Kanosue, 2017; Stefan et al., 2005).

In the present study, we used animated pictures which enabled us to dissociate between the observation of hand movements (Action-Observation Practice) or simply observing the action's consequences (Observation Without Action), i.e., keys being depressed without a hand movement. In contrast to using a visual-spatial mapping as in previous studies (Dahm and Rieger, 2023a, 2023b), the present study involved an auditive stimulus-response mapping related to the fingers (e.g., high pitch tone corresponds to index finger) rather than to the response keys (e.g., leftmost stimulus on screen corresponds to leftmost finger/key). We therefore expected effector-independent intrinsic representations to evolve more strongly than effector-independent visual-spatial representations. Still, in the observation groups, visual-spatial representations were expected due to the visual animations shown during practice. Assuming that Action-Observation Practice relies on similar mechanisms as Action-Imagery Practice (Jeannerod, 2001), we would expect that learning results in similar representation types (Osman et al., 2005). Because Action-Observation Practice involves the automatic activation of both higher level (e.g., action goals) as well as lower level (e.g., specific effectors) action elements in the observer (Massen and Prinz, 2007), we expected that effector-dependent representations can be acquired not only in Action-Imagery Practice (Dahm and Rieger, 2023a, 2023b), but also in Action-Observation Practice (Bird and Heyes, 2005). In contrast, a lack of effector-dependent representations in Action-Observation Practice would indicate that forward models predicting the action outcomes based on motor concepts are not involved. Such is expectable after Observation Without Action because it has been shown that focusing on the action rather than on the object triggers mental simulations (Ianì et al., 2024) and observing stimuli alone does not result in sequence learning (Li et al., 2024).

Using the serial reaction time paradigm, it has often been shown that participants achieve shorter RTs in the practice sequence compared to a control sequence, although they are not aware about the existence of a sequence (Reber and Squire, 1998). Still, free generation and recognition tests show that sequence awareness occurs even in implicit sequence learning settings (Dahm and Krause, 2024). Most importantly for the present study, we assumed that both Action-Imagery Practice and Action-Observation Practice result in similar sequence awareness.

2. Method

2.1. Participants

The required sample size was estimated with G*Power (Faul et al., 2007). Based on a previous learning study with the serial reaction time task (Dahm and Rieger, 2023a), we expected an effect size for effector-dependent representations (post-hoc comparisons of the practice and transfer hand in the same sequence) in Action-Imagery Practice of $d = 0.5$. Alpha was set at 0.05 (one-sided: shorter RTs in practice than transfer hand) and power (1-beta) at 0.8 which resulted in an estimated sample size of $n = 27$ per group. All participants were between 18 and 35 years old. Originally 158 participants took part in the experiment. Nine participants had technical problems and therefore aborted the experiment before the last session. From the 149 participants that had complete datasets, 23 participants showed non-compliance with the instructions, i.e. error rates above 50 % as well as infrequent and inconsistent response behavior (Maniaci and Rogge, 2014). One participant reported not having at least moderately clear and vivid movement images, assessed with the German version (Dahm, 2022; Dahm et al., 2019) of the Vividness of Movement Imagery Questionnaire (Roberts et al., 2008). Of the remaining 125 participants the distribution of sex and means of age, hand laterality index (Oldfield, 1971), and vividness of Action-Imagery (Dahm, 2022; Dahm et al., 2019) are shown in Table 1, separately for the five experimental groups. All participants gave informed consent. Ethical approval of the study was provided by the local research committee.

2.2. Serial reaction time task

In the serial reaction time task (SRTT), participants react as fast as possible to a series of stimuli (Reber and Squire, 1998). In the implicit version of the task, as used here, participants are not informed that the stimuli (and consequently also their responses) follow a predetermined sequence. In the present study a four-choice auditive serial reaction time task was used. Auditory stimuli consisted of an artificially created musical tone "A" at one of four different pitch levels (1760 Hz, 880 Hz, 440 Hz, 220 Hz). Participants responded to each tone by using the corresponding response finger as fast as possible. The index, middle, ring, and little finger were used for the highest-to-lowest tones in descending order. The response keys were the 'F', 'G', 'H', and 'J' key on the computer keyboard. Each sequence consisted of twelve elements, and four sequences were used (Dahm and Rieger, 2023b): Sequence A (GHGJFHFJHJGF) and Sequence B (JHGJGHFGFJFH), and mirrored versions of these sequences, Sequence A' (HGHFJGJFGFHJ) and Sequence B' (FGHFHGJHJFJG). In all sequences, each element appeared equally often, the same element was not repeated on successive trials, and each transition between elements occurred equally often. Thus, first order learning was not possible (Reber and Squire, 1998).

Each block consisted of 120 responses (i.e., repeating one of the 12 element sequences 10 times) and started with a fixation cross. After 500 ms the first tone was played to indicate the corresponding target key. The task was self-paced. Correct responses triggered the end of each auditory stimulus, provoking the onset of the following auditory stimulus. Upon incorrect responses, a soft noise signal (200 ms) informed the participant about the incorrect response, and the previous auditory stimulus was repeated. In each block, one of the twelve-elements was randomly chosen as starting stimulus to impede explicit learning. The response-stimulus-interval, i.e., the duration between participants' response and the subsequent stimulus tone was set at 300 ms of silence.

2.3. Procedure

The experiment ran on participants' personal computers using OpenSesame version 3.3.14 (Mathôt et al., 2012) with an out-of-the lab approach (Dahm et al., 2023b). The experimental file including all stimuli and instructions is placed at the Open Science Framework (https://osf.io/9y34k/). Participation lasted approximately 20 min in each of the eleven sessions (Fig. 2). Extensive practice over ten sessions was chosen because effector-dependent representations usually emerge at later stages of learning (Dahm and Rieger, 2023b; Panzer et al., 2009). To avoid mental fatigue, particularly during Action-Imagery Practice, practice was split up into several sessions with recommended practice phases of approximately 10 min (Driskell et al., 1994; Simonsmeier et al., 2021).

Warm-up. The first and the last session started with four warm-up blocks of 120 stimuli each, in which the participants became familiarized with the sounds and their corresponding responses. These were performed with the left and right hand (each hand two blocks), with the order of the hands being counterbalanced across participants. The order of the sound stimuli during warm-ups was random, but without stimulus repetitions.

Pretest. The familiarization phase was followed by a test phase, which consisted of the same sequence (e.g., A), mirror sequence (e.g., A′), and control sequences (e.g., B and B'). Each sequence was performed with each hand, resulting in eight blocks of 120 stimuli. The order of the hands was blocked and counterbalanced across participants. The order of the sequences was random, but equal in each hand.

Practice phase. The first ten sessions involved a practice phase in which one of the sequences was practiced with the right hand (10 blocks of 120 consecutive responses per session). Each participant practiced the same sequence over all sessions, but sequences were counterbalanced across participants and groups. Participants were randomly assigned to one of five groups. To measure RTs during Practice, the subsequent stimulus was triggered by pressing the 'Y' key with the left hand in all groups. RTs during Practice are particularly informative about participants study commitment during Action-Imagery where actual performance is not observable. In all groups, participants were not informed about the existence of sequences.

Action-Execution Practice Group: Participants were asked to place the fingers of the right hand on the target keys. They pressed the corresponding keys and simultaneously pressed the 'Y' key with their left thumb.

Action-Imagery Practice Group: Participants were asked to place the fingers of the right hand on the target keys without pressing them. They were asked to imagine pressing the corresponding key with their fingers by focusing on the feeling of the action and seeing the action through their own eyes. Participants indicated that they imagined pressing the target key with their right hand by pressing the 'Y' key with their left thumb.[1]

Action-Observation Practice Group: Participants observed a pictorial hand on the screen that pressed the keys (one finger moved downward slightly, accompanied by small lines on that finger helping to indicate motion). The moment they actually pressed the 'Y' key with the left thumb, they observed a press of the target key with the depicted right hand.

Observation without Action Group: Participants observed which key was activated (while no hand was shown). Note that this condition only included the action consequences, but not the action itself. The moment they pressed the 'Y' key with their left thumb, the target key was highlighted on the screen. A video-animation of the visual material in the observation groups can be found in the supplemental material at https://osf.io/9y34k/. In the present study, we used an animated hand on screen that created illusions of actual hand movements. These stimuli were chosen as the use of similar 'avatars' has been shown to effectively modulate the activity of the human action observation system (Miyamoto et al., 2023), and they allow precise control over the depicted material (with action and without action).

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[1] Note participants used a German QWERTZ keyboard; this key was therefore in the bottom left of the keyboard, in a natural position for the left hand.

Table 1
Sociodemographic data of the different groups.

	Action-Execution Practice	Action-Imagery Practice	Action-Observation Practice	Observation without Action	Auditory Control
Total *N* ($N_{\mathrm{female}}/N_{\mathrm{male}}$)	23 (16/7)	23 (14/9)	24 (14/10)	26 (20/6)	29 (19/10)
Age, *M*±*SD*	23.5 ± 3.6	24.3 ± 3.6	22.9 ± 2.9	22.6 ± 2.9	23.9 ± 3.7
Laterality Index, *M*±*SD*	92 ± 14	88 ± 14	92 ± 16	92 ± 13	93 ± 13
External Visual Imagery, *M*±*SD*	1.7 ± 0.7	2.4 ± 0.9	2.0 ± 0.8	2.3 ± 0.8	2.1 ± 1
Internal Visual Imagery, *M*±*SD*	1.6 ± 0.6	2.0 ± 0.7	1.9 ± 0.8	1.9 ± 0.6	1.7 ± 0.6
Kinesthetic Imagery, *M*±*SD*	1.7 ± 0.6	2.1 ± 0.6	1.9 ± 0.7	1.9 ± 0.7	1.9 ± 0.7

Auditory Control Group: Participants were asked to pay attention to the order of the sound stimuli. The moment they pressed the ‘Y’ key with their left thumb, a new sound stimulus was played.

In the Action-Observation Practice, Observation Without Action, and Auditory Control groups, participants were asked to place the right hand on their right leg. After each practice block, feedback about the median response times was given to motivate participants during practice (K. M. Wilson et al., 2017). Because errors were not trackable during Action-Imagery Practice, error feedback was not provided after practice blocks. The animations in Action-Observation Practice and Observation Without Action did not involve errors. After the feedback, participants rated their focus during practice by answering whether they (mentally) perceived a melody (auditive), whether they (mentally) perceived feelings in their fingers (kinesthetic), and whether they (mentally) perceived movements of their own fingers visually on a scale from 1 (not at all) to 9 (very much).

Posttest. The posttest started according to the same procedure as in the pretest (i.e., measures of RT during practice, mirror, and control sequence in both the practice and transfer hand). Additionally, participants performed two free generation tests. In the *acoustic generation test*, participants were asked to replicate the same sequence by selecting twelve stimuli using the mouse on the screen. Hereby, high and low buttons on the screen indicated the four stimulus sounds. In the *motor generation test*, participants were asked to press the target keys in the order of the same sequence. This was followed by two recognition tests. In the *audible recognition test*, twelve sound stimuli were presented for 500 ms in the order of each of the four sequences (no responses required). After the twelve stimuli of each sequence, participants rated whether this coincided with practice (from 1 – very unlikely to 9 – very likely). In the *motor recognition test*, participants performed each sequence block (12 responses) and rated afterwards whether this coincided with practice (from 1 – very unlikely to 9 – very likely). The order of the four blocks was randomized in the recognition tests.

2.4. Data analysis

Response time (RT) was measured as the interval between starting time of the auditory stimulus and its correct response (incorrect responses were not analyzed).[2] RTs of the first twelve responses in each block were not taken into analysis to allow participants to familiarize with the sequence of the block. Of the remaining responses, median RTs were calculated for each block (i.e., the remaining 108 trials). To analyze sequence-specific and sequence-unspecific learning effects, a mixed ANOVA with the between-factor *Group* (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation Without Action, Auditory Control) and the within-factors *Session* (Pretest, Posttest), *Sequence* (Same, Mirror, Control), and *Hand* (Practice, Transfer) was calculated on RTs. If Mauchly’s test indicated that the assumption of sphericity is violated, we report Greenhouse-Geisser corrected degrees of freedom and *p*-values. Further comparisons were conducted using *t*-tests with Holm adjusted pairwise comparisons. Statistical significance was set at $p < .05$. We expected effector-independent intrinsic representations to be indicated by differences in RTs of the transfer hand between the Same and Control Sequences. Similarly, we expected effector-independent visual-spatial representations to be indicated by differences in RTs in the transfer hand between the Mirror and Control Sequences. Further, we expected effector-dependent representations to be indicated by differences in sequence learning specifically between practice and transfer hand.

In addition to RTs, we calculated the number of triplets in the free generation test that are compatible with the Same Sequence and its Mirror Sequence. This indicates the amount of explicit learning of the sequence structure (Bird and Heyes, 2005).

2.4.1. Transparency and Openness

Data were analyzed using R version, 4.2.2 (R Development Core Team, 2019) and the packages rstatix, version 0.7.1 (Kassambara, 2021) and tidyverse version, 2.0.0 (Wickham et al., 2019). All program code and methods developed by others are cited in the text and listed in the reference section. All data, analysis code, and research materials are available at https://osf.io/9y34k/. This includes a short animation of the video material used in the AOP and OP groups. We report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study. The study was not preregistered but planned in a grant proposal.

3. Results

3.1. Manipulation check: focus during practice

Means and standard errors of the Focus Ratings are shown separately for all groups in Fig. 3. An ANOVA with the between-factor *Group* (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation Without Action, Auditory Control) and *Modality* (auditive, kinesthetic, visual) was performed on the Focus Ratings. The main effect *Modality*, $F\,(1.8, 206) = 59.2$, $p < .001$, $\eta_p^2 = .33$, was significant. The significant main effect *Group*, $F\,(4, 118) = 14.6$, $p < .001$, $\eta_p^2 = .33$, was modified by the significant interaction between *Group* and *Modality*, $F\,(7, 206) = 3.4$, $p = .001$, $\eta_p^2 = .1$. Auditive perception ratings did not differ significantly between groups ($p \geq .050$) but showed marginal tendencies of higher values in Action-Execution Practice and Action-Imagery Practice compared to Action-Observation Practice, Observation Without Action, and Auditory Control ($0.58 \leq d \leq 0.84$). Kinesthetic perception ratings were significantly higher in Action-Execution Practice and Action-Imagery Practice than in the Action-Observation Practice, Observation Without Action, and Auditory Control ($p \leq .028$, $d \geq 0.85$). Visual perception ratings of (mentally) seeing the own fingers were significantly higher in Action-Execution Practice than in Action-Imagery Practice, Action-Observation Practice, Observation Without Action, and Auditory Control ($p \leq .001$, $d \geq 1.2$). All other group comparisons were not significant ($p \geq .118$, $d \leq 0.67$).

3.1.1. Response times

Means and standard errors of RTs (in ms) of the *Groups* (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation Without Action, Auditory Control) are shown

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[2] Mind that the next stimulus only appeared after correct responses. Hence, a penalization of incorrect responses is already included in RTs, making a speed-accuracy trade-off implausible.

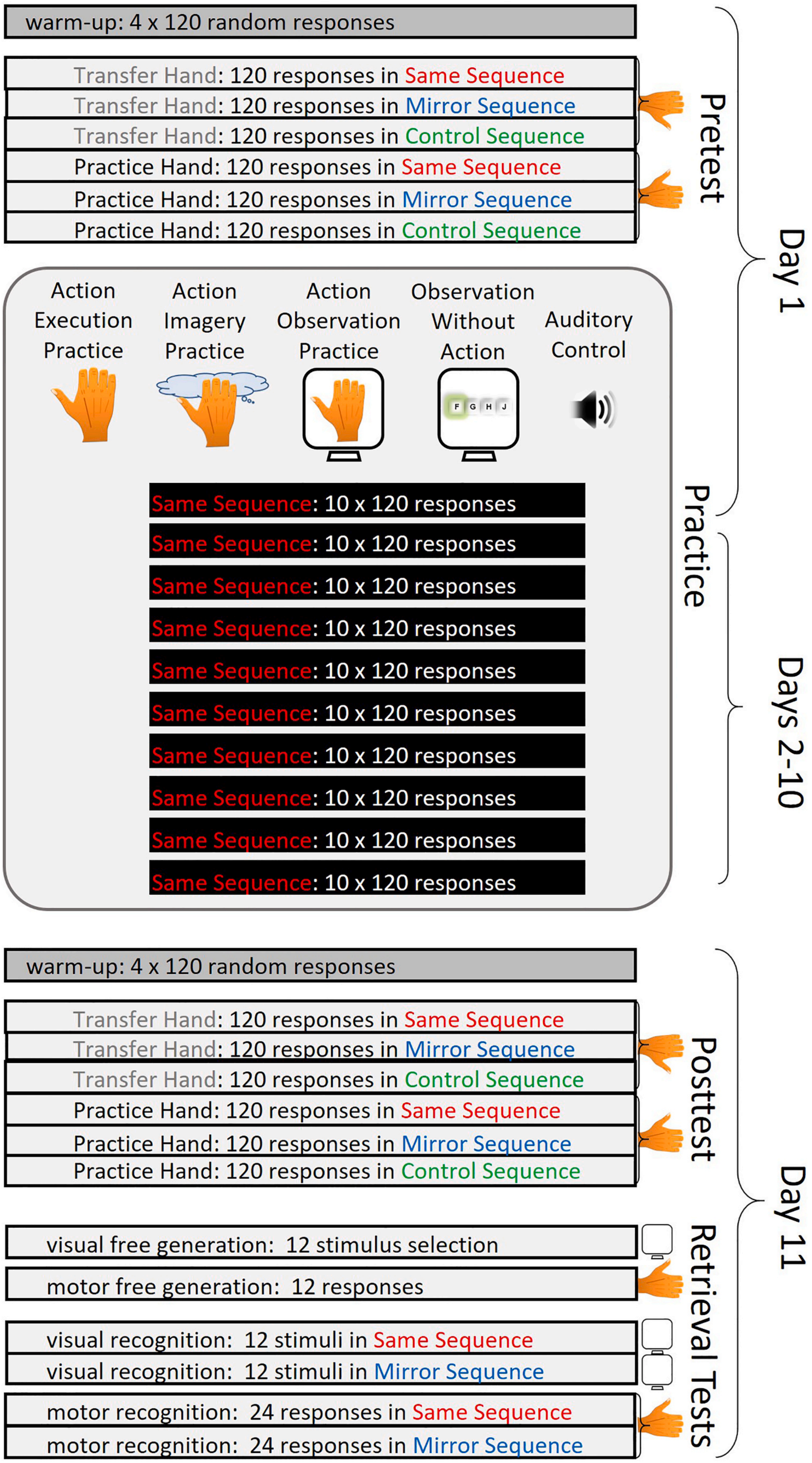

Fig. 2. The study design involved Pretest, Practice, Posttest, and Retrieval Tests. The practice conditions differed between groups. Note that the order of the sequences and hands in the tests was counterbalanced across participants.

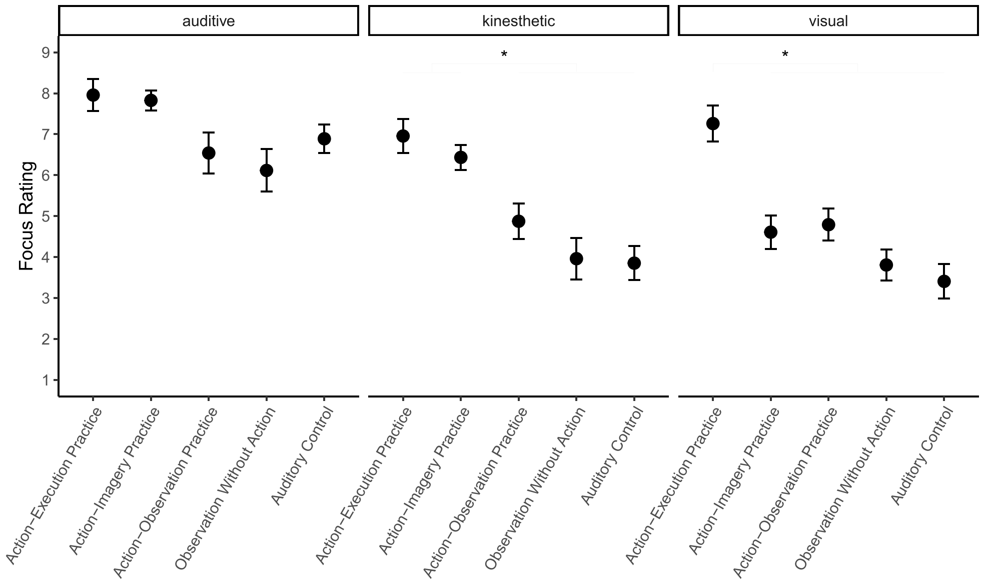

Fig. 3. Means and standard errors of Focus Ratings after practice. In all groups, participants rated whether they (mentally) perceived a melody (auditive), whether they (mentally) perceived feelings in their fingers (kinesthetic), and whether they (mentally) perceived movements of their own fingers visually.

separately for *Session* (Pretest, Posttest), *Sequence* (Same, Mirror, Control), and *Hand* (Practice, Transfer) in Fig. 4. For an overview of all main effects and interactions see Appendix A.

Sequence-unspecific learning was indicated by the significant main effect *Session, F* (1, 120) = 295, $p < .001$, $\eta_p^2 = .71$. RTs became significantly shorter from Pretest (*M*±*SD* = 755 ± 173 ms) to Posttest (*M*±*SD* = 576 ± 209 ms).

Sequence-specific learning was indicated by the significant main effect *Sequence, F* (1.8, 215.3) = 64.9, $p < .001$, $\eta_p^2 = .35$, which was modified by the significant *Session* × *Sequence* interaction, *F* (1.44, 173) = 91.4, $p < .001$, $\eta_p^2 = .43$. It indicated that the Mirror Sequence did not significantly differ from the Control Sequence ($p \geq .101$, $d \leq 0.36$). This indicates that participants did not acquire effector-independent visual-spatial representations. As an exception, the Posttest after Action-Execution Practice demonstrated significantly longer RTs in the Mirror Sequence than in the Control Sequence ($p = .040$, $d = 0.45$) which again

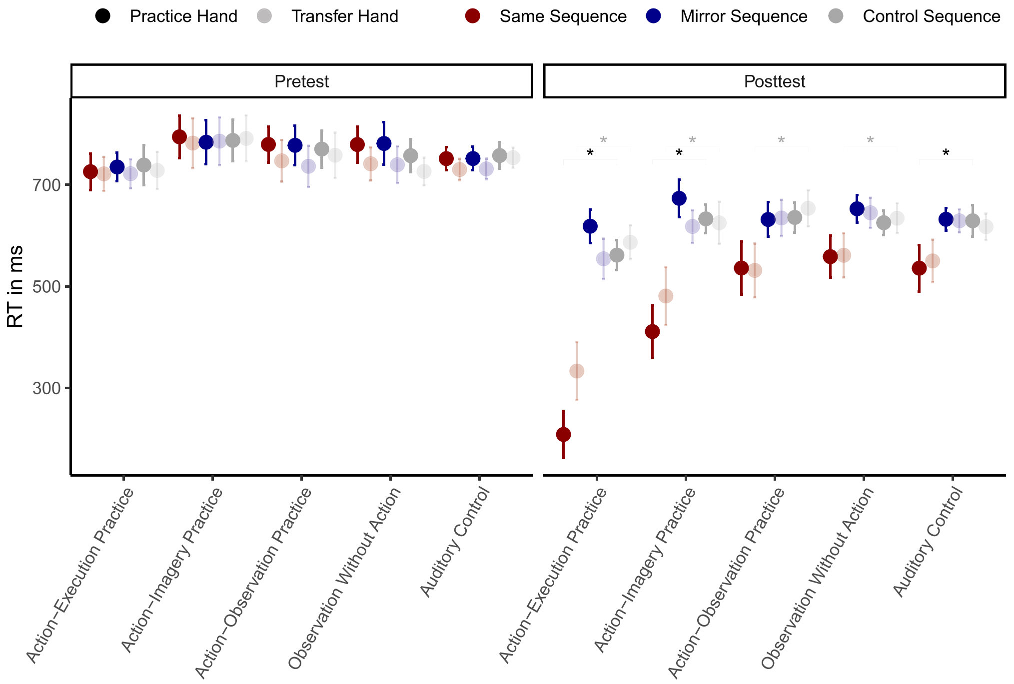

Fig. 4. Means and standard errors of response times (RT) depending on Session, Sequence (Same in red, Mirror in blue, Control in grey), and Hand (Practice in dark color, Transfer in light color), separately for the groups. The asterisks indicate significant differences between Same Sequence and Control Sequence providing evidence for effector-independent representations in the Transfer Hand.

speaks against effector-independent visual-spatial representations. Evidence for sequence-specific learning was indicated by significantly shorter RTs in the Same Sequence than in the Control Sequence in the Posttest, but not in the Pretest ($p \geq .251$, $d \leq 0.33$). In the Posttest, this difference was significant with both hands after Action-Execution Practice ($p < .001$, $d \geq 1.33$) and Action-Imagery Practice ($p \leq .003$, $d \geq 0.78$), with the practice hand after Auditory Control[3] ($p = .005$, $d = 0.65$), and with the transfer hand after Action-Observation Practice ($p = .004$, $d = 1.75$) and Observation Without Action ($p = .049$, $d = 0.47$).

Further, all interactions that included the factor sequence were significant ($\eta_p^2 \geq .07$). To analyze whether the amount of sequence-specific learning differed between groups or hands, we calculated a Sequence Learning Index (the difference between RTs in the Same Sequence and the Control Sequence) as shown in Fig. 5. The Sequence Learning Index in the Posttest with the Transfer Hand (indicating effector-independent intrinsic representations) was significantly higher after Action-Execution Practice than after Observation Without Action ($p = .007$, $d = 1.04$) and Auditory Control ($p = .007$, $d = 1.02$). Action-Imagery Practice and Action-Observation Practice did not significantly differ from the other groups ($p \geq .118$, $d \leq 0.74$).

Further, comparisons between hands indicating effector-dependent representations in the Posttest were significant after Action-Execution Practice ($p = .027$, $d = 0.5$) and Action-Imagery Practice ($p < .001$, $d = 0.81$), but not in the other groups ($p \geq .276$, $d \leq 0.23$). Additionally, we compared performance in the Practice Hand between groups. This was not significant in the Pretest ($p \geq .999$, $d \leq 0.42$). In the Posttest, the Sequence Learning Index was significantly higher after Action-Execution Practice than Action-Observation Practice ($p < .001$, $d = 1.33$), Observation Without Action ($p < .001$, $d = 1.74$), and Auditory Control ($p < .001$, $d = 1.58$). There was a non-significant tendency of a higher Sequence Learning Index in Action-Execution Practice than in Action-Imagery Practice ($p = .052$, $d = 0.71$).[4] In Action-Imagery Practice the Sequence Learning Index was significantly higher than in Observation Without Action ($p = .013$, $d = 0.94$) and Auditory Control ($p = .047$, $d = 0.78$). There was a non-significant tendency of a higher Sequence Learning Index in Action-Imagery Practice than in Action-Observation Practice ($p = .061$, $d = 0.64$).[5] The Sequence Learning Index did not significantly differ between Action-Observation Practice, Observation Without Action, and Auditory Control ($p \geq .999$, $d \leq 0.19$).

3.2. Sequence knowledge: free generation and recognition performance

Free generation performance was assessed as the number of triplets matching with the Same Sequence and the number of triplets matching with a Control Sequence. A mixed-model ANOVA with the between-factor *Group* (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation Without Action, Auditory Control) and the within-factors *Sequence* (Same, Control) and *Modality* (Acoustic, Kinesthetic) was performed on matching triplets. Means and standard errors of the number of matching triplets are shown in Fig. 6.

The significant main effect *Modality*, $F(1, 118) = 6.8$, $p = .01$, $\eta_p^2 = .05$, indicated significantly more matching triplets in the kinesthetic generation task ($M \pm SD = 5.2 \pm 3.7$) than in the acoustic generation task ($M \pm SD = 4.9 \pm 3.5$).

The significant main effect *Sequence*, $F(1, 118) = 85.3$, $p < .001$, $\eta_p^2 = .42$, indicated significantly more matching triplets for the Same Sequence ($M \pm SD = 6.9 \pm 3.8$) than for the Control Sequence ($M \pm SD = 3.2 \pm 2$). Hence, all groups were able to partially generate the Same Sequence after practice.

The significant main effect *Group*, $F(4, 118) = 3.3$, $p = .014$, $\eta_p^2 = .1$, was modified by the significant interaction between *Group* and *Sequence*, $F(4, 118) = 2.8$, $p = .027$, $\eta_p^2 = .09$. The number of matching triplets with the Control Sequence did not significantly differ between groups ($p \geq .384$, $d \leq 0.59$). However, the number of matching triplets with the Same Sequence was significantly higher after Action-Execution Practice than after Observation Without Action ($p = .019$, $d = 1.03$) and Auditory Control ($p = .022$, $d = 0.92$). All remaining comparisons between groups with the Same Sequence were not significant ($p \geq .13$, $d \leq 0.77$). The remaining interactions were not significant ($\eta_p^2 \leq .04$).

A mixed-model ANOVA with the between-factor *Group* (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation Without Action, Auditory Control) and the within-factors *Sequence* (Same, Control) and Modality (Acoustic, Kinesthetic) was performed on recognition ratings (participants' self-ratings on how likely a performed sequence coincided with the Same Sequence). Means and standard errors are shown in Fig. 7.

The significant main effect *Sequence*, $F(1, 118) = 120.8$, $p < .001$, $\eta_p^2 = .51$, indicated significantly higher ratings for the Same Sequence ($M \pm SD = 6.8 \pm 2.3$) than for the Control Sequence ($M \pm SD = 3.9 \pm 2.3$). Hence, all groups were able to partially recognize the sequence after practice.

The significant main effect *Modality*, $F(1, 118) = 5.2$, $p = .025$, $\eta_p^2 = .04$, was modified by the significant interaction between *Modality, Sequence*, and *group*, $F(4, 118) = 2.7$, $p = .034$, $\eta_p^2 = .08$. After Action-Execution Practice and Action-Imagery Practice, participants reported significantly higher ratings after performing the Same Sequence in the kinesthetic setting than after listening to the tones in the acoustic setting ($p \leq .01$, $d \geq 0.59$). This was not significant in the other groups ($p \geq .31$, $d \leq 0.22$), nor in the Control Sequence ($p \geq .067$, $d \leq 0.4$). All remaining effects and interactions were not significant ($\eta_p^2 \leq .04$).

3.3. Response times during practice

To explore participants behavior during practice, we conducted a mixed-model ANOVA with the between-factor *Group* (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation Without Action, Auditory Control) and the within-factor *Session* (1, 2,3, 4, 5, 6, 7, 8, 9, 10) on RTs. Means and standard errors of the RTs during practice are shown in Fig. 8.

The significant main effect *Group*, $F(4, 115) = 14.3$, $p < .001$, $\eta_p^2 = .33$, was modified by the significant interaction between *Session* and *Group*, $F(36, 1035) = 13.4$, $p < .001$, $\eta_p^2 = .32$. RTs during Action-Imagery Practice were significantly higher than during Action-Execution Practice from Session 4 onwards ($p = .007$, $d = 0.68$). Moreover, RTs during Action-Imagery Practice were significantly higher than during Action-Observation Practice, Observation Without Action and Auditory Control in all sessions ($p \leq .029$, $d \geq 0.7$). The latter did not significantly differ from each other ($p \geq .59$, $d \leq 0.57$). Finally, RTs during Action-Execution Practice were significantly higher than during Action-Observation Practice until Session 3 ($p = .01$, $d = 0.96$) and Observation Without Action until Session 4 ($p = .031$, $d = 0.89$), but did not significantly differ in the subsequent sessions ($p \geq .106$, $d \leq 0.58$).

The significant main effect *Session*, $F(9, 1035) = 72.6$, $p < .001$, $\eta_p^2 = .39$, was modified by the significant interaction between *Session* and *Group*. During Action-Execution Practice RTs were significantly reduced from Session 2 to Session 3 ($p = .004$, $d = 0.97$) and from Session 3 to Session 4 ($p = .002$, $d = 1.06$). During Action-Imagery Practice RTs were significantly reduced from Session 2 to Session 3 ($p = .015$, $d = 0.85$). During Action-Observation Practice, Observation Without Action, and Auditory Control, RTs did not significantly differ between subsequent sessions ($p > .999$, $d < 0.38$).

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[3] Note that in Auditory Control and Observation Without Action participants did not practice with a hand, but only focused on the tones or response keys. For the sake of consistency, we kept up with the terms practice and transfer hand in these groups.

[4] Note that due to multiple comparisons we report Holm-adjusted p-values throughout the results section. The non-adjusted p-value was significant ($p = .010$).

[5] The non-adjusted p-value was significant ($p = .015$).

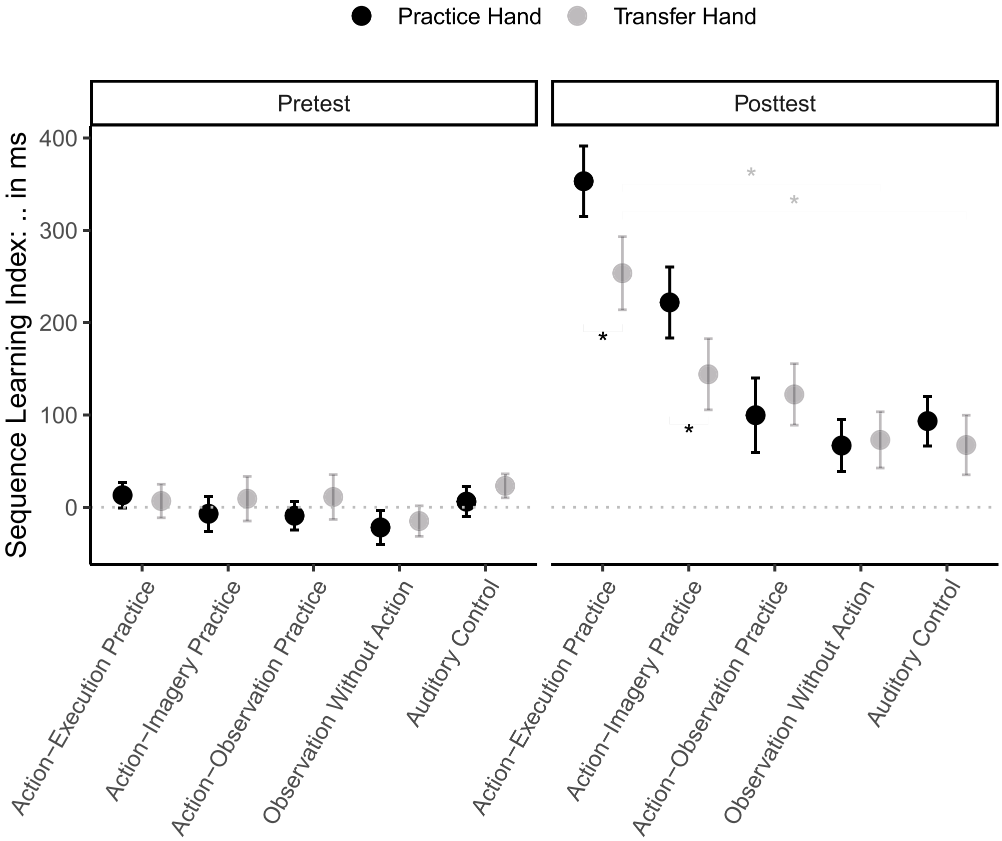

Fig. 5. Means and standard errors of the Sequence Learning Index (response time difference between Same Sequence and Control Sequence) depending on Session and Hand (Practice in dark color, Transfer in light color), separately for the groups.

4. Discussion

Using an auditory serial reaction time task, we investigated the acquired representation types in Action-Execution Practice, Action-Imagery Practice and Action-Observation Practice. Shorter RTs in the Practice hand than in the Transfer hand, indicative of effector-dependent representations, were observed after Action-Execution Practice and after Action-Imagery Practice, which is possibly caused by the focus on kinesthesis in these learning conditions. Effector-independent intrinsic representations that show up in mirror movements of the transfer hand were only observed after Action-Execution Practice. All groups were able to partially recall the Same Sequence, with the Action-Execution group showing almost perfect recall performance. In line with the focus ratings, recognition of the sequence was higher in a kinesthetic setting than in an acoustic setting after Action-Execution Practice and Action-Imagery Practice.

4.1. General sequence-unspecific learning

The results revealed a general decrease in RTs from Pretest to Posttest which was observed in all conditions and groups. Improvements in the control sequence can be explained with task familiarity that is acquired in the course of the experiment, which has been observed in previous studies using the serial reaction time task using Action-Imagery Practice (Dahm et al., 2023; Dahm and Rieger, 2023a, 2023b; Kraeutner et al., 2017) and Action-Observation Practice (Bird and Heyes, 2005; Osman et al., 2005). Participants may have become better in differentiating the four target tones (Chen et al., 2020) or due to repeated testing (Roediger and Karpicke, 2006). Further, stimulus-response coupling, which refers to the strengthening of connections between stimuli and their corresponding responses (Schneider and Shiffrin, 1977), may have led to such general improvements.

4.2. Sequence-specific learning

The shorter RTs in the Same Sequence than in the Control Sequence revealed sequence learning in all groups, including Controls. This is not particularly surprising as the Auditory Control group was an active control group in a way that they also listened to the tones during the practice phase. Participants could therefore learn the sequence pattern (the 'melody'), which may have helped them to anticipate the upcoming stimuli in the Same Sequence in the Posttest (Williamon, 2004). Such representations are not considered visual or motoric in nature. This effect is analogous to data indicating that observing visual stimulus information can enhance performance in the serial reaction time task (Bird et al., 2005). Notably, RTs in the Observation Without Action group did not significantly differ from RTs in the Auditory Control group. Similarly, while performance for all groups improved in the pre- vs posttest comparisons, we found no significant differences between the Action Observation Practice condition and either of the control groups. This pattern of learning is consistent with prior work which has argued that perceptual, non-motor mechanisms make large contributions to performance improvements in the SRTT (Howard et al., 1992; Mayr, 1996; Remillard, 2003). The present data suggest that relatively subtle changes in the delivery of perceptual information (i.e., whether it is auditory, visual, or based on the observation of action) all lead to

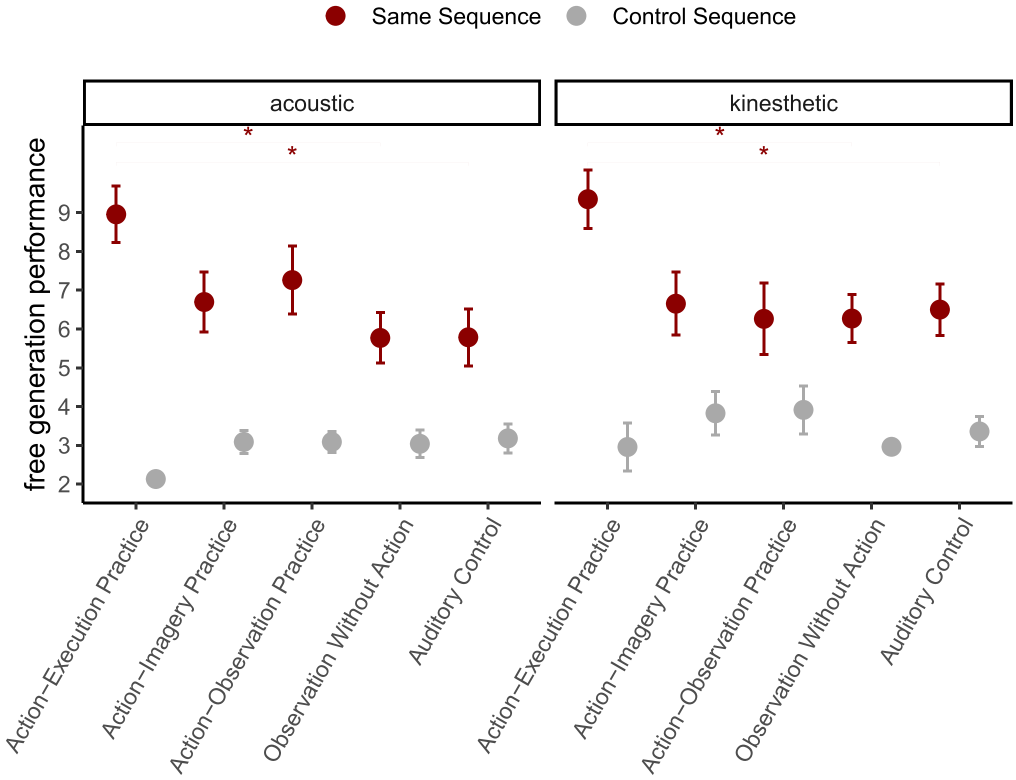

Fig. 6. Means and standard errors of free generation performance of the Practice Sequence (in red) and a Control Sequence (in grey), separately for the practice groups.

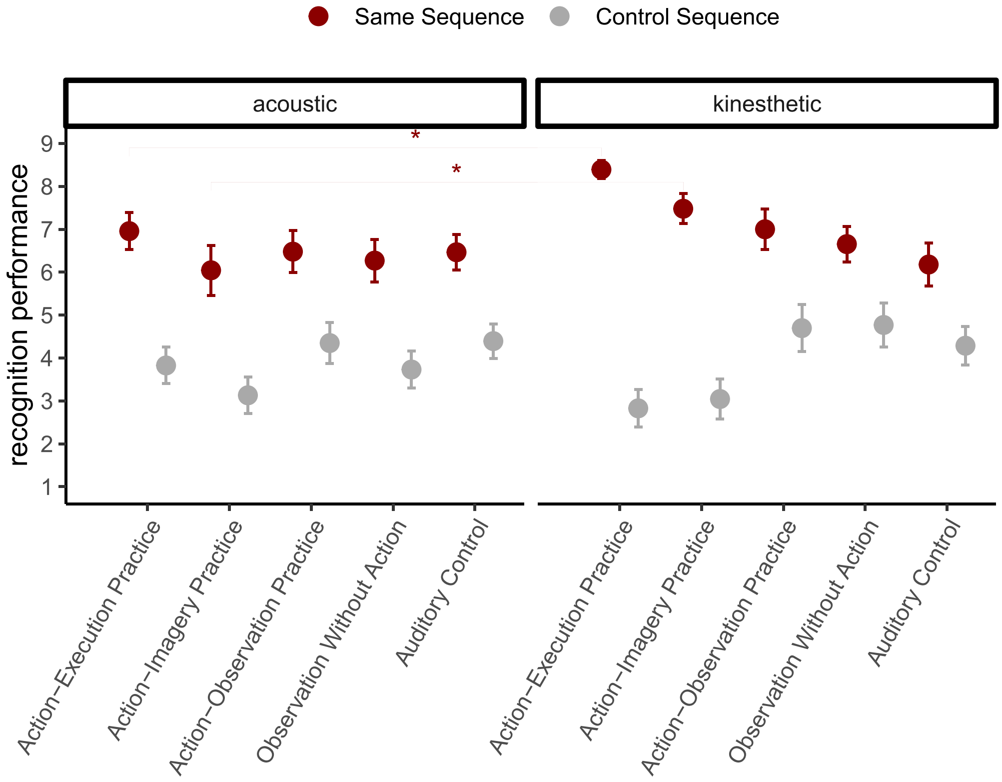

Fig. 7. Means and standard errors of recognition ratings for the Same Sequence (in red) and the Control Sequence (in grey), separately for the practice groups.

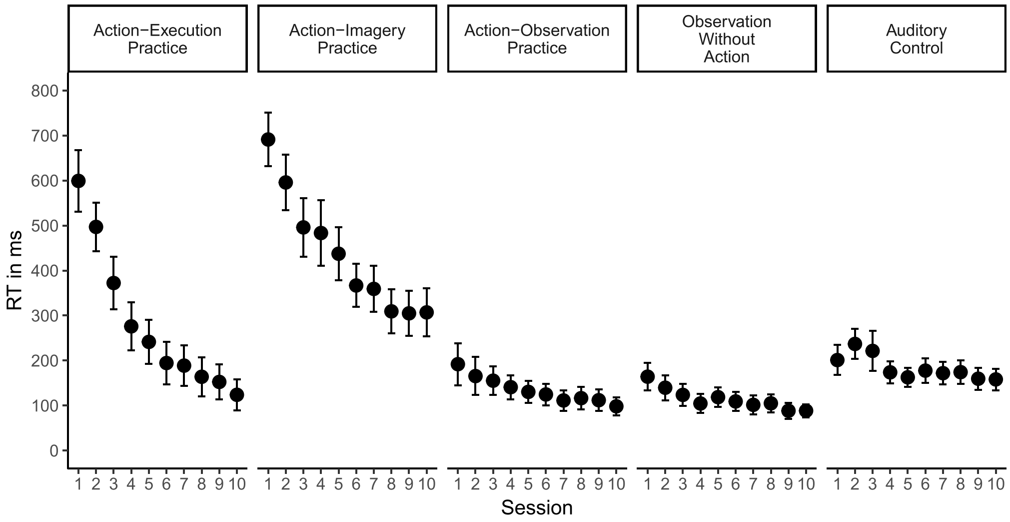

Fig. 8. Means and standard errors of response times (RT) during practice separately for the groups. During practice this is the interval between the start of the acoustic stimulus and participants' response with the 'Y' key.

improvements in performance of a similar magnitude.

In contrast to the Auditory Control and the Observation Without Action group, the Sequence Learning index in the Same Sequence of the Transfer Hand was larger in the Action-Execution group. This indicates effector-independent intrinsic representations as participants used the homologous fingers of the other hand while responding to the same tones as during practice. Such strong evidence for effector-independent intrinsic representations has not been observed in studies using visual-spatial stimulus material (Dahm et al., 2022; Dahm and Rieger, 2023a, 2023b). As assumed previously (Dahm and Rieger, 2023b), the acoustic stimulus material of the present study provoked effector-independent intrinsic representations because it was non-spatial and followed a stringent stimulus-finger mapping (independent from the keys). In line with this, the present study showed no evidence for effector-independent visual-spatial representations after Action-Execution Practice and Action-Imagery Practice. Further, evidence for effector-independent visual-spatial representations was not observed in the action observation groups, even though the animated pictures involved visual-spatial information.

Comparisons of the Sequence Learning Index in the Same Sequence in the Practice Hand revealed a non-significant tendency of shorter RTs in Action-Execution Practice than in Action-Imagery Practice. Here, the lack of significance may be caused by missing power when considering p-adjustments for multiple comparisons. The tendency goes in line with previous evidence for weaker effector-dependent representations after Action-Imagery Practice than after Action-Execution Practice (Dahm and Rieger, 2023a, 2023b; Land et al., 2016). Still, evidence for effector-dependent representations after Action-Imagery Practice was observed by comparisons of the Sequence Learning Index in the Practice Sequence between Practice Hand and Transfer Hand. Hence, learning via Action-Imagery Practice goes beyond perceptual processes (Kraeutner et al., 2016), likely because motor simulation triggers effector-dependent representations (Ingram et al., 2016, 2019). Forward models may predict the action consequences and kinesthetic perceptions in Action-Imagery Practice leading to effector-dependent improvements (Rieger et al., 2023). This goes in line with the present results from the manipulation check showing that participants reported more kinesthetic 'feelings' in Action-Imagery Practice than Controls.

Interestingly, comparisons between hands in the Sequence Learning Index were not significant after Action-Observation Practice. Visual inspection of Fig. 5 shows that there was a small opposite tendency for shorter RTs in the Transfer Hand than in the Practice Hand. Therefore, effector-dependent representations were not observed after Action-Observation Practice, which stands in contrast to previous results from Action-Observation Practice (Bird and Heyes, 2005; Osman et al., 2005). So, why was there no learning from Action-Observation Practice in the present study? In the ratings of the manipulation check, participants reported lower kinesthetic representations during Action-Observation Practice than during Action-Execution Practice and Action-Imagery Practice. Kinesthetic sensations are proposed to play a critical role in driving changes in corticospinal excitability during imagery (Stinear et al., 2006). Moreover, recent work indicates that during combined action observation and imagery (Eaves et al., 2022), it is imagery alone that drives corticospinal excitability (Chye et al., 2022; Wright and Holmes, 2024). So, action observation may rather serve as a guide supporting action imagery processes (Meers et al., 2020), especially to control for perspective and movement timing (Wright and Holmes, 2024). Assuming that the focus on kinesthetic perceptions triggers the development of effector-dependent representations, the latter could explain the lack of such representations after Action-Observation Practice. For action prediction and a subsequent acquisition of effector-dependent representations, a focus on kinematics and kinesthesis (as in Action-Execution Practice and Action-Imagery Practice) rather than a focus on the object (as in Observation Without Action) or the final action state (as in Action-Observation Practice) might be necessary (Ianì et al., 2024). For this, subcortical areas such as the cerebellum that is active in Action-Execution Practice and Action-Imagery Practice, but not in Action-Observation Practice (Caspers et al., 2010; Hardwick et al., 2018) might play a role. In line with this, the cerebellum has also been considered as the locus of forward models that predict action consequences (Ishikawa et al., 2016; Kawato, 1999; Welniarz et al., 2021).

5. Sequence knowledge

Results of the free generation and recognition test indicated that all groups were able to recall and recognize the Same Sequence at least partially. Therefore, similar as for the increased performance in RTs, the sequence knowledge was acquired even in the Auditory Control condition. Again, this can be attributed to the Auditory Control group listening to the tones during practice which enabled them to learn the sequence pattern (the 'melody') (Williamon, 2004).

In the free generation task, participants of the Action-Execution Practice group were able to recall more elements of the Same

Sequence than in the Observation Without Action and Auditory Control group. Such was not significant in the Action-Imagery Practice and Action-Observation Practice group. This stands in contrast to previous findings of similar recall performance when comparing Action-Execution Practice and Action-Imagery Practice (Dahm and Rieger, 2023b) or Action-Execution Practice and Action-Observation Practice (Bird and Heyes, 2005). Both previous studies used visual-spatial stimuli, whereas the present study applied acoustic tones. It appears that actual movement facilitates the acquisition of explicit knowledge.

In the Action-Execution Practice and Action-Imagery Practice group, participants were able to better recognize the Same Sequence after practice when they performed it than when they solely listened to the tones. This is particularly interesting, because this accounts not only for Action-Execution Practice, but also for Action-Imagery Practice, where no actual movement was performed during practice. Hence, action imagery evoked effects on kinesthetic recognition which goes beyond acoustic (or visual) perceptions (Ingram et al., 2016; Rieger et al., 2023).

6. Limitations and future directions

It could be contended that participants did not engage in imagining the actions during practice, but rather responded without actively attending to the screen and the response mapping, as evidenced by longer RTs during Action-Imagery Practice compared to Action-Execution Practice, and the inherent challenge in objectively controlling imagination processes (Cumming and Eaves, 2018; Dahm, 2020). However, examination of RTs during practice sessions revealed remarkably similar learning curves between Action-Imagery Practice and Action-Execution Practice, suggesting active engagement in mentally rehearsing the sequences during Action-Imagery Practice. Moreover, the emergence of effector-dependent representations subsequent to Action-Imagery Practice strongly implies that participants simulated the corresponding responses.

The RTs during practice sessions revealed that durations of imagination were significantly longer than those of execution which has been observed in may previous studies (for an overview see: Guillot and Collet, 2005). Still, this finding contradicts the assumption of functional equivalence proposed by Jeannerod (2001) and suggests that while imagination and execution share some underlying mechanisms (Dahm & Rieger, 2016a, 2016b; Jeannerod, 2001), they also exhibit notable differences (Dahm & Rieger, 2019a, 2019b; Glover and Baran, 2017). One potential explanation for the slower durations observed during imagination compared to execution is the involvement of inhibitory mechanisms (Rieger et al., 2017), which may impede the imagination process. This inhibition could be particularly pronounced in the current experiment, where participants had to simultaneously inhibit the motor execution of the sequence while performing a motor act involving adjacent effectors (i.e., pressing the Y-key with the thumb of the transfer hand). Another explanation is that during imagination, there is a more explicit focus on the action compared to the implicit focus during execution (Glover and Baran, 2017). Additionally, perceptual information from different modalities processed simultaneously during execution may be processed sequentially during imagination, potentially leading to prolonged imagination durations. For instance, while kinesthetic and visual information may be processed concurrently during execution, they may be processed sequentially during imagination, contributing to the observed differences in durations.

Further, RTs during practice revealed very short RTs in the observation groups, particularly at the beginning of learning. In all groups, participants were instructed to respond to the auditory stimulus as fast as possible. One might question whether participants in the Action-Observation Practice and Observation Without Action groups perceived the stimulus before pressing the button. Although the study was conducted without the presence of an experimenter, pressing the 'Y' key during practice ensured that participants could not leave the table. Therefore, listening to the auditory stimuli was inevitable. However, this does not account for the visual animation of the key press in the observation groups. In case participants willingly looked away from the screen, they may not have perceived the animations. To experimentally control for attention, future studies may include questions to check for participants attention during Action-Observation Practice. Still, RTs during observation were not overly implausible as they did not significantly differ from RTs during later stages of Action-Execution Practice.

In Action-Execution Practice and Action-Imagery Practice participants held their fingers on the target keys on the keyboard, whereas in the other groups participants held their hand on their knee. Admittedly, one may argue that the acquisition of effector-dependent representations could be provoked by the setting of the hand positions during practice. For instance, it has been shown that posture influences RTs in hand laterality judgements (Conson et al., 2015; Lorey et al., 2009). However, the setup used in the present experiment was chosen in order to reduce the possibility that spontaneous imagery occurs which would have created a confound in the observation groups (Moreno-Verdú et al., 2024; Vogt et al., 2013). The observed lower kinesthetic focus ratings in the observation groups approve this. Another methodological explanation for the absence of effector-dependent representations after Action-Observation Practice is the nature of the stimuli. Many previous studies on Action-Observation used real videos (Gatti et al., 2013; Scott et al., 2024) or pairs of participants in which one was the observer (Bird and Heyes, 2005). It is up to future studies to detect whether similar effects are detectable with other movement types (e.g., whole body movements) or other observation material (e.g., observing a real person).

7. Conclusion

Overall, this study underscores the complexity of motor learning and the varying effectiveness of different practice modalities. While auditory stimuli and kinesthetic engagement appear crucial for robust motor representations, visual observation alone may not suffice, highlighting the need for a multifaceted approach (Krüger et al., 2022) in motor learning and rehabilitation strategies. Novel findings emerged from effector-independent internal representations being acquired in both Action-Execution Practice and Action-Imagery Practice, but not in Action-Observation Practice. Similarly, effector-dependent representations were acquired in both Action-Execution Practice and Action-Imagery Practice, but not in Action-Observation Practice. This suggests that in the serial reaction time task, action imagery, but not action observation, involves a motor simulation including kinesthetic feelings which activates motor representations effectively, akin to physical execution. In motor learning (effector-dependent representations), forward modelling and prediction processes during the action itself appear to be of outmost importance. Here, attention on the action, rather than the object or the end-state, appears essential.

Disclosure of potential conflicts of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

CRediT authorship contribution statement

Stephan Frederic Dahm: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Robert Michael Hardwick:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization.

Informed consent

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

Ethical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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Appendix A

Statistical values of the ANOVA conducted with the factors Practice groups (Action-Execution Practice, Action-Imagery Practice, Action-Observation Practice, Observation, Control), Session (Pretest, Posttest), Sequence (Practice, Mirror, Control), and Hand (Practice, Transfer) on RTs.

	F	*df1, df2*	*p*	η_p^2
Practice	1.2	4, 120	0.303	0.04
Session	295	1, 120	<0.001	0.71
Hand	1.4	1, 120	0.242	0.01
Sequence	64.8	1.8, 215.3	<0.001	0.35
Practice x Session	4	4, 120	0.004	0.12
Practice x Hand	1	4, 120	0.400	0.03
Practice x Sequence	5.6	7.2, 215.3	<0.001	0.16
Session x Hand	11.3	1, 120	0.001	0.09
Session x Sequence	91.4	1.4, 173	<0.001	0.43
Hand x Sequence	8.6	1.8, 220.7	<0.001	0.07
Practice x Session x Hand	0.8	4, 120	0.543	0.03
Practice x Session x Sequence	6.9	5.8, 173	<0.001	0.19
Practice x Hand x Sequence	2.8	7.4, 220,7	0.007	0.09
Session x Hand x Sequence	9.5	1.8, 219,7	<0.001	0.07
Practice x Session x Hand x Sequence	3.3	7.3, 219.7	0.002	0.10

Data availability

A link to the data is shared in the manuscript.

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