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Research report

On the relationship between the execution, perception, and imagination of action

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HIGHLIGHTS

- It is thought that common coding systems enable action imagination and perception.
- Present work examined similarities in action execution, imagination, and perception.
- Consistencies in the speed-accuracy relationships in each task were observed.
- Amplitude of motor overflow during imagination scaled to imagined movement distance.
- Common coding account of action execution, imagination, and perception supported.

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ABSTRACT

Humans can perform, perceive, and imagine voluntary movement. Numerous investigations of these abilities have employed variants of goal-directed aiming tasks because the Fitts's law equation reliably captures the mathematical relationship between movement time (MT) and accuracy requirements. The emergence of Fitts's speed-accuracy relationship during movement execution, perception, and imagination has led to the suggestion that these processes rely on common neural codes. This common coding account is based on the notion that the neural codes used to generate an action are tightly bound to the codes that represent the perceptual consequences of that action. It is suggested that during action imagination and perception the bound codes are activated offline through an action simulation. The present study provided a comprehensive testing of this common coding hypothesis by examining the characteristics of the Fitts relationship in movement execution, perception, and imagination within the same individuals. Participants were required to imagine and perceive reciprocal aiming movements with varying accuracy requirements before and after actually executing the movements. Consistent with the common coding account, the Fitts relationship was observed in all conditions. Critically, the slopes of the regression lines across tasks were not different suggesting that the core of the speed-accuracy trade-off was consistent across conditions. In addition, it was found that incidental limb position variability scaled to the amplitude of imagined movements. This motor overflow suggests motor system activation during action imagination. Overall, the results support the hypothesis that action execution, perception, and imagination rely on a common coding system.

1. Introduction

Not only are we able to select, plan, and execute a variety of goal-directed actions, but we are also able to perceive and imagine these same movements. The nature of the potential commonalities between the processes underlying the execution, perception, and imagination of action has been considered for more than a century [1]. Also, there has been a fairly recent expansion of experimental attention to these issues [2,3]. The results of this recent work have revealed that there are similarities in the patterns of effects across tasks involving the execution, perception, and imagination of action. These similarities have led some researchers to conclude that all of these abilities rely on similar neural codes and networks.

More specifically, it has been suggested that the processes underlying action generation, perception, and imagination are enabled by an ideomotor (or common coding) network. In this common coding network, the neural codes that are responsible for generating a specific goal-directed action are tightly bound to the

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codes that represent the perceptual consequences of those actions (see Refs. [4,5] for reviews and more thorough discussions of this theory). It is thought that these codes are actively and fully engaged during the execution of action, but are run offline (i.e., at a sub-threshold level, which does not cause the actual movements to emerge) during action perception and imagination [2,6]. Although there are separate lines of research investigating the similarities in action execution and perception [2] and action execution and imagination [3], there has yet to be a systematic study of all these tasks in the same group of individuals. The purpose of the present study was to address this limitation and, thereby, provide a comprehensive testing of the common coding account of action execution, perception, and imagination.

1.1. Ideomotor coding

The common coding account of action execution, perception, and imagination is based on the tenet that the motor representation of an action is tightly bound to the representation of the perceptual consequences (effects) of that action [4,5]. The binding of action and effect codes only occurs via training and/or experience in which the individual repeatedly perceives a specific stimulus following the execution of a specific action. An important consequence of this experienced-based binding for the individual is that the activation of one code automatically activates the companion bound code [7,8]. In the context of action execution, this series of coupled activations is thought to facilitate efficient and accurate response selection. The logic behind this hypothesis is derived from the idea that conceiving of a desired effect will drive the activation of the appropriate response to bring about that effect and, likewise, formulating a specific action can activate the codes of the effect of that action to allow the individual to predict the consequences of the selected action [4]. For example, the desire to make your avatar in a video game jump will activate the action plan to press a specific button on the game controller, and the action plan to press a specific button on game controller can be used to predict that that action will cause the avatar to jump. Notably, it is only through the experience of pressing different buttons on the controller in that specific gaming environment that the individual will know and accurately characterize the specific action requirements (e.g., which button to push or joystick to manipulate) and the specific action the avatar will execute.

Researchers that have advanced the common coding account of action perception and imagination suggest that these two tasks are completed by running the common codes offline. In the case of action perception, it is thought that the observation of an action activates the perceptual representations that code for the observed motion pattern and/or the perceptual consequences of the actions. The activation of the perceptual codes subsequently leads to the excitation of the bound motor codes that would bring about the observed actions and consequences. The active effect and motor codes are then accessed by other systems to allow for a wide variety of tasks including action perception [2,6,9] and the planning of joint action [10–12]. One of the main lines of evidence that supports the hypothesized active engagement of the motor system during action perception is the repeated observation of changes in activity in primary motor cortex when people observe someone else performing an action [13–19]. Importantly, these changes in the activation of the motor system are sub-threshold and do not elicit overt movement execution.

In the case of action imagination, it has been proposed that the action/effect codes are endogenously excited and operated offline to allow the individual to experience task execution at a sub-threshold level. Consistent with the literature on action perception, the finding of sub-threshold changes in the activation of the motor system during action imagination [15,20,21] (see Ref. [22] for a review) support this common coding hypothesis. In addition to this neurophysiological evidence supporting the notion that the motor system is active during imagination and perception, there is also evidence for the hypothesis that common coding systems underlie these processes that has been derived from behavioural studies that explore the speed/accuracy trade-off that occurs during goal-directed action. These studies form the basis of the present work and will be reviewed next.

1.2. Fitts's law in execution, perception, and imagination

In a series of recent behavioural studies, researchers have exploited the well-characterized speed-accuracy trade-off that occurs when actors are attempting to execute movements of different difficulties as quickly and as accurately as possible. The essential trade-off that occurs is that actors increase movement time (MT) in an attempt to maintain comparable levels of precision across movements with increasing difficulty. This relationship between movement difficulty and movement time is captured in Fitts's law equation [23]. The formal equation is:

$$MT = a + b\left(\log_2 \quad \frac{2A}{W}\right)$$

where a and b are constants that relate the individual's base MT (y-intercept) and the increase in MT as a function of movement difficulty (the slope of the regression line). The ($\log_2 [2A/W]$) component of the equation quantifies the difficulty of the movement in bits of information. This index of difficulty (ID) is a function of the width of the target (W) and the movement amplitude (A). Effectively, ID increases as the width of the target (W) decreases and/or the movement amplitude (A) increases. Because the relationship between MT, accuracy, and specific target variables has been quantified and established, Fitts's law tasks provide an excellent control platform to develop specific predictions regarding movement execution, perception, and imagination.

One of the first studies to investigate motor imagery using the relationship between movement time and movement difficulty was conducted by Decety and Jeannerod [24]. Participants in this study were asked to imagine themselves walking through different doorways as quickly as possible and to report the time it took to walk through the door. The starting distance from the door and the width of the door was manipulated in a manner consistent with Fitts's law. The critical finding of the study was that the times reported to walk through the different doorways (i.e., the imagined walking MT) increased when the doorways were narrower and the distance to the door increased—a pattern of MTs consistent with Fitts's law. In more recent and directly relevant research, Young et al. [3] and Sirgiu et al. [25] showed that the Fitts's law relationship existed in both executed and imagined movements in a discrete goal-directed movement task. Interestingly, their data revealed that imagined MTs were longer than actual MTs. Thus, although the speed-accuracy trade-off was present in imagined movements, participants over-estimated the time in the imagined task suggesting that the offline simulation is slightly detuned or runs more slowly than the actual movements are executed.

The processes underlying action perception have been studied in a parallel, but separate, series of studies using a Fitts's law task. In a study by Grosjean et al. [6], participants watched videos of a person completing a continuous series of aiming movements with their index finger between two targets at different speeds (i.e., reciprocal aiming movements). The task of the participant was to determine if they thought it was possible or not to maintain the accurate termination of the movement on the targets while moving between the two targets at the observed speed in a given video. The videos actually consisted of two pictures (one with the finger of the model on the right target and one with the finger of the model on the left target) that were presented alternately to create apparent motion of the finger moving between the two targets. The time between the two pictures (stimulus onset asynchrony or SOA) created the apparent or perceived MT. The SOA was consistent within a trial, but was varied across trials to generate different apparent MTs. The other key manipulation was that the targets during a given trial varied in width and in distance from each other. The target width and movement amplitude were specifically varied to generate a total of 9 different target environments—3 different combinations at the 3 IDs of 2, 3, and 4. The key finding of this study was that the shortest lowest MT at which the participants judged that it was possible to move and maintain accuracy conformed to Fitts's law—the shortest MT judged as possible for the ID of 2 was shorter than that for the ID of 3, which in turn was shorter than for the ID of 4. Thus, Fitts's relationship was replicated in this action perception task.

In a recent follow-up and extension of the Grosjean et al. [6] study, Chandrasekharan et al. [2] investigated how these perceived MTs compared to actual MTs. The key additional aspect of this study was that the researchers were interested in determining the influence of recent task experience on the action perception task. It was reasoned that if the common coding account of action perception is correct and training/experience with the task increases the strength and/or accuracy of the ideomotor codes, then recent experience with the task should increase the accuracy of the action perception task. To this end, participants completed an action perception task similar to that of Grosjean et al. [6] before and after actually performing the reciprocal aiming task they observed during the action perception task. Consistent with the findings of Grosjean et al. [6], the shortest MTs judged as possible to maintain accuracy conformed to Fitts's law in both pre- and post-execution action perception tasks. The more theoretically-relevant finding was that experience at performing the action modified MTs in the perception task. Specifically, MTs in the perception task completed before the execution task (i.e., pre-execution perception MTs) were longer than actual execution MTs, whereas the MTs in the perception task completed after execution task (i.e., post-execution perception MTs) were not different from actual execution MTs. The finding that MTs in the post-execution action perception test were closely aligned with those from the action execution task supports the common coding account of action perception and suggests that the action/effect system has the ability to integrate recent experience to match perception and execution together.

1.3. Rationale for the present study

In sum, there are parallel lines of research demonstrating similarities in the relationships between MT and movement difficulty in action execution and imagination [3,24] and action execution and perception [2,6,13]. These findings suggest that a common coding system enables and underlies all three of these abilities. The goal of the present study was to test the hypothesis that there are similarities in the processes underlying action execution, perception, and imagination by asking the same set of individuals to perform each of the tasks. It was predicted that if there is a similar set of mechanisms underlying action execution, perception, and imagination, then similar relationships between MT and movement difficulty would be noted across the tasks. Of particular interest to the present aims were comparisons between the components of the regression lines (i.e., slope and intercept) in each condition. The main focus was on the slopes of the regression lines because the slope reflects the change in MT that occurs as a function of movement difficulty. Hence, focusing on the core of the relationship (i.e., emphasizing the analysis of the slope of the line over that of the y-intercept) will inform us about how the changes in MT as a function of movement difficulty are manifested in each task, independently from the base MT [9].

To conduct a more in-depth testing of the common coding account, participants completed the perception and imagination tasks before and after actually executing the task. Recall that Chandrasekharan et al. [2] found that MTs in the action perception task were longer than those in the action execution task before the participants performed the task, but were more closely related to the actual MTs after participants gained motor experience with the task. It was suggested that this experience-based modification provided support for the common coding account of action perception because the experience helped to hone or strengthen the underlying common codes. Based on these findings and associated lines of reasoning, it was predicted that if a common coding system underlies all these tasks, then any differences between MTs in the action execution, perception, and/or imagination tasks prior to gaining motor experience would be reduced or eliminated by this experience. That is, MTs in the post-execution perception and imagination tasks would be more closely aligned with actual execution MTs than the MTs in the pre-execution perception and imagination tasks. Alternatively, if different systems or some other mechanisms underlie the different tasks, then experience will not affect MTs in action perception or imagination.

Finally, as an additional testing of the potential role of ideomotor codes and the motor system in action imagination, incidental movements (i.e., motor overflow) during action imagination were analyzed. This additional analysis was possible because we recorded the displacement of the finger during the imagination tasks. Note that the participants' fingers rested on a keyboard during the action perception task, so it was not possible to perform this incidental movement analysis for action perception. It was hypothesized that if action imagination engages codes in the motor system, then the activity associated with the engagement of the motor codes may subtly surpass the threshold for muscle activation and the finger of participant may inadvertently move in a manner consistent with the imagined movement (see Refs. [26,27] for evidence of motor overflow in mental rotation tasks; see also Ref. [28] for a review of motor system involvement in other cognitive tasks). If action imagination engages motor codes, then it is possible that the amount of motor overflow (e.g., amplitude of the unintended movement) would be proportional to the amplitude of the movements that were being imagined. Thus, it was predicted that motor overflow would be larger when the participants were imagining movements of larger amplitude and smaller if they were imagining movements of smaller amplitude. Such overflow would support the contention that action imagination shares common ideomotor codes with action execution. If, however, the motor system is not engaged during action imagination or this engagement does not cause inadvertent overt action, then the amplitude of the incidental movements should not be influenced by the amplitude of the imagined movements, casting some uncertainty on the common coding accounts of action perception and imagination.

2. Materials and methods

2.1. Participants

Twenty right-handed people (9 women and 11 men) aged 18–24 years old participated in the study and received a small monetary compensation ($15) for their time. All participants had normal or corrected-to-normal vision and were naïve to the purpose of the study prior to participation. Participants provided written informed consent and the procedures of the study were approved by Office of Research Ethics at the University of Toronto.

2.2. Apparatus, stimuli, and tasks

The design of the tasks in the present study was based on previous studies [2,6]. Nine individual stimuli posters were created. Each poster consisted of a pair of identical black strips that served as a target pairs, pasted onto white poster boards (57 cm [*d*] × 72.5 cm [*w*]: see Fig. 1). The strips were 15 cm in depth and were one of three different widths (2, 4 or 8 cm) and the distance between the black target strips (center-to-center) varied (4, 8, 16, 32 or 64 cm). The distance between the targets was manipulated to generate stimuli with three IDs values (2, 3, or 4) for each of the three target widths [23]. Specifically, the targets with the width of 2 cm were paired with the amplitudes of 4, 8, and 16 to obtain IDs of 2, 3, and 4, respectively; the targets with the width of 4 cm were paired with the amplitudes of 8, 16, and 32 to obtain IDs of 2, 3, and 4, respectively; and, finally, the targets with the width of 8 cm were paired with the amplitudes of 16, 32, and 64 to obtain IDs of 2, 3, and 4, respectively.

2.2.1. Action perception task

The stimuli for the action perception task were digital photographs of an adult male sitting in front of the posters with the index finger of the right hand placed in the middle of one of the targets (see Fig. 1). Two photos were taken for each of the nine poster boards: one with the finger on the right target and one with the finger on the left target. During the perception task, the two pictures were presented alternately to create an apparent motion of the model moving the finger between the two targets. The same pair of pictures was displayed throughout a single trial so that the ID (i.e., the target width and distance) was consistent for a given trial. The time between the presentations of the two pictures (i.e., stimulus onset asynchrony [SOA]) served as the apparent MT for the perception task.

The apparent motion stimuli were presented to participants on a 19-in. CRT monitor (ViewSonic, Graphics Series—G225f) running at a resolution of 1204 × 768 pixels and a refresh rate of 100 Hz. The monitor was placed so that the center of the screen was approximately at eye level, approximately 60 cm from the participant. The SOA at the beginning of each trial was either 50 or 500 ms and participants were asked to use the cursor (arrow) keys to alter the apparent MTs (the SOAs) until the model displayed the shortest MT in which it would be possible to maintain accuracy for the displayed targets [29]. Participants used the left and right arrow keys to make relatively gross adjustments in apparent MT—a single press of the left arrow key decreased the apparent MT by 100 ms and a single press of the right arrow key increased the apparent MT by 100 ms. To increase the resolution of the measurement, the participants used the up and down arrow keys to increase and decrease, respectively, the apparent MTs in 10 ms increments. When participants identified the shortest MT at which it was possible to move and maintain accuracy, they pressed the "Enter" key and the SOA was recorded. No time limit was given for watching the stimuli and forming the decision. After the SOA was recorded, the next trial and a new set of pictures were displayed. Participants completed the task on each of the nine combinations of target width and distance three times. The order of presentation of the 27 trials completed in each of the pre- and post-execution perceptual tasks was randomized.

2.2.2. Action imagination task

In the imagination task, participants stood in front a table in the view of an optoelectric motion tracking system (Optotrak Certus, Northern Digital Inc., Waterloo, Ontario, Canada). An infrared emitting diode (IRED) was attached to the participant's right index finger. On a given trial, one of the nine randomized poster boards was clamped onto the table in front of the participant. The order of the posters was randomized. The task of the participant was to, following a verbal "GO" signal from the experimenter, imagine themselves moving between the two targets as fast and accurately as possible 10 times (i.e., movement 1 was from the right target to the left target, movement 2 was the return movement from the left to the right target, and so on...). At the beginning of the trial, the participant placed the right index finger on the middle of the right target. The participant was instructed to signal the start of the imagination of the task by lifting their finger upwards from the poster (approximately 15 cm), and to signal the end of the imagination of the 10th movement by placing the finger back on the right target. Specifically, the participants were explicitly instructed that the start of the imagination of the first movement was to be simultaneous to the lifting of the finger from the right target and the end of the last imagined movement (terminated on the right target) was to be simultaneous with the contact of the right target by the finger. Note that no specific instructions were given to the participants (i.e., to hold their finger still or to move it) while the finger was in the air and the imagination was continuing. The participant performed the imagination task three times for a single poster before that poster was removed and the next poster was placed. Thus, there were a total of 27 trials in each of the pre- and post-execution perceptual tasks.

2.2.3. Action execution task

The action execution task was consistent with the action imagination task in that participants started with the right finger on the right target and then moved between the targets 10 times (i.e., movement 1 always started from the right to the left target and so on). Participants were told to move as fast and as accurately as possible. The order of the posters was randomized and participants completed three sets of movements on a single poster before the next poster was placed on the table (a total of 27 trials). The participant rested while the experimenter changed the poster (approximately 2 min) which helped to counteract potential fatigue effects.

2.3. Procedure

Participants were tested individually and completed all tasks in a single 90 min session. There were 5 stages in the study—each stage was separated by a 3–5 min rest period. The imagination and perception tasks were completed twice; once before and once after performing the execution task. The execution task was always completed in the third stage, but the order with which participants completed the perception and imagination tasks before and after the execution task was counterbalanced across the participants. That is, one-half of the participants completed the perception task before completing the imagination task and the other half completed the imagination task before completing the perception task.

2.4. Data collection and reduction

2.4.1. Movement times in action execution, perception, and imagination

For the perception task, the SOA the participants chose as the shortest possible apparent MT that they were able to maintain accuracy was used as the MT for that trial. In both the execution and imagination tasks, the 3D coordinates of the IRED were captured by the motion-tracking camera at 250 Hz for 10 s (imagination) and 6 s (execution). The IRED data were stored for offline analysis using a custom movement-parsing program to calculate MTs written using Matlab (2011b, The MathWorks Inc.). In the analysis program, the IRED position data were differentiated using a 3-point central finite algorithm to obtain the instantaneous velocity of movement. None of the movements landed outside of the target zones for any trials

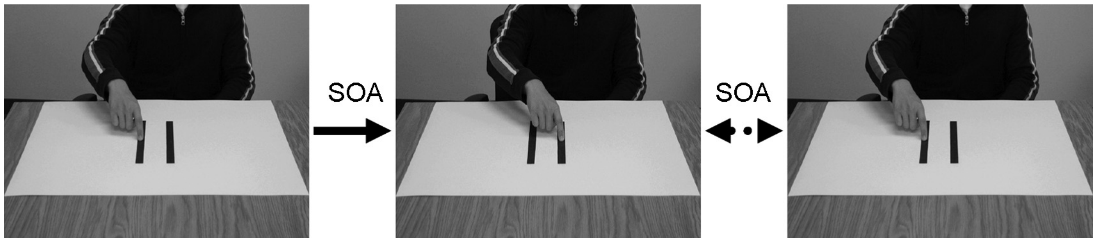

Fig. 1. (*Experimental setup for the perception task*): Exemplar right/left images and sequence of events used for the apparent motion stimuli during the action perception task. The arrows indicate the sequence of events. The first arrow indicates that the first image was of the model with their finger on the right target and that it was followed by the image with model's finger on the left target presented after the specific SOA for that trial. The two-way arrow indicates that the images were alternately presented until the participant pressed the enter key.

and, hence, no MTs were eliminated from the execution analyses. The total time for the participants to execute and imagine the 10 movements was determined by calculating the interval of time between the onset of the first movement (i.e., initial lift off from the right target) until the finger came to rest on the right target. Movement initiation was identified as the first sample on which the resultant finger velocity exceeded 30 mm/s and remained above this threshold for 12 ms (i.e., 3 samples). The end of the movement interval was identified as the first sample on which the resultant finger velocity fell below 30 mm/s and remained below this threshold for 12 ms. To determine the average MT for a single movement between a pair of targets, which would be equivalent to the SOA recorded as apparent MT in the perception task, the total time was divided by 10.

Mean MTs for a specific target combination for the execution, perception, and imagination tasks were calculated by averaging the MTs across each of the 3 trials the participant completed with that target combination. The average MTs were then submitted to a series of analyses to test specific hypotheses. These analyses are described in the following sections.

2.4.2. Motor overflow during movement imagination

To assess motor overflow in the imagination task, the standard deviation in the displacement of the IRED on the finger in the left/right axis was calculated during the movement imagination tasks. The analysis focused on the left/right displacement because this axis was the primary axis for the imagined movements and was the one that had the greatest and most relevant change in magnitude (i.e., 8–64 cm). To eliminate any potential influence of the displacement of the finger during the overtly active phases of the imagination task (i.e., the time intervals in which the finger was actually being lifted and returned to the board), the analysis focused on the time interval in which the finger was off the table and should otherwise have been in a stable position. Thus, the period of time that was analyzed was the one from the moment in which the resultant velocity fell below 30 mm/s in mid-air (i.e., following the initial lift) until the moment the finger achieved a velocity of over 30 mm/s in the direction of the target (i.e., began to move back towards the target). Because it was predicted that motor overflow should increase as the amplitude of the imagined movement increases, but should be unaffected by target width because the change in target widths were relatively small in comparison to amplitude changes, a single standard deviation value for each of the 5 amplitudes was calculated for each participant by averaging across the trials that had similar movement amplitudes, regardless of the associated target widths.

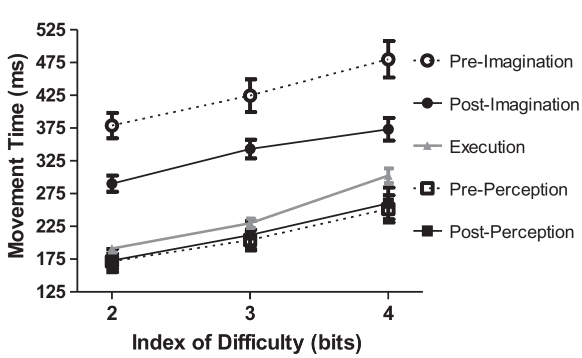

Fig. 2. (*MT for all trial conditions*): Movement time (ms) in each of the tasks as a function of index of difficulty. Open circle symbols and dashed lines represent values in the pre-execution imagination task. Closed circle symbols and solid lines represent values in the post-execution imagination task. Closed grey triangle symbols and solid lines represent values in the execution task. Open square symbols and dashed lines represent values in the pre-execution perception task. Closed square symbols and solid lines represent values in the post-execution perception task. Standard error of the mean bars are shown.

3. Results

3.1. Assessment of Fitts's law in the experimental tasks

To determine if MTs in each of the tasks conformed to Fitts's law, the initial analysis consisted of a series of linear regressions between the group mean MTs for each of the 9 combinations of target width and movement amplitude and the ID for the related combinations. A separate analysis was conducted for the data from each of the 5 conditions. Consistent with previous studies [2,3,6,23], MTs were highly and significantly correlated with ID in all five tasks: pre-execution imagination, $R^2 = 0.90$, $p < 0.001$, MT (ms) = 276 + 50.5(ID); pre-execution perception, $R^2 = 0.95$, $p < 0.001$, MT (ms) = 89 + 40.0(ID); execution, $R^2 = 0.80$, $p < 0.001$, MT (ms) = 74 + 55.6(ID); post-execution imagination, $R^2 = 0.86$, $p < 0.001$, MT (ms) = 210 + 41.5(ID); and, post-execution perception, $R^2 = 0.88$, $p < 0.001$, MT (ms) = 84 + 43.6(ID) (see Fig. 2).

Because Fitts's law was replicated in each task, we turned our attention towards the comparisons of the components of the regression lines to determine if and how the relationship between MT and ID differed across the tasks. In these analyses, the components of the regressions lines of the group performance on the different task are compared to one another based on a ratio of the residuals for each line (for details on the statistical procedure, see Chapter 18 of [30]). The results of these analyses revealed that the slopes of the regression lines for the different conditions did not significantly differ, $F(4,35) < 1$ (see previous paragraph for the specific values). On the other hand, the elevations (y-intercepts) of the lines were significantly different, $F(4,39) = 289.95$, $p < 0.001$. The nature of the differences in the elevations of the lines will be elucidated by assessing the influence of movement execution on mean MTs in the perception and imagination tasks (see following Sections 3.2 and 3.3). In sum, the results of this initial analysis support the common coding hypothesis because the Fitts relationship was observed in each task and the increase in MT that occurs with an increase in ID did not differ across tasks.

3.2. The effect of execution on action perception and imagination

To assess the influence of execution on action perception and imagination, mean MTs for each participant for the pre- and post-execution imagination and perception tasks were submitted to a 2 (time: pre-execution, post-execution) by 2 (task: imagination, perception) repeated measures ANOVA. MTs were averaged across the individual combinations of target amplitude and width for this analysis because MTs in each of the tasks conformed to Fitts's law in each task and the slopes of the regression lines did not differ (see previous section and Ref. [2]). In addition, note that order (perception task first, imagination task first) was included as a between-subjects factor in an initial omnibus 3-factor mixed ANOVA, but was not included in the final analysis because it did not have a significant influence on MTs ($ps > 0.11$ for the main effect and all interactions).

The ANOVA revealed main effects for time, $F(1,19) = 8.36$, $p < 0.01$, and task, $F(1,19) = 70.28$, $p < 0.01$. MTs in the imagination task (mean = 381 ms) were longer than those in the perception task (mean = 212 ms), and MTs assessed before completing the execution task (318 ms) were longer than those assessed after the execution task (mean = 275 ms). These main effects were qualified by a significant interaction between time and task, $F(1,19) = 26.70$, $p < 0.001$. Post-hoc analysis of this interaction revealed that it emerged because experience with the task only had a significant effect on MTs in the action imagination task (see Fig. 2). Specifically, there was a significant pre-/post-execution difference in the imagination task [mean pre-execution imagination MT = 428 ms; mean post-execution imagination MT = 335 ms; $t(19) = 5.06$, $p < 0.001$], whereas the pre-/post-execution difference was not significant for the perception task [mean pre-execution perception MT = 209 ms; mean post-execution perception MT = 215 ms; $t(19) = 0.34$, $p < 0.7$]. It is interesting to note that, even though post-execution MTs in the imagination task were closer to MTs in the execution task (mean execution MTs = 241 ms), post-execution imagination MTs were still longer than those in the execution task, $t(19) = 10.62$, $p < 0.001$. Thus, even though they are more closely aligned with the execution MTs following experience with the task, imagined MTs were still longer than actual MTs.

At first glance, the absence of a significant effect of task experience on MTs in the perception task does not seem to be consistent with the common coding explanation. As can be observed from Fig. 2, however, the absence of a significant experienced-based modulation of perception MTs seems to have occurred because the pre-execution MTs in the perception task were already congruent with execution MTs prior to gaining experience with the task. In fact, neither pre-execution perception MTs, $t(19) = 1.80$, $p > 0.08$, nor post-execution perception MTs, $t(19) = 1.42$, $p > 0.17$, were significantly different from the execution MTs. Thus, the absence of change in the MTs in the perception task may have occurred because the participants already perceived the MTs in a manner that was consistent with their own performance and, as a result, additional experience with the task could not (or did not) enhance the perceptual processes. A similar pattern of effects was observed in Experiment 2 of Chandrasekharan et al. [2] where perceived MTs for movements with an awkward instrument were not different from actual execution MTs prior to and after experience moving with the instrument.

3.3. Individual comparisons of slopes and intercepts

Although the results of the group data are consistent with predictions based on the hypothesis that similar coding systems

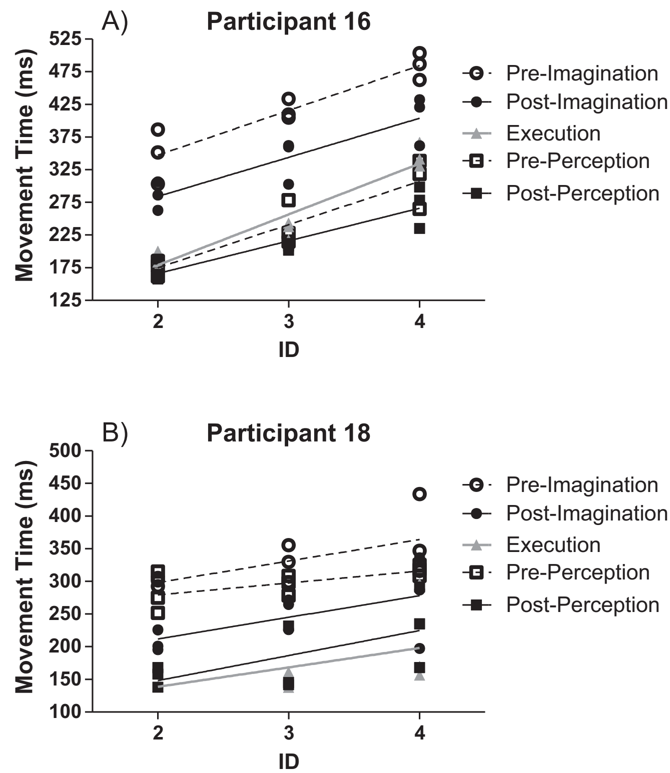

Fig. 3. (*MTs for all conditions for representative participants*): Movement time (ms) in each of the tasks as a function of index of difficulty. Open circle symbols and dashed lines represent values in the pre-execution imagination task. Closed circle symbols and solid lines represent values in the post-execution imagination task. Closed grey triangle symbols and solid lines represent values in the execution task. Open square symbols and dashed lines represent values in the pre-execution perception task. Closed square symbols and solid lines represent values in the post-execution perception task.

underlie action execution, perception, and imagination, a more stringent test of the of this hypothesis would be to assess whether or not this pattern of effects is present on the individual level. To this end, a series of additional analyses were conducted in which the components of the linear regressions between MT and ID for each individual participant in each task were compared using the method described above. For the sake of brevity and clarity, not all regression equations and associated statistics will be reported. Instead, only summary data regarding the number and direction of significant differences between the slopes and y-intercepts of the regression lines for the two tasks will be reported. For these analyses, alpha was corrected to 0.0025: 0.05 corrected for the 20 comparisons (one for each participant) conducted between a pair of tasks. Note that y-intercepts were only compared when the slopes were not different because one cannot reliably compare y-intercepts when the slopes are different. Representative plots of individual data are presented in Fig. 3.

3.3.1. Imagination and execution

The first set of analyses involved comparisons between the data for the pre- and post-execution imagination tasks and the actual execution MTs. Consistent with the main analysis, the comparisons between the individual regressions lines revealed that the majority of the participants had similar slopes, but higher y-intercepts, on imagination tasks than on the execution task. Specifically, for the comparisons of the regression lines between pre-execution imagination and execution MTs, none of the slopes for the participants were significantly different, whereas the y-intercepts were significantly lower for the Execution than for the pre-execution imagination task for 19 participants (95%). The y-intercepts for the tasks were not different for only 1 person.

Similarly, for the comparisons between post-execution imagination and execution, only one participant had a statistically different slope in the two tasks (i.e., 19 participants [or 95%] had similar slopes). On the hand, of the 19 with similar slopes, the y-intercepts for the execution task were significantly lower than for the post-execution imagination task for 16 of the participants (84%). One participant (5%) had a higher y-intercept in the imagination task and 2 participants (10%) had similar y-intercepts.

Finally, comparisons of the pre-/post-execution imagination MTs revealed that only 1 participant (5%) had different slopes in the two tasks, whereas 9 of the remaining 19 participants (48%) had different y-intercepts. Of the 9 participants with different y-intercepts, 8 of them (89%) had lower y-intercepts in the post-execution imagination task than in the pre-execution imagination task. Overall, these data are consistent with the main analysis of the group level data in that the slopes were generally not different across the tasks, but the majority of the y-intercepts decreased and were closer to the execution MTs after experience with the task.

3.3.2. Perception and execution

The comparisons between the MTs on the pre- and post-execution perception task and the execution task also revealed pattern of effects that were similar to those revealed in the group level analysis. Specifically, comparisons between the pre-execution perception and execution task revealed that only one of the participants (5%) had statistically different slopes in the two tasks. Of the 19 participants with similar slopes, 11 of them (58%) had reliably different y-intercepts. Of the 11 participants with different y-intercepts, 7 had lower y-intercepts in the pre-execution perception task than in the execution task and the other 4 had higher y-intercepts.

Likewise, for the post-execution perception task, only 1 of the participants (5%) had a slope that was different from the slope for the execution task. Eleven (58%) of the 19 participants with similar slopes had statistically different y-intercepts, with only 4 of these showing lower y-intercepts on the post-execution perception task than on the execution task.

Finally, comparisons between the pre- and post-execution perception task revealed that none of the participants had different slopes on the two tasks. Eight participants (40%) showed a difference in y-intercepts, with only 4 of these (50%) having lower y-intercepts on the post- than on the pre-execution perception task. Thus, the finding of general similarity in the slopes is replicated here. Further, there seems to greater balance in the direction of the differences in y-intercepts in that approximately half of the participants who show a pre-/post-execution differences in y-intercepts had higher values in the perception task than in the execution task.

3.3.3. Individual differences in the directions of pre-/post-execution changes

To further explore the nature of the pre-/post-execution changes in MT in the perception and imagination tasks and their relationship to actual MTs, the directions of the individual changes in imagination and perception tasks were examined. Recall the prediction that experience with the task would affect MTs in the perception and imagination tasks with MTs in these tasks being more closely aligned with actual execution MTs after experience. This effect of experience is more clearly observed in the imagination task at both the group and individual levels of analysis because significant decreases in the y-intercepts were observed in nearly all cases in which y-intercept differences emerged. This consistent direction of decrease is similar to that observed at the group level analysis and the prediction that MTs would be more closely aligned with actual MTs after execution because execution MTs were always shorter than pre-execution imagination MTs.

At first glance, the data from the perception task did not seem to be consistent with the main prediction because there was no pre/post-execution difference in MTs in the group analysis and only approximately half the participants had different MTs at the individual level analysis. A more in-depth examination of the patterns of individual differences, however, bears some interesting results. As reported in the previous section, 4 of the 8 participants with significant pre/post-execution differences in their y-intercepts showed a decrease in y-intercepts, with the remaining 4 participants having significantly higher y-intercepts in the post-execution session than in the pre-execution session. This overall pattern explains the absence of an influence of execution at the group level because: (1) the majority of participants showed no significant change; and, (2) the participants that had increases in MT averaged out the ones that had decreases in MT. The more intriguing aspect of this data is realized via a careful consideration of the y-intercepts from the execution task. Specifically, all 8 of the participants that demonstrated an influence of execution on perception MTs had changes in the y-intercepts that were in the direction of the differences between pre-execution perception and execution MTs. That is, when the y-intercept for execution MTs was higher (or lower) than the pre-execution perception MTs, the y-intercept for the post-execution perception MTs were higher (or lower) than pre-execution perception MTs. There were varying degrees of adaption with some participants having a relatively accurate adaption (e.g., the y-intercepts for P18 were: pre-execution perception = 242 ms; execution = 79 ms; post-execution perception = 71 ms (see Fig. 3b)), others over-adapting (e.g., P17: pre-execution perception = 105 ms; execution = 84 ms; post-execution perception = 45 ms), and others not adapting enough (e.g., P19: pre-execution perception = 69 ms; execution = 93 ms; post-execution perception = 79 ms). Overall, however, when differences in MTs were present, the participants adapted the MTs in the direction that would more closely align perception and execution MTs. Thus, in both the imagination and perception tasks, adaptations in MTs as a function of experience were observed at the individual level.

3.4. Motor overflow during action imagination

It was predicted that if the motor system was engaged during action imagination, then some of this activation may surpass the threshold for muscle activation and the finger of the participant may inadvertently move. If this is the case, then the magnitude of these inadvertent movements could be proportional to the amplitude of the movements that were being imagined. To test this prediction, the mean SDs of the displacement in the left/right (primary) axis were calculated and analyzed. The mean SDs in the left/right axis for the 9 combinations of width/amplitude combinations were averaged across target widths to generate mean SDs for each of the 5 amplitudes. These average SDs were then submitted to a 2 (time: pre-execution, post-execution) by 5 (amplitude: 4, 8, 16, 32, 64 cm) repeated measures ANOVA.

Consistent with the hypothesis that the motor system is engaged during imagination, the magnitude of the SD in displacement in the primary axis of the movement scaled to the amplitude of the imagined movement (Fig. 4). Post-hoc analysis (Tukey's HSD, $p < 0.05$) of the significant main effect of amplitude, $F(4,76) = 20.72$, $p < 0.001$, revealed that the SDs were larger during the imagination of movements with a 64 cm amplitude than during the imagination of all other movements. Likewise, SDs were larger during the imagination of movements with a 32 cm amplitude than during the imagination of all movements with 8 and 4 cm amplitudes. None of the other SDs were significantly different from one another. The main effect for time, $F(1,19) < 1$, and the interaction between time

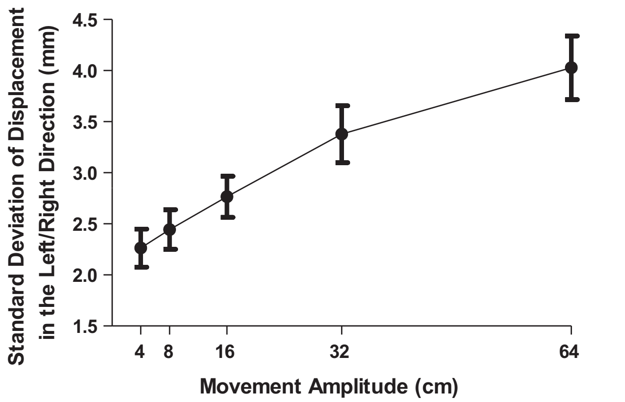

Fig. 4. (*Motor overflow during Imagination tasks*): Standard deviation of displacement of the finger in the left/right direction (mm) during the non-active phase of the imagination task as a function of the amplitude of the movements that were imagined. Standard error of the mean bars are shown.

and amplitude, $F(4,76) = 1.29$, $p > 0.28$, were not significant suggesting that the experience performing the movement task did not influence motor overflow.

4. Discussion

The purpose of the present study was to test the common coding account of the mechanisms that underlie action execution, perception, and imagination. To test this hypothesis, the same set of participant's executed, perceived, and imagined the same reciprocal tapping movements and the patterns of MTs from each of these tasks were compared. There were three patterns of effects that support the common coding account. The first main finding in support of the common coding hypothesis was that the relationship between MT and ID (i.e., the slope of the regression lines) remained consistent across each of the tasks. The consistency in the slopes suggests that the same set of codes relating the change in MT that occurs as a function of movement difficulty underlie each of these processes. The second main set of findings were related to the influence of experience with the task on imagination and perception. The effect of experience was more clear in the imagination task because MTs in the imagination task were significantly shorter and closer to actual MTs following experience executing the task on both group and individual levels of analysis. Although the results of the analysis on the group data suggested that experience did not alter MTs in the perception task, a detailed examination of the patterns of change of the *y*-intercepts on the individual level showed that when significant changes in *y*-intercepts were observed, the changes were in the direction that would align perception MTs with execution MTs. Overall, these findings suggest that experience executing the task increased the fidelity of the ideomotor codes used in the simulation process that is the basis of action perception and imagination of action The final important finding was that motor overflow in the imagination condition was scaled to the amplitude of the imagined movement. This motor overflow finding suggests that the motor system was engaged during imagination—a set of findings consistent with evidence of increased activity in motor cortex during imagery [15,21].

Overall, the patterns of effects observed here are consistent with the hypothesis that ideomotor codes are the common substrate for the execution, perception, and imagination of action. Although the findings of the present study support the common coding account, there are several aspects of the data that need to be addressed in greater detail because they are either inconsistent with previous work or, at first glance, seem not completely congruent with predictions based on the common coding account. These results include: (1) the absence of differences between pre- and post-execution MTs in the perception task at the group level of analysis; and, (2) the differences in MTs between action execution and imagination, even after motor experience.

4.1. The absence of motor experience on action perception at the group level

The first finding that needs to be addressed was that MTs in perception task did not appear to be influenced by execution when considered at the group level of analysis. The absence of an effect of execution on perception MTs in the present study is at odds with what was observed in a very similar protocol in earlier studies in which there was a significant effect in perception or judgment tasks following task experience ([2]; see also Ref. [31]). Although different from what was previously observed, this finding is not necessarily at odds with the common coding account. The reason the present finding is not at odds with the common coding account is because the MTs in the perception task were congruent with execution MTs prior to executing the movements. Thus, it appeared as though there was a ceiling effect in that experience could not increase the accuracy of the judgments because the MTs in the perception task were already generally congruent with execution MTs.

A similar pattern of results was observed in Experiment 2 of Chandrasekharan et al. [2] in which it was reported that judged MTs for movements with a weighted instrument did not change after experience moving with the instrument. Note that in that study, perceived MTs prior to experience were not different from the execution MTs (i.e., in both pre- and post-execution tasks were statistically equivalent to execution MTs). Thus, it seems that pre/post-execution changes in MTs in the action perception task should only be expected when the initial pre-execution MTs are not congruent with actual execution MTs. In other words, what is perceived as possible and impossible to perform can only be (or need only to be) fined-tuned if there was an initial discrepancy or inaccuracy. When MTs in the perception task are veridical to execution MTs, no change should be expected.

The abovementioned conclusion is supported by the results of the analysis on the individual level. Specifically, although the group analysis did not reveal any pre/post-execution changes in MT, the analysis of the individual MTs revealed that approximately half of the participants did adapt their MTs in the perception task after executing the movements. Of these individuals who adapted their MTs, approximately half increased their MTs and half decreased their MTs. This distribution of changes explains, at least in part, why no overall pre/post-execution changes were observed in the perception task—the participants that increased their MTs averaged out those who decreased their MTs. The key observation of these changes was that the adaptations were in the direction that would more closely align perception and execution MTs. That is, participants increased their MTs in the perception task after execution when their initial perception MTs were lower than execution MTs and vice versa. This pattern of adaptations is consistent with the prediction that task experience would alter perception (see also Ref. [2]). Overall, the data from the group and individual analysis are consistent with the ideomotor account of action perception and execution.

4.2. The effects of action execution on imagination

Before addressing the persistent differences between MTs in the execution and imagination tasks (see Section 4.3), the mechanisms leading to the influence of action execution on imagination needs to be discussed. Recall that previous research revealed that experience with a task hones the perception of action—there is a change in MTs in a perception task experience with the task and only occur when there are initial differences between perception and execution ([2]; see also Ref. [17]). A similar experienced-based refinement in action imagination was observed in the present study. Although we concluded that this decrease in MT in the imagination task occurred due to the experience-based refinement of the ideomotor codes that are at the core of the imagination process, it is possible that there are other explanations of the decrease in MT. Specifically, it could be that the decrease in MT occurred because of a test–retest practice influence on the imagination task, simply the passage of time, and/or the consequence of general motor system activation resulting from the intervening motor task.

To address these possibilities, a control experiment was conducted in which a new set of participants ($n = 18$) completed the same action imagination task before and after completing a different motor task. The motor task in the control experiment was a free-choice key press task in which participants pressed a left or right button in response to a white target to generate one of two effect tones. This specific task was chosen as the intervening task (opposed to having people watch a video or do nothing for ~10 min) because it was a motor task and so could control for both the effects of time and general motor system activation resulting from performing a task. Critically, this new motor task lasted approximately the same amount of time as the aiming task in the main experiment, but was not an aiming task so participants could gain no new insight into their own ability to move quickly and accurately.

A 2 (experiment: main, control) by 2 (time: pre-execution, post-execution) by 3 ID (2,3,4) mixed ANOVA was conducted on the MTs from the imagination tasks alone. This analysis revealed a main effect of time, $F(1,36) = 36.97$, $p < 0.01$, and a significant experiment by time interaction, $F(1,36) = 8.80$, $p < 0.01$. Post hoc analysis of the interaction (Tukey's HSD, $p < 0.05$) revealed that there was only a significant decrease in imagined MTs following the execution of the aiming task (i.e., as in the main experiment) and that the pre-/post-execution decrease in imagination MTs was significantly larger in the main experiment than in the control experiment. Note that there was a decrease from pre-execution (409 ms) to post-execution (378 ms) in the control data, suggesting that time or motor system activation may have a modest effect on MT, but this decrease was not significant. Overall, the results of the comparisons of the data from the main and control experiment are consistent with the conclusions that the pre-/post-execution decrease in the MTs in the imagination task in the main experiment was the result of task-specific experience, and not the effect of time, regression to the mean, a practice effect associated with multiple sessions of imagination, or general motor system activation resulting from the execution of movement.

4.3. *The persistent differences between action execution and imagination*

Overall, there are three findings that support the hypothesis that a common coding system underlies action execution and imagination. First, there were no differences in the slopes of the relationship between execution and imagination. Second, there was a pre-post execution shift in imagination MTs towards those of the execution task. Finally, and perhaps most importantly, the analysis of motor overflow during the imagination task revealed a greater degree of inadvertent movement during the imagination of longer movements than during the imagination of shorter movements. Despite this substantial support for the common coding hypothesis, it is also important to note that the longer MTs in the imagination task persisted even after gaining motor experience with the task. It is not entirely clear why the imagination MTs remained longer than MTs from the perception and execution tasks after experience. Although it is not possible to elucidate these MTs differences in this study, the following discussion outlines several potential reasons for this discrepancy to help design future experiments. The explanations will be preceded by a brief comparison with the extant literature.

The present study is, to our knowledge, the first to examine and report differences between action perception and action imagination so there are no previous findings to compare to the present observations (see Section 4.4 for a discussion of differences between perception and imagination). It is important to note, however, that the reported difference between imagination MTs and execution MTs is not atypical. Indeed, there appears to be variability in the literature with some researchers reporting similar real and imagined MTs [25,32], whereas others have found longer MTs in imagination tasks than in execution tasks [33–35]. No papers that we are aware of have reported shorter MTs in imagination tasks than in execution tasks. The reason why the differences between execution and imagination MTs are not consistently reported remains unclear (although it is always possible that some studies were under powered). The goal of the following discussion is to raise several potential methodological and mechanistic explanations for the differences that are and are not observed between action execution and imagination, and how these relate to action perception.

One possible reason for the between-experiment differences between action execution and imagination MTs are due to the motor task employed (i.e., discrete vs. reciprocal aiming movements). It seems unlikely that the use of reciprocal or discrete aiming movements can explain the differences in the MT results because differences between execution and imagination MTs have been observed in studies using both types of tasks. For example, Young et al. [35] employed a discrete movement task and, as in the present study, reported differences between imagination and execution MT. Overall, we currently conclude that methodological differences directly associated with the employed motor tasks are unlikely to have a meaningful influence on the patterns of executed and imagined MTs.

Another potential explanation of the overestimation of MT during imagination is the role of task-specific experience. Young et al. [35] suggested that participants can misperceive the time required to produce challenging goal-directed movements, especially when the performer has little-to-no direct experience with the action. That is, although the participants likely have gained a lot of experience executing discrete aiming movements in a variety contexts such as in an elevator or at a bank machine, these movements are often executed individually (i.e., not multiple times in a single session) and not under such time/accuracy pressures. The case for lack of experience is stronger for the present study because it is unlikely that people have completed reciprocal aiming movement is the distinct context of the present study. Thus, from an ideomotor perspective, the challenges in accurately imagining novel movements could be due to poorly developed or bound perception/action codes. The results of the present study support this hypothesis and the role of ideomotor coding in action imagination because the MTs in the imagination task were closer to the execution MTs after experience performing the task. To our knowledge, this present paper is the first to study and report an immediate experienced-based modulation of imagination MTs in a reciprocal aiming task (but see Ref. [2]). In sum, a lack of experience with the specific task in the present study (and associated poorly bound or formed ideomotor codes) is likely an important contributing factor to the commonly observed discordance between execution and imagination MTs.

Although the present data suggest that action execution experience improves the consistency between action execution and imagination, the MTs in these tasks were still different. One reason may be that participants did not have sufficient experience with the task. Participants only completed 3 trials (a total of 27 movements) in each combination of target width and movement amplitude. From one perspective, it is actually remarkable that the imagination MTs changed after such a relatively small amount of experience. It is possible, however, that there would have been a closer match between the execution and imagination MTs if participants had practiced more with the task. In support of this prediction, there are a number of studies indicating the action imagination of experts is much more detailed and generates different patterns of cortical activation that than of novices [16,17,20,22,36,37]. Future research could address this issue in more fundamental movement tasks such as those in the present study.

Overall, we propose that the type of motor task employed is unlikely to explain MTs differences between action execution and imagination. In contrast, prior experience with the motor task as well as the amount of practice during action execution can more likely explain the reported MTs differences. In the end, the data from the present and previous studies are consistent with the hypothesis that ideomotor coding is the basis of action imagination. The differences between action imagination and execution are likely the result of some additional processes that are yet to be defined (an issue that is addressed, in part, in the following section).

4.4. The persistent differences between action perception and imagination

The final aspect of the data that needs to be addressed is that the MTs on the imagination task were also longer than the MTs on the perception task. It was initially predicted that if perception and imagination both rely on the same simulation (i.e., an offline activation of the same perception/action codes), then similar MTs should emerge from both tasks. Such was not the case. Although there is no clear reason for this discrepancy, we suggest two possible reasons.

The first potential that MTs in the perception task are more closely aligned with actual MTs (and perhaps why imagination is also different from execution) is because there are additional sets of mechanisms that are specific to the imagination and perception tasks: (1) a visual reference provided by the apparent motion sequence on the monitor in the perception task; (2) the unlimited amount of time permitted for simulation during the perceptual task; and, (3) an emulation of expected sensory consequences in the imagination task [38]. With respect to the additional information and processing in the perceptual task, it is possible that the visual reference on the monitor during the perception task helped to fine-tune the simulation and judgment process. That is, similar to the way that experience helped to fine-tune the simulation process offline and increase the accuracy of the future simulation, participants could have used the visual reference of the apparent motion stimuli to adjust the simulation and judgment process while it was being enacted. Such a visual reference is not available to the individual in the imagination task and, hence, the simulation in the imagination task could not be adjusted online. Further, participants in the perception task had an unlimited amount of time to watch the apparent motion stimuli before determining the lowest apparent MT at which it was possible to perform the movements, whereas they were limited to a simulation of a total of 30 movements (3 trials of 10 movements each) in the imagination task. Although the amount of time each participant took on each perception trial was not recorded, it is possible that this extra amount of time and the visual reference provided participants with the opportunity to increase the accuracy of the judgments.

Finally, an alternative explanation for the difference in MT between imagination and both action perception and execution relates to actual set of processes involved in the imagination task. Based on Grush's [38] emulation theory of representation, one major difference between execution, perception and imagination is the generation of emulated sensory consequences of the action. That is, when performing or perceiving an action, internal models of both the actual and expected sensory consequences of the action are generated. In contrast, during imagination, one has to not only imagine the movement to be performed, but at the same time generate an internal model of the consequences of this movement. This extra, and perhaps noisy neural activity associated with action emulation is in addition to the activity associated with the simulation and may explain the longer MTs. Furthermore, the additional and noisy processes may decrease the efficiency and accuracy of the simulation and judgment process. Indeed, once the participant had built a realistic representation of actual action attempts, generating emulated responses could be both faster and more realistic, yet still slower than both action execution and perception. Future research efforts should be dedicated to address this possibility.

5. Conclusion

According to ideomotor theory, the codes that represent action and the perceptual consequences of those actions are tightly bound in a common code. It has been suggested that the processes underlying action perception and imagination are completed via a simulation process wherein the common codes are activated and run offline. The present findings support this hypothesis. Although it is unclear why MTs in the imagination task were longer than those in the other tasks, even after task experience, the findings of a significant decrease imagination MTs after experience and, critically, of the relationship between the amplitude of the motor overflow during imagination are consistent with the common coding hypothesis. Future work should be directed to understanding why these differences between imagination and execution exist.

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