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Article

Examining the equivalence between imagery and execution – do imagined and executed movements code relative environmental features?

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Abstract

Imagined actions engage some of the same neural substrates and related sensorimotor codes as executed actions. The equivalency between imagined and executed actions has been frequently demonstrated by the mental and physical chronometry of movements; namely, the imagination and execution of aiming movements in a Fitts paradigm. The present study aimed to examine the nature or extent of this equivalence, and more specifically, whether imagined movements encompass the relative environmental features as do executed movements. In two separate studies, participants completed a series of imagined or executed reciprocal aiming movements between standard control targets (no annuli), perceptually small targets (large annuli) and perceptually large targets (small annuli) (Ebbinghaus illusions). The findings of both studies replicated the standard positive relation between movement time and index of difficulty for imagined and executed movements. Furthermore, movement times were longer for targets with surrounding annuli compared to the movement times without the annuli suggesting a general interference effect. Hence, the surrounding annuli caused a longer time, independent of the illusory target size, most likely to avoid a potential collision and more precisely locate the endpoint. Most importantly, this feature could not be discriminated as a function of the task (imagined vs. executed). These findings lend support to the view of a common domain for imagined and executed actions, while elaborating on the precision of their equivalence.

Key words: imagery; illusion; simulated movement; allocentric

1. Introduction

The mental imagery of movements has been given substantial attention both within the literature and applied settings as it offers a potential tool for the learning of novel motor skills (Feltz & Landers, 1983; Romano-Smith, Wood, Wright, & Wakefield, 2018; Vogt, 1995) and enhancing recovery during movement rehabilitation (Crosbie, McDonough, Gilmore, & Wiggam, 2004; Dijkerman, Ietswaart, Johnston, & MacWalter, 2004; for a review, see Braun et al., 2013). As part of this body of work, there has been great consideration of the mechanisms and processes that underlie the positive effects of imagery. The dominant conceptual view holds that imagery engages many of the same representations for action as perception and execution (Jeannerod, 1994; 1999). More specifically, imagined, perceived and executed actions share a common domain such that the imagination of select movements activates a representation that is associated with the sensory consequences and motor output of that same movement (see Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997). Robust support for this conjecture is provided by neurobiological findings that suggest the imagery and execution of actions can activate common fronto-partietal areas of the brain (Filimon, Nelson, Hagler, & Sereno, 2007; Hétu et al., 2013).

From a behavioural perspective, the experimental context that is typically adopted involves the mental and physical chronometry of movements (see Guillot & Collet, 2005). Participants in these studies physically execute a series of movements and also imagine themselves performing the same movements. The context in which those movements are performed or imagined vary in difficulty and the researcher examines how the temporal characteristics change as a function of the task difficulty. Thus far, the results of these studies have indicated a consistent relation between movement difficulty and movement time for executed and imagined movements. More specifically, increasing the index of difficulty (ID) manifested in the executed and imagined movement times (MT) were also extended (e.g., Decety & Jeannerod, 1995; Papaxanthis, Pozzo, Skoura, & Schieppati, 2002; Sirigu et al., 1995; Sirigu et al., 1996; Slifkin, 2008; Wong, Manson, Tremblay, & Welsh, 2013; Yoxon, Pacione, Song, & Welsh, 2017; Yoxon, Tremblay, & Welsh, 2015). The relation between ID and MT is referred to as Fitts' Law (Fitts, 1954; Fitts & Peterson, 1964), and can be more precisely calculated using the following formula: MT = $a + b$(ID), where a and b are empirically derived constants pertaining to the base MT and the slope of the relation between MT and ID, respectively. Meanwhile, ID can be specified using the following formula: ID = $\log_2$(2A/W), where A represents the amplitude and W represents the target width. Overall, the similarity in the relation between ID and MT for executed and imagined movements has been taken as support for the hypothesized common processes.

Though these findings are highly informative with respect to the common processes for imagined and executed actions, there is still some margin for exploring the nature of the representation and the neural substrates involved. After all, despite the meaningful overlap between the neural codes engaged during imagination and execution, there are still some underlying differences in the neural recruitment and architecture occupied by each task (e.g., Nyberg, Eriksson, Larsson, & Marklund, 2006). Thus, it is possible that the current relation between ID and MT for imagined movements could result from the representation of endogenous motor parameters, where only the absolute features pertaining to the performer are encoded. Alternatively, it is possible that imagined movements additionally incorporate the relative features pertaining to the environment, which would normally factor into executed movements. To this end, we may ask, does the similarity between imagination and execution extend to neural codes that reference the absolute (egocentric) or relative (allocentric) features (see Glover, 2004)?

To explore this matter, it is possible to introduce perceptual illusions where the intended target appears perceptually different in size compared to normal, but is in fact the same size. Indeed, the use of perceptual illusions has proven an effective method to demarcate the contribution of egocentric and allocentric reference frames because the former is impervious to the direction of illusions, while the latter is responsible for imparting perceived differences. With this in mind, it is relevant to consider at least some of the evidence surrounding perceptual illusions and the planning and control of executed movements. Early evidence from this work was leveraged to support the two visual stream hypothesis (Milner & Goodale, 1995; Goodale et al., 1994). That is, visual illusions influence perceptual judgements because the relative features are coded in the ventral stream, while the online control of movement fails to reflect the nature of these illusions because their absolute features are coded in the dorsal stream. However, subsequent research findings have heavily attributed at least some influence of perceptual illusions within movement (Franz, Bülthoff, & Fahle, 2002; Glover & Dixon, 2001; 2002; Grierson & Elliott, 2009; Handlovsky, Hansen, Lee, & Elliott, 2004; Knol, Huys, Sarrazin, Spiegler, & Jirsa, 2017; Mendoza, Elliott, Meegan, Lyons, & Welsh, 2006; Roberts et al., 2013; van Donkelaar, 1999; Westwood & Goodale, 2003; see Goodale (2011), for an extensive review). For example, when adapting the Ebbinghaus (or Titchener-circles) illusion featuring large or small annuli surrounding the target, aiming movements were found to be longer or shorter in time when facing perceptually small (large annuli) or perceptually large (small annuli) targets, respectively (Handlovsky et al., 2004; Knol et al., 2017; van Donkelaar, 1999). Certainly, based on the notion that perceptual biases are contingent upon relative judgements involving the target, it is likely such judgements also impinge on the planning and/or control of target-directed movement.

Within the context of imagined movements, the evidence to-date has indicated a similar influence of relative environmental features across imagined and executed movements. Indeed, there is evidence that imagined and executed discrete movement choices

(Glover & Dixon, 2005) and times (Glover & Dixon, 2013) are consistent with the direction of an illusion (see also, Radulescu, Adam, Fischer, & Pratt, 2010; for an imagined and executed violation in Fitts' Law in the presence of a placeholder array). For example, perceptually long (tails-out) and perceptually short (tails-in) Müller-Lyer figures caused a longer and shorter time for single imagined and executed aiming movements (as indicated by a double key-press response), respectively (Glover & Dixon, 2005). Notably, this evidence surrounds contexts that strictly differ from the standard Fitts' reciprocal aiming paradigm, where a more comprehensive measure of the chronometry of imagined movements can be made. What's more, the reciprocal nature of such a task ensures the difficulty surrounding the indexing response can be comparatively limited (i.e., difference in the indexed start and end times). Hence, the present study seeks to elaborate upon this work involving imagined and executed movements and perceptual illusions. That is, the main aim of the present study is to determine if perceptual illusions influence MTs of imagined movements in a manner similar to executed movements. Thus, the (dis)similarity in the effect of the illusions on imagined and executed movement times would help to illuminate any potential differences in the processes and neural codes engaged during these tasks.

2. Experiment 1

2.1 Introduction

The aim of the present study is to examine whether imagined movements are influenced by perceptual illusions in the same way as executed movements within a Fitts aiming paradigm. Thus, participants were instructed to imagine or execute reciprocal aiming movements between two targets at varying degrees of difficulty (ID). These targets were presented with or without surrounding annuli that were designed to manipulate the perceived size of the target. That is, the large-sized surrounding annuli will foreseeably reduce the perceived size of the target, while the small-sized annuli will inversely enhance the perceived size. Providing the proposed equivalence between imagery and execution extends to the coding of relative environmental features, then we would predict a similar tendency for imagined and executed movements to be influenced by the illusion (prolonged MT for the perceptually small target and/or reduced time for perceptually large target). Alternatively, if the common codes that represent imagery and execution only encumber egocentric parameters, then there should be a limited influence of the illusion during the imagined compared to executed movements.

2.2 Method

2.2.1 Participants

There were 15 participants that agreed to take part in the study (10 male and 5 female, age range = 18-24 years, 14 self-declared right-handed). All participants had normal or corrected-to-normal vision, and were free from any known neurological impairment. Participants signed informed consent forms and the study was approved by the local ethics committee.

2.2.2 Task and Procedure

Participants were fitted with a retro-reflective marker at the index finger in order to have their movements detected by a Vicon camera system (Vicon Vantage, 16-megapixel resolution) sampling at 200 Hz for a period of 10 seconds. Target displays were printed solid black on pieces of white paper and secured to a table for participants to easily execute or imagine medio-lateral movements between two targets. Each set of targets assumed varying sizes (10, 15 mm) and amplitudes (80, 120, 160, 240, 320, 480 mm) depending on the assigned ID (4, 5, 6ID). More specifically, the 10 mm targets were spaced at 80, 160 and 320 mm, whilst the 15 mm targets were spaced at 120, 240 and 480 mm to assume IDs of 4, 5 and 6, respectively.

Some of the target displays featured surrounding annuli to create a size-contrast illusion; namely, the Ebbinghuas illusion (Figure 1). The target and annulus dimensions were primarily adapted from the studies of Aglioti et al. (1995) and Handlovsky et al. (2004). That is, the perceptually small and large targets featured 5 and 11 surrounding annuli, respectively. The diameter of each annulus was scaled to the target by a factor of 1.40 for the perceptually small target (10 mm target = 14 mm annuli, 15 mm target = 21 mm annuli) and 0.30 for the perceptually large target (10 mm target = 3 mm annuli, 15 mm target = 4.5 mm annuli). The gap size between the target and surrounding annuli was 12.5 mm and 5 mm for the perceptually small and large targets, respectively.

2.2.2.1 *Illusion Manipulation Check*

Prior to commencing the imagined and executed movement tasks, participants were tested to determine if the stimuli generated the target illusion. More specifically, participants were presented with two target circles on a computer screen; one with the sets of surrounding annuli that were used in the study and one circle without annuli. Participants were tasked with digitally adjusting the size of the target with no surrounding annuli until it appeared to be the same size as the adjacent target presented with large (perceptually small target) or small (perceptually large target) annuli. Targets were displayed diagonal to one another on an LCD monitor (spatial resolution = 1080 x 768 pixels; temporal resolution = 60 Hz) with stimuli being generated in Matlab 2018 (The Mathworks Inc., Natick, MA) running Cogent (toolbox developed by the Cogent 200 team at the FIL and ICN, and John Romaya at the LON, Wellcome Department of Imaging Neuroscience). The target without surrounding annuli could be adjusted by selecting the up (↑) and down (↓) keys to increase or decrease the size of the target by 0.5 mm per iteration (~1 pixel), respectively. Once participants perceived that they had closely matched the sizes, they had to press the ‘enter’ key to register their judgment and move on to the next trial (2 trials per target condition).

2.2.2.2 Movement Execution and Imagination Tasks

For the executed movement task, participants were instructed to execute fast and accurate aiming movements with their dominant upper-limb to each target in a reciprocal fashion (left-to-right, right-to-left, etc). There were 8 movement segments to be executed (4 cycles), although in the event participants executed too few or many segments, then the averaged segment MTs were amended accordingly (see later for details on the dependent measure). With respect to the imagined movement task, participants were instructed to imagine themselves see and feel the aiming movements between the two targets 8 times (4 cycles). To indicate the start and end of their imagined movement sequence, participants were told to lift and then return their finger to the home position in order to coincide with the imagined start and end points, respectively.

Each target display that comprised a unique combination of target size, amplitude and illusion were delivered in blocks of 3 trials in a fully randomized order (3 trials x 18 target displays). There were 18 target displays consisting of 6 combinations of the target width and movement amplitude, which derived 3 movement IDs (4, 5, and 6) for each of the individual annuli conditions (no annuli, small annuli, and large annuli). Imagined and executed blocks were delivered between participants in a counter-balanced fashion. Taken together, there were a total of 108 trials (54 trials each for imagination and execution).

[Insert Figure 1 about here]

2.2.3 Data Management and Analysis

Time-series position data were extracted and filtered using a Butterworth filter (8 Hz low-pass cut-off frequency, 2nd order, dual-pass). Resultant position was determined and velocity calculated by the three-point central difference method. Executed trials were graphically inspected for the number of movement cycles (i.e., sinusoidal transition of position across time). Both imagined and executed trials had their movements quantified in the same way. That is, movement onset was defined by parsing of individual frames from trial onset (~0 mm/s) to the moment that resultant velocity reached above 20 mm/s for at least 100 ms. Movement offset was inversely defined by parsing backwards from the end of the recorded trial (~0 mm/s) to the moment resultant velocity was above 20 mm/s.

The dependent measure of interest was the time taken to imagine or execute movements between the targets. Thus, we divided the total MT by the number of movement segments for each individual trial and calculated a mean of the MT for the trials for each condition. Imagined and executed movement trial times that were <100 ms, along with any executed trials whose endpoint error >30 mm, were removed prior to averaging (.01% trials).

Statistical analysis of the data consisted of a series of steps. First, we sought to examine whether the imagined and executed MTs were directly related to task difficulty (e.g., Decety & Jeannerod, 1995; Fitts, 1954). Thus, we correlated the IDs and mean MTs between participants for each of the imagined and executed movement tasks independent of the illusion context. With this in mind, it is important to recognise that the potentially low number of IDs being correlated comprised of varying combinations of amplitude and target width meaning any such relation would not be restricted to one particular constraint or instance of ID (for a similar procedure, see Wong et al., 2013). To determine if perceptual illusion was present, we assessed the emergence of any perceptual biases generated by the target illusions by analysing the pre-experimental size adjustments with a two-way repeated-measures ANOVA featuring factors of target size (10 mm, 15 mm) and illusion (perceptually small, perceptually large). Finally, mean MTs were analysed using a three-way repeated-measures ANOVA featuring factors of task (imagined, executed), ID (4, 5, 6) and illusion (perceptually small, control, perceptually large).

The assumption of equal variance of differences was tested using Mauchly's test of Sphericity. In the event of a violation, the Huynh-Feldt correction was issued when Epsilon was <.75, but the Greenhouse-Geisser value was adopted if otherwise. Furthermore, Fisher LSD post hoc analyses were conducted for significant effects featuring more than two means. Partial eta-squared (η^2) was used to indicate the size of any treatment effects. Statistically significant differences were declared at $p < .05$.

2.3 Results and Discussion

For executed MTs, there was a robust positive correlation with ID: $r^2 = .98$, $p < .001$, MT = -42.14 + 92.54(ID). Similarly, the imagined MTs demonstrated an equally robust positive correlation: $r^2 = .97$, $p < .001$, MT = 191.25 + 58.27(ID). These findings corroborate the vast evidence reflecting Fitts' Law for imagined and executed movements.

The pre-experimental perceptual matching task revealed a significant main effect of actual target size, $F(1, 14) = 474.47$, $p < .001$, *partial* $\eta^2 = .97$. There was also a main effect of perceptual illusion, $F(1, 14) = 62.06$, $p < .001$, *partial* $\eta^2 = .82$, which was consistent with the direction of the illusion (10 mm target: perceptually large $M = 10.38$ mm, perceptually small $M = 9.71$ mm; 15 mm target: perceptually large $M = 15.37$ mm, perceptually small $M = 14.29$ mm). The size x illusion interaction approached conventional levels of statistical significance, $F(1, 14) = 4.21$, $p = .059$, *partial* $\eta^2 = .23$, which appeared to indicate a slightly greater perceived difference in size for the larger target (15 mm). This trend may manifest as a function of Weber's stated positive relation between stimulus magnitude and *just-noticeable differences* (e.g., Holmes, Mulla, Binsted, & Heath, 2011).

Mean executed and imagined movement times are presented in Table 1. The omnibus ANOVA on MTs showed a significant main effect of task, $F(1, 14) = 5.23$, $p < .05$, *partial* $\eta^2 = .27$, which reflected longer MTs for the imagined compared to executed movements. There was also a main effect for ID, $F(2, 28) = 142.33$, $p < .001$, *partial* $\eta^2 = .91$, which indicated that there were shorter MTs for 4ID compared to 5ID, which was in turn, shorter than 6ID. In addition, there was a significant task x ID interaction, $F(2, 28) = 12.71$, $p < .001$, *partial* $\eta^2 = .48$, which indicated that the longer MTs for imagined compared to executed movements manifested in 4ID and 5ID (*ps* < .05), whereas MTs for imagined and executed movements did not differ for 6ID ($p > .05$) (Figure 2). Meanwhile, there was a significant main effect of illusion, $F(2, 28) = 3.50$, $p < .05$, *partial* $\eta^2 = .20$, which indicated a significantly shorter MT for the control ($M = 445.19$ ms, SE = 24.03) compared to the perceptually small ($M = 454.44$ ms, SE = 24.65) and perceptually large targets ($M = 455.10$ ms, $SE = 23.63$) (*ps* < .05). Critically, MTs for perceptually small and large targets did not statistically differ ($p > .05$). There were no further statistically significant interactions (task x illusion and ID x illusion, *Fs* < 1; task x ID x illusion, $F(4, 56) = 1.12$, $p > .05$, *partial* $\eta^2 = .07$).

[Insert Figure 2 and Table 1 about here]

There was a systematic tendency for the control target to have a shorter MT compared to the perceptually small and perceptually large targets, whose MTs did not differ. This direction of effects is inconsistent with those from the pre-experimental perceptual matching task. Based on the perceptual matching task, which provided evidence for a definitive perceptual bias of the illusion, one would have expected MTs to be longer for the large surrounding annuli (perceptually small target) compared to the small surrounding annuli (perceptually large target) and an intermediate time for no surrounding annuli (control target). Such changes in MTs according to the illusions did not emerge. Nevertheless, these effects are not too dissimilar from the original research findings of the execution of reaching and grasping movements toward the Ebbinghaus illusion (Aglioti, DeSouza, & Goodale, 1995; Haffenden & Goodale, 1998). Indeed, it is relevant to consider that the control target condition did not feature any surrounding annuli as was presented in the perceptually small and perceptually large target conditions. Under such circumstances, the temporal differences between target illusions may be attributed to an ecological artefact independent of the perceived size of the target (Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001; see also, Coren, 1986; Searleman, Porac, Dafoe, & Hetzel, 2005; cf. Franz, Bülthoff, & Fahle, 2002). That is, performers may have extended the time to targets with surrounding annuli compared to without the annuli because the participants required more time to avoid the annuli and ensure a precise endpoint response. This seemingly ad-hoc explanation may be likened to the avoidance of distractors (e.g., Tresilian, 1998; 1999) or inhibitory target movement effects (e.g., Howard & Tipper, 1997; Neyedli & Welsh, 2012; Welsh & Elliott, 2004), where objects that are adjacent to the intended target are overridden in favour of the intended target location. Nonetheless, it is important to note that MTs in both imagination and execution tasks were similarly affected – a finding that elaborates on the notion of equivalence, where imagined and executed actions rely on similar neural substrates.

3. Experiment 2

3.1 Introduction

To corroborate and extend the findings of Experiment 1, Experiment 2 was designed to divulge the nature of the effect of target illusions and the associated annuli during imagined and executed movements. Thus, participants completed the same imagined and executed movements toward targets with (perceptually small, perceptually large) and without (control) surrounding annuli so as to manipulate the perceived target size. In addition, a further target condition was introduced wherein the surrounding annuli appeared roughly equal to the size of the target. This additional condition with annuli of equal size diminishes the size-contrast illusion whilst retaining the potential artefact of the adjacent objects (equal annuli), and with it, the potential need to inhibit or avoid them. This context is directly adapted from previous studies that have shown no bias in the perceived size of the target, although there is a reduced grip aperture compared to normal when grasping (Haffenden & Goodale, 1998). Hence, comparisons between the MTs on the control target with no surrounding and the new target with equally-sized annuli enable us to further understand the influence of the adjacent objects on imagined and executed MTs. If the longer MTs on the perceptual illusions compared to the control target from Experiment 1 are attributed to the inadvertent avoidance of surrounding annuli, then there should be a similarly longer MT for the equally-sized annuli as for the large and small surrounding annuli conditions. What's more, the equivalence rendered for imagery and execution should mean that the effect of the surrounding annuli will not be differentiated across imagined and executed movements.

3.2 Method

3.2.1 Participants

There were 12 participants that agreed to take part in the study (7 male and 5 female, age range = 18-35 years, 10 self-declared right-handed). All participants had normal or corrected-to-normal vision, and free from any known neurological impairment. Participants signed informed consent forms and the study was approved by the local ethics committee.

3.2.2 Task and Procedure

The task and procedure were the same as in Experiment 1. However, the present study featured only target displays with a 15 mm target size to limit the number of movement amplitudes (120, 240, 480 mm) that were required to span the pre-allocated IDs (4, 5, 6ID), and to limit to overall time of data collection. In addition, there was an extra target display designed to alleviate any size-contrast illusion, whilst still presenting the surrounding annuli (Figure 1). The new target display parameters were directly adapted from the study of Haffenden and Goodale (1998). That is, there were 8 surrounding annuli with the diameter of each scaled to 0.81 with respect to the target (15 mm target = 12.2 mm annuli), which substantially reduced the contrast in size compared to the perceptually small and perceptually large target illusions. The gap size between the target and surrounding new annuli was 7.5 mm.

Once again, there were blocks of 3 trials for each target display, which were presented in a fully randomized order (3 trials x 12 target displays). Imagined and executed blocks were delivered between participants in a counter-balanced fashion. Taken together, there were 72 trials in total.

3.2.3 Data Management and Analysis

Data were handled in the same way as in Experiment 1 (.01% trials removed). Consistent with Experiment 1, we initially correlated imagined and executed MTs with ID irrespective of the illusion context. Perceptual biases from the pre-experimental size adjustments were assessed using a one-way repeated-measures ANOVA. Finally, mean participant MTs were analysed using a three-way repeated-measures ANOVA featuring the factors of task (imagined, executed), ID (4, 5, 6) and illusion (perceptually small, control, equal annuli, perceptually large).

3.3 Results and Discussion

The recordings of two participants for a single condition in execution were missing due to excessive marker loss. Rather than eradicating these cases featuring otherwise viable data, we extrapolated the MTs for the relevant illusion context based on the IDs that were successfully recorded.[1] For executed MTs, there was a robust positive correlation with ID: $r^2 = .95$, $p < .001$, MT = 10.58 + 93.27(ID). In a similar vein, the imagined MTs demonstrated an equally robust positive correlation: $r^2 = .96$, $p < .001$, MT = 193.06 + 66.45(ID).

The pre-experimental perceptual matching task revealed a significant main effect of illusion, $F(2, 22) = 49.12$, $p < .001$, *partial* $\eta^2 = .82$. Post hoc analyses indicated that the size adjustments were consistent with the direction of the illusion as the perceptually small (M = 13.99 mm) and large (M = 15.58 mm) targets were respectively made to be smaller and larger than the equally-sized annuli (M = 15.03 mm) target (*ps* < .01).

Mean executed and imagined movement times are presented in Table 2. The omnibus ANOVA on MTs showed a significant main effect of task, $F(1, 11) = 7.74$, $p < .05$, *partial* $\eta^2 = .41$, and ID, $F(2, 22) = 54.47$, $p < .001$, *partial* $\eta^2 = .83$, which reflected longer MTs for the imagined compared to executed movements, and shorter times for 4ID compared to 5ID, which was in turn, shorter than 6ID. The task x ID interaction approached conventional levels of significance, $F(2, 22) = 3.82$, $p =. 067$, *partial* $\eta^2 = .26$, which in a similar vein to Experiment 1, indicated longer times for imagined compared to executed movements primarily in 4ID and 5ID, whereas MTs for 6ID were no different between the tasks. Meanwhile, there was a significant main effect of illusion, $F(3, 33) = 3.74$, $p < .05$, *partial* $\eta^2 = .25$, which indicated significantly shorter MTs for the control (no annuli) condition (M = 486.92 ms, SE = 42.64) compared to perceptually small (M = 504.77 ms, SE = 42.90) and equally-sized annuli (M = 511.51 ms, SE = 39.04) targets (*ps* < .05), with a similar trend for the comparison with the perceptually large target (*M* = 501.25 ms, *SE* = 42.35) (p = .15). There were no further statistically significant interactions (task x illusion, $F(3, 33) = 1.78$, $p >$ .05, *partial* η^2 = .14; ID x illusion, $F(6, 66) = 1.12$, $p > .05$, *partial* η^2 = .09; task x ID x illusion, $F(6, 66) < 1$).

[Insert Table 2 about here]

These findings corroborate those from the previous Experiment 1, including the proposed influence of surrounding target annuli. That is, the presence of surrounding annuli caused performers to prolong their imagined and executed MTs, which was independent of any perceived size-contrast illusion. Presumably, the surrounding annuli were treated as adjacent objects to-be-avoided, which require a slightly prolonged time to ensure a precise terminal location on the target. For the main purpose of the present studies, however, the critical finding was that the target illusion did not interact with the nature of the task performed. Thus, the influence of the annuli on the imagined and executed movements did not systematically differ.

4. General Discussion

The present studies were designed to examine the nature of the equivalence between imagined and executed movements. More specifically, we set out to explore whether the relative environmental features impact imagined movements as they do executed movements. Based on the evidence that perceptual illusions influence certain aspects of executed movements (e.g., Glover & Dixon, 2001; 2002; Handlovsky et al., 2004; Westwood & Goodale, 2003), it was predicted that to render equivalence between imagery and execution, then there should be a similar illusion effect for imagined and executed movements. The key findings indicated that there was an effect of the stimuli that should generate perceptual illusions on MTs, but that this effect manifested in the perceptually small (large annuli) (Exp. 1-2), perceptually large (small annuli) (Exp. 1-2), and equally-sized annuli (Exp. 2) targets appearing to be slower than the control target (no annuli). Thus, the perceptual illusions did not affect MTs in a manner that was consistent with the direction of the illusions. These findings were not differentiated as function of task suggesting a similar influence of target context for the imagined and executed movements. What's more, there was a longer time for imagined compared to executed movements within the lower IDs (4, 5ID), but not for the most difficult ID (6ID). The following discussion will focus on each of these key findings.

Target context

While previous findings surrounding the mental and physical chronometry of actions may allude to similarities between imagery and execution (e.g., Decety & Jeannerod, 1995), it can be argued that the subsequent support for a common representation pertains only to studies that are independent of any environmental or contextual features. The use of illusions in movement execution has provided some valuable insight into the potential cortical areas engaged during the execution of movement. Thus, the use of perceptual illusions as targets provides further insight into whether imagined and executed movements can be equally influenced by relative features that are coded in an allocentric reference frame (e.g., contrast between the target and annulus size) (Glover, 2004). Such an influence would normally assume a shorter time for the perceptually large target compared to the control target, which may be shorter still compared to the perceptually small target (e.g., Handlovsky et al., 2004; van Donkelaar, 1999). However, the present effect of target illusions appeared to reflect a direction of effects that were not fully compatible with the nature of the perceptual illusion. Instead, it is perhaps more accurate to conceive of the current effects as a direct influence of the surrounding annuli independent of any size-contrast illusion. Consistent with these findings is evidence that when grasping a target embedded amongst equally-sized annuli, then there is a smaller grip aperture compared to a target without surrounding annuli despite the targets being perceived as similar in size (see Figure 1) (Haffenden & Goodale, 1998). Likewise, increasing the gap size between a target and small-sized annuli causes the grip aperture to be reduced while retaining the illusion of it being a large target (Haffenden et al., 2001). In this context, if the surrounding annuli accommodate movement directly to the target, then the performer will ensure that the movement avoids any potential collision.

Nevertheless, the effect of the target and surrounding annuli appeared to be consistent across imagery and execution, which would lend support to the argument that they rely on a common representational domain (Jeannerod, 1994; 1999). With this common domain in mind, the present study details the extent in which imagery may be considered equal to execution, because something as slight as irrelevant surrounding annuli can impinge on both imagined and executed movements (see Glover and Dixon, 2005; 2013 for similar context effects). With this in mind, it may be useful to elaborate on the current findings by exploring how imagined movements engender the avoidance/interference patterns as found during executed movements, where there are potentially multiple targets to choose from and only a single response is required to be programmed (e.g., Neyedli & Welsh, 2012; Tresillian, 1998; 1999; Welsh & Elliott, 2004). After all, it is relevant to consider that the present interpretation is strongly adapted from prior views on movement control with adjacent or distractor objects, and thus cannot comprehensively refute any confounding influences of the surrounding annuli (e.g., mental load, oculomotor interference, etc).

Modulation effects

The longer times for the imagined compared executed movements at the lower IDs, combined with the limited difference found at the highest ID, was unexpected. That said, the longer times found for imagined compared to executed movements is a rather ubiquitous finding within the literature (e.g., Decety, Jeannerod, & Prablanc, 1989; Slifkin, 2008). Recent evidence has suggested that additional physical practice of the movement can reduce the imagined times, and subsequently bring them closer to the executed times (Wong et al., 2013; Yoxon et al., 2015; Yoxon et al., 2017). This experience-dependent effect of imagined movements has been attributed to the development and enhancement of the codes responsible for matching imagined, perceived and executed actions, which can be built upon by sensorimotor training or exposure to the unique task environment. However, this reasoning arguably fails to explain why imagined MTs are systematically longer, as opposed to shorter or randomly varied, relative to the executed MTs. Indeed, if there were limitations to the representation of imagined movements, then it would presumably ensue in an alternative direction of effects.

As an alternative explanation, the recently coined motor-cognitive model of imagery (Glover & Baran, 2017) has been leveraged to explain such a pattern of results. This model contends that while imagined and executed movements initially converge onto a single representational domain or common code, they may become differentiated during the movement phase itself. That is, executed movements unfold naturally without the need for conscious intervention where online adjustments may unfold (Elliott, Helsen, & Chua, 2001). Alternatively, imagined movements do not feature any afferent or efferent signals, which also generate anticipatory forward models (Desmurget & Grafton, 2000; Wolpert, Ghahramani, & Jordan, 1995), meaning any simulation must be undertaken through executive and consciously accessible processes. Consequently, the increased cognitive demand for imagined movements may cause a delay in the indexing response (responsible for indicating the end of the movement). Furthermore, unlike during the perception of ongoing actions (e.g., Chandrasekharan et al., 2012; Grosjean, Shiffrar, & Knoblich, 2002; Wong et al., 2013), there is no visual input regarding the ongoing movement that could be used to recalibrate the speed of the simulations of the movement. While this model can reconcile the tendency to have longer imagined MTs, it is also possible to explain the limited differences between imagined and executed movements for our most difficult task scenario (6ID). To elucidate, when the increasing ID imposes such constraints on the control of executed movements, then the executed MTs may reach a point where they seemingly coincide with the imagined MTs. After all, there must be a margin of difficulty where the executed movements become just as difficult and slow as the imagined movements. Previous work may have failed to allude to such a relation between task and ID because of the comparatively low range of IDs (e.g., IDs of 2-4; Wong et al., 2013; Yoxon et al., 2015). Given the differences in base MTs for imagined and executed movements across the literature (imagined > executed: Decety, Jeannerod, & Prablanc, 1989; Slifkin, 2008; imagined =/< executed: Calmels, Holmes, Lopez, & Naman, 2006; Macuga & Frey, 2012; Sirigu et al., 1995), it is perhaps useful for future research to explore this complex interaction with task constraints.

Conclusion

It appears that the equivalency of imagined and executed movements extends to the coding of environmental features. This equivalence may be so precise that imagery and execution can equally capture the contextual task features, which eventually inflict slight, yet systematic, changes to the MT. In addition, the ubiquitous finding of a prolonged time for imagined movements, and it’s modulation as a function of task difficulty, may suggest that the bespoke equivalency co-exists with separate cognitive and/or movement control processes.

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Figure captions

Figure 1. Illustration of the targets for Experiment 1 and Experiment 2: perceptually small (large annuli) (A), control (no annuli) (B), perceptually large (small annuli) (C), and equally-sized annuli (D).

Figure 2. Mean times for Experiment 1 as a function of task (executed, imagined) and ID (4, 5, 6). Error bars indicate standard error of the mean.

Tables

Table 1. Mean (±SE) of the executed and imagined times as a function of ID and target illusion for Experiment 1

Execution			
ID	*Perceptually Small*	*Control*	*Perceptually Large*
4	335.18 (20.93)	333.45 (20.95)	336.62 (20.13)
5	415.12 (23.55)	402.23 (21.66)	401.79 (20.75)
6	528.26 (26.71)	508.03 (25.05)	524.17 (28.62)
Imagery			
ID	*Perceptually Small*	*Control*	*Perceptually Large*
4	422.18 (26.15)	414.00 (27.96)	436.67 (30.34)
5	490.98 (34.43)	469.00 (29.40)	488.21 (30.72)
6	534.90 (39.04)	544.42 (44.05)	543.16 (37.99)

Table 2. Mean (±SE) of the executed and imagined times as a function of ID and target illusion for Experiment 2

Execution				
ID	*Perceptually Small*	*Control*	*Equal Annuli*	*Perceptually Large*
4	388.10 (31.59)	398.57 (39.39)	397.43 (33.64)	387.27 (34.82)
5	452.44 (37.30)	449.32 (37.48)	485.65 (39.38)	446.70 (33.26)
6	582.70 (41.40)	557.05 (41.40)	600.14 (40.04)	577.61 (44.49)
Imagery				
ID	*Perceptually Small*	*Control*	*Equal Annuli*	*Perceptually Large*
4	454.38 (44.29)	452.42 (48.87)	467.18 (37.52)	472.26 (44.79)
5	533.16 (51.45)	500.52 (47.33)	516.56 (41.48)	529.41 (54.43)
6	617.85 (67.45)	563.65 (52.47)	602.09 (57.76)	594.26 (61.89)

Footnote

1) Following removal of the two cases with missing data (n = 10), the correlation between MTs and ID revealed a significant positive relation: $r^2 = 94$, $p < .001$, MT = 24.76 + 93.05(ID). The omnibus ANOVA on MTs appeared to show a similar set of findings to when all cases were included (task: $F(1, 9) = 4.64$, $p = .06$, *partial* $\eta^2 = .34$; ID: $F(2, 18) = 38.50$, $p < .001$, *partial* $\eta^2 = .81$; illusion: $F(3, 27) = 3.20$, $p < .05$, *partial* $\eta^2 = .26$; task x procedure: $F(2, 18) = 2.48$, $p = .14$, *partial* $\eta^2 = .22$).