Distinct Visual Resolution Supports Aperture Shaping in Natural and Pantomime-Grasping

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Abstract

Pantomime-grasping is a 'simulated' motor response wherein an individual grasps to an area dissociated from a physical target. The task has been used in the apraxia literature as a proxy for natural grasping (i.e., physically grasping a target); however, it is important to recognize that the task's decoupled spatial relations between stimulus and response renders the top-down processing of target features (e.g., size) that accumulating evidence has shown to be mediated by visual information functionally distinct from natural grasping. Here, we examined whether the visual information supporting pantomime-grasps exhibits a visual resolution power commensurate with natural grasps. Participants were presented with a target and non-target that differed in size below the perceptual threshold (i.e., 0.5 mm or ~1.3%) and were asked to make a perceptual judgment about the target (i.e., "smaller" or "larger" than the non-target) before and after completing natural and pantomime-grasps. Results showed that perceptual judgments "before" and "after" natural and pantomime-grasps did not reliably distinguish between target and non-target. Natural grasp peak grip apertures (PGA) scaled to target size and were comparable for "before" and "after" perceptual judgment trials – a result indicating that haptic feedback from physically grasping the target did not "boost" perceptual accuracy. Most notably, pantomime-grasp PGAs were insensitive to target size; that is, responses elicited a visual resolution power less than natural grasps. These results provide convergent evidence that pantomime-grasps are mediated by the same visual information as obligatory perceptions and do not provide a proxy for natural grasps.

Keywords: *action; perception; prehension; visual; visuomotor*

Public Significance Statement: The visual information we use to identify an apple in a bowl of fruit (i.e., a perception) is distinct from the visual information we use to grasp the apple (i.e., an action). The main finding from the current study is that a simulated grasping response (so-called pantomime) is supported by the same visual information as that supporting perceptions.

Introduction

A master watchmaker can assemble the intricate, and very small, components of a timepiece independent of knowledge about each component's absolute size and shape. In an experimental demonstration of this, Ganel et al. (2012) presented a pair of 3D circular discs 40.0 and 40.5 mm in diameter and instructed participants to precision grasp (i.e., thumb and forefinger) one of the objects (i.e., the target) and report whether it was smaller or larger than the non-target. Participants did not accurately report whether the target was smaller or larger than the non-target – an expected finding given the approximate 1% between-target size difference is less than the Weber fraction for perceptions of visual length (Teghtsoonian, 1971). In contrast, peak grip aperture (PGA) associated with grasping the target increased from the 40.0 to 40.5 mm target and was taken to reflect that the resolution power for visuomotor responses is greater than visuoperceptual judgments. Ganel et al. interpreted their findings within the perception/action model's (PAM) framework that visually guided (and natural) grasps are supported via absolute visual information specified by the dorsal pathway, whereas perceptual judgments are mediated by relative information specified by the ventral pathway (Goodale & Milner, 1992; for review see Goodale & Milner, 2018).

An interesting question arising from Ganel et al.'s (2012) work is whether pantomime-grasps exhibit the same – or different –resolution power as natural grasps. Pantomime-grasps involve responses to an area adjacent to (i.e., spatially dissociated) or previously occupied by (i.e., memory-guided) a target (Barbieri & De Renzi, 1988; Geschwind, 1975; Heath et al., 2001; Roy et al., 2000; Liepmann, 1908) or when a visual target is not physically graspable via a mirror-based apparatus (for details see, Bingham et al., 2007; Schenk, 2012). Such actions have been frequently used in the neurology and neuropsychology literature as a proxy for natural

grasps. Notably, however, accumulating literature has shown that pantomime-grasps are mediated by visual information distinct from their natural grasp counterparts. For example, Goodale et al., (1994) had neurologically healthy individuals (i.e., control group) and DF (i.e., an individual with bilateral ventral stream lesions) complete natural and pantomime-grasps (i.e., memory-guided and spatially dissociated) to differently sized targets. Control participants produced natural and pantomime-grasp (i.e., memory-guided and spatially dissociated) PGAs that scaled to target size; however, values were smaller for pantomime-grasps. In turn, DF exhibited PGA/target-size scaling during natural grasps; however, PGAs for memory-guided pantomime grasps did not scale to target size. Moreover, although DF's spatially dissociated pantomime-grasps showed some scaling to target size (see Whitwell et al., 2015a) Goodale et al. reported that they were "[…] extremely variable compared to her normal grasping movements" (p. 1174)[1]. The smaller pantomime-grasp PGAs for controls was taken as indirect evidence of aperture formation via visual information distinct from natural grasps (see also Davarpanah Jazi et al., 2015; Fukui & Inui, 2013; Heath et al., 2017; Westwood et al., 2000), whereas DF's results were interpreted as evidence that pantomime-grasps – and in particular memory-guided ones – are perception-based and mediated by the ventral pathway. In further support of this view, our group examined whether natural and pantomime-grasps to differently sized targets adhere to or violate the psychophysical principles of Weber's law (Davarpanah Jazi & Heath, 2016; Holmes et al., 2013). Weber's law asserts that the just-noticeable-difference (JND) of a stimulus is a constant ratio of the original stimulus magnitude and that the sensitivity of detecting a change between an original and a comparator stimulus is relative as opposed to absolute (see Ganel et al., 2008; Heath et al., 2015). Results demonstrated that JNDs for natural grasps did not vary with object size and thus violated Weber's law. In contrast, pantomime-grasp JNDs

increased linearly with increasing object size and thus provide law-based evidence of aperture shaping via relative visual information.

The work outlined above indicates that pantomime-grasps are mediated via relative visual information. If that contention is correct, then a logical extension would be that the resolution power for pantomime-grasps is less than natural grasps. In other words, given the proposed relative nature of visual information supporting pantomime-grasps, it is predicted that PGAs will not vary in response to changes in target size below the Weber fraction for perceptions of visual length. To address that issue, we employed the same general methods as Ganel et al. (2012) in that a pair of objects (i.e., a target and non-target) differing in size by 0.5 mm were presented and participants were required to provide a perceptual report and complete natural and spatially dissociated pantomime-grasp responses. If pantomime-grasps are perception-based, then the resolution power for such actions should be refractory to changes in target size.

Methods

Participants

Twenty individuals from the University of Western Ontario community volunteered for this study (10 female: age range 18–27 years of age) and all self-reported right-hand dominance, normal or corrected-to-normal vision and no history of neuropsychiatric/neurological disorder or movement dysfunction. Informed written consent was attained via a protocol approved by the Non-Medical Research Ethics Board, University of Western Ontario, and this work corresponded to the Declaration of Helsinki with the exception that participants were not entered into a database.

Apparatus and stimuli

Participants stood at a table (depth=760 mm, width=1060 mm) with the tabletop height adjusted to approximately 150 mm above their waist and grasped or pantomime-grasped (see details below) 3D targets. Two target sizes were used, and both were acrylic blocks painted flat black and secured to a laminated sheet of white paper with their long-axis oriented perpendicular to participants. Targets were presented as a pair and were 40.0 and 40.5 mm in length (both 10 mm in height and depth). Targets were precision manufactured and measured via University Machine Services, Department of Material and Mechanical Engineering, Western University. The target size difference (i.e., 0.5 mm or ~1.3%) used here is below the Weber fraction for judgments of visual length (for review see, Teghtsoonian, 1971) and is commensurate with Ganel et al. (2012) with the exception that the former employed discs. For each trial, one target in the pair (i.e., the target) was presented 50 mm to the right of participants' midline and 400 mm from the front edge of the table, whereas the other object (i.e., non-target) was 400 mm from the front edge of the table and 50 mm left of midline. Visual and auditory events were controlled via MATLAB (7.6: The MathWorks, Natick, MA, USA) and the Psychophysics toolbox extensions (v. 3.0) (Brainard, 1997). Participants wore liquid crystal goggles (PLATO Translucent Technologies, Toronto, ON, Canada) throughout the experiment. The goggles can be set to transparent and translucent (i.e., opaque) states without altering the level of light reaching the eyes (Milgram, 1987). In the present work, the goggles served as a necessary tool to control the amount of time stimuli were viewed by participants in advance – and following – a trial (see details below).

Prior to each trial participants rested the palm of their right (i.e., grasping) hand on a start location (i.e., MFJ-550 telegraph key) positioned 50 mm to the right of midline and 50 mm from the front edge of the table with their thumb and forefinger pinched lightly together. During this

period the goggles were translucent so that the experimenter could place the target and non-target on the tabletop. Subsequently, the goggles became transparent for a uniformly distributed randomized preview period of between 3000-4000 ms after which a tone (i.e., 2900 Hz for 50 ms) signalled participants to natural grasp or pantomime-grasp (i.e., via precision grip) the object presented to the right of midline (i.e., the target). For natural grasps, participants reached to grasp – but not lift – the target's long axis and held it for approximately 1000 ms before returning to the start location. For pantomime-grasps, participants grasped to an area approximately 100 mm to the right of the target and remained at that position for approximately 1000 ms before returning to the start location (i.e., spatially dissociated pantomime-grasp) (see **Figure 1** for schematic of grasping responses and timeline of visual, auditory and motor events). This procedure is in line with previous work examining pantomime-grasps (e.g., Goodale et al., 1994; Davarpanah Jazi & Heath, 2016; Holmes & Heath, 2013; Westwood et al., 2000; Whitwell et al., 2015b) and represents the manipulation employed in the extant apraxia literature (Liepmann, 1908). Natural and pantomime-grasps were completed in separate and randomly ordered blocks. In each block, the 40.0 mm and 40.5 mm objects served as the target and non-target on an equal number of occasions and were randomly ordered (i.e., 80 natural and 80 pantomime-grasps). Additionally, for each trial participants provided a verbal response (i.e., perceptual judgment) as to whether the target was "smaller" or "larger" than the non-target. In line with Ganel et al. (2012), perceptual judgments were completed during the preview period or after natural or pantomime-grasps (i.e., when a stable final grip aperture was achieved). Prior to each trial, the experimenter informed participants to provide a perceptual response "before" or "after" their grasp/pantomime-grasp. An equal number of "before and "after" responses were

completed with the order pseudorandomized such that a "before" or "after" response could not occur on more than three consecutive trials.

Data collection, dependent variables, and statistical analyses

An OPTOTRAK Certus (Northern Digital Inc., Waterloo, ON, Canada) sampling at 400 Hz for 2 s following the auditory cue measured the position of the right limb via infrared emitting diodes (IREDs) attached to the medial surface of the distal phalanx of the thumb, the lateral surface of the distal phalanx of the forefinger, and the styloid process of the radius. IRED data were filtered by a second-order dual-pass Butterworth filter with a low-pass cut-off frequency of 15 Hz. Displacement data were used to compute instantaneous velocities via a five-point central finite difference algorithm (Winter, 2009). Movement onset was marked by release of the start location and movement offset was determined when velocity was less than 50 mm/s for 50 ms.

Dependent variables included reaction time (RT: time from auditory cue to movement onset), movement time (MT: time from movement onset to offset), peak grip aperture (PGA: maximum resultant distance between thumb and forefinger), and time to PGA (tPGA: time from movement onset to PGA). Grasping data were examined via 2 (condition: natural vs. pantomime-grasp) by 2 (perceptual judgment: "correct" vs. "incorrect") by 2 (target size: 40.0 and 40.5 mm) fully repeated measures ANOVA. The accuracy (i.e., percentage of correct trials) of perceptual responses completed before and after natural/pantomime-grasps was contrasted via paired-samples t-tests and accuracy was contrasted to a chance level of performance via a single-sample t-test. Where appropriate, two one-sided tests (TOST) were used to determine whether natural and pantomime-grasp values were within an equivalence boundary (Lakens et al., 2017).

Results

Perceptual accuracy

Perceptual responses did not reliably vary when completed "before" or "after" natural or pantomime-grasps (all t(19)=0.57 and 0.40, ps>0.57, all d_z<0.13 and 0.09). Accordingly, perceptual data were pooled and produced an overall accuracy of 55% (SD=25) and this value did not reliably differ from a chance level of performance (t(19)=1.07, p=0.298, d=0.24).

Grasping data

The grand means for RT and MT were 323 ms (SD=52) and 635 ms (SD=97), respectively. RT and MT did not produce reliable main effects for condition, all $F(1,19)=1.16$ and 0.26 for RT and MT, respectively, ps=0.26 and 0.61, $\eta_p^2=0.05$ and 0.01, perceptual judgment, all $F(1,19)=0.65$ and 1.27, ps=0.45 and 0.27, $\eta_p^2=0.03$ and 0.06, target size, all $F(1,19)=0.52$ and 1.17 for RT and MT, respectively, ps=0.47 and 0.29, $\eta_p^2=0.02$ and 0.05, nor any higher-order two-way or three-way interactions, all $F(1,19)<0.77$ and 0.93 for RT and MT, respectively, ps>0.39 and 0.35, all $\eta_p^2<0.05$.

Figure 2 presents an exemplar participant's mean natural and pantomime-grasp grip apertures, and 95% confidence interval envelopes, as a function of target size at decile increments of normalized grasping time. The figure shows that natural condition apertures were larger than pantomime-grasp values from ~30% of MT until the end of the response, and that PGAs occurred later for pantomime-grasps. Moreover, the exemplar participant demonstrates natural grasp apertures that were smaller for the 40.0 mm than the 40.5 mm target from ~30% of MT until the end of the response, whereas pantomime-grasp apertures did not vary with target size at any stage in the unfolding response. In terms of quantitative results, group mean PGA produced a main effect for condition, $F(1,19)=69.68$, p<0.001, $\eta_p^2=0.78$, and a condition by target size interaction, $F(1,19)=19.94$, p<0.001, $\eta_p^2=0.51$. Natural grasp PGAs (45 mm, SD=4)

were larger than pantomime-grasps (37 mm, SD=6). As well, **Figure 3A** demonstrates that natural grasp PGAs increased from the 40.0 to 40.5 mm target ($t(19)=6.79$, $p<0.001$, $d_z=1.52$), whereas pantomime-grasp values did not reliably differ ($t(19)=0.88$, $p=0.38$ $d_z=0.19$) and a two-one side test (TOST) indicated that values were within an equivalence boundary ($t(19)=1.91$, $p=0.038$). **Figure 3C** shows PGA target size difference scores (i.e., 40.5 minus 40.0 mm target) – and 95% between-participant confidence intervals – for natural and pantomime-grasps associated with "correct" and "incorrect" perceptual judgments as well as their pooled averages. The figure demonstrates that natural grasp, but not pantomime-grasp, values reliably differed from zero and was a result that did not vary across trials involving "correct" and "incorrect" perceptual responses. The ANOVA model did not reveal a main effect for perceptual judgment (i.e., "correct" vs. "incorrect"), $F(1,19)=1.34$, $p=0.26$, $\eta_p^2=0.06$, nor any higher-order interaction, involving this variable, $F(1,19)=0.72$, $p=0.41$, $\eta_p^2=0.03$. Results for tPGA produced a main effect of condition, $F(1,19)=11.79$, $p=0.003$, $\eta_p^2=0.38$: tPGA occurred earlier for natural (504 ms, SD=98; i.e., 79% of MT) than pantomime-grasps (583 ms, SD=134; i.e., 90% of MT) (**Figures 3B and 3D**) . tPGA did not produce reliable main effects for perceptual judgment, $F(1,19)=1.08$, $p=0.31$, $\eta_p^2=0.05$, target size, $F(1,19)=1.34$, $p=0.26$, $\eta_p^2=0.02$, nor any higher-order interactions, all $F(1,19)<0.49$, $ps>0.47$, all $\eta_p^2<03$.

Discussion

Our primary objective was to contrast the resolution power of the visual information supporting natural and pantomime-grasps. Before addressing that primary objective, we first outline the general differences – and similarities – between natural and pantomime-grasps.

PGAs for natural grasps were larger and occurred earlier than pantomime-grasps. These results were independent of any between-condition difference in movement planning (i.e., RT) or

execution (i.e., MT) times and thus cannot be attributed to a speed-accuracy trade-off (Fitts, 1954). Instead, results are in keeping with a wealth of evidence showing that natural grasps require orthogonal thumb and forefinger approach vectors so that the opposing forces of each effector are parallel to one another at the time of contact (i.e., prevents target 'slipping') (for review see, Smeets & Brenner, 1999). As well, the timing of PGA onset for natural grasps (79% of MT) evinces a safety-margin task-set designed to prevent an object collision (Jeannerod, 1984) and allowing for the integration of online feedback during the later stages of aperture formation (Marteniuk et al., 1987; Wallace & Weeks, 1998; Wing et al., 1986; for review see, Elliott et al., 2010). In turn, it has been proposed that the smaller and later occurring (90% of MT%) PGAs for pantomime-grasps reflects that there is no need to approach the object orthogonally or employ a safety-margin task-set (Cavina-Pratesi et al., 2011; Goodale et al., 1994; Holmes et al., 2013; Westwood et al., 2000). After all, the participant – and not the physical properties of a target – determines the tolerance parameter for a successful pantomime-grasp (Holmes & Heath, 2013; Ozana & Ganel, 2017).

The most salient comparisons in this study relates to the interplay between target size 'awareness' and natural and pantomime-grasp PGA/target-size scaling. As expected, participants' perceptual reports provided "before" and "after" natural and pantomime-grasps did not differentiate between the 40.0 mm and 40.5 mm targets. Moreover, that the accuracy of perceptual reports did not improve following a natural grasp (i.e., an "after" trial) indicates that physical interaction with the target did not "boost" perceptual resolution. The results for the perceptual task are an expected finding given that the between-target size difference used here is below the accepted Weber fraction for judgments of visual length (for review see, Teghtsoonian, 1971). In spite of the lack of explicit target-size knowledge, natural grasp PGAs for the 40.5 mm

target were larger than the 40.0 mm target. This result provides a direct replication of Ganel et al. (2012) and supports the PAM's assertion that the dorsal pathway provides the visuomotor system absolute visual information to mediate metrically precise hand-target interactions (for review see, Goodale & Milner, 2018). Thus, the present findings, those of Ganel et al., and the extant grasping literature (for reviews see, Goodale, 2011; Smeets & Brenner, 1999) demonstrate that PGAs scale to veridical target size across stimuli that are below – and above (see Ayala et al., 2018; Heath & Manzone, 2017) – the Weber fraction for the discrimination of line length. Notably, however, pantomime-grasp PGAs for the 40.0 mm and 40.5 mm targets did not reliably differ and a TOST statistic indicated that values were within an equivalence boundary. Thus, null *and* equivalence tests indicate that the visual information mediating pantomime-grasps provides decreased resolution power for PGA/target-size scaling.

As briefly outlined in the Introduction, Goodale et al. (1994) had healthy controls complete natural and pantomime-grasps (i.e., memory-guided and spatially dissociated) to targets that were 25 mm, 35 mm and 50 mm in width and observed decreased PGA/target-size scaling in the former (see also Whitwell et al., 2015a). As well, Westwood et al. (2000) and Rinsma et al. (2017) had healthy participants complete natural and pantomime-grasps to targets embedded within fins-in and fins-out configurations of the Müller-Lyer illusion and the former employed targets that were 50 mm and 70 mm in width, whereas the latter employed targets that were 60 mm, 80 mm and 100 mm in width. In both experiments, natural grasp PGAs were mostly refractory to the illusion, whereas pantomime-grasps were biased in a direction consistent with the illusion's perceptual effects. In turn, work by our group has shown that natural and pantomime-grasps to targets 20, 30, 40 and 50 mm in width violate and adhere to, respectively, the psychophysical principles of Weber's law (Holmes et al., 2011; Manzone et al., 2017).

Accordingly, that pantomime-grasps show reduced PGA/target size scaling, are 'tricked' by pictorial illusions, and adhere to Weber's law evince the perceptual nature of the task and their mediation by relative visual information. In the present investigation, we propose that the null pantomime-grasp PGA/target size scaling provides convergent evidence of aperture shaping via relative information. What is more, we believe that our results add importantly to the literature insomuch as they provide the first direct evidence that the visual resolution power for pantomime-grasps is less than natural grasps. As indicated above, this issue has not been addressed given that the between-target size differences used previously ranged from 10 mm and 20 mm (see details above) and are magnitudes above the documented threshold for perceptual estimations of line length (Teghtsoonian, 1971).

We recognize that our study is limited by at least two important methodological traits. First, we employed only a single stimulus-set (i.e., 40.0 mm and 40.5 mm target and non/target) and thus we cannot conclude that the decreased resolution for pantomime-grasp PGAs extends across the continuum of 'graspable' target (and non-target) sizes. Further, the application of a single stimulus-set does not provide a means to determine whether the resolution findings for natural and pantomime-grasps reflect a between-condition difference in the neuromotor noise associated with aperture shaping (e.g., Sternand, Abe, Hu & Müller 2011). Second, terminal haptic feedback was available during natural but not pantomime-grasps and this was done so that the latter task matched that used in previous work (Goodale et al., 1994; Holmes et al., 2011; Westwood et al., 2000) and the extant apraxia literature (Liepmann, 1908). That said, we recognize the salience of this issue given work by our group and others showing that haptic feedback on trial N can – in some instances –support an absolute visuo-haptic calibration for trial N+1 and beyond (Bingham et al., 2007; Davarpanah Jazi & Heath, 2016; Heath et al., 2019;

Schenk, 2012; Whitwell et al., 2020). Based on the above, it would be interesting to determine whether a continuum of targets that differ by as little as 0.5 mm provide the requisite feedback for an absolute visuo-haptic calibration. Such an investigation would provide the combined benefit of identifying whether possible between-condition differences in neuromotor noise and/or haptic feedback contribute to the reduced resolution of pantomime-grasps.

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Footnote

1. Whitwell et al. (2015a) re-examined DF's data originally reported in Goodale et al. (1994) and reported that DF's PGA/target size slopes in spatially dissociated pantomime-grasps were not different from controls, whereas DF's memory-guided grasps reliably differed from controls. Based on these results it was argued that target vision provided in spatially dissociated pantomime-grasps permitted DF an opportunity to engage real time visuomotor networks to support the scaling of grip aperture to object size. That said, Figure 6 of Goodale et al. demonstrates that DF's trial-to-trial PGAs for spatially dissociated pantomime-grasps are greater than natural grasps, and Figure 2 of Whitwell et al., show that DF's PGA/target size slopes for spatially dissociated pantomime-grasps are less than counterpart natural grasps.

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Disclosure statement

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Figure Captions

1. Schematic of natural and pantomime-grasping (**Panel A**) and the timeline of visual and motor events for each trial (**Panel B**). For Panel B, the shaded grey rectangle in the line denoted by the "Vision" textbox indicates when the goggles were set to their translucent state. Once a stimulus-set was positioned, the goggles were set to their transparent state for the remainder of a trial and a 3000-4000 ms preview was initiated after which a tone (see textbox labelled "Imperative") served as the movement imperative. Subsequently, participants completed natural or pantomime-grasps (denoted via velocity profile in the "Grasp" textbox). The first velocity profile represents the response to the stimulus and the second represents a return to the start location.
2. Mean natural (circle symbols) and pantomime-grasp (P-Grasp: square symbols) grip aperture for an exemplar participant for the 40.0 mm (open symbols) and 40.5 mm (closed symbols) targets at decile increments of normalized grasping time. Error envelopes represent 95% confidence intervals. Natural grasps produced larger apertures than pantomime-grasps beyond ~30% of grasping time and showed an early aperture to target-size scaling.
3. Natural and pantomime-grasp (P-Grasp) group mean peak grip aperture (PGA: **Panel A**) and time to PGA (tPGA: **Panel B**) for the 40.0 mm and 40.5 mm targets. Error bars represent 95% within-participants confidence intervals computed via the mean-squared error term for the condition by target size interaction. The right panels show natural and pantomime-grasp PGA (**Panel C**) and tPGA (**Panel D**) target size difference scores (i.e., 40.5 mm minus 40.0 mm), respectively, for "Correct" and "Incorrect" perceptual judgments as well as the pooled difference score (see shaded grey region labelled "Overall). Error bars represent 95% between-participant

confidence intervals and the absence of overlap between a confidence interval and zero (i.e., the horizontal dashed line) represents a reliable effect inclusive to a test of the null hypothesis.

Figure 1

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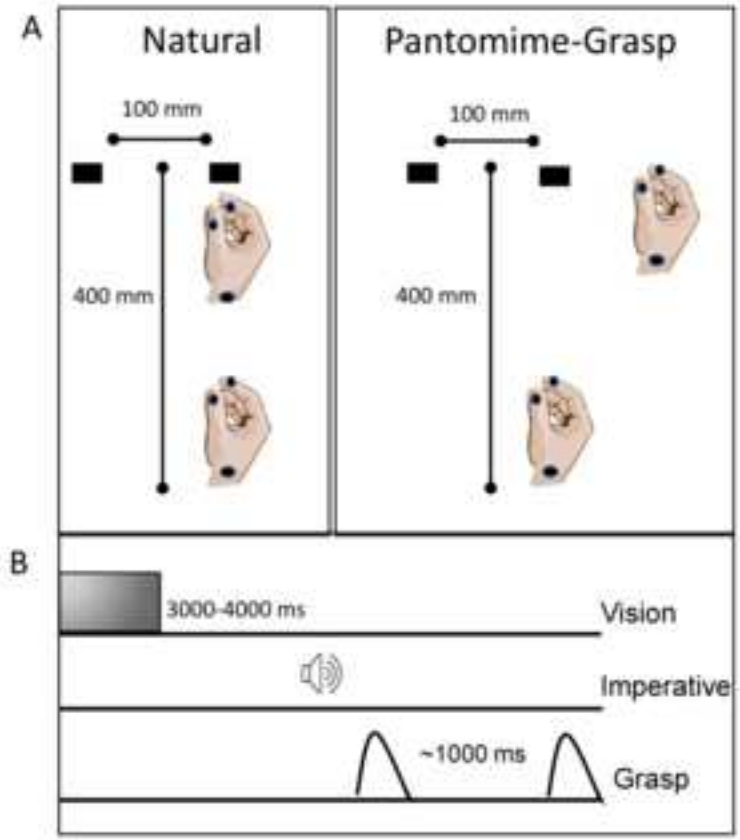

Figure 2

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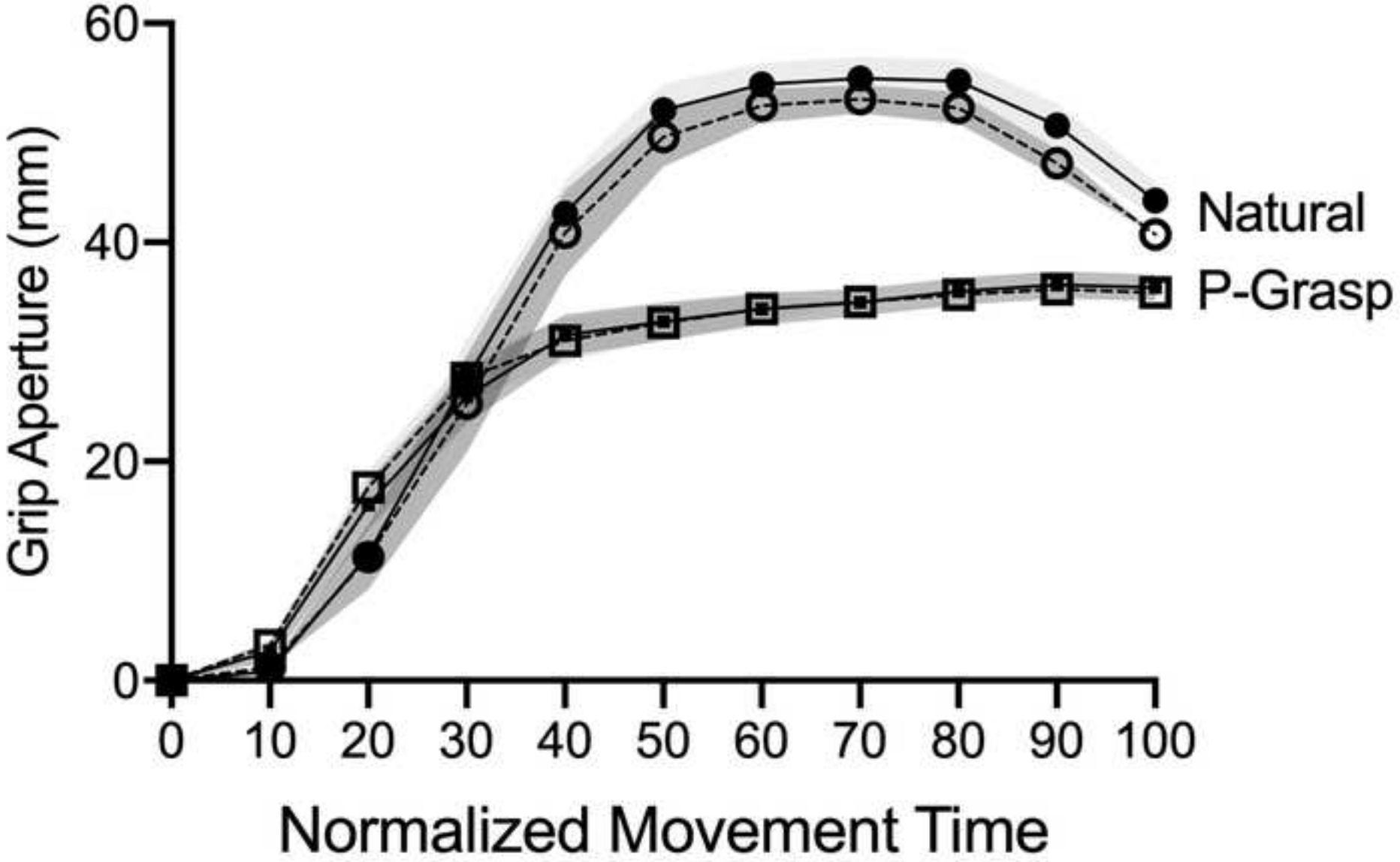

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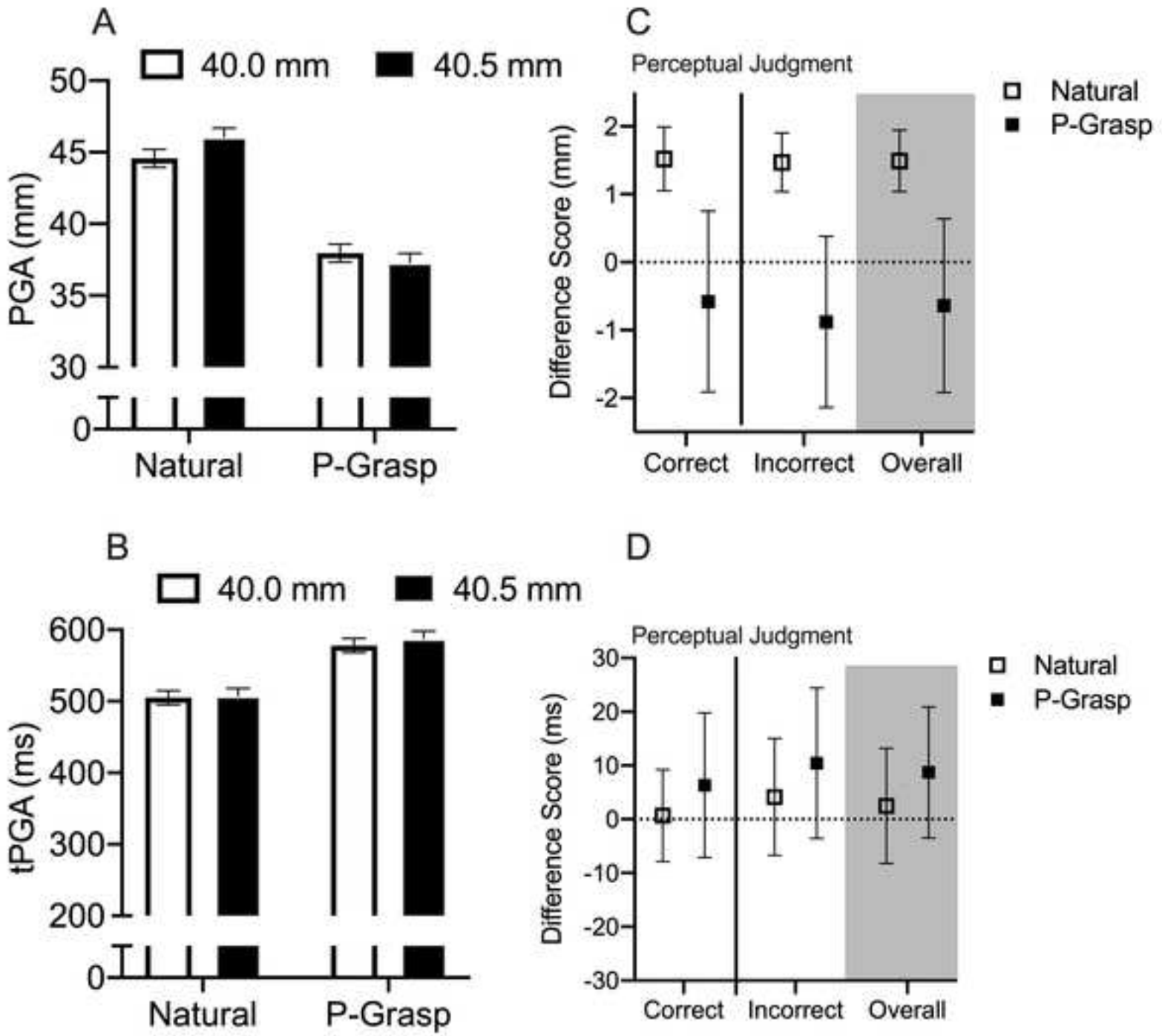
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