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Both vision-for-perception and vision-for-action follow Weber's law at small object sizes, but violate it at larger sizes

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Abstract

According to a previous report, the visual coding of size does not obey Weber's law when aimed at guiding a grasp (Ganel et al, 2008, Current Biology, 18, R599-601). This result has been interpreted as evidence for a fundamental difference between sensory processing in vision-for-perception, which needs to compress a wide range of physical objects to a restricted range of percepts, and vision-for-action when applied to the much narrower range of graspable and reachable objects. We compared finger aperture in a motor task (precision grip) and perceptual task (cross modal matching or "manual estimation" of the object's size). Crucially, we tested the whole range of graspable objects. We report that both grips and estimations clearly violate Weber's law with medium-to-large objects, but are essentially consistent with Weber's law with smaller objects. These results differ from previous characterizations of perception-action dissociations in the precision of representations of object size. Implications for current functional interpretations of the dorsal and ventral processing streams in the human visual system are discussed.

Introduction

Hands can be used to operate or they can be used to inform. For instance, we can reach for a small object and pick it up with two fingers. This is a performative action, and its goal is to change the state of the environment with respect to us. Alternatively, we might want to tell a friend about the object -- for instance, we might want to report its size. One way to do that would be to shape our two fingers to match the size of the object, and show the friend. This a communicative action, and its goal is to provide information about what we saw to someone who did not see what we saw. The distinction between performative and communicative actions was first introduced by Gibson (1966), who also discussed a third broad category, exploratory actions, which are beyond the scope of this paper.

Performative and communicative actions correspond to different motor functions. For this reason, it is natural to speculate that their brain basis might involve different forms of processing. This speculation was turned into a full-fledged model of the visual brain by Milner & Goodale (Milner and Goodale, 1995). In this paper, we investigate one specific prediction of this model, namely, that performative manual actions should not obey Weber's law (the psychophysical principle dictating that sensory precision decreases as stimulus intensity increases; see Gescheider, 1997), whereas communicative actions should. To this aim, we compared two actions that are both visually guided, use two fingers (the index and the thumb), and involve reaching out and opening the fingers. These correspond to the movements that were described in the previous paragraphs, and to the tasks that are commonly referred to as precision grip and manual estimation. Crucially, and in contrast with previous work, we examine the full range of potentially graspable objects from very small to close to the graspability limit. In both tasks, we observe non-Weber behavior with medium-to-large objects, but Weber-compatible behavior with smaller objects. These results have implications for the current debate on Milner & Goodale’s model.

Rationale for the current study

A large and controversial literature has been published on behavioral dissociations between vision-for-action and vision-for-perception over the last twenty years (see Bruno, 2001; Cardoso-Leite & Gorea, 2010; de'Sperati & Baud-Bovy 2008; Franz and Gegenfurtner, 2008; Schenk and Mcintosh, 2010; Schenk, Franz and Bruno, 2011; Smeets and Brenner, 2006). One especially provoking claim has been that the precision of vision-for-action remains essentially constant over changes in the size of stimuli (Ganel, Chajut and Algom, 2008), whereas the precision of vision-for-perception does not. Because this claim is the focus of the current paper, we start by analyzing it in detail.

Ganel and his colleagues presented objects of different sizes in two tasks. The first was a cross-modal match ("match the size of the object by the aperture of your index and thumb"), often called "manual estimation" (see Haffenden and Goodale, 1998). The second was a precision grip ("pick up the object by its length using the thumb and index fingers"). In both tasks, a measure of finger aperture was collected as the dependent variable of interest. In the estimation task, this was simply the matched finger aperture, which was assumed to reflect a "readout" of the internal representation of perceived size. In the grip task, it was the maximum in-flight grip aperture between the thumb and the finger. This is a much-studied kinematic marker of reach-to-grasp actions, and it is generally believed to reflect the representation of size that was computed from visual information before beginning the movement (Jeannerod, 1981; Marteniuk et al, 1987; Jeannerod, Arbib, Rizzolatti and Sakata, 1995). Ganel and colleagues reported that their observed pattern of variable errors (inverse of precision, as measured by the standard deviation of the distributions of the finger aperture data) was markedly different in the two tasks. In manual estimations, variable error grew with object size as one would expect from Weber's law. In precision grips, conversely, it remained constant over the tested range of sizes. Thus, Ganel and colleagues reported a striking dissociation between vision-for-action and vision-for-perception. They proposed that visual coding for a performative action violates Weber's law, a fundamental psychophysical principle, whereas visual coding for a communicative action adheres to this principle as is commonly observed in perception.

Ganel and colleagues proposed that their observed result reflects a key difference between visual functional modules. Because vision-for-perception operates over a wide range of physical distances and sizes, scaling is needed to compress such wide range into a narrower range of percepts. Thus, scaling laws apply as they do in many other cognitive tasks (Chater & Brown, 1999, Kello, 2010). Conversely, vision-for-action operates on restricted ranges that are defined by the action possibilities of effectors. For instance, grasping actions can be performed only on graspable objects in near space. Therefore, there is no need for a compressing mechanism and scaling laws do not apply. This interpretation is very much in accord with the functional characterization of the higher-level primate visual system proposed by Milner & Goodale (Milner and Goodale, 1995; for recent reviews, see Goodale and Westwood, 2004; Goodale, 2008; 2010; Goodale and Milner, 2008). Milner & Goodale's model, which identifies vision-for-action with the dorsal stream from primary visual (V1) to posterior parietal (PPT) cortex, and vision-for-perception with the ventral stream from V1 to the inferotemporal (IT) cortex , indeed proposes that the visual codings of spatial properties in the two functional modules obey different principles, resulting in context-sensitive, object-relative representations in perception but in context-blind, effector-relative representations in action. Such different spatial coding might well result in different patterns of precision, and for this reason Ganel's result has been often cited as key evidence in support of Milner & Goodale's model (see Westwood and Goodale, 2011).

Although Ganel's findings are in accord with Milner and Goodale's model, other explanations are possible. For instance, it is possible to model grasping as coarticulation of two pointing movements (one for each finger) aimed at the chosen contact points on the object (Smeets & Brenner, 1999). Within this model, no internal representation of size is used to control the grasp. Therefore, there is no reason to expect effects on the variability of the finger aperture. In a reanalysis of Ganel's initially reported data, Smeets & Brenner (2008) argued that the grasping-as-double-pointing model can predict Ganel's data. In a rebuttal paper, however, Ganel, Chajut, Tanzer and Algom (2008) argued that Smeets & Brenner's alternative model only applies to closed-loop grasping, namely, to an action performed with full visual information during execution. Ganel's original data were based on a closed-loop grasping task. In their rebuttal paper, however, Ganel and colleagues used an open-loop grasping procedure, and showed that even in these conditions the variable error was constant over a range object sizes. The open-loop procedure involved removing visual information as soon as the action started, thereby preventing any on-line adjustment of the finger trajectories during the grasp and forcing participants to use the visual information that had been acquired before beginning the movement.

We stress that only open-loop data can provide evidence supporting a perception-action dissociation between perception and action visual modules. Under closed-loop conditions, on-line adjustments can be performed on the basis of visual and motor feedback, modifying earlier spatial representations that were computed before starting to move. The influence of these adjustments will depend on the speed of the movement, with more ballistic movements being less affected in comparison to slow movements. Other things being equal, it could be argued that violations of Weber's law might occurr in these conditions because of these on-line adjustments, which are based on feedback loops. This argument has received some empirical support (Heath et al, 2011; but see Foster & Franz, 2013). For this reason, it is critical to examine visuomotor and perceptual precisions under similar open-loop conditions.

Yet another possible explanation has been advanced in a recent paper by Utz et al (2015). In a series of open-loop grasping experiments, Utz and colleagues observed that variable errors did not remain constant as observed by Ganel but decreased as the size of the target object increased. They interpreted this finding as evidence that a biomechanical factor, in addition to sensory factors, affects finger aperture in grasping. Suppose the desired maximum finger aperture as a function of object size depends on the size of the object, plus a random error that can be more or less than the "true" desired finger aperture. As objects get bigger and approach the maximum graspable object for a given participant, a random error in excess of the true value will become increasingly unlikely, whereas a random error in defect of the true value will remain unaffected. Thus, this sort of ceiling effect will increasingly reduce the variability of finger apertures as object size increases, and this is exactly what was observed by Utz and collaborators. This interpretation deserves to be taken seriously. However, the data provided by Utz et al (2015) leave several issues unresolved.

Firstly, Utz et al observed a “reverse Weber law” pattern when using interquartile ranges to estimate variable error, but this was less clear (although qualitatively in accord with reverse Weber) when using standard deviations. A plausible explanation for this is that standard deviations are not robust estimators; they are affected by the presence of outliers and by distributional asymmetries. This might explain why Ganel and colleagues observed more-or-less constant variable errors (measured as standard deviations) as a function of object size. Interquartile ranges instead are robust estimators which are less affected by outliers and distributional asymmetries, and this is presumably a reason why the interquartile ranges of Utz and colleagues showed a clearer pattern.

Second, the open-loop procedure used by Utz and colleagues involved a mirror apparatus that allowed participants to see the target object continuously but did not allow them to see their hands. This is different from the procedure employed by Ganel et al, which involved occluding spectacles to remove vision of both target and hand at movement initiation (for a discussion of the effects of these subtle differences in visual feedback during reaching and grasping, see Bruno, Bernardis & Gentilucci, 2008; Bruno & Franz, 2009). To validate the proposed interpretation of Ganel’s data, it is necessary to collect precision data using a fully comparable open-loop procedure.

Third, Utz et al (2015) performed several elegant manipulations of the conditions for performing precision grips but did not include a condition tapping into explicit visual processing as comparison. This comparison would be especially informative as the key theoretical prediction is a dissociation between two tasks.

Fourth, we note that the studies of Utz et al, Ganel et al, and indeed most studies of precision grips (see for instance the meta-analysis in Smeets & Brenner, 1999) collected data for object widths in the range between 20 and 70 mm: We are aware of only two experiments (Marteniuk et al, 1990; Hesse & Franz, 2009) that included 10 mm widths. The choice of this range is justified by the fact that this appears to be, under informal observation, a range of sizes that allows for natural, comfortable grasping by most participants. However, most of us (depending on the size of one's hand) can perform a two-finger grip with objects as wide as 120 - 150 mm, although with increasing difficulty. And even more notably, we can readily grasp objects smaller than a 20mm width. In animal studies, recordings of "precision grip" motor neurons are typically performed in monkeys that pick up and bring to the mouth quite small food items, such as raisins or pine nuts. Although this is probably not a serious limitation when interested in the actual magnitude of the finger apertures, it becomes relevant when interested in studying errors, because very small objects, being farther away from graspability limits, should provide data that are most free from ceiling effects.

Specific objectives and predictions

The above-listed considerations motivate our study. Specifically, we seek to do three things. First, we are interested in evaluating how vision-for-action might violate Weber's law. In particular, we want to determine whether the precision of maximum grip aperture is constant over different object sizes, as suggested by Ganel and collaborators, or rather increases with object size as suggested by Utz and collaborators. Second, we are interested in comparing the pattern of precision in the action task with that observed in a perception task, the manual estimation task that was also studied by Ganel and collaborators. Third, we seek to evaluate to what extent violations of Weber's law, if applicable, depend on biomechanical constraints as opposed to properties of the visual coding of size.

Methods

Participants

We recruited 14 volunteers (7 females, age range 21- 46) from the University of Parma community. All were right-handed, had normal or corrected-to-normal eyesight, no history of neurological disease, and were unaware of the purpose of the study.

Tasks

We compared two tasks. The first task (open loop precision grip, OLPG) consisted in grasping disks of variable diameters with the thumb and finger of the right hand. Visual information was removed as soon as the grasping movement started, such that the grasp was completed based on what had been visually processed before the initiation of the movement. Once the participant had grasped the disk, he or she was required to lift it, move the hand sideways to the right by approximately 10 cm, and then rest the disk again on the table. The second task (open loop manual estimation, OLME) consisted in matching the visible size of the disks by opening the thumb and index fingers, while keeping the hand near to the body. As for the OLPG task, visual information was removed as soon as the matching movement began. After recording the match, the participant was also similarly required to reach for the disk, grasp it and move it sideways. This insured that participants received equal amounts of information from actually touching the object with the hand in both conditions.

Apparatus

The target disks were a series of six custom-made wooden disk, each 1 cm high, having diameters ranging from very small to very large: 5, 10, 20, 40, 80, and 120 mm. Participants sat on an adjustable chair in front of the short side of a small (45 x 100 cm) rectangular table. A button box was placed on the table in front of the participant. A faint cross-mark drawn on the table marked the position for the target disks. The center of the cross mark was placed at exactly 23 cm from the edge of the table (approximately 20 cm from the starting button, corresponding to a viewing distance of approximately 50 cm). Visual feedback was removed using PLATO visual occlusion spectacles (Translucent Technologies Inc.) which have a transparent-to-opaque latency of 3-4ms. Response kinematics were recorded using a Qualysis ProReflex MCU1000 (sampling rate 240 Hz, spatial precision at least 0.4 mm with four cameras at distances of 1 to 2 m from the participant hand) using three markers (one on the wrist, one on the tip of index finger, and one on the tip of the thumb). A personal computer running MatLab R2011b under Windows 7 was used to control stimulus presentation and to manage trigger signals to the Plato spectacles and the Qualysis motion tracking system.

Design

The design resulted from crossing two within-participant independent variables: disk diameter (six levels, see previous section) and task (OLPG and OLME). Tasks were performed in two separate blocks which were randomized between participants. Order was counterbalanced across participants. Disk diameters were randomized within each block. The presentation of each diameter was repeated 20 times, resulting in a total of 240 (120/block) trials. In each trial, the dependent variable consisted in a measure of the index-thumb aperture, taken in the manner appropriate to the task. In the OLPG task, this was the maximum in-flight grip aperture (MGA) between the thumb and index. In the OLME, this was simply the aperture of the thumb and index as shown by the participant to match the disk diameter.

Procedure

Each block began with a brief verbal and motor explanation of the task, followed by five practice trials using randomly chosen diameters. Practice trials were not recorded. The structure of each trial in the two tasks is schematized in Figure 1. Up to a point the procedure was the same for the two tasks. At the beginning of each trial, the shutter spectacles were turned off (opaque). The experimenter read off the MatLab on-screen console the disk diameter for the current trial, placed the appropriate disk on a preset mark in front of the participant, and verbally gave a go signal. At this point, the participant pressed a key on a button box to turn on the shutter spectacles (transparent), observed the target disk as long as needed (typical preview periods were of the order of 500ms), and then released the button by lifting the hand to initiate the response. The button release turned off again the shutter spectacles (opaque). From now on, there were some slight differences in the procedure according to task. In the OLPG task, the button release also triggered the kinematic recording. The system recorded for 3 seconds, giving the participant ample time to grasp the disk and complete the trial. In the OLME task, the button release did not trigger recording but merely turned off the goggles. The participant performed the match by opening the fingers as deemed appropriate, then pressed a second button with the left hand to record the response. It was this second button press that triggered the system, which in this case recorded for only 0.1 seconds. Once recording was complete, a computer-generated beep informed the participant that he or she could bring the hand back to the starting position on the button box. If an error occurred for whatever reason, the experimenter recorded the conditions of the relevant trial. All trials classified as errors were repeated in random order at the end of the block.

< insert figure 1 about here >

Data validation and analysis

Recordings from all trials of all participants were analyzed off-line firstly to check for errors that may have escaped the experimenters' attention during runs. Given that no obvious mistakes were identified in this first stage, all recordings were further analyzed to compute maximum grip aperture, in the OLPG condition, and manual estimation, in the OLME condition. This analysis was performed by means of R scripts which allowed visualizing finger trajectories, velocity profiles, and thumb-index apertures as a function of time to double-check computations. In the OLPG condition, the maximum grip aperture could be reliably found by computing MAX(finger aperture) within the initial 1000 ms of the response. In the OLME condition, finger aperture was computed as the average aperture within the recorded 100 ms. Finally, the aperture data for each participant in each task as a function of disk diameter were screened individually for outliers. Outliers were defined as observations larger (smaller) than the third (first) quartile plus (minus) 3 times the interquartile range. These values correspond to datapoints depicted as "extreme" in a Tukey box plot (Tukey, 1977; McGill, Tukey & Larsen, 1978). All responses identified as such were removed from that individual set. This resulted in the exclusion of 24/1680 grips and of 9/1680 manual estimations in total. All statistics used in further analyses were therefore computed on these outlier-free individual sets (for further details see Appendix).

Results

Figure 2 presents finger aperture data in the OLPG (grip) and OLME (estimation) tasks. In OLPG, these correspond to the maximum in-flight index-thumb aperture before grasping each disk; in OLME, to the index-thumb aperture matching the perceived size of each disk. We display arithmetic mean apertures for each participant in each task at each level of disk diameter, as well as group arithmetic means at each level of disk diameter.

< insert figure 2 about here >

In both tasks, finger aperture was an approximately linear function of disk size. Given the within-participant design of our study, we measured the average trend by first fitting linear regressions individually to each participant in each condition, computing the average slope and intercept from the individual fits, and then plotting line with these average slope and intercept. Interval estimates (confidence level = 0.95) of slopes and intercept were 0.75 +- 0.05 mm/mm and 37.8 +- 5 mm in the OLPG task; 0.88 +- 0.04 mm/mm and 9.1 +- 3.2 mm in the OLME task. One sample t-tests indicated that both parameters were significantly different from zero in both tasks, OLPG slope: $t(13) = 33.6$, $p < 0.001$; OLPG intercept: $t(13) =16.4$, $p < 0.001$; OLME slope: $t(13) = 41.8$, $p < 0.001$; OLME intercept: $t(13) = 6$, $p < 0.001$. A paired t-test indicated that the OLME slope was significantly larger than the OLPG slope, $t(13) = 5.7$, $p < 0.001$.

Figure 3 presents the variable error data, based on robust estimates of each participant's standard deviation (see Appendix) in each task at each level of disk diameter.

< insert figure 3 about here >

To subject the variable error data to statistical analysis, we did two things. First, the OLPG and OLME datasets were entered jointly into a 2 (task) x 6 (size) repeated-measures ANOVA. This analysis revealed a significant main effect of size, $F(5, 65) = 13.7$, $p < 0.001$, and a significant task X size interaction, $F(5, 65) = 31.4$, $p < 0.001$, whereas the main effect of the task failed to reach statistical significance, $F(1, 13) = 3.6$, $p = 0.080$. As a second step in the analysis, we noted that in both conditions the pattern of variable errors may be characterized as an initial increase at small disk sizes, followed by a reduction or tapering off. To model this behavior, we applied two-component piecewise linear spline regressions (see Lundgren, 2007) to the OLPG and OLME data. This is equivalent to fitting a multiple regression model with three parameters (one intercept and two slopes), constrained such that a change of slope occurs at a predetermined value (the “knot”) of the independent variable. The knot is chosen, before performing the analysis, on the basis of the apparent structure of the data and the model’s residuals at different plausible values (see Harrell, 2015). Our chosen knot values were 20 mm for the OLPG dataset and 40 mm for the OLME dataset. The model was fitted individually to the data from each participant. Group average parameters were then used to plot the model results in Figure 3. One-sample t-tests confirmed that initial slopes were statistically different from zero in both conditions (OLPG: initial slope = 0.064, $t(13) = 2.544$, $p = 0.024$; OLME: initial slope = 0.136, $t(13) = 9.861$, $p < 0.001$) and that the second slope was different from zero in the OLPG group (second slope = -0.025, $t(13) = -7.012$, $p < 0.001$) but not in the OLME group (second slope = 0.004, $t(13) = 0.295$, $p = 0.772$). Thus, these analyses confirmed that at small object sizes variable errors increased in both groups. In addition, paired t-tests comparing initial parameters across the two conditions failed to provide evidence for a difference in the initial slope ($t(13) = 2.159$, $p = 0.050$) or in the second slope ($t(13) = 2.082$, $p = 0.058$) in the OLME condition relative to the OLPG condition.

< insert Figure 4 about here >

Figure 4, finally, presents measures of distributional asymmetry (skewness), again in the individual data as well as condition averages. In the OLPG task, the effect of object diameter on skewness failed to reach significance, $F(5, 65) = 1.9$, $p = 0.090$. In the OLME task, conversely, there was evidence for a significant effect, $F(5, 65) = 3.138$, $p = 0.013$.

After submission of the present paper, one reviewer suggested that we compare our results with previous estimates of variable error. Estimates of variable error in grasps were reported in three earlier papers (Ganel, Chajut & Algom, 2008; Ganel, Chajut, Tanzer & Algom, 2008; Utz et al, 2015). Of these, the first reported data from a closed-loop grasping task (vision remained available during movement) which is fundamentally different from our open-loop task (see Introduction). The second and third did report data from open-loop tasks and these are compared with ours in Figure 5. The comparison requires additional caution. While the apparatus and procedure employed by Ganel et al (2014) were similar to ours, those employed by Utz et (2015) involved a mirror apparatus that was markedly different from Ganel’s or ours. In addition, Ganel's reported data are averages of non-robust estimates (ordinary standard deviations), whereas Utz’s data included both robust nonparametric estimates (interquartile ranges) and non-robust estimates (ordinary standard deviations). Given these differences, the absolute values of the variable error are likely to be not completely comparable across the three studies. Absolute values aside, inspecting the patterns of variable error displayed in Figure 5 suggests that our observed decrease in variable error is similar, within comparable ranges of object sizes, to those observed by Utz et al. The pattern reported by Ganel et al, on the other hand, does not show a similar negative trend.

Discussion

We compared a perception and an action task using a standard open-loop procedure, testing the whole range of graspable objects from very small (5 mm) to almost beyond the graspability limit for most of us (120 mm). Observed finger apertures in both tasks were nicely consistent with previous estimates (for a meta-analysis on precision grips, see Smeets & Brenner, 1999; for a discussion of differences with manual estimates, see Schenk, Franz & Bruno, 2011). In contrast with previous reports, however, in our action task we did not observe constant (Ganel, Chajut & Algom, 2008), or constantly decreasing variable errors (Utz et al, 2015). Rather, our results suggest that variable errors in both perception and action increase as a function of object size with relatively small objects, and then decrease or taper off. We will first review our evidence for these two claims, and then move on to a proposed interpretation.

Support for the idea that in both tasks variable errors increase at small sizes is provided by the qualitative pattern in Figure 3, as well by tests revealing that in both conditions slopes fitted to the first half of the data are significantly different from zero. While this trend seems evident, it remains less clear whether OLPG and OLME slopes, in addition to being both different from zero, also differ from each other. Although we did measure somewhat different average trends in Figure 3, this difference failed to reach statistical significance. Technically, therefore, it seems correct to interpret the current results as i) evidence that there is a Weber-like effect on variable errors at smaller object sizes, and ii) lack of evidence that this effect is different in perception and action. However, this interpretation requires caution, as statistical tests may suffer from insufficient power to detect a small difference between OLPG and OLME. Either way, it seems justifiable to claim that our results are consistent with similar or at least not-too-dissimilar Weber-like effects at small object sizes. We note further that, even if the two slopes were indeed slightly different, this would not necessarily damage our key claim that variable errors at small sizes follow Weber's law in both perception and action. There can be many reasons why errors might increase at different rates in the OLPG and OLME data as the tasks were not completely equivalent in terms of hand movement. Lacking evidence that one of the slopes might be zero or negative, our conclusion still stands.

Support for the idea that variable errors decrease or taper off once size reaches a certain value is also provided by the qualitative pattern in Figure 3, as well as by statistical analyses suggesting that both changes in slopes after the critical size value are statistically different from zero, but cannot be distinguished statistically from each other. Although a caveat about statistical power is appropriate also regarding this last claim, it seems nonetheless appropriate to conclude that the second half of our data demonstrate that the Weber-like effect at small sizes is counteracted, at medium and larger sizes, by some other factor that tends to reduce variable error.

A likely candidate factor accounting for the reduction of variable error at medium to large sizes is hand biomechanics. As the physical size of an object approaches the limit size that one’s hand can grasp, a ceiling is effectively placed on variable errors in excess of the targeted finger aperture. Thus, variable error is increasingly reduced as size increases. This hypothesis was first advanced by Utz et al (2015) who measured variable errors over the 20 -70 mm range and observed a regular decrease. Our data are nicely consistent with Utz’s observations in that they also suggest a progressive reduction of variable error starting at 20mm and extending to the 80 and 120mm objects, where the reduction is maximum as one would expect. Our results however also go beyond Utz's data in that they show that hand biomechanics may have an effect also on manual estimations, although in this case, at least in our data, a tapering off of variable error appears to occurr after size reaches 40mm rather than 20mm.

An important difference between the two tasks is related to the motor strategies involved in emitting the manual response. In a precision grip, absolute values of maximum in-flight apertures are always much larger than the physical size of the target object (see, for instance, Smeets & Brenner, 1999). It is generally agreed that this feature of precision grips reflects a key component of grasping actions. Grasps are typically performed in two stages: in the initial, fast stage, the hand accelerates and the fingers open progressively until the peak velocity is reached somewhere near the target. At this point, the hand slows down and a second, control stage begins whereby the fingers close to make contact on the object. Given random noise, if the maximum aperture were programmed to approximately equate the size of the object, in many trials the maximum aperture would be insufficient to initiate the closing stage and the fingers would have to be opened again, such that the resulting movement would be inefficient and cumbersome. A more efficient strategy, therefore, is to open the fingers much more than the target size, allowing a "safety margin". Thus constant error in grips are the sum of two components: a constant safety margin (the intercept in the linear fit) and a scaling component that depends on size (the slope of the linear fit). Because of the safety margin, the physical limit of the hand is not too far even when responding to medium sizes. In a manual estimation, conversely, constant error depends solely on a scaling component (the intercept of the linear fit is expected to be close to zero). For this reason, the physical limit is approached more slowly as size increases, but apparently becomes relevant even in manual estimations once size is large enough.

A plausible interpretation of our results is that, in both perception and action, the representation of size that drives the response behaves in accord with Weber's law, yielding approximately linear increases of variable error at small sizes. As size grows due to hand biomechanics variable errors are then increasingly reduced, causing the pattern to turn downward. There is however a final feature of our data suggesting that hand biomechanics may not be the only factor at play, especially in precision grips. Given that the biomechanical explanation entails an upper ceiling on variable errors, a key prediction of this proposal is that variable error distributions should be increasingly compressed on the high end of the distribution; i.e., they should “morph” from approximately symmetrical to left-tailed, such that their skewness becomes increasingly negative as size increases. In our final analysis, however, we failed to observe a clear trend of distributional skewnesses from zero to negative. Instead (Figure 4), in both tasks skewness remained essentially zero at small to medium sizes, and became only very slightly negative at larger sizes. In the action task, this pattern failed to reach statistical significance, suggesting that the skewness data are not actually consistent with a biomechanical explanation. In the perception task, conversely, we found statistical support for a change in skewness between responses to large and small objects. This suggests that biomechanics might affect manual estimations more clearly than they do grips.

Thus, the current results suggest that, in the action task, the pattern observed with larger sizes may not be completely ascribable to biomechanics. We propose that an additional factor may involve a motor strategy relating to the selection of a precision-accuracy tradeoff. Recall that, in grips, the role of adopting a safety margin is to free the system from having to compute a very precise maximum aperture. The task of precisely guiding the fingers near the appropriate contact points can be left to the slower second phase that can be controlled online based on sensory feedback or on feedforward predictive models (Desmurget & Grafton, 2000; Wolpert, 1997). As objects get larger, however, possible safety margins become inadequate. To avoid undershooting the target size and therefore preserve the efficiency of the movement, the system might now opt to compute a more precise maximum aperture. If this were the case, one would expect to observe a reduction of variable error with larger objects, but not necessarily a change in skewness as the reduction is strategic and not merely a byproduct of an upper ceiling on random variations. While this hypothesis remains speculative (and post-hoc) at present, empirical tests are possible by manipulations enforcing accuracy-precision tradeoffs. Such tests may well be worth performing in future studies.

Conclusions

Our results have implications for current functional models of vision-for-action and vision-for-perception. According to an earlier proposal (Ganel et al, 2008), the precision of the internal representation of object size which is utilized by vision-for-action does not obey Weber's law. Our results with larger target objects do support this conclusion, but our results with smaller target objects do not. Instead, it seems that precision grips do obey Weber's law, but the Weber effect is increasingly counteracted by biomechanics or, possibly, by task-related changes in motor strategic programming, as object size increases. The combination of these two effects produces an increasing pattern in variable errors at small sizes, but a decreasing or tapering pattern at larger sizes. In this, vision-for-action tasks appear to differ from otherwise comparable vision-for-perception tasks, which may reflect a similar strategic change. Thus, we report a dissociation between perception and action. However, we suggest that this is not related to differences in the sensory coding of size (as predicted by the model of Milner & Goodale, 1995) but to different effects of biomechanical or possibly strategic factors.

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Appendix

To estimate variable errors in our data, we used standard deviations that were computed after removing extreme outliers. Extreme outliers were defined as observations less or more than 3 times the interquartile range from the first or third quartile (that is, as the datapoints marked as asterisks in a Tukey box plot; see Tukey, 1977; McGill, Tukey & Larsen, 1978). This procedure provides a method for computing robust estimates of standard deviations. The advantage lies in the possibility of applying parametric methods for statistical inference as we do in the present paper. This procedure however might be questioned on two grounds: i) the criterion for identifying outliers could be questioned; ii) other methods for computing robust estimates could be used; for instance, Utz et al (2015) compared standard deviations to interquartile ranges.

To verify how our suggested method compares with other possibilities, we computed alternative robust measures of spread and compared them with standard deviations computed on the full dataset (that is, before removing outliers). The robust measures we considered are the interquartile range (IQR), the median absolute deviation (MAD), and the standard deviation after removing outliers (the measure of variable error plotted in Figure 2). Although the IQR is more resistant than a simple standard deviation to outliers as it is based on the central 50% of the data, it is unclear whether it provides the best estimate of variable error. Furthermore, parametric methods for statistical inference may not be fully applicable (Huber, 1981). The MAD is generally considered the most robust estimator of spread (Tukey, 1977). As for the IQR, however, it is not clear how parametric methods could be applied for statistical inference.

< insert Figure A1 about here >

The results of the comparison are presented in Figure A1. The pattern, as well as the absolute values, of the standard deviations once outliers are removed is very similar to that of the MAD’s. The IQR’s also show the same pattern but tend to yield larger estimates. Standard deviations computed on all the data, conversely, fail to fully capture the pattern exhibited by robust estimators, especially at very large disk diameters, although they remain roughly consistent with it.

Figure Captions

Figure 1. Trial structure in the two tasks that were compared in the study: Open-Loop Precision Grip (OLPG) and Open-Loop Manual Estimation (OLME).

Figure 2. Average finger aperture as a function of disk diameter in the OLPG (left) and OLME (right) tasks. Dotted light grey lines: individual averages. Solid black line: line obtained by fitting linear regressions individually to each of the 14 participants, and then plotting the line with the average slope and average intercept from the 14 fits. Filled black circles: averages of individual data at each of the 6 diameter levels. Error bars: sem. Dashed black line: y = x baseline.

Figure 3. Average variable error (standard deviations) as a function of disk diameter in the OLPG and OLME tasks. All plotting conventions as in Figure 2. The solid black lines were obtained by applying linear spline regression individually to each of the 14 participants, and then plotting the two lines using the averages of the spline parameters from the 14 fits.

Figure 4. Average skewness as a function of disk diameter in the OLPG and OLME tasks. All plotting conventions as in Figure 2.

Figure 5. Variable error estimates in our study (solid black line) and in the two previous studies that reported comparable assessments. Blue line: average standard deviations from Ganel, Chajut, Tanzer & Algom (2008), Figure 1. Red dotted line: average standard deviations from Utz et al (2015), Figure 3, Task 1. Red dashed line: average interquartile ranges from Utz et al (2015), Figure 3, Task 1.

Figure A1. Comparing four estimators of variable error. Dotted lines refer to the OLPG data, whereas solid lines refer to the OLME data. Ordinary standard deviations are plotted in blue as a thick line for reference. The three robust estimators are plotted as thin lines and are labelled by color: the red thin lines are the IQR’s; the green lines are the MAD’s; the black lines, finally, are the standard deviations computed after removing extreme outliers (that is, the variable errors plotted in Figure 3).