

Biomechanical factors may explain why grasping violates Weber's law

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Abstract

For grasping, Ganel, Chajut, and Algom(2008) demonstrated that the variability of the maximum grip aperture (MGA) does not increase with the size of the target object. This seems to violate Weber's law, a fundamental law of psychophysics. They concluded that the visual representations guiding grasping are distinct from representations used for perceptual judgments. Weber's law is however only relevant for one component of the measurable variability of MGA, namely the variability in the sensory system. We argue that when looking at the relationship between object size and grasping, the gain (often called slope) governing the relationship between target size and MGA can be used as an approximation to estimate the contribution of sensory noise to MGA variability. To test the idea that differences in gain modulate the relationship between target size and MGA variability, we examined grasping under a variety of conditions. We found that gain varied quite significantly across different tasks, but irrespective of gain Weber's law could not be found in any of the grasping tasks. Instead we repeatedly found an inverse relationship between variability and object size, i.e. variability decreased for bigger objects. This trend may reflect the reduced biomechanical freedom found for movements at the end of an effector's effective range of motion. MGA variability may thus be dominated by non-sensory factors and therefore may constitute a poor choice to estimate the variability of the visual signals used by the brain to guide our grasping actions.

Key words: Action, perception, grasping, Weber's law, haptic, slope, biomechanical

1. Introduction

When we grasp objects, we adjust the opening of our hand to the size of the object to be grasped. A common measure of the anticipated size of the object is the maximum grip aperture (MGA) which is the maximal distance between index finger and thumb during the grasping movement (Jeannerod, 1984, 1986). Ganel, Chajut, and Algom (2008) investigated the influence of object size on the MGA in grasping and compared it to its influence on perceptual judgments. The perceptual tasks included a visual adjustment task in which participants were asked to adjust the length of a visual stimulus presented on a computer screen to the length of a target object, and a manual estimation task in which participants had to indicate object size by the opening between index finger and thumb. Ganel et al. found that the “just noticeable difference (JND)”, indicating the smallest quantity of a change in stimulus intensity that causes a noticeable change in sensation, increased with the object size for both the visual adjustment and manual estimation task in accordance to Weber’s law. Weber’s law describes a fundamental psycho-physical law underlying human perception, namely that in all sensory domains the JND is a constant ratio of the stimulus intensity. In other words, the JND increases for larger stimulus magnitudes. In contrast, when participants were asked to grasp objects varying in size, Ganel et al. observed that the JND, measured as standard deviation of the MGA, remained relatively stable over all object sizes, therefore contradicting Weber’s law. The authors concluded that physical size is represented differentially for action and perception, which is in accordance with the perception-action model (Goodale, 2011). Within the perception-action model, formulated by Milner and Goodale (1995, 2006), it is supposed that the visual system is separated in two different sub-systems or streams. According to this view, the dorsal stream mediates visually-guided actions and represents the actual size of objects in relation to the body (egocentrically), whereas the ventral stream subserves visual perception and processes size and location of an object in relation to other objects (allocentrically).

While the perception-action model provides one possible account for the failure of grasping to conform to Weber’s law, other accounts have also been offered. Smeets and Brenner (2008) argued that for grasping grip positions, not object sizes, are computed (see their model on grasping described in Smeets & Brenner, 1999). If size is not used in the visual control of grasping then there is no reason to assume that the noise of the visual signal for size should dictate the variability of the hand-opening.

In this study we aim to test yet another alternative account. Similarly as Smeets and Brenner (2008), we want to test an alternative explanation of Ganel et al.'s findings (Ganel, Chajut, & Algom, 2008) that does not require the assumption that perception and action use distinct visual representations. We start with the observation that the failure to find a linear relationship between object size and the variability of the MGA is only surprising if we assume that MGA variability directly and primarily reflects the precision with which visual size can be discriminated. However, it is very likely that MGA variability is a compound measure to which a number of noise sources contribute, for example sensory noise, biomechanical factors and neuromuscular noise. Weber's law determines only the relationship between object size and that part of the sensory noise that is related to the visual signal for the target size. In grasping, other sources of noise contribute to the final variability of the MGA and may thus cancel out the effect of object size on sensory noise. Following this reasoning, we might expect to observe Weber's law for grasping tasks in which noise in the visual system forms a large part of MGA variability but not for grasping in conditions in which this visual noise contributes only in a minor way to MGA variability. To identify tasks in which visual noise is a crucial factor in MGA variability we need to find conditions in which changes in represented visual size are faithfully reflected in corresponding changes in MGA. The underlying assumption is that when a large change of visual size has only minor effects on MGA, large visual errors will also make only a minor contribution to MGA-variability. Conversely, if large changes of visual size produce large changes in MGA, large visual errors will have a substantial impact on MGA-variability under the assumption that the contribution of other non-visual sources of variability remain roughly the same. In summary, when the slope of the function relating visual size and MGA is shallow, we expect that Weber's Law-induced increases in variability of visual size will be harder to detect than when the slope of this function is steeper. Since we cannot easily measure the representation of an object's size in the brain's visual system, it is difficult to determine the slope of the above transformation function. However, we can use the slope of the function relating physical size and grip aperture as a rough estimate for the slope relating represented visual size and MGA (Franz & Gegenfurtner, 2008). We can then predict that grasping tasks that are associated with steep slopes are more likely to display a Weber's law-like relationship between object size and MGA variability than tasks with shallow slopes.

In fact, we can extend this concept beyond grasping and also include behavioural measures which are obtained in perceptual tasks, such as manual estimation and visual adjustment tasks (Franz

& Gegenfurtner, 2008). At the moment the evidence for this hypothesis is mixed with some findings supporting our hypothesis and others disagreeing with it. For example, reviewing the literature seems to suggest that the slope-values for classical grasping (slope: 0.8 [Smeets & Brenner, 1999]) are smaller than those for visual adjustment (slope: 1.0 [Franz, 2003]) or manual estimation (slope: 1.6 [Franz, 2003]; 1.85 [Haffenden, Schiff, & Goodale, 2001]). Given that Weber's law is found for adjustment and estimation tasks but not for grasping, these findings on slope seem to support the predicted trend of finding Weber's law primarily in tasks with larger slopes. However, not all studies are in agreement with our prediction. In a series of studies by Heath and colleagues, JNDs were examined in different grasping and size-estimation tasks. With respect to our hypothesis, mixed results were obtained. Holmes et al., (2013) found that pantomime grasping but not classical grasping obeyed Weber's law. However, in contradiction to our hypothesis, the observed grip-aperture-size slopes were of comparable size in both tasks. Furthermore, Davarpanah Jazi and Heath (2014) reported JNDs for several visuomotor and perceptual tasks with some, but not all, conditions following our predicted trend. Hence, the evidence for the slope-JND hypothesis is mixed at the moment. In this study, we aimed at bringing more clarity to this issue by examining the JNDs in a large set of grasping tasks that produced a wide range of grip-aperture-object size slopes. Our own experience suggested that the manipulation of haptic feedback might be a promising way to create size-MGA functions with varying slopes. In standard grasping tasks haptic feedback is provided at the end of a trial. By using a mirror-setup it is possible to present one object that is seen and use another object as the object that is grasped at the end of the movement (see for example Mon-Williams & Bingham, 2007). We can thereby dissociate visual and haptic information during grasping. A previous study has shown that the slope is increased when haptic feedback is only intermittently provided and further increased when no haptic feedback is provided (Schenk, 2012). Furthermore, it is expected that the slope can be substantially reduced when random haptic feedback (i.e. no correlation between the size of the visually perceived object and the size of the haptically perceived object) or constant haptic feedback (i.e. same haptic object irrespective of the visual object) is provided (see, Whitwell, Milner, Cavina-Pratesi, Byrne, & Goodale, 2014). Therefore by changing the haptic conditions, we hoped to create a range of conditions that vary substantially with respect to slope and thereby create an opportunity to test the relationship between slope magnitude and the emergence of Weber's law.

We also aimed to address two more questions. Firstly, we aimed to test Smeets and Brenner's (2008) alternative account. In Smeets and Brenner's model of grasping, the explicit computation of an object's size is not required to determine the relevant parameters for a reach-to-grasp movement. From this they conclude that increased errors in the representation of size will not lead to increased MGA variability. Thus, in their opinion, the observation that MGA-variability does not increase with object size in a Weber's law fashion simply reflects the fact that the variable in question, namely object size, is not used in the control of grasping. It does not demonstrate that psychophysical laws do not apply to the visual representations used in the control of action. Following this logic one might expect to find Weber's law for a grasping task in which visual size becomes an indispensable cue.

Pantomime grasping provides one example for a grasping-like task in which visual size becomes an indispensable cue. The location of the object and the location of the grasp are dissociated. The strategy of simply directing the fingers to the perceived grip points on the target object will not work when the perceived locations of the grip points and the actual locations of the grasping endpoints are dissociated. For a more extensive discussion of why tasks with dissociated positions require the use of visual size, see Schenk, 2012a,b. Holmes et al. (2013) compared the relationship between JNDs for grip aperture in standard and pantomimed grasping and found Weber's law for pantomimed but not for standard grasping. This interesting finding suggests that real and pantomimed grasping utilize different visual cues (Holmes et al., 2013). Interestingly, this finding is compatible with Smeets and Brenner's alternative account, but it is also compatible with the perception-action model since pantomimed grasping is conventionally seen as a perceptual task guided by ventral-stream information (e.g. Goodale, Jakobson, & Keillor, 1994; Goodale et al., 1994; Milner & Goodale, 2008). The pantomime task in the study by Holmes et al. (2013) differed from the real grasping task in two further respects. Participants encountered a real object and thus received veridical haptic feedback in the real grasping task, but not in the pantomime task. Furthermore, participants were allowed to see their hand during the movement. However, hand-sight is possibly more useful when the observed finger positions can be directly related to the target positions and thus hand-sight might prove more useful when target and grasping location are not dissociated, as they were in the pantomime but not in the real grasping condition. To address some of these issues we introduced two new grasping conditions.

In one task (task 5) participants saw the object at location A but were asked to direct their grasp to location B. Similarly, as in Holmes et al. (2013) study target and grasping location were thus dissociated. However, in our experiment, participants encountered a real object at location B and therefore received veridical haptic feedback at the end of each grasp. We also introduced another condition, namely task 6. Here, target and grasping locations were identical, but this time no real object was encountered and thus no haptic feedback was present. Hand-sight was prevented in both conditions, therefore differences in the usefulness of visual feedback between the normal and the dissociated grasping task could not contribute to performance differences in our experiment. Before we can describe our predictions for these conditions we first need to be clear about our understanding of pantomimed grasping.

To our knowledge, there is no real consensus on what defines a pantomime and thus a grasp guided by ventral-stream information as compared to a real grasp that is supposed to rely on dorsal-stream information. We base our understanding of pantomime grasping on Goldenberg's (2014) contention that the key feature of pantomime acts is their communicative nature. In this view, pantomime acts are pretended movements intended to convey information to an audience. Pantomime acts are not intended to interact directly with the actor's physical environment. Instead, they are primarily constrained by the need to convey information clearly. Real acts are intended to interact with our environment and the physical constraints of that environment will shape the parameters of those acts. Thus, one might argue that in the case of grasping, the known presence of a real target-object will ensure that a real grasp is performed. In contrast, when such an object is missing, relevant physical constraints are missing and the act's primary purpose becomes communicative. Assuming that real acts are dorsal-stream driven and pantomime acts are ventral-stream dependent, we might predict that the absence of real objects will turn a grasping task into a pantomime task and thus into a task dependent on ventral-stream visual representations. Now, we are in a position to describe the different predictions that can be derived from Ganel et al.'s (2008) versus Smeets and Brenner's (2008) accounts. Ganel et al.'s prediction for our task 5 is not clear, but for task 6 we expect them to predict compliance with Weber's law given that the absence of a real object requires participants to perform pretended grasps in this condition. In contrast, Smeets and Brenner would have to predict violation of Weber's law in task 6 given that task 6 provides veridical visual information about the required grip position at the intended location for the grasping movement and hence provides the

necessary information to guide the grasp purely on the basis of egocentrically-defined position information. Task 5 in contrast dissociates visible target information and grasping location and thereby prevents a strategy based on visual positions alone, making the use of size cues indispensable. We would therefore expect that Smeets and Brenner predicted adherence to Weber's law in task 5 but not in task 6. Our set of grasping conditions allows us to dissociate these two competing accounts. It is also hoped that our study will shed further light on the role of haptic feedback in the emergence or disappearance of Weber's law in grasping.

2. Materials and Methods

2.1. Participants

Twenty-four healthy women with a mean age of 26 years (age range: 21-34) were recruited for the study. All participants were self-reported right-handers and had normal or corrected-to-normal vision. Informed consent was obtained from all participants prior to the investigation. The study was approved by the ethics committee of the medical faculty of the Friedrich-Alexander University Erlangen-Nuremberg and conducted in accordance with the Declaration of Helsinki II.

2.2. Setup and procedure

For all grasping tasks a mirror apparatus was used (see Figure 1). All objects were plastic blocks with a height of 30 mm and a width of 20 mm; their depth¹ was 20, 30, 40, 50, or 70 mm. The object depth of 60 mm was omitted to keep the amount of trials manageable for participants.

There was one set of those objects with a constant weight for all objects (37 g) and another set in which the weight increased with object size (21.6, 32.0, 42.0, 52.4, 72.8 g). Participants were seated in front of the mirror apparatus and used their right dominant hand for all tasks.

One marker of a miniBIRD (Ascension Technology Corporation, Shelburne, VT, USA) was placed at the participants' index finger and another one at the thumb. Their hand was placed behind the mirror; thus they could not see their hand during the grasping tasks. At the beginning of each trial, participants pressed a start button with their hand, with thumb and index finger in contact. The target objects were presented with their short side parallel to the front edge of the desk and the long side

¹ In the following we will use the term 'size' to refer to object depth.

(which varied) parallel to the sagittal axis of the participants. Participants were required to wait for the start signal and then to grasp the object with the shorter edge aligned horizontally by its depth as quickly and accurately as possible and to lift it.

Grasping movements were recorded with the miniBird system using a sampling rate of 100 Hz. Data collection was controlled with the Motion Monitor software (Innovative Sports, Chicago, IL, USA). Each participant was tested twice on separate days. In each testing session all six tasks (see below) were performed with the order of trials and tasks being counterbalanced across sessions and participants. All tasks were preceded by 10 practice trials.

2.3. Tasks

2.3.1. Task 1: Standard grasping

An object was placed at the distant position in front of the mirror and another object with the same size was placed at the corresponding position behind the mirror (see Figure 1). Therefore the position of the reflected image of the object corresponded with the position at which an object was placed behind the mirror. There were 20 trials for every object size and thus a total of 100 trials in this task (50 per test session).

2.3.2. Task 2: Grasping with constant weight

Task 2 differed from task 1 only in one respect: the grasping objects behind the mirror always had the same weight (37 g) irrespective of object size. Again 100 trials were performed (50 per test session), 20 for every object size.

2.3.3. Task 3: Grasping with random haptic feedback

An object was placed at the distant position in front of the mirror and another object with the same weight was placed at the corresponding position behind the mirror. However, the size of the objects before and behind the mirror were not correlated, but randomly paired. For example the participant may have seen an object with a size of 20 mm in front of the mirror but grasped an object with a size of 50 mm behind the mirror. The object with a size of 40 mm was not used in this task. For this task the set of objects with identical weight was used. There were 20 trials for every object size and thus a total of 80 trials (40 per test session).

2.3.4. Task 4: Grasping with constant haptic feedback

An object was placed at the distant position in front of the mirror but always paired with an object with a size of 40 mm behind the mirror. Again in this task, the object with a size of 40 mm was never presented in front of the mirror. Twenty trials per object size were presented in a randomized order, resulting in 80 trials in total (40 per test session).

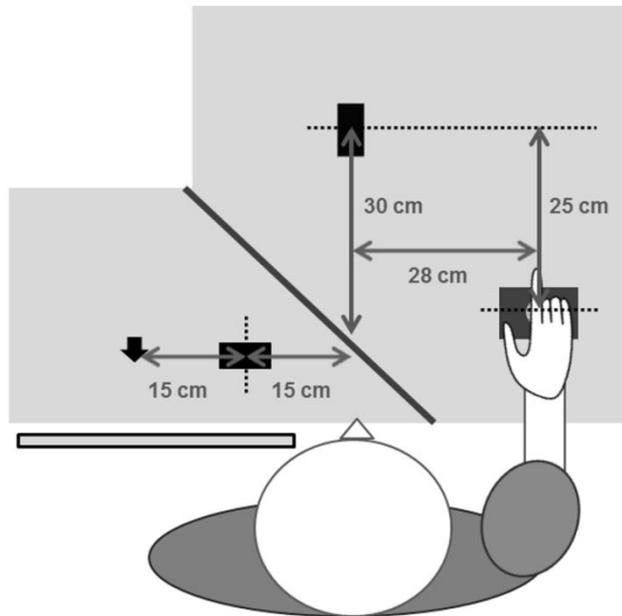


Figure 1: Mirror apparatus, seen from above. The diagonal line represents the mirror. Objects were placed at one position behind (30 cm away from the mirror) and two different positions in front of the mirror (15 or 30 cm away from the mirror), depending on the respective task. Direct view of the object in front of the mirror was prevented by a visual cover (horizontal grey line). Only the reflection of the object (and the black arrow) in the mirror was seen by participants. They perceived the object at its mirror-symmetrical position behind the mirror. In task 5 (dissociated positions) an arrow indicated the location of the object behind the mirror. The grasping hand was placed behind the mirror and could not be seen by the participants. The start-position of the hand was located 28 cm to the right and 25 cm in front of the object placed behind the mirror (far position). Head position was not fixed. Distance between the participants' eyes and the position on the mirror located straight ahead from their eyes was approximately 26 cm.

2.3.5. Task 5: Grasping with dissociated positions

An object was placed at the near position (see Figure 1) in front of the mirror and another object of the same size was placed behind the mirror at the far position. Therefore, the object was seen at one position but had to be grasped at a different position. The mirror-reflection of an arrow located at the far position and presented in front of the mirror (but perceived as being behind the mirror) indicated to the participants the position at which the target object had to be grasped. At the position of the arrow, as reflected by the mirror, participants encountered an object which was identical to the object presented

in front of the mirror meaning that participants received veridical haptic feedback. The object with a size of 40 mm was not used in this task. Eighty trials were conducted (40 per test session), 20 for each object size. For this task the set of objects with varying weights was used.

2.3.6. Task 6: Grasping without haptic feedback

In this task no object was present behind the mirror. Hence, participants received no haptic feedback. The object with a size of 40 mm was not used in this task. Eighty trials were performed (40 per test session), 20 for each object size. In all other respects the task was identical to task 1.

2.4. Data analysis

The maximum distance between index finger and thumb (MGA) was determined for each trial. Furthermore, the mean, standard deviation (SD) of the MGA and interquartile range (IQR) of MGA were computed separately for each task and object size. While previous studies on this topic used SD as their measure of variability, we were encouraged by an anonymous reviewer to use IQRs in addition to SDs. IQRs are less affected by outliers and might thus provide a more robust measure of variability. We used the means of the MGA as the dependent variable in linear regression analyses with object size as predictor variable. The non-standardized Beta-Parameter was used as our estimate for the slope of the size-MGA function. Using this procedure, we obtained slope values for each task and participant.

To test whether task conditions had an influence on the slopes a one-way repeated-measures ANOVA with the factor task and the dependent variable slope was conducted. Furthermore, one-way repeated-measures ANOVAs with the factor object size (20, 30, 50, 70) and the dependent variable SD of MGA were computed, one for each task, to explore whether Weber's law emerged in any of the six grasping tasks. Contrasts were used to test for a linear trend using SPSS' polynomial contrast function. We specified coefficients for the polynomial contrasts to correct for the unequal spacing between different levels of factor size. The same analyses were conducted for IQR of MGA as dependent variable. Data of the object with a length of 40 mm was discarded from the second analysis because this object size was only used in tasks 1 and 2. In case the assumption of sphericity was violated, the Greenhouse-Geisser corrected p -values are reported. Dependent t-tests were used for pairwise comparisons.

All analyses were computed with IBM SPSS Statistics 21 and alpha level was set at $p = .05$. In case of multiple comparisons p was adjusted via sequential Bonferroni correction according to Holm (1979); and in those cases the corrected alpha levels are presented.

3. Results

3.1. Slope

In this section we computed the slopes for each task and examined whether we succeeded in creating a range of tasks that differed in the value of the associated size-MGA slopes. There was a significant main effect of task, $F(5,115) = 90.189$, $p < .001$. Figure 2 shows the mean slopes for the six different tasks and Table 1 presents the mean MGA for each object size and task.

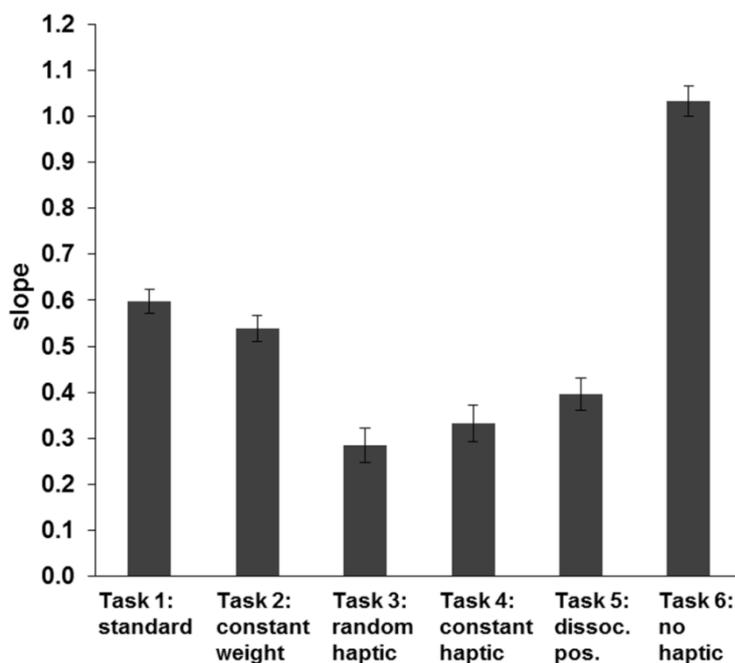


Figure 2: Mean slopes for the different grasping tasks. Slopes are indicated by the unstandardized Beta-Parameter of the linear function between object size and MGA. Error bars indicate between-participant standard errors of the mean.

The largest slope was observed for grasping without haptic feedback (task 6; $M = 1.03$, $SD = 0.16$), followed by standard grasping (task 1; $M = 0.60$, $SD = 0.13$), grasping with constant weight (task

2; $M = 0.54$, $SD = 0.14$), grasping with dissociated positions (task 5; $M = 0.40$, $SD = 0.17$), grasping with constant haptic feedback (task 4; $M = 0.33$, $SD = 0.20$), and the smallest slope was found for grasping with random haptic feedback (task 3; $M = 0.28$, $SD = 0.18$). The slopes differed between all tasks (all $ps < \text{corrected alpha level of } .013$), except between task 3 and task 4 ($p = .048 > \text{corrected alpha level} = .025$), between task 3 and task 5 ($p = .038 > \text{corrected alpha level} = .017$), and between task 4 and task 5 ($p = .220$).

Table 1: Mean MGA [mm] of the different object sizes in the grasping tasks, corrected for initial distance of the markers.

Task no.	Object size	20	30	40	50	70
1		70.3	76.6	83.8	90.2	99.9
2		70.9	77.1	83.3	88.5	97.9
3		82.3	85.1		90.7	96.5
4		77.7	79.7		86.9	93.9
5		77.5	82.3		91.0	97.3
6		37.3	47.7		66.7	89.5

3.2. Variability as a function of object size (testing Weber's law)

In this section we explored the variability of MGA as a function of object size to find out under which conditions Weber's law could be found. We employed two measures for MGA-variability: standard deviation (SD) and interquartile range (IQR), a measure of variability that is less susceptible to outliers. Figure 3 shows the SD of MGA for the different object sizes, separately for each task. Table 2 displays the test statistics (ANOVAs) for the different tasks. There was a significant main effect of object size for grasping with random feedback (task 3), grasping with constant feedback (task 4), as well as for grasping with dissociated positions (task 5), indicating that changes in object size influenced the variability of MGA in those tasks. Linear contrasts showed a significant linear trend for task 4 and 5 ($p < .05$) and a linear trend approaching significance for task 3 ($p = .064$).

Additionally, we also analysed the interquartile range (IQR) of MGA as an alternative measure of the JND. The results are displayed in Table 2 and Figure 3. The analyses confirmed our results obtained for the SDs of MGA: There was again a significant main effect of object size for grasping with

random feedback (task 3), grasping with constant feedback (task 4), as well as for grasping with dissociated positions (task 5), indicating that changes in object size influenced the variability of MGA in those tasks. Additionally, there was a significant main effect of object size for standard grasping (task 1). Linear contrasts showed a significant linear trend for task 1, 3, 4 and 5 (all $p < .05$).

Interestingly, in all of those cases in which a significant influence of object size on MGA was obtained, the relationship was opposite to what is expected on the basis of Weber's law, i.e., the SD of MGA decreased instead of increased with increasing object size (see Figure 3, tasks 3, 4, 5). In fact, when we used IQR as our JND-estimate we found a significant inverse trend for all tasks but task 2 and 6.

Table 2: Results of the ANOVAS with the *factor* object size and the *dependent* variables SD of MGA or Interquartile range (IQR) of MGA

Task no.	Task	Result of ANOVA with SD of MGA	p	Result of ANOVA with IQR of MGA	p
1	Standard grasping	$F(3,69) = 2.19$.135	$F(3,69) = 8.44$	<.001*
2	Grasping with constant weight	$F(3,69) = 1.29$.284	$F(3,69) = 1.62$.193
3	Grasping with random haptic feedback	$F(3,69) = 2.80$.046*	$F(3,69) = 3.86$.013*
4	Grasping with constant haptic feedback	$F(3,69) = 7.93$.001*	$F(3,69) = 4.18$.025*
5	Grasping with dissociated positions	$F(3,69) = 3.15$.030*	$F(3,69) = 3.38$.035*
6	Grasping without haptic feedback	$F(3,69) = 0.66$.582	$F(3,69) = 0.18$.913

Note: *indicates statistical significance.

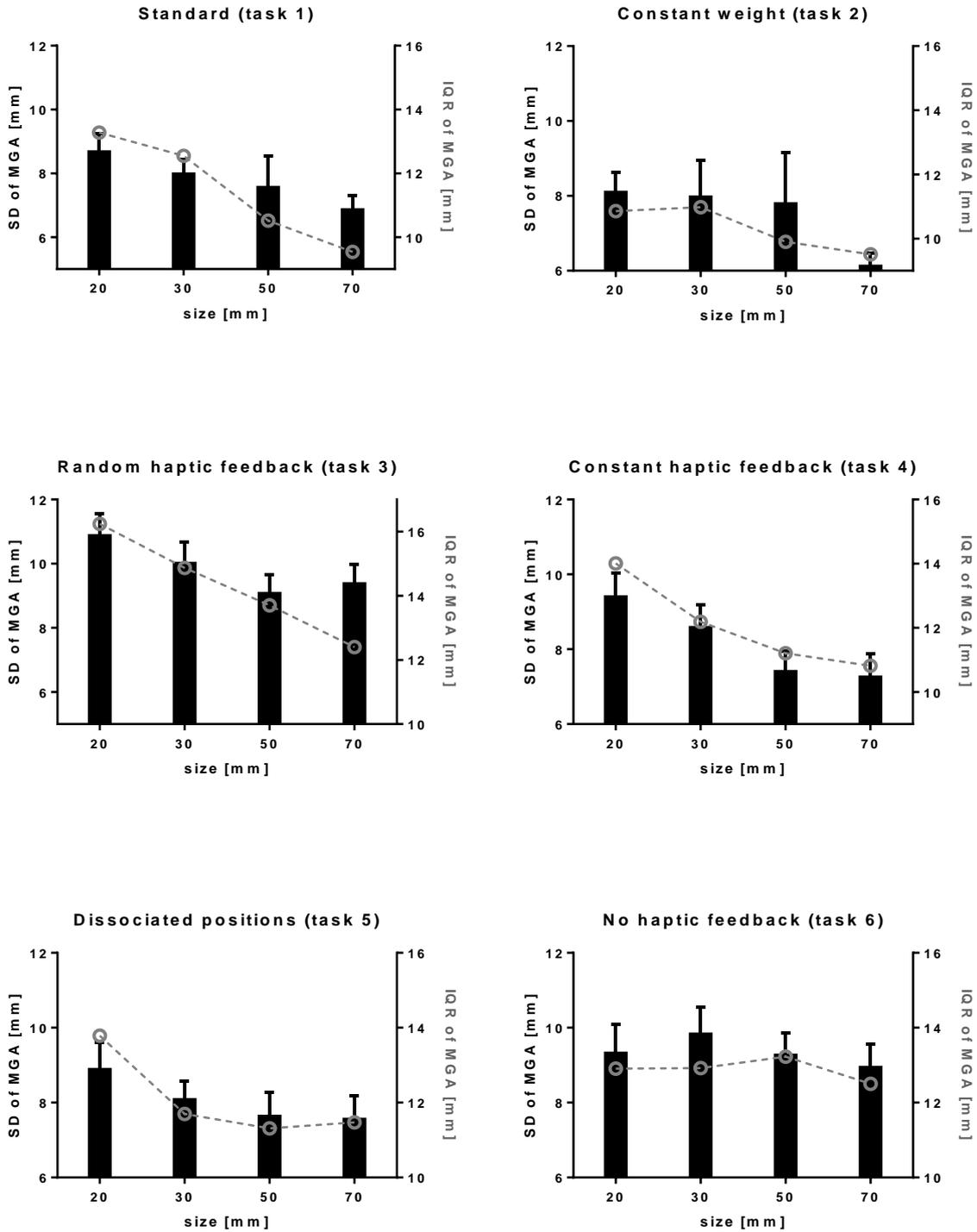


Figure 3: Mean standard deviations (mm) of MGA (maximum grip aperture) and IQR (interquartile range) for the different object sizes and different grasping tasks. SD of MGA are represented by black bars; IQR of MGA are represented by grey circles. Error bars indicate standard error of the mean and reflect the variance of the variability measured in the sample. With the exception of task 6, there was a trend towards smaller variability for larger object sizes. For SD of MGA, this trend was significant for task 4 and 5; and approaching significance for task 3. For IQR of MGA, this trend proved significant for task 1, 3, 4 and 5.

We were quite surprised to see that Weber's law could not be observed in any of the six tasks but that in fact in several tasks the opposite of Weber's law was found, namely a trend for smaller MGA-variability in the case of larger objects. Possibly, there is a straightforward explanation for this. For large objects the MGA will come close to the opening of the hand that is comfortable given the anatomical constraints of our hands. This means there is an upper ceiling for MGAs and consequently once the mean MGA gets close to this ceiling, trial-to-trial deviations from the mean towards smaller MGAs are possible, but deviations towards larger MGAs are strictly limited. In sum, biomechanical constraints will reduce variability for larger objects, thereby leading to an inverse relationship between variability and object size. This inverse trend may not only compensate for the positive relationship between variability and object size, that is expected on the basis of Weber's law, but can in fact lead to an overall negative relationship between size and variability (as seems to be the case in most of our tasks). Encouraged by an anonymous reviewer we explored this hypothesis further. While we do not know the anatomical limits of our participants' hands it is clear that, for any given individual, larger MGAs will be closer to the limit of the maximal hand opening than smaller MGAs. Assuming our biomechanical hypothesis is correct, we can thus predict that for each participant MGA-variability will be smallest for the task in which the MGA for the large object is largest and variability will be highest for that task in which MGA for the large object is smallest. To test this prediction, we therefore selected for each participant the task with the highest average MGA in the 70-mm condition and the task with the lowest average MGA in the 70 mm condition. The lowest MGA ($M = 112.20$ mm, $SD = 8.61$ mm) differed significantly from the highest MGA ($M = 131.19$ mm, $SD = 8.67$ mm; $t(23) = -12.283$, $p < .001$). We then computed MGA-SDs for those tasks and compared the average MGA-SDs across all participants in the high- MGA condition with that in the low-MGA condition using a paired-samples t -test. The results confirmed our prediction. MGA-SDs for the high-MGA condition was significantly smaller than those in the low-MGA condition (SD of MGA: high-MGA: 6.68 mm versus low-MGA: 8.99 mm; $t(23) = 2.658$, $p = .014$).

Further tentative support for our biomechanical hypothesis can be found in Table 3. We would expect that the trend for reduced variability for larger objects will be particularly pronounced in tasks that use great safety margins thus leading to larger MGAs. In contrast, in tasks that encourage less generous safety margins and thus produce lower average MGAs the negative relationship between object size and variability should be attenuated. To put it differently, it is more likely to find a negative

size-variability trend for tasks with large average MGAs than in tasks with small average MGAs. This is exactly what we observed in our study. The only task that clearly failed to show a negative trend between object size and MGA variability is task 6 which is also the task with the smallest average MGAs recorded.

Table 3: Mean and (SD) of the different measures in the grasping tasks.

Task no.	Task	MGA in mm	Time to MGA in ms	Movement time in ms	Movement amplitude in ms
1	Standard grasping	83.4 (16.3)	615 (133)	1011 (351)	0.34 (0.07)
2	Grasping with constant weight	83.1 (15.5)	633 (130)	1005 (318)	0.33 (0.07)
3	Grasping with random haptic feedback	89.7 (14.4)	664 (119)	1034 (298)	0.34 (0.05)
4	Grasping with constant haptic feedback	83.7 (14.3)	637 (131)	1013 (318)	0.33 (0.07)
5	Grasping with dissociated positions	86.6 (15.3)	640 (134)	1031 (307)	0.34 (0.06)
6	Grasping without haptic feedback	61.5 (24.5)	722 (129)	935 (238)	0.31 (0.07)

Note, that MGA was corrected for the initial distance of the markers. It should also be noted that in each trial, the experimenter first started the MiniBird recording and then signalled to the participant (verbally) that they could now start with their grasping response. Afterwards we used an automated procedure to identify the start of the grasping response. Movement-onset was determined as the first frame in which hand velocity exceeded a threshold of 0.05 m/s. Unfortunately, participants frequently moved their hands before the start signal. This resulted in the recording of artificially long movement times. In fact once they properly started with their movement, they typically proceeded at normal speed. The average peak velocity across all trials was above 900 mm/s – a value that is in the range of that found for other grasping experiments.

4. Discussion

We found that our manipulations of haptic feedback, weight of objects and object positions affected the slopes of the function relating object size to MGA. However, despite of our success in creating a range of tasks differing significantly in slope values, Weber's law was not found in any of the

conditions. This clearly contradicted our own predictions, since we hypothesized that Weber's law would be found in conditions with large slope values. The evidence from previous studies is mixed in this regard. Holmes, Lohmus, McKinnon, Mulla, and Heath (2013) found similar slopes for grasping and pantomime grasping and nevertheless observed a clear difference with respect to the JNDs: JNDs increased with object size for pantomime but not for real grasping. However, work from the same lab also produced findings that were in line with our expected correlation between slope size and the likelihood of observing Weber's law (Davaranah Jazi & Heath, 2014). Together with our current findings, there is therefore no consistent evidence to support the claim that Weber's law can only be found in tasks with large slopes.

The fact that we did not find Weber's law in any of our grasping tasks, at first sight seems to constitute an impressive endorsement of Ganel et al.'s (2008) claim that Weber's law only affects the visual signals governing perceptual tasks but not the signals responsible for the visual control of action. Ganel and his colleagues (Ganel, Chajut, & Algom, 2008; Ganel, Chajut, Tanzer, et al., 2008) argued that given the universal presence of Weber's law in perceptual processes, its failure to turn up in grasping suggests that grasping is governed by visual processes that are quite distinct from those involved in visual perception. According to this view, the presence of Weber's law can be taken as indication of the involvement of perceptual processes and its absence as evidence of the disengagement of perceptual processes from a given task, such as grasping. Therefore, it seems our findings provide further support for the idea that perception and action are served by distinct visual processes (Milner & Goodale, 1995, 2006).

However, closer inspection of our findings reveals aspects that are not in line with the interpretation derived from the perception-action model. Firstly, it should be noted that our six grasping tasks also included one task, namely task 5 (grasping at dissociated positions), that shares important features with pantomimed grasping—a form of grasping that according to the perception-action model engages the perceptual visual stream (Goodale et al., 1994). Incidentally, the failure to find Weber's law in Task 5 also contradicts the predictions derived from Smeets and Brenner's (2008) alternative account. Specifically, Task 5 required participants to pick up the object at a position which was different from the position at which the object was seen. Milner and Goodale (2008) argue that movements which are not directed at the location of the target object are pantomimed and hence controlled by the ventral stream and not by the dorsal, visuomotor system. As according to Ganel et al.

(2008) the presence of Weber's law indicates the involvement of the ventral stream grasping in task 5 should be subject to Weber's law. Clearly, this was not the case.

For different reasons, Smeets and Brenner's (2008) account would predict to find Weber's law in task 5. They argue that classical grasping is immune to Weber's law as object size is usually not used in the control of grasping. The flip-side of this argument is that if you create a grasping task that requires the use of size information, Weber's law should emerge. We argued above, that in a condition in which the object has to be picked up at location that is different from the location where it is seen, grasping can no longer be planned based on contact-positions and instead object size needs to be considered (see Smeets & Brenner, 1999). As object size was therefore relevant for grasping in Task 5, Weber's law should have emerged.

More importantly, it seems that neither the perception-action model nor Smeets and Brenner's (2008) interpretation can provide an explanation for the most interesting aspect of our findings, namely that in some tasks variability of MGA *decreased* with *increasing* object size. In fact this trend was found in four out of six tasks when IQR of MGA was used as measure of variability. How can this trend be explained? We think that the biomechanical constraints of our hand provide the most obvious explanation. During the typical course of a grasping movement, the fingers open up to a certain maximum (i.e. MGA) at mid-flight and then close again to converge on the actual size of the objects. Safe grasping requires that the fingers converge onto the object from opposing directions so that the end-trajectories of the finger movements are orthogonal to the grip-surface. With such a movement the impact of the index-finger will push the object towards the thumb and vice versa, thereby creating two counter-acting forces that produce a stable grip formation. To achieve such a sidewise approach the hand opening on approach needs to be bigger than the distance between the two grip points. This explains why the hand-opening on approach is typically substantially wider than the distance between the two grip points, i.e. the length of the target object. This difference between MGA and target length is called the safety margin. It is obvious that participants can use different safety margins for objects of the same size and this probably explains a substantial proportion of the variability observed in the MGA. There is however a clear upper limit given by the anatomical dimensions of the grasping hand. The maximum hand opening cannot exceed the distance between two fingers in a fully extended hand and this means that the safety distance cannot be bigger than the difference between maximum hand extension and object-length. From this it follows that for small objects the possible range of safety

margin values is wider than for big objects. Since we measure the maximum hand opening, we effectively sample the range of safety values when we calculate the SD of the grasping movements. Therefore, a bigger range of possible safety values will lead to a larger range of maximal hand openings, thus resulting in a larger SDs of the MGA. Accordingly, we can expect that smaller objects, allowing a greater range of safety values, are correlated with a larger SD and big objects are associated with a smaller SD. This biomechanical constraint induces a trend that runs opposite to the trend predicted by Weber's law and might thereby mask the influence of Weber's law on the visual signals used in grasping. This account would lead us to expect that for tasks where the MGA for the big object is closer to the biomechanical limit of a given individual the accompanying variability in MGA (SD) is smaller than for tasks where the MGA is further below this individual's biomechanical ceiling level. This prediction was confirmed in our study.

Interestingly, findings reported in previous studies can also be explained by this biomechanical account. Holmes, Lohmus, McKinnon, Mulla, and Heath (2013) for example found that pantomime grasping obeys Weber's law while grasping does not. It seems at first quite surprising that we did not find a similar dissociation between standard grasping (task 1) and grasping with dissociated positions which is similar to pantomimed grasping (task 5). There is however a critical difference between the two studies. In the study by Holmes et al., MGAs for pantomime grasping were on average 38% smaller than MGAs for real grasping. In our case MGAs for task 1 and task 2 were comparable (difference: 3%). Thus, in the context of our current hypothesis we would argue that Holmes et al. found evidence of Weber's law in pantomime grasping only because MGAs in pantomime grasping were substantially smaller than for real grasping. Hence the MGAs in pantomimed grasping were further away from the anatomical limit, thereby providing more room for variability. This explanation is supported by findings in our study. The one task that clearly failed to show an *inverse* Weber's law trend was also the task with the lowest average MGAs (Task 6) and thus the task which provided the most room for variability even for the big objects.

Moreover, an interesting finding from Holmes and Heath (2013) could also possibly be explained in terms of biomechanical constraints. Holmes and Heath reported a dissociation between grasping for 2D and 3D objects. Whereas grasping for 2D objects obeyed Weber's law, grasping for 3D objects did not. They interpret their findings as evidence that grasping of 2D and 3D objects is guided by different sets of visual cues. However, our biomechanical hypothesis could also explain

these findings since in this study MGAs for 2D objects were consistently smaller (in fact almost halved in value) than the corresponding MGAs for 3D objects of the same size. Thus, we would argue that the critical factor in this study is not the dimensionality of the object but the absolute values of the MGAs. This interpretation is further supported by findings from another study on 2D grasping. Christiansen et al. (2014) asked their participants to grasp bars of different lengths that were presented as 2D images on a computer monitor. In contrast to Holmes and Heath (2013), they found a clear violation of Weber's law. Importantly, Christiansen and colleagues employed long bars (up to 9.6 cm) which were presumably fairly close to the aperture limit of many participants. Thus, taking both studies on 2D grasping into account it seems that the absolute values of the MGAs and not the dimensionality of the target object is the critical factor. Note that the biomechanical hypothesis cannot account for all aspects of Holmes and Heath's findings. For example, it seems surprising that while the MGA values for 3D grasping were almost twice as large as those for 2D grasping, they still did not observe an inverse relationship between MGA values and object size.

Before we conclude, we need to address one final question: While the failure to find Weber's law in grasping clearly is not new (see Ganel, Chajut, & Algom, 2008, but also others), we observed that in fact Weber's law can be inverted in grasping. How can it be explained that we found this negative relationship but others did not? Firstly, we should point out that this trend became only significant for standard grasping once we adopted a different measure for variability, namely IQR instead of SDs or SEMs that were used in previous studies. Furthermore, our participants could not see their hand while performing their grasping movements. Numerous studies have shown that withdrawal of hand-sight results in increased MGAs (e.g. Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Churchill, Hopkins, Ronnqvist, & Vogt, 2000; Gentilucci, Toni, Chieffi, & Pavesi, 1994). This is in line with the fact that MGAs in our study were larger than in other studies on this topic (e.g., Holmes et al., 2013). This might explain why we found a negative trend for Weber's law while other did not.

While the absence of hand-sight is a likely factor to explain why our findings differ from those found in other labs, we cannot exclude the possibility that the mirror-setup has also introduced additional changes. It might be of interest to explore such additional factors by directly comparing grasping performance in a standard and mirror-setup. However, we think it is unlikely that the inverse Weber's law trend is an artefact of the mirror-setup. A similar trend was also observed by Christiansen et al. (2014) who did not use a mirror-apparatus in their experiment. Besides, it is important to note

that the biomechanical hypothesis is insufficient to account for all instances when Weber's law was observed to be violated in grasping studies. For example, Davarpanah Jazi and Heath (2014) found that regardless of whether objects were placed on the palm or the forearm, slopes relating JNDs to object size were fairly flat. Interestingly, the MGAs for grasping objects on the palm were however much smaller than the MGAs for the forearm condition. Thus, while the biomechanical hypothesis is most probably too narrow to account for the diverse findings on Weber's law in grasping research, it is in our view an important reminder that variability of movement parameters (such as MGAs) reflect many sources of noise of which noise in the sensory system is just one. This shows that we have to be very careful when drawing conclusions about the neural representation of sensory parameters on the basis of observed variability in motor parameters. Ganel et al.'s (2008) interpretation of their findings on Weber's law and grasping is based on one unstated assumption, namely that the variability of the hand-opening in grasping reflects primarily and faithfully variability of the sensory information about the target objects. Such an assumption ignores the possibility that other sources of motor noise may dominate and render changes in sensory noise undetectable. It also ignores the possibility that other non-sensory factors impose further constraints on motor variability that may run counter to the expected increase of variability with increasing object size and might thereby neutralize the expected size-dependent variability-increase. We would argue that the negative relationship between variability and object size found in several of our tasks suggests such neutralizing, and hence indicates that additional constraints do in fact exist. This means that the variability of motor parameters is governed by factors that can compensate for increases in sensory noise and thereby make it difficult to detect the potential impact of Weber's law on sensory variables in visuomotor tasks.

To sum up, variability of MGA when grasping 3D objects seems contaminated by non-visual sources of noise, such as the size of the safety margin. Hence, the variability of MGA becomes subject to influences that are not only unrelated to object size but can cancel out the influence of psychophysical laws. One solution might be to use a different measure to characterize the relationship between object size and grasping performance. Heath and colleagues published a number of studies in which they measured hand apertures across the entire time course of the grasping action (Heath, Mulla, Holmes, & Smuskowitz, 2011; Holmes & Heath, 2013; Holmes, Lohmus, McKinnon, Mulla, & Heath, 2013; Holmes, Mulla, Binsted, & Heath, 2011). To do this they computed time-normalized movement trajectories and calculated mean hand aperture for predefined portions of the entire

movement duration. They found that Weber's law holds for grip apertures during the early parts of the movement but disappears later on. In line with Glover's planning-vs-control model (Glover, 2004), Holmes, Heath and colleagues take this as evidence that perceptual processes determine only the early part of a grasping movement. However, such a continuous measure of grasping aperture is not free of problems either. Whitwell and colleagues (Whitwell & Goodale, 2013) demonstrated that time-normalized grasping trajectories can give rise to spurious correlations between movement parameters and object size. Ganel et al. (2014) demonstrated empirically that the early measures of grip apertures are confounded with the grasping finger's velocity and significantly affected by the initial starting position of the hand. Foster and Franz (2013) presented a computer-simulation to demonstrate the mathematical link between finger-velocity and early measures of grip aperture. They argued on the basis of their computer simulation that MGA is still the best indicator of the motor system's estimate of object size.

It therefore appears that quite a few authors argue that MGA is the best available measure to characterize how the grasping response is adjusted to the size of the target object. However, our findings also show that MGA is certainly not a pure measure of the visual cues that are used in guiding our grasping response. As we argued above, MGAs are also affected by non-visual factors and these factors may counteract the influence of sensory laws and thereby mask their influence on the grasping response.

Finally, we would like to point out an additional interesting aspect of our findings. In our experiment, the grasping performance as measured by the slope was not substantially different from that found in classical grasping when the target object's weight remained constant and did not vary with object size. Whitwell et al. (2014) argued that the co-variance between object weight and object size might be used as a critical cue to adjust our hand-opening to the size of the object. Our findings do not support this idea. The comparative irrelevance of weight as a cue to object size becomes particularly obvious when we contrast the fairly minor changes observed when the co-variance of weight and size is abolished with the fairly dramatic changes found when haptic feedback is withdrawn or distorted.

To be clear, our findings neither invalidate the perception-action model nor do they contradict Smeets and Brenner's model of grasping, but they suggest that variability of the MGA cannot be used to infer the variability of the underlying visual representation. Therefore, we suggest that so-called

violations of Weber's law cannot be used as tools to probe the nature of visual representations underlying the control of grasping movements. Consequently, such violations cannot be used either to support or criticize the perception-action model.

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