



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 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.

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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).

Abbreviations: EL, estimated length; MGA, maximum grip aperture; JND, just noticeable difference.

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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 behavioral 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, 2012a). 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 et al., 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, 2012b. 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, Meenan, et al., 1994; Milner & Goodale, 2008). The pantomime task in the study by Holmes et al. (2013) differed from the real grasping

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