Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia





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ARTICLE INFO

Article history: Received 17 October 2014 Received in revised form 2 February 2015 Accepted 27 February 2015 Available online 28 February 2015

Keywords: Action Grasping Perception Semantic Visual Weber's law

ABSTRACT

According to Weber's law, the just noticeable difference between stimuli increases proportionally with stimulus magnitude, suggesting that perception becomes more variable when a stimulus becomes larger. Surprisingly, this basic psychophysical principle appears to be violated in grasping because the variability of grasping movements does not increase with object size. This dissociation between perception and grasping has been interpreted either as evidence for different neuronal processing of real-time visual size information [Ganel, T., Chajut, E., Algom, D. (2008a). Current Biology, 18(14), R599–R601], or for the idea that grasping ignores stimulus size and is based on position information only [Smeets, J. B. J., and Brenner, E. (2008). Current Biology, 18(23), R1089–R1090]. Both accounts assume that it is the processing of visual information that leads to the absence of Weber's law in grasping. We show that even if neither visual nor any real-time sensory information about the stimulus is presented (but only abstract, semantic information about its size), grasping does not follow Weber's law. This indicates that other mechanisms must be responsible for the unexpected behavior of grasping.

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1. Introduction

According to Weber's law (Baird and Noma, 1978; Fechner, 1860), the just noticeable difference between stimuli increases proportionally with stimulus magnitude. In other words, the uncertainty of the stimulus estimate increases with the magnitude of the stimuli. Weber's law is a basic psychophysical principle, which can be found in almost all sensory dimensions and is supported by a vast amount of data (Baird and Noma, 1978).

Therefore, the finding of Ganel et al. (2008a) that visually guided grasping does not follow Weber's law is particularly astonishing. In their experiments participants performed three different tasks. In the first task, participants estimated the visual size of six randomly presented objects of different sizes (20, 30, 40, 50, 60, and 70 mm) by adjusting the length of a comparison line on a monitor (perceptual adjustment). As predicted by Weber's law, the uncertainty of the size estimates (i.e., standard deviation of the estimates) increased with the object's size. In the second task, participants estimated the size of these objects by adjusting the span between index finger and thumb (manual estimation, assumed to be comparable with perceptual adjustment, but with the advantage of using the same effector as grasping; Goodale, 2011;

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.02.037 0028-3932/© 2015 Elsevier Ltd. All rights reserved. but see also Franz, 2003). Again, in this task the within-participants standard deviation of the estimates increased with increasing object size, thus, following Weber's law. In the third task, participants grasped these objects. As a measure of uncertainty in grasping, the within-participants standard deviation of the maximum grip apertures (i.e., the maximum opening between index finger and thumb during the grasping movements taken to be a measure of motor-estimated size) was calculated. Astonishingly, this measure did not scale with the object's size. Thus, visually guided grasping does not follow Weber's law. While this result seems like a violation of a very fundamental principle in psychological science, it has been replicated in many studies (Ganel et al., 2008b; Hadad et al., 2012; Heath et al., 2012, 2011; Holmes and Heath, 2013; Holmes et al., 2013, 2011).

Current explanations of the violation of Weber's law in grasping and, hence, the dissociation between grasping and manual estimation regarding Weber's law focus on differences in the processing of the sensory information about the object. At present, there are two influential accounts, the relative–absolute coding account (Davarpanah Jazi and Heath, 2014; Ganel et al., 2008a) and the size–position account (Smeets and Brenner, 2008).

The relative–absolute coding account is based on the perception–action model (Goodale and Milner, 1992; Goodale, 2008, 2011; Milner and Goodale, 1995, 2008). According to the perception–action model, visual information is processed in two largely independent visual pathways. Visual information used for perception is processed in the ventral visual pathway and visual





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information used for action in the dorsal visual pathway. The perception-action model has received support from a comprehensive data base from behavioral, neuropsychological and neuroimaging studies with patients and healthy participants (for review see Goodale, 2011). A fundamental assumption of the perception-action model is that perception and action rely on different neuronal computations of the visual signal (Ganel and Goodale, 2003). Accordingly, the coding of visual size information used for perception (e.g., manual estimation) is based on relative metrics. That is, the neuronal computation of visual size in perception is dependent on the size of surrounding objects or other aspects of the visual scene and on the dimensions of the object itself (i.e., scene-based or allocentric frame of reference). In contrast, the coding of visual size information used for action (e.g., grasping) rests on absolute metrics computed in a body-centered coordinate system (i.e., egocentric frame of reference). That is, the neuronal computation of visual size in action is independent of aspects of the visual scene and the irrelevant dimensions of the object.

This fundamental difference in the neuronal processing of the visual signal has received support from patient studies (e.g., Goodale et al., 1991), studies with healthy participants using pictorial illusions (e.g., Aglioti et al., 1995; Haffenden and Goodale, 1998), and Garner's speeded classification task (Ganel and Goodale, 2003, 2014). However, findings of other authors challenge the conclusions of these studies and provide alternative explanations of the apparent dissociation between perception and action in patient studies (Schenk, 2006, 2012) as well as in studies with healthy participants using pictorial illusions (Franz et al., 2000; for reviews see Bruno and Franz, 2009; Franz and Gegenfurtner, 2008; Schenk and McIntosh, 2010) and Garner's speeded classification task (Eloka et al., in press; Hesse and Schenk, 2013; Janczyk et al., 2010; see also Janczyk and Kunde, 2012).

More direct psychophysical evidence for a fundamental difference in the processing of perception and action is thought to be given by the finding that perceptual tasks, such as perceptual adjustment or manual estimation, adhere to Weber's law, while grasping does not (Ganel et al., 2008a, 2008b; Goodale, 2011). Within the framework of this theory, it is concluded that grasping violates Weber's law because it utilizes absolute visual size information. Manual estimation, in contrast, is assumed to follow Weber's law because it relies on relative visual size information.

According to the perception–action model, only grasping guided by real-time visual information in the movement programming is based on absolute metrics. Memory-based grasping (i.e., after a certain time delay without vision, thus, without visual information at the time of movement programming) rests on relative metrics (Goodale, 2011; Hu and Goodale, 2000). As a consequence, memory-based grasping should follow Weber's law, which was demonstrated empirically (Ganel et al., 2008a, 2008b). However, this finding could not be replicated by other authors (Holmes et al., 2011).

The relative–absolute coding account is not exclusively used to describe differences in the processing within the visual modality. Recently, Davarpanah Jazi and Heath (2014) found a dissociation regarding Weber's law between tactually guided manual estimation and grasping. They placed objects on the participant's left palm (i.e., real-time tactile size information) and asked them to manually estimate the size of these objects or grasp these objects with index finger and thumb of their right hand. Whereas tactually guided grasping did not. In line with the sensory processing model of Dijkerman and de Haan (2007), they conclude that relative size information is used in tactually guided grasping.

A second approach to explain the dissociation regarding

Weber's law was made by the size-position account of Smeets and Brenner (2008). According to their "double-pointing"-hypothesis, grasping can be described as guiding the finger and thumb independently to the grasp points on the object. Consequently, grasping is based on egocentric position information about the grasp points of the object. Thus, in grasping, the computation and the use of the visual size is not necessary. As Weber's law holds for size information, but not for position information, grasping does not follow Weber's law. Manual estimation, in contrast, is based on size information. As a consequence, manual estimation follows Weber's law. Thus, the dissociation regarding Weber's law between manual estimation and grasping is attributed to the use of size information in manual estimation and egocentric position information in grasping. Further, according to Smeets and Brenner (2008), memory-based grasping is based on size information. This is because the memory for size information is assumed to be more accurate than the memory for egocentric position information. While information about object size is not influenced by our own movements, egocentric position information should be updated when we move, which is not possible in memory-based grasping. Accordingly, grasping without real-time visual information about the object is based on relative size information instead of egocentric position information and should follow Weber's law.

In summary, current explanations of the dissociation regarding Weber's law focus on differences in the processing of the sensory information used in manual estimation and grasping. Whereas relative size information is used in manual estimation, either absolute size or egocentric position information is thought to be used in real-time grasping. Memory-based grasping, however, is also thought to be based on relative size information.

However, according to the relative–absolute coding account as well as the size–position account, the violation of Weber's law in grasping is dependent on the availability of real-time sensory information about the object (i.e., concrete sensory information about the object at the time of movement programming; typically visual but also tactile information as in the case of Davarpanah Jazi and Heath, 2014). If no real-time sensory information would be available at the time of movement programming, grasping would be based on relative size information. Thus, both accounts agree that without real-time sensory information grasping should follow Weber's law and the dissociation between manual estimation and grasping should disappear.

To test these accounts, we measured manual estimation and grasping in a visual and a non-visual, semantic condition. In the visual condition, the movement programming of manual estimation and grasping was based on real-time visual information about the objects. In the semantic condition, numbers were presented over headphones indicating the size of objects without vision of these objects. Thus, in the semantic condition neither visual nor real-time (only abstract, memory-based) information about the object was available. According to both accounts, a dissociation between manual estimation and grasping regarding Weber's law is expected in the visual condition but not in the semantic condition.

We also used our experiments to test alternative ideas for the apparent absence of Weber's law in grasping. We hypothesized that there might be other task differences between manual estimation and grasping that could explain the dissociation regarding Weber's law.

First, late noise could mask Weber's law in grasping. This could be noise that occurs in the processing after size is estimated and that does not follow Weber's law (e.g., motor noise). Such late noise will reduce the scaling of the standard deviation, thereby leading to an underestimation of Weber's fraction. If there were more late noise in grasping than in manual estimation, this could account for a smaller Weber's fraction in grasping than in manual estimation. We tested this notion and found that late noise alone cannot explain the dissociation regarding Weber's law (see below). Second, ceiling effects might reduce the scaling of the standard deviation. Ceiling effects could result from the natural limitation of the finger span and a tendency to avoid uncomfortable large finger apertures, such that the frequency of large responses should decrease for larger object sizes and the distribution of the responses should become negatively skewed (i.e., heavier left tail). Because responses in grasping (as measured by the MGA) are usually considerably larger than in manual estimation, ceiling effects are likely to be more pronounced in grasping than in manual estimation. To test for such differential influences of ceiling effects, we compared the scaling and the mean skewness of grasping and manual estimation and found that ceiling effects might indeed be an important factor (see below).

Four experiments were performed. Visually guided manual estimation was performed in experiment 1, visually guided grasping in experiment 2, semantically guided manual estimation in experiment 3, and semantically guided grasping in experiment 4.

2. Experiment 1

The purpose of the first experiment was to replicate the finding of Ganel et al. (2008a) that visually guided manual estimation follows Weber's law. Participants manually estimated the size of different objects. To provide haptic feedback about object size, participants grasped every object immediately after manual estimation (this is the usual procedure, cf. Haffenden and Goodale, 1998). As in the original study of Ganel et al. (2008a), six visual object sizes (i.e., 20, 30, 40, 50, 60, and 70 mm) were used and 20 trials per object size were applied. Visual information about object size was provided in advance of movement onset.

The mean, standard deviation, and the skewness of the manual estimate (ME) were determined for each participant at each object size. According to Weber's law, we would expect an increase of the standard deviation of the ME across object size.

In addition, the mean, the standard deviation, and the skewness of the maximum grip aperture (MGA) of the grasping response following manual estimation, hereafter referred to as MGA of post-estimation-grasping (MGA_{post-est}), were determined for each participant at each object size.¹ Because sight of the objects was prevented as soon as participants initiated their manual estimation response, in this experiment the post-estimation-grasping response is memory-based (i.e., a temporal delay between the availability of the visual information and the possibility to respond). In keeping with the assumption that memory-based grasping is based on relative visual metrics (Goodale, 2011; Hu and Goodale, 2000) and the finding that memory-based grasping follows Weber's law (Ganel et al., 2008a, 2008b; but see Holmes et al., 2011), we would expect an increase of the standard deviation of the MGA_{post-est} across object size, that is, Weber's law.

2.1. Methods

2.1.1. Participants

Fifteen participants (10 females, 5 males; age range: 19–32 years) were included in the data analysis. One participant was excluded because the infrared emitting diode on her thumb was detached during the experiment. In all experiments, participants were either undergraduate students who received course credits or were paid volunteers. In all experiments, participants were native German speakers, self-declared right-handed dominant and with normal or corrected-to-normal vision.

2.1.2. Ethics statement

In each experiment, written informed consent was obtained from all participants. All experiments were conducted in accordance with the 1964 Declaration of Helsinki and in keeping with the ethical guidelines of the Professional Association of German Psychologists (BDP) (2005, C.III) and the German Psychological Society (DGPs). This study was conducted within the International Graduate Research Group "Cross-modal Interaction in Natural and Artificial Cognitive Systems" (CINACS) that was reviewed and approved by the German Research Foundation (DFG, project number IGK-1247).

2.1.3. Apparatus and procedures

The experimental setup of experiments 1 and 2 is illustrated in Fig. 1a. Participants sat at a table with their heads positioned in a fixed chin rest. To control the timing of visual presentation, participants wore liquid-crystal shutter goggles (PLATO, Translucent Technologies Inc., Toronto, Ontario, Canada, cf. Milgram, 1987). To present the acoustic start signal and shield from possible sounds of stimulus placement, participants wore headphones with isolation against ambience attenuation of 35 dB (beyerdynamic, DT 770 M 80 Ω , Heilbronn, Germany). In all experiments, target objects were blocks of rigid plastic that were 20, 30, 40, 50, 60 and 70 mm in length and 15 mm in width and depth. They were loosely attached lengthwise at a 40° sloped platform.

At the beginning of each trial, participants were asked to place their right index finger and thumb pinched together at a start position 29 cm in front of the target object. When the experimenter pressed a button, the shutter goggles became transparent to enable full vision of a single object lying on the sloped platform. In all experiments, the start of the response was indicated by a single 1000 Hz tone after an unpredictable time interval with a mean of 1200 ms. This time interval consisted of a fixed interval of 960 ms and an additional random duration drawn from an exponential distribution with a mean of 240 ms. (The exponential distribution was used because of its memoryless property, which is the property that the probability to wait a time interval *t* does not depend on the time *s* that already elapsed before the time interval *t*, making the start tone unpredictable in terms of the time that had already elapsed). In experiment 1, the start tone indicated the start of manual estimation. Then the participants moved their right hand approximately 5 cm to the right of the start position and accomplished manual estimation as accurately and spontaneously as possible by indicating the visual size of the object with the span between index finger and thumb. Movement onset immediately caused the shutter goggles to close preventing any sight on the object during manual estimation (i.e., open-loop manual estimation; Haffenden and Goodale, 1998). The ME in this experiment and experiment 3 was confirmed by the participant by pressing a button with the left hand. If the button press did not occur within 2.5 s after the start tone or movement velocity between index finger and thumb at the time of the button press was larger than 30 mm/s (Franz, 2003), the trial was considered invalid and repeated at a random, later time.

¹ To our knowledge, it is the first time that the MGA of the grasping response that follows manual estimation (post-estimation-grasping) is measured, although it has been used in many studies as a standard means to provide haptic feedback during ME (Ganel et al., 2008a; Haffenden and Goodale, 1998; Heath et al., 2011; Holmes et al., 2011). We are aware that post-estimation-grasping differs from normal grasping (i.e., without manual estimation in advance). In our experiments the start of post-estimation-grasping is defined as the time when the manual estimation is made. Thus, the start aperture of post-estimation-grasping equals the ME, which is usually dependent on object size. For this reason and due to the fact that manual estimation and post-estimation-grasping are two responses at one stimulus presentation, both responses cannot be considered as independent. However, precisely because manual estimation and the following grasping response are two different responses to the same stimulus presentation, in our view, the comparison between both responses is interesting – especially if they nevertheless show different behaviors in our results.

Immediately after the confirmation of the ME, that is, without returning to the start position, participants grasped the object lengthwise with index finger and thumb of the right hand (postestimation-grasping). This grasping procedure was performed to establish a comparable situation regarding the use of haptic feedback between the manual estimation tasks of experiment 1 and 3 and the grasping tasks of experiment 2 and 4. This is a standard procedure used in previous investigations (e.g., Ganel et al., 2008a; Haffenden and Goodale, 1998; Heath et al., 2011; Holmes et al., 2011). After lifting the object and putting it on the desk in front of the sloped platform participants returned their finger and thumb to the start position. The goggles remained closed until the experimenter set up the next object and started the following trial. In all experiments, the six target objects were presented randomly and each of the target objects was repeated 5 times during practice trials (i.e., 30 trials) and 20 times during experimental trials (i.e., 120 trials).

2.1.4. Data analysis

An Optotrak Certus (Northern Digital Inc., Canada) with a sampling rate of 200 Hz resulting in a temporal resolution of 5 ms was used to record the trajectories of the infrared emitting diodes (IREDs). Three IREDs were placed on the platform to build up a spatial reference frame. Further two IREDs were fixed with adhesive putty (UHU-Patafix, UHU GmbH, Bühl, Germany) on the finger nail of index finger and thumb (see Fig. 1c). Control of stimulus presentation and data recording was obtained with the Psychophysics Toolbox (Brainard, 1997) and the Optotrak Toolbox by V. H. Franz (http://webapp6.rrz.uni-hamburg.de/allpsy/vf/Opto trakToolbox) within Matlab (The MathWorks, Natick, MA, USA).

In all experiments, movement onset was determined when at least one IRED crossed a sphere with a radius of 40 mm around the start position and movement velocity in at least one IRED exceeded 0.025 m/s. The ME in experiment 1 and experiment 3 was determined as the distance between the IRED of the index finger and thumb at the time when participants pressed the button to confirm their manual estimation. In experiment 1 and experiment 3, the MGA_{post-est} was defined as the peak distance between the IREDs of index finger and thumb within the time of the ME and movement offset. In all experiments, movement offset was determined when at least one finger IRED reached the area within 80 mm around the center of the object position and less than 5 mm above the platform. In all experiments, a trial was considered invalid and repeated randomly later in the experiment if movement onset occurred before the start signal or if the IRED signal happened to be occluded. In all experiments, practice trials were performed to give the participant the opportunity to get used to the instructions and the procedure of the tasks in the visual as well as the more unfamiliar semantic conditions. Practice trials were not included into our analyzes to avoid outliers in the responses due to a participant's uncertainty about the task procedure. Nonetheless, we did analyzes including practice trials, which yielded essentially the same outcomes.

The mean, standard deviation, and the skewness (Type 2; for details see Joanes and Gill, 1998) of ME as well as $MGA_{post-est}$ were calculated for each object size for each participant. To determine the scaling of these measures across object size, linear regressions were fitted for each participant. One-sample *t*-tests were used to test the slopes of these within-participants regressions.

Statistical analyzes of all experiments were conducted using R (R Core Team, 2014). In all experiments, for all statistical analyzes, a significance level of α =0.05 was applied and *p*-values of 0.001 or less are depicted as *p* < 0.001. Between-participants means and corresponding standard errors are depicted as mean ± 1SEM. For the linear regressions, the parameter *b* always corresponds to the slope.

2.2. Results and discussion

The scaling of the mean responses across object size of visually guided manual estimation and post-estimation-grasping are presented in the top center and right panels of Fig. 2a. The ME increased linearly as a function of object size, t(14)=25.97, p < 0.001, $b=1.014 \pm 0.039$. This means that ME scales nearly perfectly with object size when using visual size information. The mean of MGA_{post-est} also increased linearly with object size, t(14)=27.07, p < 0.001, $b=0.85 \pm 0.031$.

The standard deviation of ME increased linearly with object size, t(14)=9.07, p < 0.001, $b=0.063 \pm 0.007$ (see top center panel of Fig. 2b). Thus, we replicated the finding of previous studies showing that visually guided manual estimation follows Weber's law (Ganel et al., 2008a; Heath et al., 2011; Holmes et al., 2011; Holmes and Heath, 2013). The within-participants standard deviation of MGA_{post-est} did not scale with object size, t(14)=0.31, p=0.764, $b=0.004 \pm 0.013$ (see top right panel of Fig. 2b). Thus, visually guided post-estimation-grasping violates Weber's law.

Note that in this experiment the post-estimation-grasping response was memory-based. This is because the shutter goggles were closed on average 860 ms (SEM=61 ms) before the visual size was estimated manually and the post-estimation-grasping response could be started. As a consequence, there was a temporal delay between the last available sensory experience and the start of the post-estimation-grasping response. Our post-estimationgrasping could therefore be considered a form of memory-based grasping, which means we were not able to replicate the finding that memory-based grasping follows Weber's law (Ganel et al., 2008a, 2008b). This is even more surprising given that post-estimation-grasping immediately followed ME (see also footnote 1).

Although there were negative slopes of the scaling of the skewness of ME, $b = -0.0055 \pm 0.0045$ (see top center panel of Fig. 2c), and MGA_{post-est}, $b = -0.007 \pm 0.0038$ (see top right panel of Fig. 2c), they did not reach significance for either ME,



Fig. 1. Experimental setup of (a) visual conditions of experiment 1 and 2 and (b) semantic conditions of experiment 3 and 4. Note that in the semantic conditions a covering panel was mounted to prevent the participant from viewing the object. (c) Infrared emitting diodes were fixed at finger and thumb to record the trajectories of the grasping movement.



Fig. 2. Results of the (a) mean, (b) standard deviation, and (c) skewness of the responses in experiments 1–4. Regression analyzes of the (a) mean, (b) standard deviation, and (c) skewness of the responses in Grasping (left panels), Manual estimation (center panels), and Post-estimation-grasping that follow manual estimation (right panels) over object size in the visual conditions (top panels) and the semantic conditions (bottom panels). The data points are pooled over subjects. All error bars depict \pm 1SEM (between subjects). (a) Note that the mean responses of Grasping, Manual estimation, and Post-estimation-grasping scale quite well with object size in the visual as well as in the semantic conditions. (b) The standard deviation in the grasping tasks (Grasping, Post-estimation-grasping) does not scale with object size in the visual condition, and thus violates Weber's law. The standard deviation of Manual estimation, in contrast, increases with object size in the semantic conditions, and thus violates Weber's law in both cases. (c) Positive skewness values denotes distributions that are skewed toward the left (i.e., larger right tail) and negative skewness values denotes distributions that are skewed toward the left (i.e., larger left tail). Descriptively, the skewness scaled negatively with object size in all tasks and conditions. The slope of this negative relationship became significant in visually guided grasping, semantically guided grasping, semantically guided grasping tasks (Center panels), and the mean level of the skewness between the grasping tasks (left panels) and the manual estimation tasks (center panels), which indicates larger influences of ceiling effects in grasping than in manual estimation. This difference cannot be seen when comparing manual estimation and post-estimation-grasping.

t(14) = -1.22, p = 0.241, or MGA_{post-est}, t(14) = -1.83, p = 0.088. Thus, although descriptively there is a pattern of negative scaling in both tasks (which is also consistent with the skewness scaling pattern in the following experiments), the results of our statistical analyzes are not sufficient to clarify whether there are ceiling effects in visual guided manual estimation or post-estimation-grasping.

3. Experiment 2

In experiment 2, we wanted to replicate the finding that Weber's law is violated during visually guided grasping. Participants grasped the six target objects directly (i.e., without estimating its size in advance). Visual information about object size was provided prior to movement onset. For each participant at each object size, the mean, standard deviation, and skewness of the MGA of the grasping response were determined. An increase of the withinparticipants standard deviation of the MGA across object size would indicate the presence of Weber's law.

3.1. Methods

3.1.1. Participants

Fifteen new participants (8 females, 7 males; age range: 19–33 years) took part in the second experiment.

3.1.2. Apparatus, procedure, and data analysis

The same experimental setup as in experiment 1 was used. In contrast to experiment 1, participants grasped the objects immediately without estimating its size. At the beginning of each trial, participants placed their right index finger and thumb at the start position. When the experimenter pressed a button, the shutter goggles became transparent to enable full vision on a single object lying on the sloped platform. After the start signal, participants grasped the object lengthwise with index finger and thumb of the right hand. Movement onset immediately caused the shutter goggles to close preventing any sight of the object during the grasping response (i.e., open-loop grasping). After lifting the object and putting it on the desk in front of the sloped platform, the participants returned their finger and thumb to the start position. The goggles remained closed until the experimenter set up the next object and started the following trial manually. The MGA in experiment 2 and experiment 4 was defined as the peak distance between the IREDs of index finger and thumb within the time of the movement onset and offset.

3.2. Results and discussion

MGA increased linearly with object size, t(14)=35.55, p < 0.001, $b = 0.835 \pm 0.023$ (see top left panel of Fig. 2a). The within-participants standard deviation of MGA did not scale with object size, t(14) = -1.73, p = 0.106, $b = -0.018 \pm 0.01$ (see top left panel of Fig. 2b). Thus, we replicated the finding of previous studies showing that visually guided grasping violates Weber's law (Ganel et, 2008a, 2008b; Hadad et al., 2012; Heath et al., 2012, 2011; Holmes and Heath, 2013; Holmes et al., 2013, 2011). Although not statistically significant, the scaling of the standard deviation of MGA was slightly negative. Interestingly, other studies report similar negative values of the scaling that approach statistical significance (Holmes et al., 2011) or reach statistical significance (Pettypiece et al., 2010). The skewness of the MGA scaled negatively with object size, t(14) = -2.23, p = 0.043, $b = -0.0078 \pm 0.0035$ (see top left panel of Fig. 2c). In addition, all values of the skewness of the MGA for objects larger than 30 mm were negative (larger left tail). Thus, there are indications of ceiling effects in the motor response of visually guided grasping.

Ceiling effects might constrain the variability of the responses especially for larger object sizes, which would lead to a reduction of the scaling of the standard deviation. This might provide an alternative explanation for the apparent violation of Weber's law in visually guided grasping (see discussion below).

4. Experiment 3

We performed experiment 3 to test whether non-visually, semantically guided manual estimation follows Weber's law. Without any visual information about objects, participants manually estimated the size of objects using semantic information (i.e., numbers presented over headphones indicating the size of unseen objects). As in experiment 1, participants grasped every object immediately after manual estimation (post-estimation-grasping).

According to Weber's law, we would expect an increase of the within-participants standard deviation of the ME across object size. For post-estimation-grasping we would also expect Weber's law (according to the relative-absolute and the size-position account) because it is even more memory-based as in the visual condition of experiment 1.

4.1. Methods

4.1.1. Participants

Fifteen new participants (9 females, 6 males; age range: 19–36 years) were included in the data analysis. One was excluded because she reported not being able to follow the instructions.

4.1.2. Apparatus, procedure, and data analysis

In experiment 3 and 4 we slightly modified the setup of experiments 1 and 2 by mounting a covering panel approximately 26 cm in front of participant's eyes to prevent the participant from viewing the target objects (see Fig. 1b). Apart from this, the experimental setup in experiments 3 and 4 was the same as in experiments 1 and 2.

At the beginning of each trial, participants were asked to place their right index finger and thumb pinched together at the start position. When the experimenter pressed a button, the shutter goggles became transparent to enable vision of the sloped platform and the panel covering the object. Thus, the participant could see the setup but not the object. 500 ms later, a single spoken number was presented via headphones. Participants were instructed to use the number as an indicator of the object's length in centimeters, e.g. the spoken "five" meant an object length of 5 cm. In addition, they were explicitly instructed to use the auditorily presented number to estimate the physical size of the object they would be grasping immediately after their estimation. After the start signal, participants estimated the size of the covered object manually. In all other aspects, the procedure was identical to experiment 1.

4.2. Results and discussion

The scaling of the mean responses across object size of semantically guided manual estimation and post-estimation-grasping is depicted in the bottom center and right panels of Fig. 2a. ME increased linearly as a function of object size, t(14)=16.67, p < 0.001, $b = 1.43 \pm 0.086$. MGA_{post-est} also increased linearly with object size, t(14)=14.88, p < 0.001, $b = 1.088 \pm 0.073$.

The within-participants standard deviation of ME increased linearly with object size, t(14)=2.87, p=0.012, $b=0.038 \pm 0.013$ (see bottom center panel of Fig. 2b). Thus, semantically guided manual estimation follows Weber's law. Although the slope of the linear regressions of the standard deviation of ME across object

size was significant, the relationship appears to be rather logarithmic than linear. We will discuss this result in the context of the skewness of ME in the next paragraph of this section. The standard deviation of MGA_{post-est} decreased linearly as a function of object size, t(14)=-2.82, p=0.014, $b=-0.053 \pm 0.019$ (see bottom right panel of Fig. 2b). Thus, post-estimation-grasping not only violates Weber's law, but we even found a negative scaling of the standard deviation of MGA_{post-est}. As mentioned in Section 3.2, negative scaling was also found in other studies (Holmes et al., 2011; Pettypiece et al., 2010). We will discuss this finding in Section 7.

The skewness of ME scaled negatively with object size, t(14) = -4.35. p < 0.001. b = -0.0136 + 0.0031 (see bottom center panel of Fig. 2c). Additionally, all values of the skewness of the ME for objects larger than 40 mm were negative (larger left tail). This finding indicates that there might be ceiling effects in the responses of semantically guided manual estimation as well. The influence of ceiling effects could explain why the scaling of the standard deviation seems to be logarithmic rather than linear. That is, for larger object sizes ceiling effects might have prevented an increase of the standard deviation in semantically guided manual estimation. The skewness of MGApost-est scaled negatively with object size, t(14) = -4.51, p < 0.001, $b = -0.014 \pm 0.0031$ (see bottom right panel of Fig. 2c). All values of the skewness of the MGA_{post-est} for objects larger than 40 mm were negative. Thus, ceiling effects might have affected the scaling of the standard deviation in semantically guided post-estimation-grasping. Whereas current explanations of the violation of Weber's law in grasping would only predict a zero-scaling of the standard deviation, ceiling effects in the motor responses could also account for a decrease of the standard deviation across object sizes (see below in Sections 6.3 and 7).

5. Experiment 4

In experiment 4, we tested whether non-visually, semantically guided grasping follows Weber's law. Participants grasped objects covered from view using auditorily presented numbers indicating the size of these objects. According to Weber's law, we would expect an increase of the within-participants standard deviation of the MGA across object size.

5.1. Method

5.1.1. Participants

Fifteen new volunteers (10 females, 5 males; age range: 20–39 years) participated in the experiment.

5.1.2. Apparatus, procedure, and data analysis

The same setup as in experiment 3 was used in experiment 4 (see Fig. 1b). At the beginning of each trial, participants were asked to place their right index finger and thumb pinched together at the start position. When the experimenter pressed a button, the shutter goggles became transparent to enable vision of the sloped platform and the panel covering the object. Thus, the participant saw the setup but could not see the object. 500 ms later, a single spoken number was presented via headphones. Participants were instructed to use the number as an indicator of the object's length in centimeters, e.g. the spoken "five" meant an object length of 5 cm. After the start signal, the participants grasped the object. In all other aspects, the procedure was identical to experiment 2.

5.2.. Results and discussion

MGA increased linearly as a function of object size, t(14) = 19.51, p < 0.001, $b = 0.709 \pm 0.036$ (see bottom left panel of Fig. 2a). Thus,

semantic information about object size can be used effectively to guide the grasping of covered objects. Interestingly, the slope is comparable with slopes found in studies on visually guided grasping. In the meta-analysis of Smeets and Brenner (1999), about half of the studies on visually guided grasping reported slopes lower than 0.8 and a fifth of the studies reported slopes lower than 0.7.

The standard deviation of the MGA decreased significantly with object size, t(14) = -5.75, p < 0.001, $b = -0.064 \pm 0.011$ (see bottom left panel of Fig. 2b). Accordingly, semantically guided grasping does not follow the prediction of Weber's law. Interestingly, this decrease of the standard deviation of the MGA with object size was also found for semantically guided post-estimation-grasping.

The skewness of MGA scaled negatively with object size, t (14)= -3.46, p=0.004, b= -0.0151 \pm 0.0044 (see bottom left panel of Fig. 2c). In addition, all values of the skewness of the MGA for objects larger than 20 mm were negative. This finding indicates that there might be ceiling effects in the motor response of semantically guided grasping, which can explain the decrease of the standard deviation across object size (see below in Sections 6.3, 6.4, and 7).

6. Comparisons between experiments

In experiments 1–4 we tested the scaling of the mean, standard deviation, and skewness in three tasks (grasping, manual estimation, and post-estimation-grasping) and two conditions (visual and semantic). We found that the mean scaled well with object size in all tasks and conditions, which means that the information about object size could be used effectively to guide the responses in all tasks and conditions. The standard deviation increased with object size for manual estimation (thus following Weber's law), but not for grasping or post-estimation-grasping (thus violating Weber's law). The scaling of the skewness was negative in visually guided grasping and in all three semantically guided tasks. Moreover, the skewness was found to scale negatively with object size were negative, which indicates that there might be ceiling effects in grasping and the semantic tasks.

In addition to the aforementioned analyzes, our experimental design also allows for direct comparisons of the effects of task and information conditions between experiments. Two ANOVAs were performed. First, to test the task effect between manual estimation and grasping, we analyzed the data of all experiments using a 2×2 ANOVA design, with task (manual estimation, grasping) and information (visual, semantic) as between-subjects variables. Second, to test the task effect between manual estimation and post-estimation-grasping, we analyzed the data of experiment 1 and 3 using a mixed 2×2 ANOVA design, with task (manual estimation, post-estimation-grasping) as a within-subjects variable and information (visual, semantic) as a between-subjects variable.

6.1. Effects on the scaling of the standard deviation

First, we asked whether there is a difference in the scaling of the standard deviation between manual estimation and the two grasping tasks (grasping, post-estimation-grasping), and whether this scaling is modulated by the type of information about object size (visual, semantic). An analysis of the scaling of the standard deviation between manual estimation and grasping yielded a main effect of task F(1,56)=73.7, p < 0.001, a main effect of information F(1,56)=11.18, p=0.001, and no interaction between task and information F(1,56)=1.03, p=0.315. Scaling of ME (b=0.05) was

overall larger than for MGA (b=-0.041). Scaling in the visual conditions (b=0.023) was larger than in the semantic conditions (b=-0.013). The analysis of the scaling of the standard deviation between manual estimation and post-estimation-grasping revealed a main effect of task F(1,28) = 37.94, p < 0.001, a main effect of information F(1,28) = 7.6, p = 0.017, and no interaction between task and information F(1,28)=1.74, p=0.198. Scaling in ME (b=0.05) was overall larger than in MGA_{post-est} (b=-0.025). Scaling in the visual conditions (b=0.033) was larger than in the semantic conditions (b = -0.008). Thus, the scaling of the standard deviation was larger in manual estimation than in grasping and post-estimation-grasping. Interestingly, also the type of information affected the scaling of the standard deviation. In both between- and within-subjects task comparisons, the scaling was larger in the visual than the semantic conditions. These results will be discussed in the following subsections of Sections 6 and 7.

6.2. Effects on the mean standard deviation

Weber's law may be masked by late noise. Late noise will reduce the measured scaling of the standard deviation, thus resulting in an underestimation of Weber's fraction. Larger late noise in grasping than in manual estimation might explain the apparent absence of Weber's law in grasping. To test for this possibility, we tested whether there is a difference in the mean standard deviation between manual estimation and the grasping tasks (grasping, post-estimation-grasping). Moreover, we tested for differences in the mean standard deviation between visual and semantic conditions, which might explain differences in the scaling of the standard deviation between these conditions.

The analysis of the mean standard deviation between manual estimation and grasping yielded no main effect of task F(1,56)= 1.04, p=0.312, a main effect of information F(1,56)=27.49, p < 0.001, and no interaction between task and information F (1,56)=0.35, p=0.555. The mean standard deviation in the visual conditions (6.17 mm) was smaller than in the semantic conditions (8.62 mm). Because there is no main effect of task, there is no evidence of a larger extra source of late noise in grasping compared with manual estimation, so this cannot explain the difference in the scaling of the standard deviation found between the tasks. The main effect of information will be discussed at the end of this section.

The analysis of the mean standard deviation between manual estimation and post-estimation-grasping yielded a main effect of task F(1,28)=4.89, p=0.035, a main effect of information F(1,28)=10.02, p=0.004, and no interaction between task and information F(1,28)=1.18, p=0.287. The mean standard deviation of the ME (7.63 mm) was smaller than for the MGA_{post-est} (8.54 mm). The mean standard deviation in the visual conditions (6.95 mm) was smaller than in the semantic conditions (9.23 mm). Thus, there is evidence of larger late noise in post-estimation-grasping compared with manual estimation. However, the difference in the late noise is rather small and while it might contribute to the difference in the scaling of the standard deviation between both tasks, it is likely not large enough to explain the absence of Weber's law in grasping, but not in manual estimation.

The larger mean standard deviation in the semantic conditions (i.e., in both between- and within-subjects task comparisons) might be a consequence of larger late noise in the semantic conditions compared with the visual conditions. A difference in the late noise might have contributed to the difference in the scaling of the standard deviation we found between the two conditions.

6.3. Effects on the scaling of skewness

As suggested above, ceiling effects in the motor responses

might reduce the scaling of the standard deviation as well. Because the mean responses are usually larger in grasping than in manual estimation, we expect larger influences of ceiling effects in the grasping tasks than in manual estimation (indicated by more negative scaling of the skewness). Furthermore, differences in the scaling of the skewness might also explain differences in the scaling of the standard deviation between visual and semantic conditions.

In the analysis of the scaling of the skewness between manual estimation and grasping there was no main effect of task F(1,56) = 0.23, p = 0.632, no main effect of information F(1,56) = 3.85, p = 0.055, and no interaction between task and information F(1,56) = 0.01, p = 0.925. Note that the main effect of information, that is, the difference in the scaling of the skewness between the visual conditions (b = -0.0066) and semantic conditions (b = -0.0143) did approach significance.

In the analysis of the scaling of the skewness between manual estimation and post-estimation-grasping there were no significant differences between tasks F(1,28)=0.08, p=0.777, between information conditions F(1,28)=3.69, p=0.065, and no interaction between task and information F(1,28)=0.02, p=0.884. Again the difference in the scaling of the skewness between visual conditions (b=-0.0063) and semantic conditions (b=-0.0137) approached significance.

A smaller scaling of the skewness in the semantic conditions compared with the visual conditions would indicate larger ceiling effects in the semantic conditions. These larger ceiling effects could in turn explain the smaller slopes of the scaling of the standard deviation in the semantic conditions compared with the visual conditions. Larger ceiling effects in the semantic conditions relative to the visual conditions might explain that there was a negative scaling of the standard deviation in semantically guided grasping and post-estimation-grasping, but not in visually guided grasping and post-estimation-grasping.

6.4. Effects on the mean skewness

Differences in the influence of ceiling effects can be also indicated by differences in the mean skewness of the response distributions. Because we hypothesized that there might be larger ceiling effects in grasping than in manual estimation, we would expect the skewness to be more negative in the grasping tasks than in manual estimation. Differences in the mean skewness between visual and semantic conditions, might also explain differences in the scaling of the standard deviation between these conditions.

The analysis of the mean skewness between manual estimation and grasping yielded a main effect of task F(1,56)=10.54, p=0.002, no main effect of information F(1,56)=0.11, p=0.738, and no interaction between task and information F(1,56)=0.77, p=0.383. The mean skewness was larger for the ME (0.062) than the MGA (-0.147). That is, the distributions of the responses in grasping are generally more skewed toward the left than in manual estimation, indicating that there are larger ceiling effects in grasping than in manual estimation. A differential influence of ceiling effects might explain that there is a failure of Weber's law in grasping, but not in manual estimation.

In the analysis of the mean of skewness between manual estimation and post-estimation-grasping there were no significant differences between tasks F(1,28)=0.43, p=0.517, between information conditions F(1,28)=0.2, p=0.657, and no interaction between task and information F(1,28)=0.01, p=0.937. Thus, unlike the between-subject comparison between manual estimation and grasping, the within-subject comparison of the mean skewness between manual estimation and post-estimation-grasping revealed no indications of differences in the influence of ceiling

effects between both tasks.

7. General discussion

Our results show a dissociation regarding Weber's law between manual estimation and grasping in the visual as well as in the semantic conditions: manual estimation always follows Weber's law, whereas grasping always violates Weber's law: even if only semantic information is available and even if grasping is performed after manual estimation.

Current approaches to explaining the violation of Weber's law in grasping cannot explain the violation of Weber's law we found in semantically guided grasping. To explain the violation of Weber's law in visually guided grasping, the relative-absolute coding account assumes that grasping is based on absolute metrics (Ganel et al., 2008a) and the size-position account assumes that grasping is based on egocentric position instead of size information (Smeets and Brenner, 2008). However, according to both accounts, the violation of Weber's law in visually guided grasping is dependent on the availability of real-time sensory information about the object (i.e., concrete sensory information about the object at the time of movement programming); without real-time sensory information, grasping should be based on relative size information and follow Weber's law. In semantically guided grasping real-time sensory information about the object is not available. Thus, according to both accounts, semantically guided grasping should be based on relative size information and follow Weber's law. Thus, neither the relative-absolute coding account nor the size-position account can explain the violation of Weber's law we found in semantically guided grasping.

The violation of Weber's law in semantically guided grasping cannot be attributed to a general violation of Weber's law when using semantic information, because semantically guided manual estimation, in contrast, follows Weber's law. Moreover, empirical evidence that symbolic representations of numbers follow Weber's law is provided by the size effect (i.e., for equal distance, the decreasing ability to discriminate between two numbers with increasing size of these numbers; Dehaene et al., 1998; Fias et al., 2003). The size effect has been demonstrated for digits (Buckley and Gillman, 1974; Parkman, 1971) and written number names (Foltz et al., 1984).

We also found that grasping that follows manual estimation (post-estimation-grasping) violates Weber's law in the visual as well as in the semantic condition, just like standard grasping. It is important to note that even in the visual condition, post-estimation-grasping is a delayed, memory-based response. Thus, at the time of movement programming, real-time information about the object was not available. Because both explanations, the relativeabsolute coding account and the size-position account, assume the availability of real-time information about the object to account for the violation of Weber's law, they cannot explain the violation of Weber's law of post-estimation-grasping in the semantic or visual condition. Because post-estimation-grasping in the visual condition is memory-based, the violation of Weber's law in the visual condition contradicts the finding that memory-based, visually guided grasping follows Weber's law (Ganel et al., 2008a, 2008b). However, this finding could not be replicated by other authors as well (Holmes et al., 2011).

We found an influence of the available information on the scaling of the standard deviation of the responses across object size. That is, there was a larger scaling in the visual than in the semantic conditions. In our view, there are two possible non-exclusive explanations of this result. First, this effect could be attributed to differences in the late noise between visual and semantic conditions. Although the scaling of the standard deviation was smaller in the semantic conditions than in the visual conditions, the mean noise level was considerably larger in the semantic conditions. Thus, there are indications of larger late noise in the semantic conditions, which might lead to a difference in the scaling of the standard deviation, that is, a greater underestimation of Weber's law in the semantic conditions. The negative scaling of the responses we found in semantically guided grasping and post-estimation-grasping, however, cannot be explained solely by the influence of late noise. This negative scaling and a further reason for the difference in the scaling of the standard deviation between visual conditions and semantic conditions might be the presence of ceiling effects. Ceiling effects, which may arise as a consequence of the natural limitation of the span between index finger and thumb and an avoidance of uncomfortable finger apertures, would bound response variability especially when estimating or grasping larger object sizes, with larger responses, and especially when uncertainty is high. Consistent with this idea, we found larger overall means and standard deviations of the responses in the semantic than in the visual conditions. In addition, there were indications that the scaling of the skewness in the semantic conditions was more negative than in the visual conditions. This was found for the comparison of manual estimation with grasping as well as manual estimation with post-estimation-grasping. Thus, ceiling effects could be more pronounced in the semantic than in the visual conditions, which would explain a lower scaling of the standard deviation in the semantic than in the visual conditions. Thus, differential influences of ceiling effects between visual and semantic conditions might have prevented an increase of the standard deviation of the ME for larger object sizes in the semantic condition, but not in the visual condition. Additionally, it might even explain that the scaling of the standard deviation of the grasping tasks were negative in the semantic conditions, but not in the visual conditions.

We were able to show that, whether visual or semantic information is provided, manual estimation follows Weber's law and grasping and post-estimation-grasping violate Weber's law. Thus, the dissociation regarding Weber's law between manual estimation and grasping as well as between manual estimation and postestimation-grasping is independent of the availability of real-time information as well as visual information about the object.

To explain the dissociation, other differences between manual estimation and grasping should be taken into account. There are several possible differences that might affect the scaling of the standard deviation selectively.

First, apart from sensory noise according to Weber's law, there is late noise (i.e., additional noise in the task, which is not due to Weber's law; e.g., motor noise) in the measured responses, which might differ between both tasks. Late noise is a critical factor that should be considered because it reduces the measured slope of the scaling of the standard deviation. That is, late noise leads to an underestimation of Weber's law. Thus, even if there is no difference in the sensory noise according to Weber's law (i.e., same Weber's fraction), differences in late noise could cause a difference in the measured slope of the scaling of the standard deviation between manual estimation and grasping. In this study, we did not find a difference in the mean noise level between grasping and manual estimation and only a slightly larger mean noise level in post-estimation-grasping compared with manual estimation. Thus, we found no evidence of a large extra source of noise in the grasping tasks compared with manual estimation, which means this cannot explain our failure to find Weber's law in grasping, but not in manual estimation. Nevertheless, a potential differential influence of late noise on the measured slope in manual estimation and grasping should always be considered and tested before interpreting the difference in the scaling of the standard deviation between the tasks.

Second, manual estimation and grasping differ in the necessity to act upon the object. To complete the task successfully, no action upon the actual, physical object is necessary in manual estimation. In grasping, in contrast, the successful action upon the physical object is an essential part of the task and this necessity to act upon the object might affect the motor response. For instance, to avoid failure in grasping, adding a safety-margin between object size and MGA is highly functional. In manual estimation, this is not necessary because there is no object to act upon. Individual estimates that are smaller than the object's size do not compromise a successful completion of the task and the mean ME theoretically could match the object's size. Thus, it is not surprising that the mean response is usually larger in grasping than in manual estimation. As a consequence, ceiling effects might be more pronounced in grasping than in manual estimation. And indeed, we did find evidence for larger ceiling effects in grasping than in manual estimation. That is, the distributions of the responses in grasping were on average more skewed toward the left than in manual estimation. This was found in the visual as well as semantic conditions. Larger ceiling effects in grasping than in manual estimation could explain the apparent dissociation regarding Weber's law. Note however, that we did not find differences in the skewness of the responses between manual estimation and postestimation-grasping. Therefore, further work is required to investigate the potential difference of ceiling effects between both tasks as well as the influence of ceiling effects on the scaling of the standard deviation and skewness of the responses in more detail. Interestingly, the mean responses in grasping tasks without necessity to act upon the object, like pantomimed-grasping (Holmes et al., 2013) or 2D grasping (Holmes and Heath, 2013), approximates those in manual estimation and, thus, are considerably smaller than in normal grasping. As a consequence, ceiling effects might be less pronounced in pantomimed-grasping or 2D grasping than in normal grasping, which could explain why the standard deviation in pantomimed-grasping and 2D grasping increases across object size, but not in normal grasping. Moreover, not only when responses are larger would ceiling effects be more pronounced. As mentioned above, ceiling effects might reduce the scaling of the standard deviation especially when objects are large and the response variability is high. Consistent with this idea is the finding that 2D grasping apparently violated Weber's law when larger objects (6.6–9.6 cm) were presented and the response variability was high (Christiansen et al., 2014).

Third, there might be differences in the use of haptic feedback between manual estimation and grasping. Whereas an additional grasping response (i.e., post-estimation-grasping) is necessary to provide something like haptic feedback in manual estimation, haptic feedback is automatically available in grasping at the time of the contact with the object. Strong evidence that haptic feedback about object size can influence the grasping response comes from patient studies (Gentilucci et al., 1994; Schenk, 2012; but see also Whitwell and Buckingham, 2013; Whitwell et al., 2014) and studies with healthy participants (Bingham et al., 2007; Gentilucci et al., 1997). To establish a comparable situation regarding the availability of haptic feedback we and other authors (Ganel et al., 2008a; Heath et al., 2011; Holmes et al., 2011) provided haptic feedback after manual estimation by instructing the participant to grasp the object immediately after manual estimation. However, even if haptic feedback is available in manual estimation and grasping, there might be differences in the trial-by-trial update (i.e., learning) of haptic feedback information between both tasks. To date, there are only few perturbation studies showing that haptic feedback about object size can lead to learning across trials in visually guided grasping (Coats et al., 2008; Gentilucci et al., 1995; Säfström and Edin, 2004, 2008; Weigelt and Bock, 2007). Unfortunately, these studies use relatively large (artificial)

perturbations of haptic object size. To study more natural, lowlevel update mechanism of haptic feedback about object size in grasping or manual estimation (and to be able to compare them), newly developed methods of feedback perturbation and data analysis should be applied (e.g., Hudson and Landy, 2012). To our knowledge, the influence of haptic feedback on manual estimation has neither been investigated nor compared with the influence of haptic feedback on grasping.

8. Conclusions

The finding that semantically guided grasping violates Weber's law although semantically guided manual estimation adheres to Weber's law cannot be explained by the relative–absolute coding or the size–position account. Other differences between manual estimation and grasping, such as the influence of late noise, ceiling effects, or haptic feedback should be studied to understand the apparent absence of Weber's law in grasping.

Acknowledgements

This work was supported by a Ph.D. scholarship within the International Graduate Research Training Group (No. IKG-1247) on Cross-Modal Interaction in Natural and Artificial Cognitive Systems (CINACS) from the German Research Foundation (DFG).

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