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On the Origin of Body-Related Influences on Visual Perception

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The human body and the potential to move it affect the way we perceive the world. Here we explored a possible origin of such action-specific effects on perception. Participants were asked to enclose a virtual object by movements of their index finger and thumb and judged either the actual finger-thumb distance or the size of the virtual object subsequently. The visual-haptic discrepancy that comes with such virtual grasping resulted in a mutual impact of visual and body-related signals: the visual judgments of object's size were attracted by the felt finger posture and vice versa, judged finger distance was attracted by the size of the grasped object. This pattern was observed in spite of a clear spatial separation between somatic and visual signals and was conceptually replicated using a virtual reaching paradigm. The results indicate that basic mechanisms of multisensory integration accompany the emergence of action-specific effects on perception.

Public Significance Statement

Previous research indicated body-related changes in visual perception of distant objects manipulated by motor actions. The present study explored whether well-studied principles of multimodal integration contribute to these phenomena. Our participants repeatedly enclosed a virtual rectangle by movements of their index finger and thumb and we measured their perception of the rectangle size and of the finger-thumb distance subsequently. Thereby the finger distance was either smaller or larger than the rectangle. The rectangle perception was biased toward the actual finger distance whereas the perception of the finger distance was biased toward the actual rectangle size. This result was observed even though the rectangle was at a substantial distance to the fingers. Moreover, a conceptually similar result was observed in a virtual reaching task. These results indicate that body-related changes in visual perception are a consequence of weighting and integration of multimodal signals which relate to the same external object.

Keywords: action-specific perception, multisensory integration, visual perception, body perception

It has been assumed for long that the body and its potential or real movement provide a basic reference for visual perception (Berkeley, 1709; cited in Scheerer, 1984). A bulk of recent empirical research provided results which were interpreted in accordance with this notion (see, e.g., Harris et al., 2015; Proffitt & Linkenauger, 2013; Witt, 2011a; Witt & Riley, 2014; for reviews). In a typical study, a certain variable related to the morphological, physiological, or action-related state of the body is experimentally manipulated (motor variable hereafter) and the effects of this manipulation on judgments of a certain visual attribute are examined. Finding that motor variables affect the visual estimate is often considered as indication that visual perception grounds in motor units. At present, this action-specific approach is not generally accepted and recently caused intensive debates (e.g., Firestone, 2013; Firestone & Scholl, 2015).

One reason for these debates relates to the still underspecified mechanisms which bring about influences of action on perception. Consider, for example, the fact that many reported effects are rather small in magnitude and are not proportional to the magnitude of the experimentally introduced body-related changes (cf. also Firestone, 2013). This cannot readily be explained by a direct (i.e., 1-to-1) scaling of early visual information in motor units. In the present study we asked whether mechanisms of multisensory integration could provide a theoretical basis to explain such influences of action on perception. We studied the impact of multisensory integration in a situation that conceptually corresponds to a setting often used to demonstrate action-related effects on perception, namely the perception of a distant object which is manipulated by variously transformed motor actions. By this approach we do not aim to dissociate action-specific accounts of perception from a multisensory approach, which are not necessarily mutually exclusive (cf. e.g., Atkins, Jacobs, & Knill, 2003). Also, we do not want to question that influences of action on perception were "real" (cf. Firestone & Scholl, 2015). Rather we want to bring into the debate a set of well-studied mechanisms that explain that and

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why action under certain conditions can actually change visual perception.

One such basic principle holds that multimodal signals are integrated in a statistically optimal fashion, whereby information is weighted based on its reliability (Ernst & Banks, 2002; see also e.g., Ernst & Bülthoff, 2004, for a review). Frequently, visual signals dominate presumably due to their higher reliability compared with other modalities. However, under certain conditions, the percept of a visible object feature may heavily be affected, for example, by the haptic perception of that object. Thus, this line of research strongly suggests that variables related to the body and its action can in principle affect what we see. Moreover, although the general experimental approach supporting this claim is often more sophisticated, it is still quite similar to that used in studies on action-specific perception: a body-related input is varied, for example, by the manipulation of the hand posture during grasping of a visible object, and the impact of this variation on the judgments of object's attributes is examined (e.g., Ernst & Banks, 2002).

Multisensory integration and action-specific influences on perception have been barely considered together so far because of apparently different paradigms used in these research domains. In studies on multisensory integration the origins of multimodal signals are usually in a close spatial correspondence while increasing spatial distance between visual and haptic signals typically decreases integration (Gepshtein, Burge, Ernst, & Banks, 2005). In studies on action-specific perception, in contrast, effects of motor variables are often observed in spite of a clear spatial separation between the body and the objects being judged. The primary goal of the present study was thus to show that body-related and visual signals can be integrated despite considerable spatial separation.

Some recent studies already indicate that multisensory integration can survive spatial separation under conditions of a systematic and predictable relation between redundant sensory signals (Rand & Heuer, 2013, 2016; Takahashi, Diedrichsen, & Watt, 2009; Takahashi & Watt, 2014). However, experimental conditions implemented in these studies did not match typical action-specific setups (see also Exp. 1). Nevertheless, these studies speak for flexibility of sensory integration and suggest that the signals are integrated based upon their distal causes rather than on spatial proximity (e.g., Takahashi & Watt, 2014; cf. also Körding et al., 2007). In other words, considered from a multisensory perspective, a body-related signal can have impact on the visual perception of an object if the (potential or real) consequence of the body's action has a similar spatial origin as the object itself. This precondition is fulfilled in many studies on action-specific perception.[1] There are thus good reasons to assume that multisensory integration plays a role in action-specific effects on perception (cf. also White, Shockley, & Riley, 2013). The present study aimed to explore this possibility.

Accordingly, we used a paradigm which can be considered as an instance of a multisensory setup as well as a rather usual setup for study of action-specific effects on perception in one series of the present experiments. Participants performed a task resembling virtual grasping of a visual object using their index finger and thumb. In particular, they moved a pair of cursors by their fingers until the cursors "grabbed" the object (i.e., touched the object at certain sites) and an auditory feedback appeared. The critical manipulation was related to the transformation of finger movements into the movements of visual feedback. The gain between the finger distance and object size was manipulated so that virtual grasping of one and the same object could be achieved either by smaller or larger hand openings corresponding to a larger and smaller gain respectively (see Figure 1, left part). Here, participants were asked to judge the size of the object while the impact of the varying hand posture was examined.

Although this experimental setup may not directly map onto all paradigms used to study action-specific perception, it includes all essential features of such paradigms. The general rationale behind the majority of action-specific studies on perception is to manipulate a variable related to body (such as effective arm length, bioenergetics costs, jumping ability etc.) and to measure the impact of this manipulation on visual perception as mentioned. The present setting follows the same logic: visual judgments of objects' size are collected following manipulation of a motor variable (related to finger movements) and the impact of this variable is examined. Thus, the present paradigm contains nothing special what can a priori separate it from studies discussed under the umbrella of action-specific perception.

Action-specific effects are often thought to reflect an influence of perceiver's action ability (e.g., Witt, 2011a; see also General Discussion). In the present setup a larger gain can be construed to increase the actual action ability because more and larger objects become (virtually) graspable with large as compared to small gain. Because an increase in action ability is typically associated with a decrease in perceived object's size (e.g., Linkenauger, Leyrer, Bülthoff, & Mohler, 2013; Linkenauger, Witt, & Proffitt, 2011; Taylor & Witt, 2010), a larger gain can be assumed to decrease the size estimate of the to be grasped object (cf. also Linkenauger, Bülthoff, & Mohler, 2015; Witt, 2011b; Witt & Proffitt, 2008; Witt, Proffitt, & Epstein, 2005; for related logic in distance perception). The same prediction can be derived from the multisensory approach because larger gains go along with smaller hand openings: an integration

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[1] For example, judgments of object's size depend on the quality and success of motor actions aimed at these objects (Cañal-Bruland & van der Kamp, 2009; Wesp, Cichello, Gracia, & Davis, 2004; Witt & Dorsch, 2009; Witt, Linkenauger, Bakdash, & Proffitt, 2008; Witt & Proffitt, 2005). The spatial position of the judged objects (such as of golf holes) in these studies is comparable with the spatial position of the effects caused by perceivers' actions (such as spatial positions of the balls after strokes). Consider also, for example, the observation that hills are judged as steeper when wearing a heavy backpack (e.g., Bhalla, & Proffitt, 1999). The consequence of the potential action here is climbing the hill (this is proposed to be a necessary condition for the effect to emerge). Accordingly, the visual stimulus (i.e., the hill) and the action effect have the same spatial origin. The same argument can be applied to related observations where certain body attributes, such as jumping ability, proved to affect judgments of certain features of visual objects, to which those attributes were assumed to be related (e.g., Taylor & Witt, 2010).

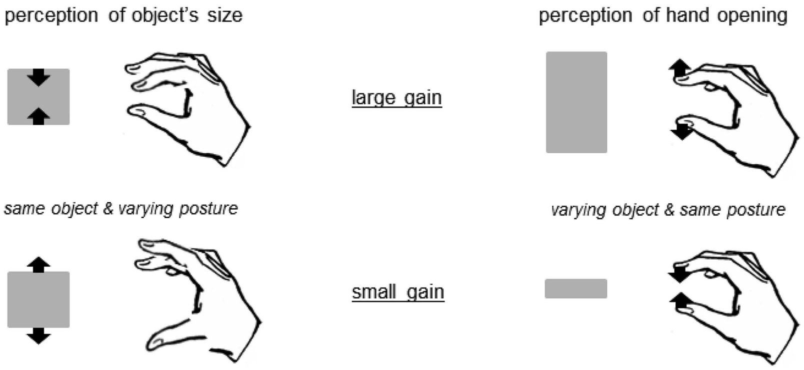

Figure 1. Rationale of the present experiments. Left: Identical objects should appear visually smaller when they can be grasped with a small hand opening (large gain) than when they can be grasped with a large hand opening (small gain). Right: Identical hand openings should appear larger, when they allow grasping visually large objects (large gain) than when they only allow grasping small objects (small gain).

of the posture with the visual object information can here result in a decrease of the perceived object' size.[2]

To recap, an impact of a body-related variable on perception is predicted by the action-specific account as well as by a multisensory account for the present setup. The multisensory perspective, however, makes the unique prediction that not only perceived object's size can be altered by hand opening, but also that the perception of the hand opening can be altered by the size of the grasped object: Grasping of a larger object can be expected to increase the perceived hand opening as compared with grasping of a smaller object. That is, one and the same process (multisensory integration) predicts two distinct behavioral effects. Thus, demonstrating both effects with a similar setup would provide evidence for sensory integration of body-related and visual signals. To explore this issue, different gains were assigned to different sizes of graspable objects in another series of experiments. That is, with a given hand opening either small (small gain) or large (large gain) objects could now be grasped (see Figure 1, right part). The task here was to estimate the perceived magnitude of the hand opening and the impact of the size of the grasped objects on this measure was examined.

Five experiments are reported below. In Experiment 1, multimodal integration was explored with a virtual grasping setup using a rather close spatial proximity between the origins of haptic and visual signals. Experiment 2 was a control experiment thought to confirm the existence of a small but reliable effect observed in Experiment 1. Experiments 1 and 2 revealed effects consistent with the multisensory integration account. In Experiment 3, a substantial spatial discrepancy was introduced between the visual and haptic signals. Nevertheless, the results remained comparable to Experiments 1 and 2. Experiment 4 tested then the possibility that memory rather than perception of the object was affected by the body-related manipulation. Finally, Experiment 5 explored whether the results generalize from virtual grasping task to virtual reaching. In sum, the results revealed evidence for multisensory integration under conditions similar to those in which action-related effects in visual judgments are observed.

Experiment 1

Holding an object in the hand while looking at it provides visual as well as haptic information about the object which are integrated, as mentioned earlier. Moreover, some recent studies indicated that multimodal integration also occurs when the hand is offset in respect to the object being grasped, however, only if a tool, such as plier or tong, is used for grasping (Takahashi et al., 2009; Takahashi & Watt, 2014). In these studies, participants saw the tools before and/or during grasping movements. Moreover, in the critical conditions the visual illustrations of tools connected the spatial position of the hand with the spatial position of the object being judged. Thus, the examined conditions resemble situations in which external objects are judged after being manipulated by "physical" tools.

Many effects of motor variables on visual judgments, however, are observed in the absence of any physical connection between body and to be judged objects. Accordingly, a paradigm of "virtual" rather than of physical grasping was used in which no visible tool linked the hand and the to-be judged object but only movement consequences were visually presented. Although there is no direct evidence to our knowledge that haptic signals of the hand and visual object information are integrated under these conditions, some previous reports clearly suggest this possibility (Kirsch, Pfister, & Kunde, 2016; Rand & Heuer, 2013, 2016).

In the study of Rand and Heuer (2013), for example, participants were asked to perform arm movements on a horizontal plane while the visual feedback was displayed in the vertical plane. Following

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[2] Please note that one might consider "grasping ability" to be confounded here with finger posture. However, this argument does not hold given that ability-related effects might be due to sensory integration of motor and visual signals. In other words, the same critique can be applied to several studies where action ability was varied. This is because a certain change in action ability has to entail a certain change in a body-related representation, otherwise no effect in visual perception will be found, or this effect will have nothing to do with body and its action. Moreover, whether or not the gain manipulation is considered as an index of grasping ability there is still a (motor) variable related to the body (hand posture) which should affect visual perception according to action-specific accounts (cf. e.g., Proffitt & Linkenauger, 2013).

misalignment of the visual movement direction in respect to the actual movement direction the judgment of the felt hand direction shifted toward the seen cursor direction and, vice versa, the judged cursor direction shifted (albeit much less) toward the felt hand direction. This and related results indicate that multimodal integration is not restricted to physical tools and can also occur when virtual tools are used. However, in this and related studies (unlike studies on action-specific perception) perceptual judgments were made in respect to the felt body part and its visual equivalent rather than to an external object being manipulated by some action.

In Experiment 1, participants manipulated a movement device mounted behind a monitor using the thumb and index finger of the right hand (see Figure 2). Thereby, the position of the fingers was offset in depth by approximately 10.5 cm with respect to the position of the screen. The finger movements were transformed into movements of two visual dots displayed roughly above the hand. The task was to place the dots at the shorter sides of a rectangle and then to judge either the current hand opening or the height of the rectangle. The gain between hand opening and the dots was varied so that either one and the same hand opening was judged after a rather small or a rather large rectangle had been “grasped” (Exp. 1A) or so that one and the same rectangle was associated with a rather small or a rather large hand opening (Exp. 1B). We hypothesized that the judgment of the rectangle size will be attracted by the actual size of the hand opening and vice versa, the judgment of the hand opening will be attracted by the size of the rectangle. Both observations would indicate sensory integration of visual and body-related signals.

The present study goes beyond standard multisensory tasks in that it examines sensory integration under conditions approximating set-ups used in research on action-specific perception, in which observers manipulate spatially distant external objects by certain motor actions (i.e., where sources of multimodal signals are spatially separated and there is no physical connection between them like, e.g., in several sports, in which action ability proved to affect objects’ estimates, see also Footnote 1).

Method

Participants. Twenty-four right-handed participants participated in Experiment 1. Participants gave their informed consent for the procedures and received monetary compensation for their participation. The sample included 12 males and 12 females (M_{age} = 27 years, SD = 6).

Apparatus and stimuli. The apparatus consisted of a 19′ monitor (Fujitsu Siemens P19-1) and a finger movement device mounted behind the monitor (see Figure 2). This apparatus was positioned on a table at an angle of about 40 degrees. One pixel (px) of the monitor was 0.294 mm in size. The finger movement device was manipulated by the index finger and the thumb of the right hand. The fingers were placed on U-shaped metal plates with a “horizontal” distance of about 1.7 cm between both sites (i.e., fingers were not completely fixed). Both metal plates were interlocked so that moving one plate/finger resulted in a mirror-symmetric movement of the second plate/finger.

Visual stimuli were a gray rectangle of 26 mm in width (line thickness $\sim$ 1.2 mm), a pair of gray bars of about 7 mm length and 1.2 mm width, and a pair of green circles about 2.5 mm in diameter presented on a black background. The rectangle was always shown on the right side of the screen approximately above the fingers. The pair of the bars was always on the left side of the screen (about 14.7 cm apart from the middle of the rectangle). The horizontal position of the green circles corresponded to the middle of the rectangle.

Participants were seated at a distance of approximately 41 cm from the screen with their head supported by a combined chin-and-forehead rest. Moreover, headphones were used for the presentation of acoustic signals and to minimize external noise. A conventional computer mouse lay on the table left to the main apparatus and was manipulated by the left hand.

Procedure and design. Experiment 1 consisted of two parts, namely of Experiment 1A and Experiment 1B. Each participant performed both experiments within one single session. The order of the Experiments 1A and 1B was counterbalanced across the participants.

Experiment 1A. Participants were asked to place the green circles at the shorter sides of the rectangle by moving their fingers of the right hand inserted into the finger movement device (i.e., they were virtually asked to grasp the rectangle by visual movement cursors). The initial distance between the circles corresponded to the current distance between the fingers modified by the current gain factor (see below). That is the starting position of these stimuli varied trial by trial. The circles always moved in the same direction as the fingers (i.e., to each other or away from each other) and when they reached the shorter sides of the rectangle a clicking noise was presented. Participants were instructed to maintain this finger position and to perform corrective movements when the noise disappeared (i.e., when the circles left the shorter sides of the rectangle). Note that this task

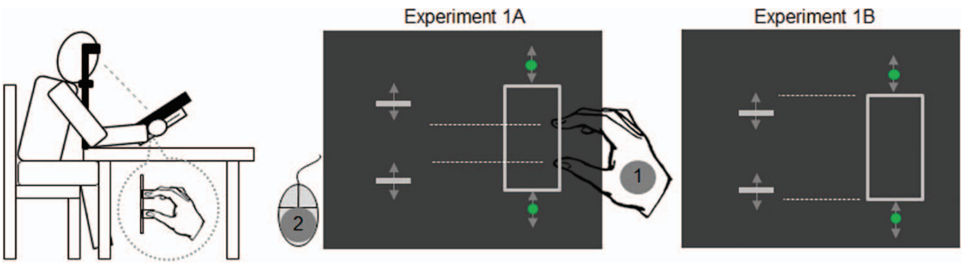

Figure 2. Apparatus and stimuli used in Experiment 1. Digits indicate the succession of participant’s actions. Initially, the fingers of the right hand moved the cursors (green circles) toward the shorter sides of the rectangle. Then, either the current hand opening (Exp. 1A) or the height of the rectangle (Exp. 1B) were judged with the left hand using a computer mouse. See the online article for the color version of this figure.

does not contain all the features of unrestricted and "natural" grasping movements (such as hand transportation, hand preshape, and motion of the object relative to the environment). However, given the adjustment of the cursors (i.e., of finger opening) according to the current size of the object as well as auditory feedback (indicating that the object has been actually grabbed) we speak of virtual grasping here.

Following a period of 1.5 sec in which the noise was presented the green circles disappeared and the gray bars appeared at the left side of the screen. The initial distance between those bars randomly amounted either approximately 50% or 150% of the actual finger distance (as measured between the inner plates of the movement device). The task was to adjust the distance between the bars so that it corresponded to the *distance between the fingers*. This judgment was made per pressing buttons of a computer mouse. Pressing the left/right button led to an increase/a decrease of the distance. The judgment was confirmed by pressing the middle mouse button (scroll wheel).

When participants changed the fingers' posture of their right hand during the judgments, or when the left or the right mouse buttons were pressed before the bars on the left side appeared, or when the middle mouse button was pressed before an estimate was made, an error feedback was presented and the trial was repeated.

The question of interest was whether the perceived finger distance varies as a function of the size of the object being grasped. Accordingly, the critical experimental variation was related to the transformation of the finger movements to the movements of the circles. The distance between the fingers was divided either by the factor of 2/3 or by 2. That is, in one condition the actual finger distance was always larger than the distance between the circles (small gain). In another condition, the finger distance was smaller than the distance between the circles (large gain). This ensured that for a given finger distance two rectangles could be grasped the height of which corresponded to either 50% (small gain) or 150% (large gain) of the actual finger distance.

Additionally, three different finger distances were used (about 34, 40, and 46 mm, as measured between the inner plates of the movement device). Thus, the experiment included two independent variables (gain and finger distance) which yielded six experimental conditions.

The main experiment included 4 blocks of trials with 36 trials each (6 repetitions of each condition). The order of conditions was random (with the constraint that no immediate repetitions of the same condition were possible and all conditions should be completed before a next repetition was possible). Before the main experiment started participants performed 12 practice trials which were not included in the analyses.

Experiment 1B. In Experiment 1B, participants were asked to judge the *size of the rectangle* (instead of the finger distance). That is, the task was to adjust the distance between the bars so that it corresponded to the height of the rectangle. The initial distance between the bars randomly amounted either 50% or 150% of the current rectangle height.

The critical experimental variation was similar as in Experiment 1A. That is, the distance between the circles either increased or decreased in respect to the distance between the fingers (i.e., the gain was again large or small). The main question of interest here, however, was whether virtual grasping with a varying hand opening affects the perceived size of the grasped object. Accordingly, the gain was adjusted so (by multiplying the actual finger distance by 2/3 or by 2) that for a given rectangle size there were two finger distances corresponding to either 50% (large gain) or 150% (small gain) of the rectangle height. Note that for a given rectangle size the visual input was identical for both gain conditions during the judgment procedure.

Additionally, the height of the rectangle was also varied and could be about 34, 40, or 46 mm. Thus, as in Experiment 1A, there were two independent variables (gain and size of rectangle) which yielded six experimental conditions. The rest of the procedure and design of Experiment 1B was identical to the procedure and design of Experiment 1A. Accordingly, the rectangle was visible throughout the trial. This does not limit the used judgment method because the perception of the rectangle but not of the test bars can be assumed to be affected by the hand opening (see also Footnote 3).

Results

For each experiment, each participant and each experimental condition medians of the judged distances were calculated. These values were then subjected to a within-subjects analysis of variance (ANOVA) performed for each experiment separately. For the data of Experiment 1A this analysis revealed significant main effects for the factor finger distance, $F(2, 46) = 123.1$, $p < .001$, $\eta_p^2 = .843$, and for gain, $F(1, 23) = 13.8$, $p = .001$, $\eta_p^2 = .374$, and a significant interaction between both factors, $F(2, 46) = 18.8$, $p < .001$, $\eta_p^2 = .449$. Judgments of the *finger distance* increased with finger distance and, more importantly, with an increase in gain (see left part of Figure 3 for the letter result). Also an impact of gain increased with an increase in finger distance (see Figure S1 for all mean values).

The analysis of the data of Experiment 1B yielded a significant main effect for rectangle size $F(2, 46) = 1502.0$, $p < .001$, $\eta_p^2 = .985$, and a significant main effect for gain, $F(1, 23) = 5.4$, $p = .030$, $\eta_p^2 = .189$. The interaction was not significant ($F(2, 46) = 2.5$, $p = .094$, $\eta_p^2 = .098$). The judgments of *rectangle height* increased with an increase in rectangle height and, more importantly, decreased with an increase in gain (see right part of Figure 3 for the letter result and Figure S1 for all mean values).

Discussion

Participants virtually grasped an object with a pair of cursors controlled by their finger movements and subsequently judged either their hand opening (Exp. 1A) or the size of the object (Exp. 1B). One and the same hand opening was judged as larger after a large object was grasped as compared with grasping a smaller object. Moreover, one and the same object was judged as larger when it was associated with a larger hand opening (and smaller action ability) as compared with a smaller hand opening (and larger action ability).

These results indicate that visual and haptic signals were integrated after using a virtual tool. The observation that the rectangle judgments were far less affected than the hand judgments further support this possibility. People usually have no precise knowledge about an effector in the absence of visual information (e.g., Longo & Haggard, 2010; Müsseler & Sutter, 2009; Saulton, Dodds, Bülthoff, & de la Rosa, 2015). Thus, it can be assumed that the visual input was much more reliable than the haptic input and received thus more weight under the present conditions (see, e.g., Ernst & Banks, 2002).

An increase of the effect in the hand judgments with an increase in the hand opening does not speak against this conclusion. The (abso-

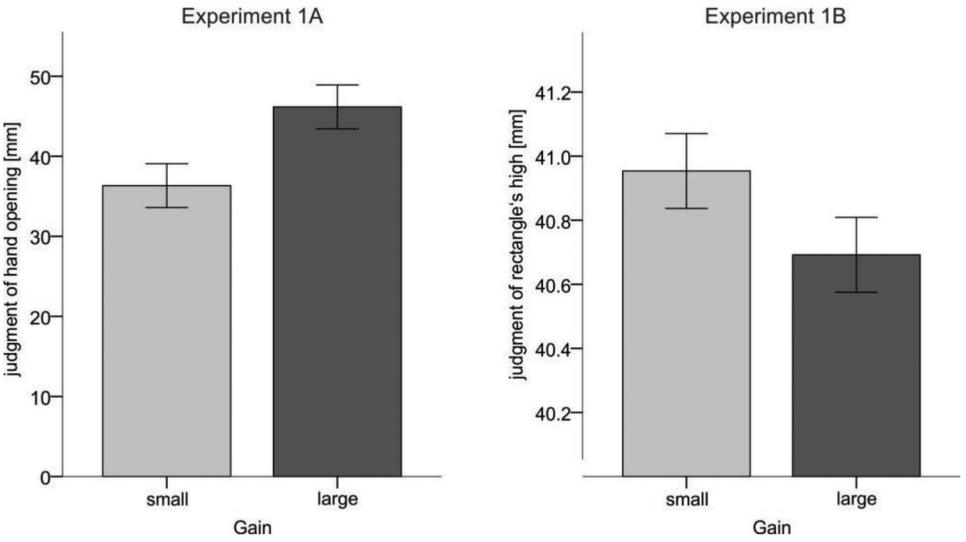

Figure 3. Main results of Experiment 1. Error bars indicate within-participants confidence intervals (95%) computed according to Cousineau (2005). According to the multisensory approach the perception of hand opening should be biased toward the actual object size and conversely the perceived object size should be biased toward the actual hand opening. Note that in the large gain conditions the hand opening was smaller than the object in both experiments (cf. Figure 1). Accordingly, an increase or decrease in estimates in Exp. 1A/Exp. 1B for the large gain condition as compared with the low gain condition is consistent with the multisensory approach.

lute) difference between the rectangles being grasped with the same hand opening increased with an increase in hand opening (due to the gain manipulation). Thus, the observed interaction between the magnitude of hand opening and gain probably reflects a procedurally induced increase in the impact of the critical manipulation with an increase in the hand opening.

Experiment 2

The results of Experiment 1 revealed evidence for a mutual impact of visual and body-related signals as predicted. However, given that the effect observed in rectangle judgments was rather small some caveats remain whether it really exists. Moreover, finger and rectangle judgments were made by each participant within one single session. Thus, carry over influences cannot be ruled out. Also, the adjustment method used in Experiment 1 might have been rather suggestive because the bars used as comparison objects moved along a similar trajectory as the fingers and the dots.

Given these caveats Experiment 2 served as a control experiment to ensure that the mentioned effect is replicable and is not confined to the conditions of Experiment 1. In Experiment 2, only judgments of the rectangle were requested. Moreover, the adjustment method used in Experiment 1 was replaced by a two-alternative forced choice procedure.

Method

Participants. Twelve right-handed participants participated in Experiment 2. They gave their informed consent for the procedures and received monetary compensation or course credit for their participation. The sample included three males and nine females ($M_{age} = 27$ years, $SD = 7$).

Apparatus and stimuli. Apparatus and stimuli were the same as in Experiment 1 with one marginal exception: the edges of the rectangle were somewhat thinner (~ 0.3 mm) in Experiment 2.

Procedure and design. Participants moved the cursors (i.e., green circles) toward the shorter sides of the rectangle (standard stimulus) as in Experiment 1. Then, following an interval of 1.5 sec in which the clicking noise was presented two bars appeared (test stimulus) and the circles disappeared. The distance between the bars varied by steps of 2 mm from -7 to $+ 7$ mm in respect to the height of the rectangle. The task was to indicate whether the distance between the bars is larger than the height of the rectangle or vice versa by pressing the left or the right mouse button, respectively. After one of the buttons was pressed the chosen stimulus (either the standard or the test) changed its color from gray to yellow for 500 msec. As in Experiment 1B, the height of the rectangle could be 34, 40 or 46 mm and the gain either "small" or "large."

The experiment included 10 blocks of trials with 48 trials each. Each experimental condition was repeated 10 times. Participants performed 12 practice trials at the beginning which were not included in the analyses.

Results

Figure 4 (left part) shows the percentage of decisions for the test stimulus (i.e., where the distance between the bars was judged as larger than the height of the rectangle) depending on movement gain (see also Figure S2 for all means). An increase in gain was associated with a small but reliable shift of the psychometric function toward smaller test distances. To quantify this effect the data (proportions of "test larger than standard") of each participant and each condition were fitted using a local model-free fitting

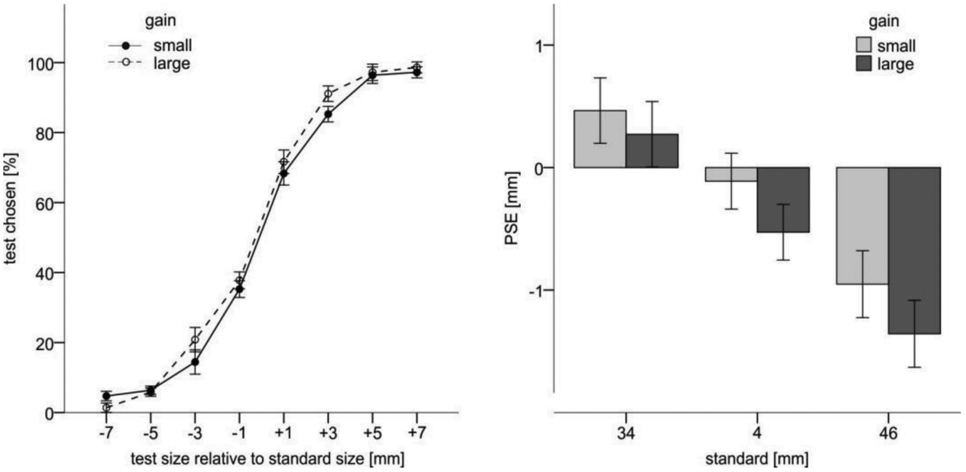

Figure 4. Main results of Experiment 2. Error bars indicate within-participants confidence intervals (95%) computed according to Cousineau (2005).

procedure (mean $r^2 = .97$, $SD = .04$) and the point of subjective equality (PSE) was computed (Zychaluk & Foster, 2009). PSE were then analyzed by means of a two-way ANOVA with gain and height of rectangle as within-subjects factors.

An increase in rectangle size was associated with a significant shift of the PSE toward negative values, $F(2, 22) = 9.\ 2$, $p = .001$, $\eta_p^2 = .457$. More importantly, an increase in gain significantly biased the PSE toward more negative values, $F(1, 11) = 5.6$, $p = .038$, $\eta_p^2 = .336$. Both factors did not interact significantly ($F(2, 22) = .3$, $p = .734$, $\eta_p^2 = .028$). Figure 4 (right part) shows mean values from this analysis.

Discussion

Experiment 2 conceptually replicated the results of Experiment 1B using a different procedure. Thus, in spite of a rather small magnitude the effect of the varying movement gain on visual judgments of object size is well replicable and is not confined to the conditions of Experiment 1. Moreover, possible carry over effects of haptic judgment can also not explain this effect because there were no haptic judgments in Experiment 2.

In Experiment 2, PSE shifted toward more negative values with an increase in object's size. This effect probably reflect two tendencies, a slight general tendency to underestimate the object's size which is obviously due to some optical factors and a tendency toward a mean object's size often observed in perceptual tasks (e.g., Helson, 1964).

Experiment 3

Experiments 1 and 2 suggested that virtually manipulating an external object triggers sensorimotor integration processes between this object and body-related signals. However, the spatial distance between the hand and the object was rather small in these experiments. Accordingly, the previous results might be attributable to spatial proximity of visual objects and body rather than to using a type of virtual tool. The main purpose of Experiment 3 was, thus, to demonstrate that manipulating a motor variable affects the perception of external objects as well as the perception of own body, even though the body and the objects are spatially clearly separated.

We thus mounted an additional monitor in front of the participants and displayed all visual stimuli on this monitor (see Figure 5, left part). After virtual grasping of the rectangle, one group of the participants judged the magnitude of the hand opening as in Experiment 1A (Exp. 3A), whereas the other group judged the size of the rectangle as in Experiments 1B and 2 (Exp. 3B). For the sake of consistency we used two-alternative forced choice methods in both experiments. Also, we tried to improve the judgment procedure. In particular, the test stimulus was now present in the

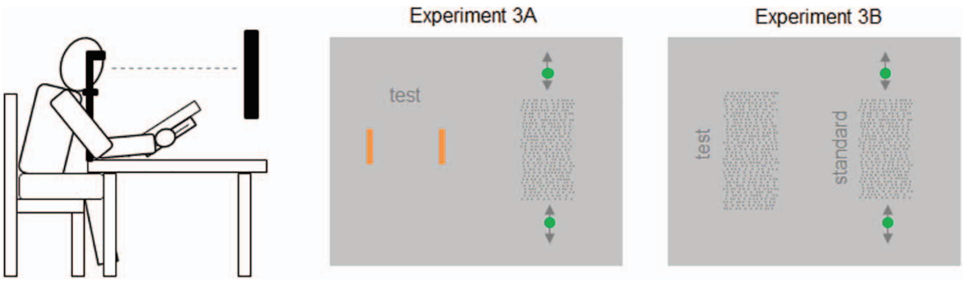

Figure 5. Apparatus and stimuli used in Experiment 3. See the online article for the color version of this figure.

absence of and orthogonally to the grasped rectangle in Experiment 3A (see Figure 5, middle part). Moreover, the test stimulus used in Experiment 3B was now an additional rectangle varying in size[3] (see Figure 5, right part).

We were also interested in how changes in visual cue reliability might affect the visual and haptic judgments. The multisensory approach suggests that a decrease in the quality of the visual signal can increase the impact (or weighting) of signals from other modalities. Accordingly, we varied the contrast of the rectangles and reasoned that a lower contrast (less visual reliability) could be associated with a larger impact of gain (i.e., of hand opening) in Exp. 3B, but with a lower impact of gain (i.e., of rectangle size) in Exp. 3A.

Method

Participants. Sixteen right-handed participants participated in Experiment 3A and another 16 right-handed participants participated in Experiment 3B. They gave their informed consent for the procedures and received monetary compensation or course credit for their participation. The sample included four males and 12 females in Experiment 3A (M_{age} = 28 years, *SD* = 6) and four males and 12 females in Experiment 3B (M_{age} = 27 years, *SD* = 6).

Apparatus and stimuli. An additional monitor (Fujitsu Siemens P19-1) was placed uprightly in front of the participants in a distance of about 68 cm (see Figure 5). All visual stimuli were presented on this screen, while the slanted and previously used monitor was inactive in Experiment 3. The rest of the apparatus was the same as in the previous experiments.

Visual stimuli were dark gray rectangles (see below), a pair of orange bars (7 mm in length and 1.2 mm in width) and a pair of green circles of about 2.5 mm in diameter presented on a light gray background[4] (with coordinates “128, 128, 128” in the RGB color space). The rectangles were composed of dots with random distances between 1.2 and 2.9 mm along the horizontal and with a fixed distance of 1.5 mm along the vertical (see Figure 5 for examples). The maximal width of the rectangles was about 26 mm.

Procedure and design.

Experiment 3A. Participants moved the green circles toward the shorter sides of the rectangle (standard stimulus) by means of finger movements and a clicking noise was presented when the circles reached the shorter sides of the rectangle as in all previous experiments.[5] Then the rectangle as well as the circles disappeared and two bars appeared (test stimulus). The bars were oriented vertically and were displaced horizontally by steps of 10 mm from −20 to +20 mm in respect to the current distance between the fingers. The current distance between the fingers was here defined as the distance between the inner plates of the movement device plus 1 cm (based on pilot tests). The distance between the middle of the test stimulus and the middle of the previously shown rectangle was always constant and was about 17.5 cm. The vertical position of the bars corresponded to the middle of the rectangle. Participants' task was to indicate whether the distance between the bars is larger than the distance between the fingers (left mouse button) or vice versa (right mouse button). When participants changed the fingers' posture during the judgments or when one of the mouse buttons was pressed before the test stimulus appeared then an error feedback was presented and the trial was repeated.

There were two gain condition (small and large) corresponding to grasping of larger (150% of the finger distance) and smaller (50%) rectangles and three different finger distances (34, 40, and 46 mm) as in Experiment 1A. Additionally the color contrast of the rectangle was varied by using different levels of the grayscale (RGB color space: “36, 36, 36” and “99, 99, 99”). Also, there were five different test distances. Thus, overall there were 60 experimental conditions.

The main experiment included 12 blocks of trials with 60 trials each (one repetition of each condition in each block). The order of conditions was random. Before the main experiment started participants performed 12 practice trials which were not included in the analyses.

Experiment 3B. After participants placed the green circles at the shorter sides of the rectangle (standard stimulus) the circles and the standard stimulus disappeared, and another rectangle appeared on the left side of the screen (about 17.5 cm apart) for 1.5 sec (test stimulus, see Figure 5). The task was to indicate which rectangle appears larger by pressing the left or the right mouse button (for the left and the right rectangle respectively).

Analogously to Experiments 1B and 2, there were two gain conditions, which corresponded to different finger postures after grasping of the same rectangle. Three different rectangle sizes (34, 40 and 46 mm) and two color contrast conditions were used (see also above). Both rectangles (i.e., test and standard) had the same contrast in each trial. Moreover, the height of the test rectangle varied by steps of 4 mm from −8 and + 8 mm in respect to the height of the standard rectangle. Thus, as in Experiment 1A, there were 60 conditions which were randomly presented and repeated 12 times within 12 blocks of trials. The experiment also included 12 practice trials which were not included in the analyses.

Results

Figure 6 (left parts) shows the percentage of decisions for the test stimulus depending on the size of the test stimulus and the movement gain in Experiments 3A and 3B (see also Figure S3 for all mean values). As predicted, the psychometric function shifted to larger test distances with an increase in gain in Experiment 3A and to smaller test distances in Experiment 3B. Using a local model-free fitting procedure (Zychaluk & Foster, 2009) the PSE were derived for each participant, each condition and each experiment (Exp. 3A: mean r^2 = .91, *SD* = .17; Exp. 3B: mean r^2 = .98, *SD* = .03).

Analyses of variance (ANOVAs) indicated a significantly more negative PSE for the smaller gain than for the larger gain in

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[3] Note that only the standard stimulus is virtually grasped but not the test stimulus (see Figure 5, right panel). Accordingly perception of the standard stimulus can be assumed to be affected by the finger movement, but not the perception of the test stimulus. Thus, any objections that perception cannot be measured by this procedure (such as El Greco fallacy, Firestone & Scholl, 2015) are not justified.

[4] Black background used in Experiments 1 and 2 proved rather unsuitable for the present setup (because of salient differences in lightness between the left and right rectangles in Exp. 3B) and we thus decided to display stimuli on a light background.

[5] In Experiment 3 the circles disappeared as soon as they reached the right position. In the previous experiments, they remain visible as long as the sound was presented. This marginal change was aimed to improve the procedure (i.e., to strengthen the effect of finger movements on the rectangle).

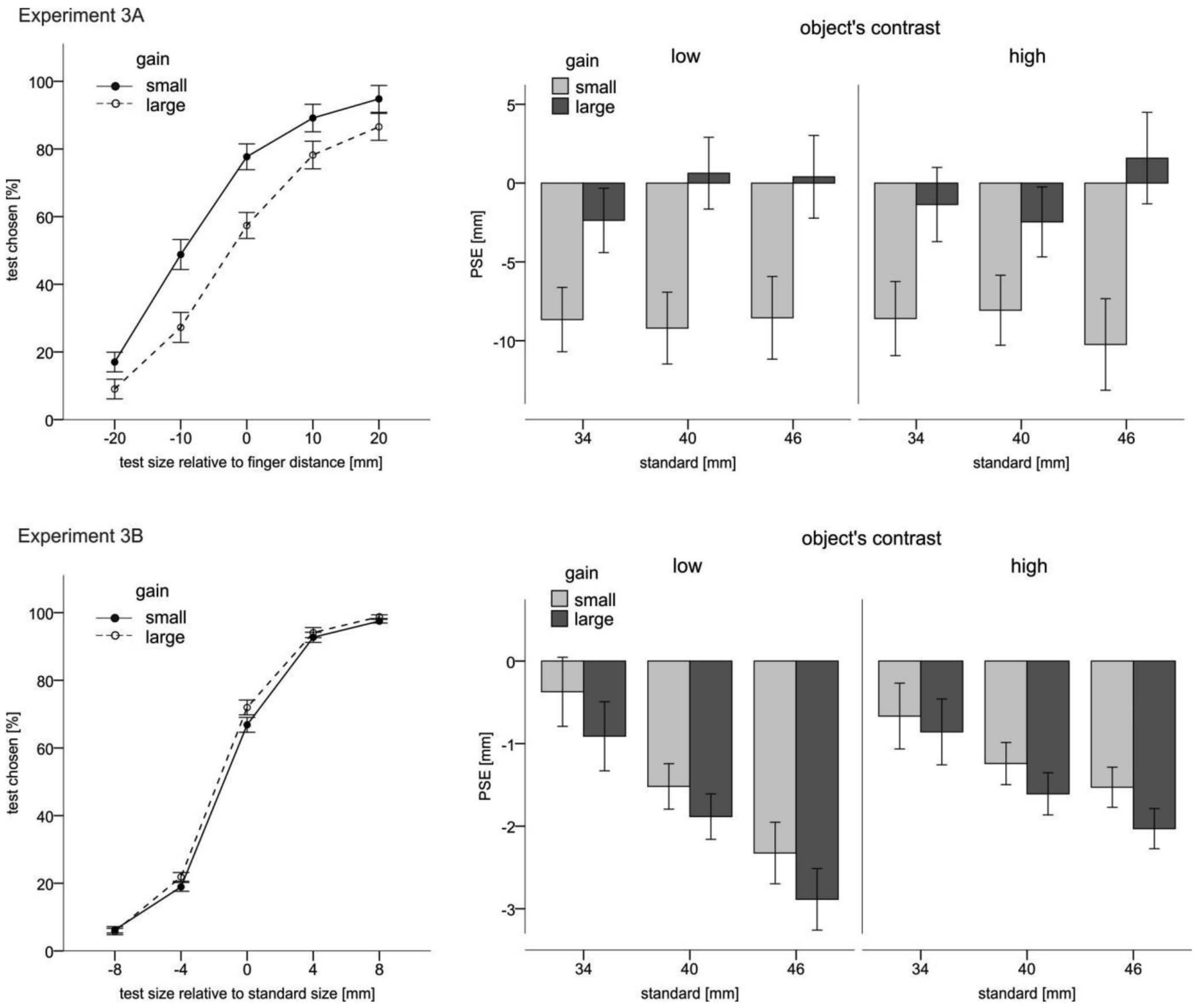

Figure 6. Main results of Experiment 2. Error bars indicate within-participants confidence intervals (95%) computed according to Cousineau (2005).

Experiment 3A, $F(1, 15) = 16.6$, $p < .001$, $\eta_p^2 = .525$, and a significantly more positive PSE for the for the smaller gain than for the larger gain in Experiment 3B, $F(1, 15) = 6.6$, $p = .022$, $\eta_p^2 = .305$.

In Experiment 3A, the impact of gain also depended to some extent on the size of the standard (i.e., on the actual finger distance) and on rectangle's contrast, as indicated by significant interactions between the factors gain and standard size, $F(2, 30) = 8.2$, $p = .001$, $\eta_p^2 = .352$, and between all three factors, $F(2, 30) = 4.1$, $p = .027$, $\eta_p^2 = .213$ (see the top right part of Figure 6 for means). The main effects of standard size and of contrast as well as the interactions between standard size and contrast, and between gain and contrast were not significant with $F(2, 30) = .5$, $p = .627$, $\eta_p^2 = .031$; $F(1, 15) = 1.2$, $p = .291$, $\eta_p^2 = .074$; $F(2, 30) = 1.3$, $p = .294$, $\eta_p^2 = .078$; $F(1, 15) = .03$, $p = .877$, $\eta_p^2 = .002$, respectively.

In Experiment 3B, the main effect of standard size and an interaction between contrast and standard size were significant with $F(2, 30) = 17.3$, $p < .001$, $\eta_p^2 = .536$, and $F(2, 30) = 5.1$, $p = .012$, $\eta_p^2 = .254$. The PSE generally decreased with an increase in standard size and this effect was less pronounced for the high contrast condition (see the lower right part of Figure 6 for means). The main effect of contrast and the interactions between gain and standard size, gain and contrast, and between all of the factors were not significant with $F(1, 15) = 2.4$, $p = .142$, $\eta_p^2 = .138$; $F(2, 30) = .2$, $p = .813$, $\eta_p^2 = .014$; $F(1, 15) = .3$, $p = .582$, $\eta_p^2 = .021$; and $F(2, 30) = .2$, $p = .816$, $\eta_p^2 = .014$, respectively.

Discussion

The main results of Experiment 3 were an increase in the estimates of the current hand opening after virtual grasping of a larger as compared with a smaller rectangle and an increase in the size estimates of the rectangle being grasped using a larger as compared with a smaller hand opening. These results thus support the claim that the results observed in Experiments 1 and 2 generalize to conditions with strict spatial separation between body and visual objects.

Rectangles' contrast affected the estimates to some extent. In Experiment 3B, the low contrast condition was associated with larger differences across the three rectangle sizes than the high contrast condition. This indicates a stronger tendency toward the middle of the rectangles' range with a decrease in stimulus quality (cf. also Exp. 2). As predicted, the effect of gain was larger for the low contrast condition than for the high contrast condition, however, only descriptively. This might be an index for a rather small magnitude of the contrast variation under the present task conditions.

In Experiment 3A, the contrast affected the magnitude of the gain effect, however, not consistently across the sizes of the hand opening. The predicted decrease in gain effect with lower contrast was thus not consistently evident. There may be several reasons for such a complex pattern and we suppose that the (unaltered) contrast of the movement cursors (i.e., green dots) could be more important here than the manipulated contrast of the object being grasped.

Experiment 4

One might still raise some concerns over the Experiment 3B. In particular, the standard and test stimuli were successively presented and thus, the judgment had to be made based upon a memory representation. Accordingly the observed impact of the gain manipulation of the size estimates might reflect a bias in memory rather than in perception. To test for this possibility, we performed Experiment 4. This experiment was nearly identical to Experiment 3B with the exception that the standard and test stimuli were simultaneously visible before the size judgment was made.

This change can be assumed to generally enhance the relative reliability of visual information, and thus to reduce the probability to find an impact of body-related signals. This should especially be true for the high contrast condition where stimuli are clearly visible. However, if object's contrast is reduced, finger signals could be used in an attempt to make the size estimate more reliable. In other words, if the effect observed in Experiment 3B is perceptual then it should be observed particularly in the low contrast condition of Experiment 4 and be reduced or even disappear in the high contrast condition.

Method

Participants. Sixteen right-handed participants participated in Experiment 4. They gave their informed consent for the procedures and received monetary compensation for their participation. The sample included seven males and nine females (M_{age} = 28 years, SD = 4).

Apparatus and stimuli. Apparatus and stimuli were the same as in Experiment 3B.

Procedure and design. Procedure and design were the same as in Experiment 3B with one exception. After participants placed the green circles at the shorter sides of the rectangle this standard stimulus did not disappear as in Experiment 3B while another rectangle (test stimulus) appeared on the left side of the screen. Both rectangles remained visible for 1.5 sec.

Results

The main results are shown in Figure 7 (mean r^2 = .99, SD = .02). The gain manipulation did not generally affect participants' judgment behavior (i.e., the PSE) as in the previous experiments. However, there was a significant effect of gain in the low contrast condition, $F(1, 15) = 3.9$, $p = .067$,[6] $\eta_p^2 = .206$, but no effect in the high contrast condition, $F(1, 15) = .2$, $p = .648$, $\eta_p^2 = .014$, when both contrast conditions were separately analyzed (see also Figure S4 for mean decision rates of all conditions; the main effect of standard size was significant in the low as well as in the high contrast condition, $F(2, 30) = 6.5$, $p = .005$, $\eta_p^2 = .302$; $F(2, 30) = 7.3$, $p = .003$, $\eta_p^2 = .328$; the interactions were not significant with $F(2, 30) = .9$, $p = .424$, $\eta_p^2 = .056$, and $F(2, 30) = .1$, $p = .935$, $\eta_p^2 = .004$). This is also supported by an ANOVA including all conditions and indicating a significant interaction between the factors gain and contrast, $F(1, 15) = 5.7$, $p = .031$, $\eta_p^2 = .275$. In this analysis the main effect of standard size was significant with $F(2, 30) = 10.8$, $p > .001$, $\eta_p^2 = .418$; whereas the main effects of gain and of contrast as well as the interactions between standard size and gain, standard size and contrast, and between all of the factors were not significant, $F(1, 15) = .8$, $p = .399$, $\eta_p^2 = .048$; $F(1, 15) = .7$, $p = .422$, $\eta_p^2 = .043$; $F(2, 30) = .8$, $p = .442$, $\eta_p^2 = .053$; $F(2, 30) = .5$, $p = .590$, $\eta_p^2 = .035$; $F(2, 30) = .2$, $p = .815$, $\eta_p^2 = .014$. Note that although the PSE tended to be of the same magnitude for the large standard rectangle in the low contrast condition (see the lower left part of Figure 7) there were no indications that the size of the rectangle interacted with the factor gain (all according p values > .4, see above, cf. also Figure S4).[7]

Discussion

The results of Experiment 4 were in line with our prediction. The varying hand opening affected the size estimates when the visibility of the stimuli was reduced. This outcome suggests that the impact of the hand manipulation observed in this and in the previous experiments is perceptual in nature.

The fact that related effects were observed with rather high contrast stimuli in Experiments 1B, 2, and 3 does not necessarily speak against this conclusion since the used stimuli and task varied considerably. For example, in Experiments 1B and 2, a pair of bars served as test stimuli can be assumed to produce more uncertainty during the estimate than a comparison rectangle used in Experiments 3 and 4. Accordingly, in a more difficult (visual) task the impact of the same motor variable might be increased. In a similar vein, when standard and test stimuli are simultaneously presented (as in Experiment 4) the task is easier as when they are not (as in Experiment 3; cf. also the slopes in Figures 6 and 7). Thus, the

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[6] Note that this is a predicted effect that can be tested using one-tailed tests. Accordingly, we consider this marginally significant ANOVA outcome as a significant effect.

[7] To approve this pattern of results and related conclusions, we also run an ANOVA on the percentage of decisions for the test stimulus including all experimental conditions. A main effect of gain as well as the Gain × Contrast interaction were significant with $p = .028$ and .038, respectively. Moreover, the factor gain as well as a Gain × Test stimulus interactions were significant when the low contrast condition was analyzed separately (with $p = .012$ and $p = .012$, respectively). In the high contrast condition, in contrast, the factor gain did not affect the judgment behavior (all $p > .6$).

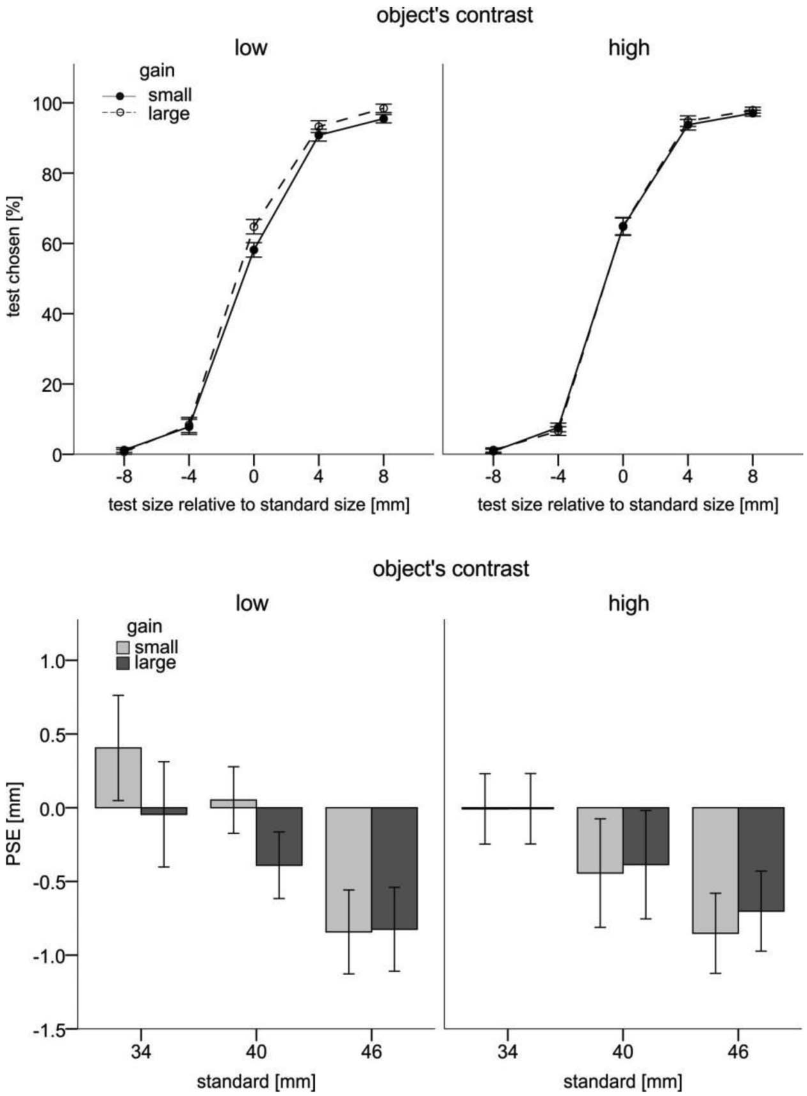

Figure 7. Main results of Experiment 4. Error bars indicate within-participants confidence intervals (95%) computed according to Cousineau (2005).

haptic signal might generally be stronger weighted in the later than in the former case.

Experiment 5

One might be not fully convinced that the virtual grasping task used in the previous experiments adequately represents an action-specific paradigm. We therefore used a different task in Experiment 5 in which the dynamic of the body's action rather than its end state was emphasized. Participants moved a digitizing stylus on a graphics tablet placed on a horizontal plane and saw a visual consequence of their movements (i.e., cursor) as well as additional stimuli on a monitor similar to Experiments 3 and 4 (see Figure 8). In each trial participants moved the cursor from a central start position toward a first lateral target line and back to the start position. Then, after a short interval they moved the cursor to another target line displayed on the opposite side of the screen and back to the start position. The task was to indicate on which side of the screen the visual distance (i.e., between start position and target line; Exp. 5B) or the extent of the stylus movement (Exp. 5A) was larger. The critical experimental variation again concerned the transformation of stylus movement to cursor movement (i.e., gain). Specifically, the extent of the stylus movement could be larger (small gain) or smaller (large gain) than the extent of the cursor movement.

In our previous studies on action-specific effects in perception we already showed that increasing movement amplitudes increase the estimates of visual distances to which those movements are related (e.g., Kirsch & Kunde, 2013, 2015). The present reaching task additionally shares characteristics with studies on tool use which demonstrated that visual distances are judged as smaller, when effective arm length is extended by a tool (e.g., Witt, 2011b;

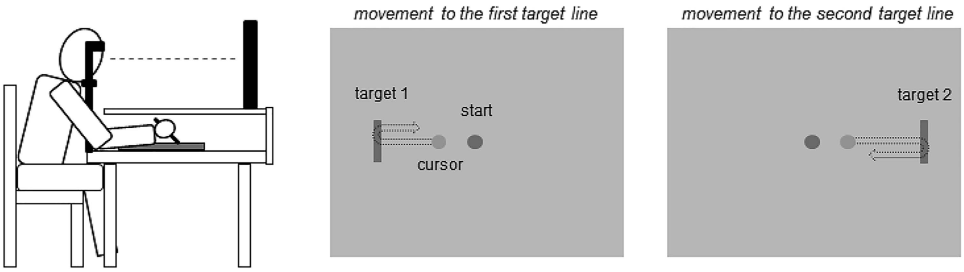

Figure 8. Apparatus and main events in a single trial of Experiment 5.

Witt & Proffitt, 2008). According to this research, a larger stylus distance (small gain) can be expected to increase the visual distance estimate in Exp. 5B as compared with a smaller stylus distance (large gain). In other words, extending the reaching distance of the arm by a virtual tool can here be assumed to compress the apparent distance between two visual objects to which reaching movements are related. The multisensory perspective suggests the same perceptual bias toward the current somatosensory signal. However, a unique prediction of the multisensory perspective is, that the perceived amplitude of the stylus movement should be biased toward the visual distance. Thus, a larger cursor distance (large gain) should produce an increase in the perceived amplitude of the stylus movement as compared with a smaller cursor distance (small gain) in Exp. 5A.

Method

Participants. Sixteen right-handed participants participated in Experiment 5A and another 16 right-handed participants participated in Experiment 5B. They gave their informed consent for the procedures and received monetary compensation or course credit for their participation. The sample included three males and 13 females in Experiment 5A ($M_{age} = 25$ years, $SD = 5$) and five males and 11 females in Experiment 5B ($M_{age} = 26$ years, $SD = 4$).

Apparatus and stimuli. Stimuli were displayed on a 19′ monitor (Samtron 96 B, Samsung). One pixel measured about 0.35[8] mm on the screen. Observers were seated at a 65-cm distance from the screen with their head supported by a combined chin-and-forehead rest. The monitor stood on a wooden superstructure that was positioned on a table (cf. Figure 8). A graphics tablet (Intuos 4 A4, Wacom) was positioned in-between the table and the superstructure. Hand movements were performed on the tablet with the right hand holding a digitizing stylus. The superstructure prevented the vision of the hand during the movements. A computer mouse fixed to the left of the tablet was used for recording of perceptual judgments. The mouse buttons were pressed using the left hand.

Main visual stimuli were small circles (about 2 mm in diameter) and vertically oriented lines (about 7.2 mm in length and 0.7 mm in width) which were presented on a light gray background (RGB coordinates: "128, 128, 128"). One dark gray ("81, 81, 81") and stationary circle served as a starting position for movements and as a landmark for distance judgments. The other somewhat brighter circle ("120, 120, 120") served as a movement cursor. The lines ("81, 81, 81") represented movement targets and boundaries of the to be judged distances (see below).

Procedure and Design.

Experiment 5A. At the beginning of each trial the movement cursor appeared at the starting position (i.e., in the middle of the screen) together with a target line which was shown in some distance to the left or to the right of the starting position. Participants had to move the cursor to that line and then back to the start positon. As soon as the cursor touched the line, it changed its color from dark gray to yellow for 50 ms. Then the line disappeared and the start position appeared. After the cursor reached the start position its color changed from dark gray to orange for 1000 ms. Participants had to keep the stylus at the start position for this time period. Then another target line appeared on the opposite side of the screen. This was a signal to move the stylus to this second target and then back to the start position. As for the movement to the first target, the line got yellow and then disappeared after the cursor reached the line. After the cursor reached the start position displayed subsequently, the start position got orange again and the participants were required to indicate the side of larger movement extent by "R/L?" shown in red at the top part of the screen. The instruction stressed that the judgment is related to the movement of the stylus and that the visual distances should be ignored. After the judgments was made by pressing a mouse button an intertrial interval followed (1000 ms) in which number sign symbols (###) were shown in the middle of the screen.

If the participants left the start position as long as it was orange (max. allowed position difference was about 3.6 mm) or substantially overshot the target (by more than 5 mm) an error feedback was presented and the trial was repeated. Also, if the start position was left during the intertrial interval an error feedback appeared and that interval was repeated (after the cursor returned to the start).

The amplitude of one of the two stylus movements (i.e., the distance between the start position and the stylus position when the target was reached) was always 65 mm (standard distance). The amplitude of the stylus movement to the target on the opposite side varied between 30 and 100 mm in eight steps (test distance). The first movement could contain either the test or the standard distance and could be directed to the target either on the left or on the right side (random order).

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[8] Because of a small measurement and rounding error the reported mm values slightly overestimated the real measures (were computed according to 0.36).

The main question of interest was whether the perceived movement extent varies as a function of the visual target distance covered by the cursor (see also Exp. 1A and 3A). Accordingly, the gain was adjusted so that for each amplitude of the stylus movement the cursor covered either a shorter (70%; small gain) or a larger (130%; large gain) distance before it reached the target. These two gain conditions were implemented in each trial. That is, if the first movement was performed using the small gain, the large gain was used for the second movement and vice versa (random order).

The main experiment included 4 blocks of trials with 64 trials each. Overall, there were 16 critical conditions (2 (gain) × 8 (test distance)) which were repeated 16 times. Before the main experiment started 16 practice trials were performed.

Experiment 5B. In Experiment 5B, participants indicated which start-line distance is larger (left or right) and the impact of different gains assigned to the stylus movements was examined. That is, each visual distance could be covered by a smaller (large gain) or by a larger (small gain) stylus movement. Here we pursued a conservative approach and tried to minimize using of explicit strategies by a rather small gain manipulation: the amplitude of the stylus movements deviated by only 15% from the amplitude of the cursor movement. For example, if the distance between the start position and the target line amounted 65 mm, the required stylus movement was either 55 (large gain) or 75 mm (small gain).

In each trial one of the start-line distances always amounted about 65 mm (standard distance), whereas the other start-line distance varied between 47 and 82 mm in eight steps (test distance). The rest of the procedure and design was the same as in Experiment 5A.

Results

Figure 9 shows the percentage of decisions for the test distance as a function of the test distance and movement gain applied to the standard distance in Experiments 5A and 5B. As in previous experiments, the psychometric function shifted to larger test distances with an increase in gain in Experiment 5A and to smaller test distances in Experiment 5B (Exp. 5A: mean $r^2 = .90$, $SD = .15$; Exp. 5B: mean $r^2 = .98$, $SD = .02$).

Statistical analyses indicated a significantly more negative PSE for the smaller gain (−17) than for the larger gain (20) in Experiment 5A, $t(15) = 9.4$, $p < .001$, and a significantly more positive PSE for the smaller gain (2) than for the larger gain (−2) in Experiment 5B, $t(15) = 4.4$, $p = .001$. It is also notable that none of the participants of Experiment 5B except for one noticed the critical manipulation of gain as indicated by post experimental reports. This participant "felt" that the cursor sometimes moved faster. Excluding this participant from the analyses did not affect the results substantially (the effect was still significant with $t(15) = 4.6$, $p < .001$).

Discussion

The task used in Experiment 5 required the participants to judge the distances moved either by a visual cursor or by the hand operating the cursor. The judgments of the cursor movements were attracted by the actual hand movement and vice versa, the judgments of the hand movement were attracted by the distance covered by the cursor. Thus, the pattern of results observed with a virtual grasping task in the previous experiments was reproduced using a virtual reaching task being conceptually very similar to action-specific paradigms used previously. Thus, the link between the present results and the action-specific approaches appears to be well justified.

General Discussion

A considerable number of studies using diverse paradigms reported changes in observers' judgments of visual attributes following variations of observers' bodies or body movements. According to one widely held view, changes in body-related states determine changes in

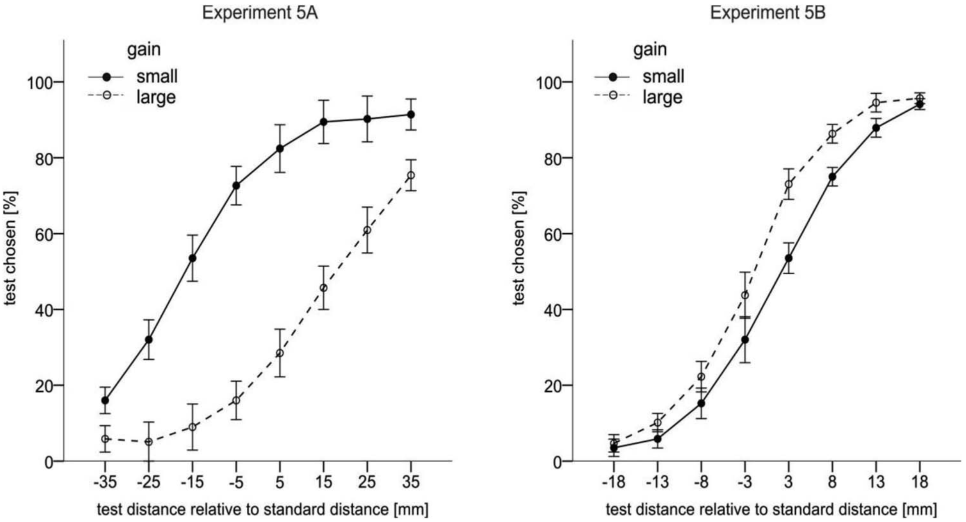

Figure 9. Main results of Experiment 5. Note that the movement gain refers to the standard distance and that the test distance in the same trial was always associated with the opposite gain factor. Error bars indicate within-participants confidence intervals (95%) computed according to Cousineau (2005).

visual perception due to a kind of direct scaling of initial visual input in motor units (e.g., Proffitt & Linkenauger, 2013). This approach thus postulates a certain kind of integration of visual and motor signals which gives rise to changes in visual perception following changes in motor variables. However, this critical integration process (if existent) is not well understood. Here we tested whether well-known principles of sensory integration of multimodal signals could characterize the proposed mechanism and thus, could in principle explain action-specific effects in visual judgments.

The sensory integration approach predicts a mutual impact of visual and body-related signals if there is a discrepancy between them: What is visually perceived should be attracted by what is bodily sensed and vice versa, the body-related feeling should be attracted by the visual information. We took up this rationale and explored whether these mutual biases are observed when somatic and visual information relate to the same external object but are spatially separated (like in many studies on action-specific perception). Participants virtually grasped an object and judged either the size of the object or the magnitude of the hand opening they used to enclose it. The main results were clear and straightforward. The hand had a small but systematic impact on object judgments, whereas the haptic estimates were much more affected by the size of the visual object. A comparable pattern was observed in a virtual reaching task. Thus, in spite of considerable spatial separation of hand and manipulated object, there was a strong indication of multisensory integration. Visual signals were more heavily weighted, conceivably because of a higher reliability, as compared with body-related information.

The multisensory perspective is a powerful framework which can in principle be applied to several sorts of body-related effects on visual perception. It provides a basis for quantitative predictions and explanations of how visual and body-related signal are integrated, and thus, for example, of which magnitude action-specific effects can be expected in a particular situation. One of the key predictions is that the impact of motor variables on visual judgments should critically depend upon the reliability (i.e., quality) of visual and body-related information: it should increase with a decrease in reliability of visual signals and with an increase in reliability of body-related signals. This can potentially explain why the effects in studies on action-specific perception are often relatively small in magnitude (e.g., Kirsch & Kunde, 2013; cf. also Firestone, 2013) or even undetectable at all (de Grave, Brenner, & Smeets, 2011; see also Exp. 4).

Beyond the weighed sensory sampling approach[9] which we considered so far to explain the mutual effects of body-related and visual information the multisensory research offers more comprehensive models which can help to describe how several stages of the integration process could look like. For example, the system has initially to decide whether signals relate to the same object or event (i.e., it has to solve the so called “correspondence problem”). Such a decision can be modeled within a Bayesian framework as an expectation (i.e., “coupling” or “interaction” prior) which determines to what extent the signals will be integrated based on knowledge about the co-occurrence statistics such as redundancy or signal correlation (Ernst, 2006, 2007; Roach, Heron, & McGraw, 2006). The outcome of this process could vary on a continuum from a complete fusion of the signals into a single percept via partial fusion through to a complete independence (see also e.g., Hillis, Ernst, Banks, & Landy, 2002). Applied to the research on action-specific perception in general and on tool use in particular, body-related and visual signals often relate to the same external object. Accordingly, in spite of spatial distance between the body and the object it could be advantageous to integrate both signals in order to enhance the quality of object perception (see also e.g., Takahashi et al., 2009). Thus, a mutual influence between the sensory modalities and thus action-specific effects can in principle be expected to emerge in such situations and multisensory approaches can be applied to formalize the involved processes in more detail (see also Rohde, van Dam, & Ernst, 2016 for a tutorial on cue integration).

This reasoning as well as the present finding correspond well with the studies on the impact of tool-use on visual and somatic perception. One line of research indicated that egocentric distances to visible objects are judged as smaller when those objects are manipulated by a tool extending the effective arm length (Davoli, Brockmole, & Witt, 2012; Witt, 2011b; Witt & Proffitt, 2008; Witt et al., 2005). Using a tool, however, also proved to change the perception of the body (e.g., Cardinali et al., 2009). The arm, for example, feels elongated after using a rake-like tool to reach otherwise unreachable objects (Sposito, Bolognini, Vallar, & Maravita, 2012). The former result was explained in terms of action-specific perception whereas the later was explained in terms of a malleable body schema. The present results suggest that both types of observations may have a common origin. In particular, the somatic signal indicating, for example, the end position of the arm might be combined with the object location provided by vision during multisensory integration. Asking for the felt arm position could then result in a bias toward the visual object position, whereas judgments of the object’s positon can be expected to be biased by the actual arm position. Reasoning this way does not speak against an often assumed incorporation of tools into the body schema (e.g., Iriki et al., 1996; Maravita & Iriki, 2004). Rather it implies that such an integration of the kinematic tool transformation into a body representation might be a prerequisite to relate signals of an external object and a spatially displaced body to each other (cf. also Takahashi et al., 2009).

The effects of action on perception are often discussed as contrast-like phenomena using the term “ability” (e.g., Witt, 2011a). The mentioned *decrease* of the visual distance estimate following tool use was assumed to emerge as a result of an *increased* reaching ability, increased jumping ability was supposed to decrease the perceived height of walls (Taylor & Witt, 2010), increased grasping ability was associated with a decrease in perceived size of graspable objects (Linkenauger et al., 2011), and so on. In contrast, the multisensory perspective emphasized by the present approach indicates the “assimilative” nature of such phenomena. Does it mean that these views are mutually exclusive? We believe it does not. Consider, for example, the finding that hills are judged as steeper when wearing a heavy backpack (e.g., Bhalla, & Proffitt, 1999). In terms of hill’s “walkability” this effect is certainly a contrast phenomenon. However, assuming that a certain motor variable related, for example, to some energetic parameters (e.g., Proffitt, 2006) is taken into account in perception of a hill, rather than hill’s walkability per se, turns this effect from a contrast to an assimilation phenomenon (because *high* movement costs are now associated with an *increase* in perceived slope). This makes the effect appear conceptually not very different

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[9] Formally, the Maximum Likelihood Estimation (MLE) was successfully applied to model the integration of redundant sensory signals (e.g., Ernst & Bülthoff, 2004). In essence, the MLE provides a weighted average of unimodal signals where the weight of each signal depends on the reliability of sensory information. Thereby the integrated estimate achieves a higher precision than the unimodal signals alone.

from the finding well explained by the multisensory integration that the visual perception of slant in grasping space is attracted by the slant experienced through haptics (Ernst, Banks, & Bülthoff, 2000). Thus, reasoning in terms of lower level motor variables rather than in higher level abstract concepts could in principle resolve apparent differences.

It has been claimed that (action-specific) perception prepares the perceiver for a subsequent action by signaling opportunities and costs associated with that action (e.g., Proffitt, 2006; Witt, 2011a). For example, perceptual changes after putting a heavy backpack might help to select an appropriate speed of walking and to avoid excessive demands. Such a facilitation of adaptive behavior is readily explained within a multisensory framework (cf. e.g., Ernst, 2006). Because of sensory noise representations mediated by different modalities are not exact and can provide divergent information about the same external object. Weighting and integration of information has been thought (and empirically proved) to enhance the accuracy of the final estimate and thus, to facilitate an optimal decision (or action). Accordingly, the apparently adaptive nature of action related changes in perception could be considered as a natural consequence of effort to reduce variance of the perceptual estimate through sensory integration.

It has been supposed that action-specific effects reflect biases related to response behavior or memory rather than changes in perception (e.g., Cooper, Sterling, Bacon, & Bridgeman, 2012; Durgin, Klein, Spiegel, Strawser, & Williams, 2012; Firestone, 2013; Firestone & Scholl, 2015). We did not examine this issue in detail in the present study and thus cannot evaluate it with certainty. However, the fact that we consistently observed effects notwithstanding different judgment methods speaks for the perceptual nature of the investigated phenomena. Consider, for example, that a forced choice procedure used in Exp. 3 could measure a decision bias rather than perceptual changes: if two objects are similar in size, participants could choose a larger one based on some (motor) cues devoid of perceptual changes. However, given that the same effect is observed using a method of adjustments (in Exp. 1) which is far less susceptible to such decision biases makes this possible concern implausible. Also, it has often been claimed that participants merely respond in accordance with their guess of the experiments' purpose. This possible objection also seems not applicable not least because the participants of Exp. 5 were unaware of the critical manipulation and the purpose of the other experiments can be assumed to be not very obvious to the participants.

To sum up, we show that a systematic effect of a motor variable on visual judgments of size and distance observed under conditions of a clear spatial separation between body and to be judged objects is accompanied by changes in body-related perception. This indicates that the former effect as well as related observations are linked to known processes of multisensory integration. Thus, the present results provide new insights into the nature of body-related changes in visual perception and shed new light on their possible origin.

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