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RESEARCH ARTICLE

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When does action resist visual illusions? Effector position modulates illusory influences on motor responses

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Abstract Actors viewed horizontal segments either in isolation or embedded in patterns that produce spatial illusory effects (Kanizsa's compression illusion and the "dumbbell" version of the Müller-Lyer compression-expansion illusion). They were asked to reproduce the apparent horizontal extent of these segments by the amplitude of open- or closed-loop motor responses (after having positioned a finger on position A, choose a position B on the right of A such that apparent width = B–A). A touchmonitor was used to present the displays and to record movement amplitudes and times. In open-loop motor responses, displays were turned off as soon as actors raised their finger from position A. In closed-loop responses, displays could be viewed continuously during the actions. Four conditions were investigated: (1) open-loop responses starting from A at the right endpoint of the segment; (2) closed-loop responses from A at the right endpoint of the segment; (3) open-loop responses from A at the left endpoint of the segment; and (4) open-loop responses from A aligned horizontally with the left endpoint of the segment but displaced vertically below that segment. With both kinds of display, results in conditions (1) and (2) demonstrated illusory effects comparable to those measured in standard visual matching experiments, whereas results in conditions (3) and (4) showed essentially no illusory effects. Implications for models of visuomotor transformations in peripersonal space are discussed.

Keywords Perception · Action · Illusions · Dorsal · Ventral

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Introduction

According to a currently popular hypothesis, the primate higher-level visual system is divided into two subsystems that are distinguishable both anatomically and functionally (Milner and Goodale 1995). The dorsal stream of projection from V1 to PPC processes visual information aimed at planning and executing actions. Conversely, the ventral stream from V1 to IT processes visual information aimed at recognition and identification. Dorsal processes are hypothesized to be fast, not necessarily conscious, and to code spatial features using egocentric frames of reference. Ventral processes are hypothesized to operate on a slower timescale, to require consciousness, and to use allocentric coding. We will refer to this hypothesis as the two-visual-system hypothesis, or TVSH (see also Norman 2002). According to the TVSH, the ventral stream uses allocentric coordinates because they are easier to compute for all objects in the scene and critical for perceptual constancies. Conversely, the dorsal stream computes egocentric coordinates for target objects (and perhaps some objects nearby) to allow for fast and accurate transport during grasping or locomotion.

For some years, there has been agreement that the TVSH is supported by demonstrations that "actions resist visual illusions". Interest on action responses on visual illusory patterns stems from the fact that, in the TVSH framework, visuomotor mechanism (dorsal) should be able to access accurate spatial information even when that information is not available at levels mediating symbolic decisions (ventral). For instance, in the Müller-Lyer illusion the same segment appears wider when flanked by outward-pointing arrows, and narrower when surrounded by inward-pointing ones. In the TVSH framework, this illusory effect is due to allocentric (object-relative) coding of spatial extensions in the ventral subsystem. However, actions such as picking up a bar should involve egocentric (body- or effector-relative) coding of spatial features by the dorsal subsystem. Therefore, motor measures of bar length should be unaffected by spatial relations with flanking elements even if conscious judgments are. Following on the footsteps of pioneering work by Bridgeman and Mack (see, for instance, Bridgeman et al. 1979; Wong and Mack 1981), a substantial body of experimental work has attempted to test the TVSH predictions concerning motor responses to geometrical illusions. At present, however, a consensual interpretation for this large body of data is lacking. In fact, at least three different positions can be distinguished.

According to the first of these (Carey 2001), the bulk of the evidence on actions and illusions is compatible with the TVSH, provided that one limits dorsal involvement to “dumb” motor responses, namely, fast movements based on 3D orientations in egocentric coordinates. The idea that “less direct” motor responses (for instance, those performed on the basis of memory or of spatial imagery) should recruit higher-level perceptual resources is plausible and has received support from several studies (Goodale et al. 1994; Gentilucci et al. 1996; Hu and Goodale 2000; Westwood et al. 2000). There is evidence suggesting that “motor estimation” responses (intermodally matching seen extent with finger aperture, without performing an actual grasp) recruit ventral resources (Haffenden and Goodale 1998). This distinction is supported also by neuropsychological work with patient DF, who can grasp solids accurately but fails to intermodally match their size (Goodale et al. 1991). However, an obvious difficulty faced by this view is that clear a priori criteria for deciding when an action is “dorsal” are not specified by the TVSH.

According to a second, diametrically opposite view the evidence is not consistent with the TVSH (Franz 2001). This second position relies on studies showing that perceptual judgments and visually guided motor responses are affected by spatial illusions equally if experimental artifacts are controlled (Pavani et al. 1999; Franz et al. 2000a, 2000b). However, the scope of this proposal is limited to one action, reaching, and one motoric measure of manipulation, the maximum pre-shape grip aperture (MGA) of the index and thumb. This focus is understandable, because the MGA was used in studies that have been widely cited as evidence supporting the TVSH (Aglioti et al. 1995). However, the MGA is only one of several possible motor measures of a reaching action. In a recent study of bilateral open-loop reaching, we found that the final position of the hands was completely immune from a compression illusion affecting perceptual judgements (Bruno and Bernardis 2002). Other results involving hand transport in open-loop pointing tasks (Burr et al. 2001) as well as body transport in open-loop walking responses (Loomis et al. 1992) also support the TVSH prediction.

According to a third position, finally, the evidence indicates that the distinction proposed by the TVSH is too rigid and needs to be relaxed. In this view, the crucial factor is not the mode of response (verbal vs. motor) but the selection of a specific mode of representation either in perception or action, or in both. For instance, some studies have suggested that several apparent dissociations between perceptual judgement and motor response may be interpreted as differences between tasks requiring representations that are typical of verbally expressed perceptual judgements, such as judgements of size, length, or speed, vs. responses simply requiring representations of position as is typical of several reaching responses (Brenner and Smeets 1994, 1996). Other investigators have suggested that the crucial distinction may lie in the selection of a specific frame of reference (Vishton et al. 1999; Wraga et al. 2000; Bruno 2001). In this view, several verbal judgements tend to select allocentric frames, whereas motor responses tend to select egocentric frames thereby causing immunity from certain illusions. A variant of this proposal suggests that the selection of a frame of reference depends on the phase of the visuomotor process, with action planning relying on object-relative spatial properties and online visuomotor control of the action on effector-relative properties (Glover and Dixon 2001). An in-depth theoretical analysis of the similarities and differences between these specific proposals is beyond the scope of the present work. We note, however, that although these proposals provide a potential account for seeming contradictions in the reaching data, they also face a difficulty similar to that faced by the first account until we clarify how tasks should be mapped on modes of representation.

Thus, there is a great deal of disagreement on the status of the TVSH given the present evidence. Given this disagreement, it is important to continue examining motor responses to visual illusory patterns. In this paper, we report data on a length reproduction visuomotor task. In this task, actors are required to position their index finger on a predefined position A and to reproduce the horizontal extent of a segment by raising the finger and transporting the hand sideways until they can touch a second position B such that (B–A) equals the apparent extent of the segment. We used two patterns that produce robust illusions of extent in conscious perception: the “dumbbell” version of the Müller-Lyer illusion and a compression illusion discovered by Kanizsa (1975). For each pattern, we started by assessing the strength of the perceptual effect using a standard matching task. Next, we measured the corresponding effect on motor length reproduction in one closed-loop and three open-loop conditions. All open-loop conditions were completely equivalent except for one critical feature: the starting position of the index finger. We show that this simple manipulation has a dramatic effect on the accuracy of the open-loop action. The motor reproduction is essentially immune from the illusion when actors start at one segment terminator and move to the other. However, it becomes as biased by the illusion as the perceptual judgments when actors start at one terminator and move away from the segment, so that a mental translation of the perceived extent is needed to define the aim point. The closed-loop condition was exactly equivalent to one of the open-loop conditions, except for the availability of visual feedback during the execution of the action. Here we also show that there is essentially no difference in susceptibility to the illusion between these two modes of performing the action.

Experiment 1: perceptual matches to segments in "dumbbell" patterns

In the "dumbbell" version of the Müller-Lyer illusion pattern (Fig. 1a), a segment with hoops drawn on the top of its outer parts (the "hoop-in" version) appears narrower than a physically identical segment with hoops drawn outside its terminators (the "hoop-out" version). As a preliminary step to a comparison with motor responses, we sought to quantify this illusory effect. To this end, we performed an experiment using a standard matching task.

Materials and methods

Observers

Ten members of the University of Trieste community participated. All had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Equipment

A Macintosh G4 computer was used for controlling the presentation of experimental displays and for recording responses. Responses were entered by participants using the computer console. Displays were presented on an Elo Entuitive 1726C 17" CRT Desktop Touchmonitor, set at a spatial resolution of 1024×768 pixels, a temporal resolution of 85 Hz, and 8-bit color. The Elo Entuitive touchmonitor uses infrared technology to record direct finger contact with the CRT surface but is otherwise fully equivalent to a standard CRT monitor in both appearance and function. Thus, although observers did not interact with the software by touching the monitor in this study, the displays were presented under conditions comparable to other studies of visual illusions and exactly under the same visual conditions used in the subsequent motor experiments.

Displays

Experimental displays consisted of seven horizontal segments having lengths equal to 150, 180, 210, 240, 270, 300, and 330 pixels, subtending 4.7, 5.6, 6.5, 7.4, 8.3, 9.2, and 10.4 degrees of visual angle, respectively, at a viewing distance of 57 cm. In the standard stimuli these segments were presented with circles having radii equal to 16% of the segment length. In the "in" version of the display, these circles were drawn as in the top pattern of Fig. 1a. In the "out" version, as in the bottom pattern, the standard stimuli were presented always on the left half of the monitor, whereas an adjustable test segment was presented on the right half of the monitor. The initial length of this test segment was set at a random value either above or below the length of the standard. Both the standard pattern and the adjustable test segment were colored middle gray whereas the background was white.

Procedure

In each trial, observers adjusted the horizontal extension of the test segment on the right to match the width of the standard segment (with hoops) on the left. The adjustment was performed by pressing keys on the computer keyboard, which was also used to record the adjustment and advance the procedure to the next trial. Each observer served in two blocks of 35 trials, each block resulting from 5 presentations of each of the 7 lengths, in a completely randomized order. One of the blocks served to assess the "in" version of the pattern whereas the other was used to assess the "out" version. The order of blocks was randomized across participants. Before initiating the experimental blocks, a brief training session was administered to illustrate the task and the use of the keyboard for interacting with the experimental software.

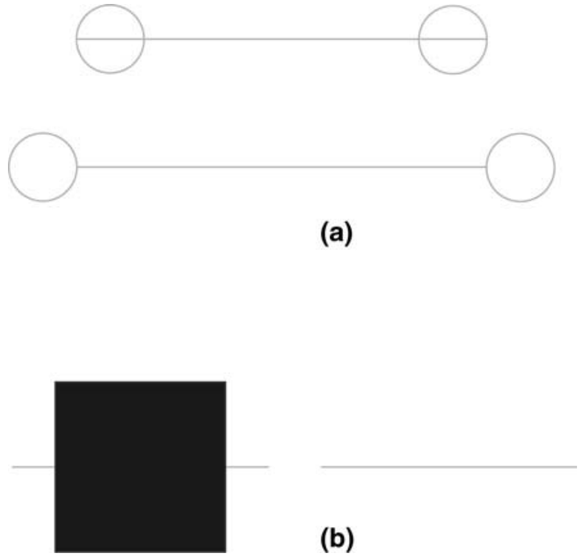

Fig. 1 Versions of the dumbbell illusion **(a)** and of Kanizsa's compression illusion **(b)** used in the present experiments. In the dumbbell illusion, the same segment appears narrower when presented with inner hoops and wider when presented with outer hoops. In Kanizsa's illusion, a segment presented behind an occluding square appears narrower than the same unoccluded segment

Experimental design and data analysis

Adjustments were recorded as a function of two independent variables, actual extension of the segment (from 150 to 330 pixels) and type of display (hoop-in or hoop-out). We expected adjustments to vary as a function of actual extension, but at different rates depending on the type of display. Specifically, we expected the rate of change of adjustments when matching the hoop-out version to be higher than the corresponding rate for the hoop-in version, yielding two linear functions diverging from a common origin at (0, 0). To test this model, the data were subjected to a multiple regression with no constant and two predictor variables: the actual horizontal extension of the segment, and an interaction term computed by assigning a dummy code of 0 to the hoop-in data and of 1 to the hoop-out data. The interaction term is of chief interest here in that the associated parameter measures the difference in slope between the two data groups. Thus, we can take this parameter as a measure of the strength of the relational effect in the present conditions.

Results and discussion

Average matches from the ten participants are presented in Fig. 2. Empty circles represent average matches to the hoop-in version of the display. Filled circles represent matches to the hoop-out version. Individuals are not identified by different symbols as there was complete consistency in the relative pattern of results: For all participants, average matches to the hoop-in version grew more slowly than the corresponding matches to the hoop-

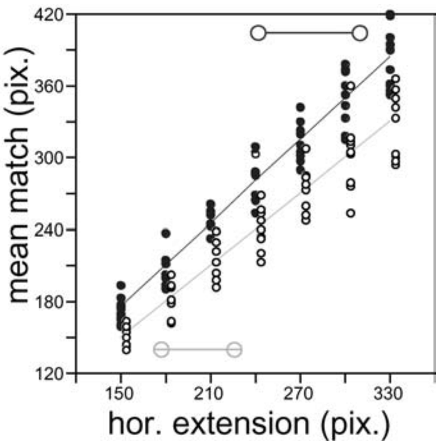

Fig. 2 The dumbbell illusion: effect of hoop position on the perception of a segments' horizontal extent in a standard matching task. Each data point is the average of four matches by one of the ten participants (*empty circles* hoop-in version, *filled circles* hoop-out version). Individuals are not identified by different symbols in that all showed the same trend (see text). Empty-circle data points are displaced to the right to reveal the density of the data. Regression lines were estimated by fitting a linear model with two parameters (effect of actual extension, effect of the extension by display type interaction) and no constant to the (undisplaced) data

out version. The partial overlap observed in the data is due to individual biases towards under- or overestimation, but these biases affected matches to the two display types in the same way in all observers. Also plotted are lines of best fit derived from the two-predictor model described in the "Data Analysis" section above. The fit of this model was statistically significant, $F_{(2,138)}$=15,418, p<0.001, and excellent, multiple R^2=0.996. In fact, the proportion of explained variance was so large that essentially no room was left for improvement from the addition of the type of display as a third predictor, whereas including the intercept in the model reduced the observed R^2 to 0.935. Linear fit parameters indicated that matches to the hoop-in version of the display were slightly compressed (slope = 0.99), whereas matches to the hoop-out version were substantially expanded relative to the true length of the matched segment (slope = 1.163). Comparing these two slopes indicates that hoop position caused an average 16.4% perceptual expansion of the hoop-out segments relative to the corresponding hoop-in segments. Thus, a substantial perceptual effect could be observed. This is a desirable feature of the present methodology if we want to make comparisons with potential effects on motor responses.

Experiment 2: motor responses to segments in "dumbbell" patterns

Having obtained an estimate of the relational effect on the apparent length of segments in the dumbbell illusion in a standard perceptual task, we proceeded to investigate whether a comparable relational effect could be found on visuomotor responses to segment length. To this end, we investigated a length reproduction task. Actors viewed the same displays that were investigated in the previous experiment. They were instructed to position their index finger on a predefined position, which varied in different experimental conditions. From that position, they were required to raise their finger and move their hand horizontally and to the right to point their finger to a new position such that the distance between this new position and the experimentally defined starting position reproduced the apparent length of the segment. Starting positions as well as motor modality (open- or closed-loop) were manipulated to determine whether the motor responses were affected by spatial relations in the pattern and, if so, under what conditions.

Materials and methods

Observers

Ten members of the University of Trieste community participated. All were right-handed and had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiments were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Equipment

A Macintosh G4 computer was used for controlling the presentation of experimental displays and for recording responses. Actors recorded their responses simply by touching the monitor with their index finger. Displays were presented on the same monitor that was used in the previous experiment, set at the same spatial, temporal, and color resolutions.

Displays

Experimental displays were the same as in the previous experiment. The only difference was that in the present motor task observers saw only one version of the standard stimuli (either the "in" or the "out" version) in any given trial. These stimuli were presented on a random position on the monitor. Randomization was adjusted to insure that enough room was available in all trials on the right of the starting position.

Procedure

In each trial, actors were requested to reproduce the horizontal extension of the segment in either the "hoop-in" or "hoop-out" version of the dumbbell illusion pattern by the amplitude of a hand movement. The movement was always performed as follows. At the beginning of each trial, actors rested their hand on a fixed position in front of the touchmonitor. After a beep, one of the experimental displays was presented. Actors responded by first positioning their right index finger on the condition-specific initial position on the monitor; they lifted it from the monitor, and moved their hand rightwards to touch the monitor on a second position, such that the horizontal distance between the second and first position reproduced the apparent horizontal extension of the segment. Each observer served in 4 pairs of blocks, each block consisting of 140 actions (20 repetitions or each segment length) in completely randomized order. In each pair, one block served to assess motor responses to the "in" version of the pattern whereas the other was used to assess the "out" version. The order or blocks within pairs was randomized across observers. The four pairs of blocks served to assess the four different motor conditions described below, which were also randomized across observers. Before initiating the block pair for each condition, a brief training session was administered to illustrate the task and the use of the touchmonitor. In all conditions, actors were encouraged to perform the task as was natural for them, but to try to adopt a constant pace in their responses and to keep it throughout a given block pair. Actors were allowed to rest between block pairs if they wished, but not within them to minimize the possibility of changes in their response criteria across responses to be compared.

Conditions

Each participant served in all four motor conditions. Conditions differed in only two aspects of the task, namely, the initial position of the action and whether this was performed open- or closed-loop. In the right endpoint open-loop (ROL) condition, actors were requested to reproduce the length starting from the right endpoint of the segment and moving horizontally to the right. As soon as they lifted the finger to initiate the action, the experimental software erased the display from the monitor leaving a blank white screen. Thus, the ROL condition measured the internal measure of horizontal extent that was used to program hand transport, when actors had to perform a sort of "mental translation" of the internally represented extent rather than simply point to a position that they had seen. In the right endpoint closed-loop (RCL) condition, actors were again requested to reproduce the length starting from the right endpoint of the segment. However, in this condition the software did not erase the display. Therefore, they could modify their aim while looking at the display until they were satisfied with a position to be touched. Thus, the RCL condition captured the potential additional contribution of online control based on visual feedback acquired during the execution of the action. In the left endpoint open-loop (LOL) condition, actors were requested to reproduce the extension of the segment starting from the left endpoint of the segment. Again, as soon as they lifted the finger to initiate the action, the experimental software erased the display from the monitor leaving a blank white screen. Thus, LOL condition measured the internal measure of horizontal extent that was used to program hand transport, when this could be represented efficiently by an effector-relative map of position. Finally, in the vertically-offset open-loop (VOL) condition, actors were requested to reproduce the length starting from a position that was aligned horizontally to the left endpoint, but offset vertically below the segment of an amount equal to 80% of segment length. (This position was marked by a small gray dot.)

Experimental design and data analysis

Movement amplitudes were recorded as a function of three independent variables: actual segment extension (from 150 to 330 pixels, in steps of 30 pixels), type of display (hoop-in or hoop-out), and motor condition (ROL, RCL, LOL, or VOL). We expected adjustments to vary as a function of actual extension, but at different rates depending on the type of display and condition. Specifically, if the motor response is affected by spatial relations between the segments and the hoops, we should expect the rate of change of adjustments when matching the hoop-out version to be higher than the corresponding rate for the hoop-in version, as in the previous study. Conversely, if the motor response is not affected by such relations, we expect the rate of change of adjustments to be comparable for the hoop-in and hoop-out versions. A natural way to test these predictions is to subject the data to multiple regressions similar to those used in experiment 1, performing separate tests for each motor condition. If motor responses behave in the same way as perceptual matches, we expect to find significant interaction terms and a good fit of the two-predictor model used in experiment 1. Conversely, if motor responses are not affected by the position of the hoop, we expect to find that the interaction term does not improve the fit of a one-predictor model (equal slopes in both data groups).

Data validation

Before subjecting amplitudes to statistical analysis, the motor data were validated by inspection of individual plots of average movement times as a function of actual extension, type of display, and motor condition. Typically, these plots showed monotonic increases of movement times as a function of segment extension, as one would expect given that motor matches to longer segments required larger displacements of the hand. However, they also showed marked individual differences in the rate of change of these times, and no consistent trends across motor conditions when comparing responses to the hoop-in and hoop-out versions of the pattern. We interpreted this lack of consistency as a consequence of two features of the task: first, that participants were instructed to keep a constant pace in their responses but no real constraint was posed on movement times by the nature of the task; and, second, that actors inexperienced with this kind of task were presumably gaining speed as they progressed through the (randomly ordered) conditions. Given that we were not interested in such order effects in the present study, we did not analyze these individual differences further. Instead, individual plots of movement times were scanned carefully for averages showing abnormally large error bars as these may be symptomatic of invalid measures contributing to the average. Invalid data points could arise in the present task for two main reasons. Actors could accidentally touch the monitor twice at the starting point (resulting in ultra fast times and near zero amplitudes), or they could touch the monitor too lightly after transporting the hand to the new position, causing a failure to record the second touch by the experimental software and a temporary interruption of the sequence of trials. In this second case, actors would realize that the program had not recorded the response after a few seconds, and touch the monitor again. Nine such invalid responses were detected by this validation procedure, one corresponding to an ultra fast invalid response and eight to excessively slow ones. Movement amplitudes corresponding to these invalid trials were removed from the data set and the data were replotted. Given that the exclusion of these (temporally) anomalous data points did not affect the position of the single average amplitudes in any appreciable fashion, the whole recorded data were kept for the statistical analysis.

Results and discussion

Results from the ten observers are presented in the four plots of Fig. 3, each plot corresponding to one of the four motor conditions. Plots follow the same conventions used in Fig. 2. Thus, open circles represent matches to the hoop-in displays, filled circles represent matches to the hoop-out displays, and individuals are not identified by different symbols. As is clearly visible in the plots, we observed substantial consistency in the relative pattern of the data although individual motor responses proved more prone to idiosyncratic biases than perceptual matches. Despite this increase in overlap, results clearly demonstrated that the position of the hoops affected the length reproduction action in the ROL and RCL conditions, but not in the LOL and the VOL conditions.

In the ROL condition (top-left of Fig. 3), the data could be fit well by the same model fit to the perceptual matches, $F_{(2,138)}$=2489, p<0.001, multiple R^2=0.973. This fit was not improved by adding the display type as a third predictor or by including a constant parameter in the model. In fact, including the constant in the model reduced the proportion of variance accounted for by a substantial amount, multiple R^2=0.6. The lines of best fit

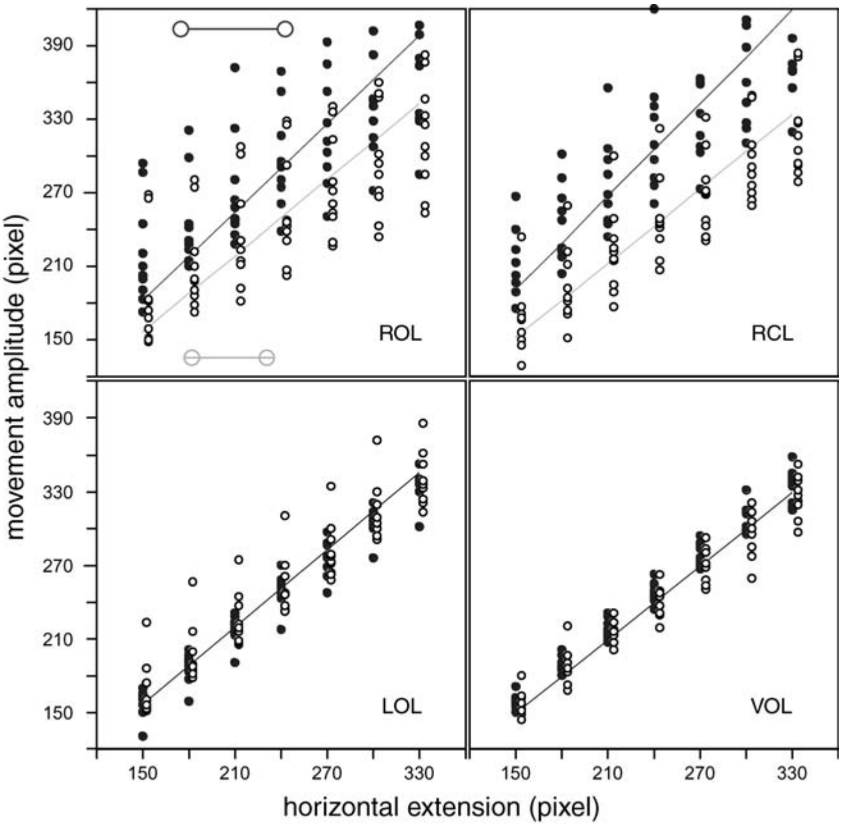

Fig. 3 Effector position modulates the influence of the dumbbell illusory effect (*ROL* right initial position, open loop movement, *RCL* right, closed loop movement, *LOL* left initial position, open loop, *VOL* initial position aligned horizontally on left endpoint but displaced vertically, open loop). Each data point is the average of 20 matches by one of the 10 participants. All plotting conventions are the same as those of experiment 2

to the hoop-in and hoop-out responses are also plotted on the graph. The slopes of these lines were 1.034 for the hoop-in data and 1.204 for the hoop-out data, yielding an effect of hoop position equal to 17% of the actual extension of the segments. A similar outcome was observed in the analysis of the RCL data (top right of Fig. 3), which were also fit very well by the two-predictor model of experiment 1, $F_{(2,138)}$=3635.556, p<0.001, multiple R^2=0.981, with no improvement from the addition of a third predictor and a substantial reduction of the accounted-for variance from the inclusion of the constant in the model, multiple R^2=0.755. The slopes associated with the two groups of data were 1.006 (hoop-in) and 1.265 (hoop-out), corresponding to an effect of hoop position equal to 25.6% of the actual length. Thus, in the two motor conditions where the length reproduction action required a form of mental translation the effect of the hoops was comparable, and in fact somewhat larger, than the effect on perceptual matches.

In the LOL condition, conversely, the data were fit almost perfectly by a one-predictor model estimating only the slope associated with the effect of segment extension and neglecting the hoop-in, hoop-out classification. This model was significant, $F_{(1,139)}$=27,248, p<0.001, and it accounted for essentially all the variance of the data, multiple R^2=0.995. Including the interaction term used to model the ROL and RCL data did not improve on this figure, whereas including a constant parameter actually reduced the proportion of accounted-for variance to 0.914. Forcing the inclusion of the interaction term in the model to obtain separate slope estimates for the two types of display yielded a slope of 1.047 for the hoop-in data and of 1.024 for the hoop-out data. Thus, comparing the two slopes in this case yielded a (non-significant) effect equal to 2.3% of segment extension and in the direction opposite to the dumbbell illusion effect. A very similar picture emerged from the analysis of the VOL condition data. The fit of the one-predictor model proved statistically significant, $F_{(1,139)}$=55595, p<0.001, and excellent, R^2=0.998. Again, there was essentially no room for improvement from adding the interaction term or the constant in the model. By forcing the inclusion of the interaction, estimations of separate slopes for the hoop-in and -out groups were equal to 1.002 and 1.03, respectively. These corresponded to a (non-significant) effect of hoop position equal to 2.8% of actual segment extension. Thus, in the two conditions that favored an effector-centered coding of extent, the position of the hoops exerted essentially no effect on the motor representation used to program hand transport.

Experiment 3: perceptual matches to segments in the Kanizsa pattern

In Kanizsa's compression illusion (Fig. 1b), the presence of an occluding surface produces a perceptual compression of the covered segment, relative to an unoccluded segment of the same length. As in experiment 1, we sought to quantify this relational effect for later comparison with motor responses. To this end, we performed a second matching experiment.

Materials and methods

Observers

Twelve members of the University of Trieste community participated. All had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Equipment, experimental design, procedure, and data analysis

These were the same as in experiment 1.

Displays

As in experiments 1 and 2, experimental displays consisted of seven horizontal segments having lengths equal to 150, 180, 210, 240, 270, 300, and 330 pixels, subtending 4.7, 5.6, 6.5, 7.4, 8.3, 9.2, and 10.4 degrees of visual angle, respectively, at a viewing distance of 57 cm. In the standard stimuli these segments were presented together with an occluding square centered on the middle of the segment, and having sides equal to two-thirds of the segment length. As in experiment 1, the standard stimuli were presented always on the left half of the monitor, whereas an adjustable test segment was presented on the right half of the monitor. The initial length of this test segment was set at a random value either above or below the length of the standard. Both the standard pattern and the adjustable test segment were colored middle gray, the occluding squares were colored bright green, and the background was white as in the previous experiments.

Results and discussion

Inspection of the individual data demonstrated that 8 of the 12 observers showed a clear compression effect, 2 showed essentially no effect, whereas 2 showed expansion—in the direction opposite to Kanizsa's illusion. At debriefing, these two observers were shown instances of Kanizsa's compression illusion (see again Fig. 1b) on paper, to verify that they did actually experience expansion rather than compression. When observing these demonstrations of the illusion on paper, both participants agreed that the occluded segment appeared shorter than the unoccluded one and manifested surprise at their matching results. Given the outcome of the debriefing, we decided to drop these two observers from the analysis.

Results from the ten remaining observers are presented in Fig. 4, adopting the same conventions used for the previous plots. The trend was essentially the same as that observed with the dumbbell illusion data of experiment 1 (compare with Fig. 2): Matches to occluded segments tended to grow more slowly as a function of horizontal extension, relative to comparable unoccluded segments. Confirming these qualitative impressions, the linear

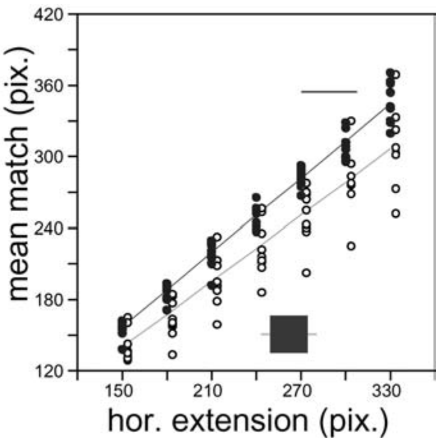

Fig. 4 Kanizsa's compression illusion: effect of the occluding square on the perception of a segments' horizontal extent in a standard matching task. Each data point is the average of four matches by one of the ten participants. All plotting conventions are the same as those of experiment 2

model used to fit the results of experiment 1 again proved statistically significant, $F_{(2,138)}$=14,192, p<0.001, and capable of capturing essentially all the variability in the data, multiple R^2=0.995. Again, including the display type as a third predictor failed to modify the proportion of variance accounted for, whereas including the constant actually reduced this proportion by more than 10%, yielding a multiple R^2=0.876. The estimated slope for the matches to the unoccluded segment data was 1.038. Conversely, the estimated slope for the matches to the occluded segment data was 0.924. Comparing these two slopes yielded an estimate of the compression effect equal to 11.4% of actual segment extension. Thus, the strength of the perceptual compression effect was about two-thirds the effect observed with the dumbbell illusion, but more than twice the typical effect size found in Kanizsa's compression illusion (about 5%, see Kanizsa 1975; Bruno and Bernardis 2002). The difference relative to the effect observed in the dumbbell pattern of experiment 1 is readily explained by noting that in the first experiment the effect was assessed by comparing the expanding (hoop-out) version of the pattern with the compressing (hoop-in) version, whereas in the case of Kanizsa's illusion the assessment of the relational effect was based on comparing the compressing pattern with a baseline segment which should not show dimensional biases. The difference with previous measures of Kanizsa's compression illusion may be attributed to the geometry of the present display, which involved a segment rather than a rectangular surface. To our knowledge, an enhancement of Kanizsa's illusion with occluded segments has not been reported so far (but see Luccio 1983; Vezzani 1999) and it may have an interest in its own. For the purposes of the present work, however, we were not interested in interpreting this potential difference but only in obtaining a measure of the perceptual effect in conditions that can meaningfully be compared with those for motor responses.

Experiment 4: motor responses to segments in the Kanizsa pattern

As we did for the dumbbell patterns, after assessing the strength of the Kanizsa illusion effect on perceptual matches we proceeded to investigate whether a comparable relational effect can be found on visuomotor responses to length. To this end, we investigated the same length reproduction task and used in experiment 2, this time using the patterns that were investigated in experiment 3.

Materials and methods

Observers

Forty members of the University of Trieste community participated. They were randomly divided into four equal-sized groups. Each group served in one motor condition only. All participants were right-handed and had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Equipment and displays

Experimental equipment and displays were the same as in the previous experiment. The only difference was that in the present motor task observers saw only one version of the standard stimuli (either the "occluded" or the "unoccluded" version) in any given trial. These stimuli were presented on a random position on the monitor. Randomization was adjusted to insure that enough room was available in all trials on the right of the starting position.

Procedure

The experimental procedure was identical to that of experiment 2. In each trial, actors were requested to reproduce the horizontal extension of the segment in either the "occluded" or "unoccluded" version of the Kanizsa illusion pattern by the amplitude of a hand movement. The movement was performed as in experiment 2. At the beginning of each trial, actors rested their hand on a fixed position on the table in front of the touchmonitor. After a beep, one of the experimental displays was presented. Actors responded by first positioning their right index finger on the condition-specific initial position on the monitor, they lifted it from the monitor, and moved their hand rightwards to touch the monitor on a second position, such that the horizontal distance between the second and first position reproduced the apparent width of the segment. As in experiment 2, each observer served in 4 pairs of blocks, each block consisting of 140 actions (20 repetitions for each segment length) in completely randomized order. In each pair, one block served to assess motor responses to the "occluded" version of the pattern whereas the other was used to assess the "unoccluded" version. The order or blocks within pairs was randomized across observers. The four pairs of blocks served to assess the four different motor conditions described below, which were also randomized across observers. Also as in experiment 2, before initiating the block pair for each condition a brief training session was administered.

Conditions

Each participant served in four motor conditions, which were the same as in experiment 2.

Data validation and analysis

They were performed in a manner analogous to that of experiment 2. As in the previous experiment, ultra fast and slow responses were identified. After checking that their presence did not alter the overall trends in the individual data, they were left in the data set. Also as in the previous experiments, the data were analyzed by fitting linear models and testing whether an interaction term was needed to account for the results. The effect associated with this interaction term was used as a measure of the relational effect of the occluded surface, if present.

Results and discussion

Figure 5 presents the results in the four motor conditions. The data are plotted following the same conventions of Fig. 3, with the only difference that in this case ten separate groups of observers contributed to each panel and therefore to each experimental condition. Although each condition was completed by different groups of observers, the pattern of results was almost exactly identical to that observed in the responses to the dumbbell illusion pattern: Length reproduction actions were substantially affected by the illusory compression effect in the ROL and RCL conditions, whereas they were essentially immune from the illusory effect in the LOL and the VOL conditions. This qualitative assessment was confirmed by comparing the fits of the two-predictor (extension plus extension by display type interaction) and single-predictor (extension effect only) models, as was done in experiment 2. The outcome of this comparison was similar to what we found in our previous analysis.

In the ROL condition, the fit of the two predictor model was statistically significant, $F_{(2,138)}=4709$, $p<0.001$, and extremely good, multiple $R^2=0.986$. Slope estimates for the lines of best fit to the two groups of data were 1.053 for the unoccluded segment data and 0.915 for the occluded segment data, yielding a compression effect equal to 13.8% of actual length. In the RCL condition, the two-predictor fit was equally good, $F_{(2,138)}=7733$, $p<0.001$, multiple $R^2=0.991$, with slope estimates equal to 1.148 for the unoccluded segments and 1.009 for the occluded ones. These estimates corresponded to a compression effect equal to 13.9%. Thus, in the two conditions requiring a mental translation length reproduction actions were influenced by the illusory compression effect in a manner comparable to the effect observed in perceptual matches.

In the LOL condition, one predictor was instead sufficient to fit the data significantly, $F_{(1,139)}=34,875$, $p<0.001$, and to account for essentially all the variance, multiple $R^2=0.996$. The same was true of the VOL condition, where again the one-predictor model fit the data significantly, $F_{(1,139)}=66,488$, $p<0.001$, and explained essentially all the variance, multiple $R^2=0.998$. In the

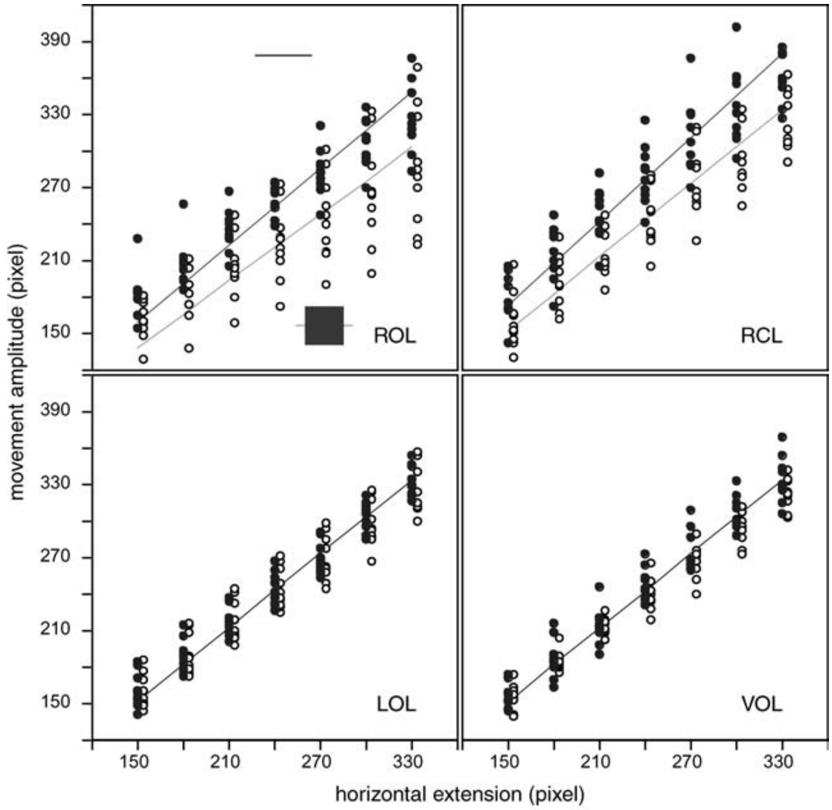

Fig. 5 Effector position modulates the influence of Kanizsa's illusory effect on a length of reproduction action. Observers performed the same actions studied in experiment 2 (Fig. 3). Each data point is the average of 20 matches by one of the 40 participants. All plotting conventions are the same as those of experiment 2

LOL condition, forcing the inclusion of the interaction term yielded almost identical slope estimates (1.011 and 1.007), corresponding to a practically null compression effect (0.4% of segment length). In the VOL condition, including the interaction term yielded slopes equal to 1.006 and 0.981, which correspond to a 2.5% compression estimate. Thus, as in experiment 2 there was essentially no effect of the illusion on the LOL and VOL motor responses.

General discussion 1–4

Overall, results from experiments 1–4 indicate that motor responses can use accurate effector-relative representations of spatial extents, provided that certain relations hold between the starting position of the effector, the direction of the action, and the orientation of the acted-upon spatial extent. A synopsis of our findings is presented in Tables 1 and 2.

Summary of results

Table 1 presents the percentages of variance explained by the two alternative linear models that can be fit to our motor data. The one-predictor model assumes that movement amplitudes depend on a single independent variable, the actual extension of the viewed segment. The two-predictor model assumes that amplitudes also depend on the type of display, as one would expect if the motor response was influenced by the illusory effect, and therefore includes an interaction term. As can be seen from the table, in both illusions all conditions are fit well by the one-predictor model, as one would expect given that the main source of variability in the amplitudes is the actual extension to be matched. In the ROL and RCL conditions, however, in both illusions adding the interac-

Table 1 Percentages of variance explained by the two alternative linear models that can be fit to the motor data

	Predictors in model	Motor condition			
		ROL	RCL	LOL	VOL
Dumbbell	1	96.7%	96.9%	99.5%	99.8%
	2	97.3%	98.1%	99.5%	99.8%
Kanizsa	1	98.1%	98.7%	99.6%	99.8%
	2	98.6%	99.1%	99.6%	99.8%

Table 2 Comparison of the size of the illusory effects, as measured by the difference between the slopes fit to the two types of display in each illusion, in the perceptual matches and in the four motor conditions studied

	Perceptual condition	Motor condition			
		ROL	RCL	LOL	VOL
Dumbbell	16.4%	17.0%	25.6%	−2.3%	2.8%
Kanizsa	11.4%	13.8%	11.8%	0.4%	2.5%

tion term provides a small, but not negligible, increase in the percentage of variance accounted for by the model. In the LOL and VOL conditions, conversely, no advantage is gained by adding the interaction term. Table 2 compares the size of the illusory effects, as measured by the difference between the slopes fit to the two types of display in each illusion, in the perceptual matches and in the four motor conditions studied. As can be seen again from these summary measures, relational effects producing the dumbbell and the Kanizsa illusions were robust in the ROL and RCL motor conditions, and comparable in size to those observed in the corresponding perceptual matches. However, essentially no relational effects were observed in the LOL motor condition. Finally, in the VOL motor condition we obtained relational effects that were an order of magnitude smaller than those observed in the ROL, RCL, or perceptual data. In fact, they were so small that the effect of the illusion proved unnecessary to model the VOL data, as was true also of the LOL data. The possibility remains that, with a much larger data set, some difference would emerge between the LOL and VOL conditions. Even if this turned out to be true, however, the conclusion seems warranted that the LOL and VOL conditions differ in some crucial way from the perceptual and the other motor conditions, and reflect spatial representations for hand transport that are essentially immune from the illusory effect.

Relationship to Gentilucci et al. (1996)

The present results may appear at odds with those of a well-cited study of motor responses to the Müller-Lyer illusion (Gentilucci et al. 1996). Gentilucci and coworkers examined pointing to one of the extremes of segments embedded in the Müller-Lyer patterns. They examined four conditions, aimed at providing a graded increase in the involvement of visual memory. In the "full-vision" condition, pointing was performed closed-loop while viewing the pattern. In the "no visual feedback condition", actors saw the pattern and their hand before starting to move, but could not see the hand during the action. In the "0-s delay" condition, they could not see the hand or the pattern (lights were turned off), but they could start as soon as vision was prevented. Finally, in the "5-s delay" condition, actors had to wait for 5 s after lights were turned off and then they could start. Given that the results of this study are often reported as evidence that the Müller-Lyer illusion affects pointing responses, they may appear in contradiction to our finding that actors were able to point to the other end of the dumbbell segments accurately in at least two conditions.

To address this point, we have reanalyzed the data published by Gentilucci et al. by computing percent measures of their illusory effects. These measures were obtained by subtracting average amplitudes in their compressing version of the illusion from the corresponding amplitudes in the expanding version, and then by normalizing with the amplitudes in the compressing version. This normalized difference can be interpreted in the same fashion as our difference between slopes (in fact, it can be shown that the difference between slopes corresponds to the average normalized difference between related points in our two groups). The outcome of this reanalysis is presented in Table 3. As can be shown from the table, Gentilucci's actors were essentially accurate in the "full vision" condition, whereas they showed a substantial effect of the illusion in the "5-s" delay condition. These latter two conditions, however, have no comparable counterpart in our study. For this reason, we will not discuss them further. More relevant here are the "no visual feedback" and "zero delay" conditions, which most closely resembled our LOL condition. As can be seen from the table, in these conditions, Gentilucci's actors were somewhat less accurate than our actors in the LOL and VOL condition, but still much more accurate than our estimates of illusion strength in perceptual matching. Thus, the outcome of Gentilucci's measurements was not substantially different, at least in its general pattern, from that observed by us.

Table 3 Reanalysis of the data published by Gentilucci et al. by computing percentage measures of their illusory effects

Full vision	No visual feedback	0 s delay	5 s delay
1.8%	3.5%	4.6%	9.9%

In addition, consider that conditions for performing the pointing actions were not fully equivalent in our and in Gentilucci's study. First of all, in Gentilucci's study pointing was performed from an initial position that was aligned with the orientation of the segment, but at some distance from its endpoint. This small, but critical, difference may have introduced at least two sources of bias in the results. On one hand, it is possible that starting from a position that is not exactly coincident with one of the endpoints of the extent to be reproduced prevented fully efficient effector-relative encoding of this extent. On the other, having to "imagine" the extent to be travelled on the illusion pattern, plus a small additional extent to cover the distance from the finger's position to the first endpoint, may have introduced a cognitive element in the direction of our effects in the ROL and RCL conditions. Furthermore, in the paradigm used by Gentilucci, actors started moving at a go signal given by the experimenter, not when they decided to as in our study. Given that in the "0-s delay" condition the go signal coincided with the exclusion of vision, it is not plausible that the formulation of the motor program preceded the exclusion of visual information. Thus, even in the zero delay condition, Gentilucci's actors were at least in part planning on the basis of memory, rather than using presently available visual information. In our study, visual information was excluded only upon the initiation of the action. Thus, our actors could comfortably plan the movement while actually viewing the display. Once these considerations are taken into account, we suggest that there is no contradiction between the results of Gentilucci and ours.

Alternative interpretations

Two alternative interpretations are also worth considering. The first is an issue raised by Mon-Williams and Bull (2000). These authors suggested that partial occlusion by the reaching hand might change the visual information available during a reaching action, and this would make the motor condition difficult to compare with the perceptual task, where no occlusion can take place. This is a valid concern, especially in studies of grasping on patterns such as the Ebbinghaus illusion. To pick up the disk in the Ebbinghaus pattern, one clearly has to move the hand and the forearm over the flankers of the disk. In the present studies, however, our actors reached for the initial positions from below the monitor and placed a single finger on the segment terminator, covering only a minimal amount of the circle abutting it. In addition, if occlusion by the finger had affected the results, we should have observed an increase of the illusory effect with larger displays, which we did not.

A second alternative interpretation is that observers did not code segment extension relative to the initial position of the effector, but used instead information from the oculomotor system to "mark" the position they had to point to (Post and Welch 1996; Carey 2000). In this view, accurate performance in the LOL and VOL conditions results from a sort of positional memory, achieved by recording the seen position in the oculomotor system and then using this information to guide the finger to the correct place. Although it seems unlikely that such coding would be based on the afferent output from mechanoreceptors in oculomotor muscles (Festinger and Canon 1965), it is possible in principle that the hand transport system could use efferent copies (Bridgeman and Graziano 1989; Bridgeman and Stark 1991) of programs for saccadic movements to guide the finger to the correct effector-relative position. We think that this is an interesting alternative, not only because it fits some physiological data on eye-hand coordination (see Carey 2000), but also because oculomotor coding of positions would provide an efficient way of controlling hand transport relative to an internal model, allowing for fast reaching movements with minimal feedforward planning (Desmurget and Grafton 2000). Given that this possibility is relatively easy to test in our paradigm, we performed a control experiment.

Experiment 5: testing oculomotor coding

We collected additional data on the LOL condition using again the dumbbell illusion pattern. In this experiment, however, actors viewed the displays monocularly and were instructed to keep their gaze fixed on the nail of their index finger once they had positioned the finger on the left endpoint of the segments to start the action. This is natural way of performing the action, given that one tends to spontaneously foveate where one is pointing. Once the action had begun, there was also a spontaneous tendency to pursue the finger but at this point the display was removed from the screen. Thus, actors did not saccade to the final endpoint of the segment in this experiment, but programmed hand transport using visual input from the peripheral retina. Using peripheral information implied that the final aim point could be more or less out of focus, depending on the actual extent of the segment. Given that there was ample opportunity to observe the display before placing the finger on the initial position, however, this appeared not to disturb the participants.

Materials and methods

Observers

Six members of the University of Trieste community participated. Three of them were familiar with the task and had participated in some of the previous experiments. All were right handed and had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Equipment and displays

Experimental equipment and displays were the same as in experiment 2.

Procedure

The experimental procedure was identical to that of experiment 2. There were only two differences. The first was that observers performed using only their preferred eye and wearing a blindfold on the other. The second was that they were instructed to keep their gaze on their fingernail after they had placed the finger on the initial position.

Conditions

Each participant served in only one motor condition, which was the same as the LOL condition in experiment 2.

Data validation and analysis

These were performed as in experiment 2.

Results and discussion

Our results were identical to those of experiment 2, as can be seen from Fig. 6. As in experiment 2, these data were fit perfectly by the simplest model using only actual width and no constant as the predictor, $F_{(1,83)}$=18,161, p<0.001, R^2=0.995. Thus, there was no hint of an illusory effect despite the fact that the task prevented oculomotor coding of the aim point. Thus, the results of this control experiment support the idea that effector-relative coding of extents was sufficient to produce immunity to the illusion in the LOL condition. Of course, even if oculomotor coding is not necessary for accurate pointing in these conditions, it remains plausible that interactions between frames of references used for reaching and

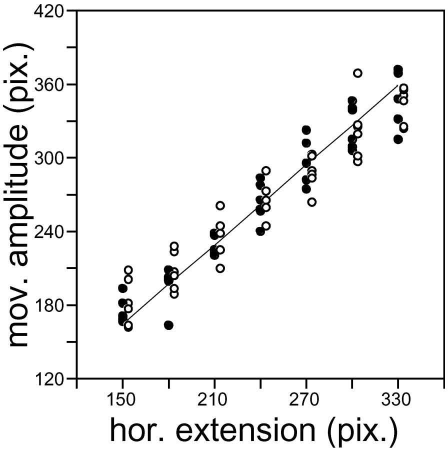

Fig. 6 Motor responses to the dumbbell pattern remained immune from the illusion even when preventing oculomotor coding of aim points. Each data point is the average of 20 matches by one of the six participants. As in the LOL condition of experiment 2, the regression line was estimated by fitting a linear model with a single parameter (effect of actual extension) and no constant. All plotting conventions are the same as those of experiment 2

oculomotor codings of positions play an important role in planning reaching actions in normal conditions. For this reason, the issue clearly deserves further investigation.

Conclusions

Organisms use vision to program and execute meaningful actions directed to environmental objects. Motor responses require that visual information be transformed into a set of motor commands appropriate to whatever action will be performed. The problem of transforming visual information into appropriate motor commands remains one of the least understood issues in motor control research (Jackson and Shaw 2000) and is a critical issue in visual cognition insofar as we accept that brain processes involved in visual perception should be understood in relation to the capacity that an embodied organism has for action (Trevarthen 1968; Gibson 1979). How do organisms solve this problem, and what cortical subsystems are involved?

Our goal in the present studies was to determine whether motor programs used for hand transport are affected by visual illusory effects and, if so, under what conditions. Our results showed a clear functional dissociation between perceptual matches, showing a robust illusory effect, and the LOL and VOL motor conditions which were essentially accurate. In addition, we also demonstrated a clear dissociation between the LOL condition and the ROL condition, which again showed the illusory effect. The present pattern of results have several implications for current evaluations of so-called perception-action dissociations when responding to visual illusions.

Consider first the proposal that seeming dissociations are, in fact, artifacts due to non-comparable perceptual and motor tasks (Franz 2001). This proposal rests on reanalyses of grasping studies suggesting that, when properly matched, perceptual judgements and grasps are affected in similar ways by illusions. Given that the perceptual and motor responses investigated in our studies were fully comparable according to Franz's criteria, at least in the present conditions it seems that the perception and action responses were indeed based on different internal representations. In this, our data did support a distinction between actions directed to the location of the stimulus (our LOL condition) and actions performed after an internal transformation (our ROL condition, involving a mental translation). Thus, this feature of our data is consistent with similar results concerning grasping (see, for instance Goodale et al. 1994; Haffenden and Goodale 1998) and does support the TVSH hypothesis of dorsal function for fast, egocentric actions directed to seen stimulus locations (Carey 2001). Note, however, that we also found accurate pointing in our VOL condition. Given that pointing was not directed to the object in the VOL condition, this result implies that the current characterization of dorsal" actions within the TVSH is incomplete.

The current pattern of results is best accounted for by a compromise solution involving either a distinction between representations of length vs. position (Brenner and Smeets 1996) or between different spatial frames of reference (Vishton et al. 1999; Bruno 2001). Consider the first of these possibilities. Although the ROL and VOL conditions were comparable in the sense that they both required an additional transformation (a form of mental translation), they also entailed a critical difference, namely, that the ROL required translating to a terminating position that was displaced an equivalent amount from the starting point as the length of the segment, whereas the VOL involved translating to a terminating position that was directly below the actual endpoint of the line. To the extent that this mode of presentation of the display made such a position salient to the visuomotor system, it may be argued that the difference between the ROL condition, on one hand, and the LOL and VOL conditions on the other, reflect a distinction between actions aimed at reproducing lengths and actions aimed at specific positions. Alternatively, it may be that the dorsal system plans horizontal transport using an egocentric reference frame centered on the body's midline. Given that the relationship between the initial position of the effector, the target position, and the body midline was equivalent in the LOL and VOL conditions, but not in the LOL and ROL conditions, this hypothesis would predict similar results in the former pair of conditions, but not in the latter. Further work is needed to distinguish between these two possibilities.

Finally, assuming that visuomotor programs were tapped by open-loop measures in our paradigm, our data also showed that motor planning is not necessarily based on allocentric coding of spatial extents as predicted by Glover and Dixon (2001). In our LOL and VOL conditions, open-loop movement amplitudes were consistent with accurate effector-relative representations of spatial extent. It remains possible, however, that even though the LOL and VOL conditions were visually open-loop, observers used kinesthetic or efferent information for online control at least to some extent.

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