RESEARCH ARTICLE

Allocentric and egocentric reference frames in the processing of three-dimensional haptic space

Robert Volcic · Astrid M. L. Kappers

Abstract The main goal of our study is to gain insight into the reference frames involved in three-dimensional haptic spatial processing. Previous research has shown that two-dimensional haptic spatial processing is prone to large systematic deviations. A weighted average model that identifies the origin of the systematic error patterns in the biasing influence of an egocentric reference frame on the allocentric reference frame was proposed as an explanation of the results. The basis of the egocentric reference frame was linked either to the hand or to the body. In the present study participants had to construct a field of parallel bars that could be oriented in three dimensions. First, systematic error patterns were found also in this three-dimensional haptic parallelity task. Second, among the different models tested for their accuracy in explaining the error patterns, the Hand-centered weighted average model proved to most closely resemble the data. A participant-specific weighting factor determined the biasing influence of the hand-centered egocentric reference frame. A shift from the allocentric towards the egocentric frame of reference of approximately 20% was observed. These results support the hypothesis that haptic spatial processing is a product of the interplay of diverse, but synergistically operating frames of reference.

Keywords Haptic · Space perpception ·
Reference frames · Egocentric · Allocentric

R. Volcic (✉) · A. M. L. Kappers
Helmholtz Institute, Utrecht University, Princetonplein 5,
3584 CC Utrecht, The Netherlands
e-mail: r.volcic@phys.uu.nl

Introduction

Our subjective experience generally supports the idea that our perception of space is veridical, since we efficiently move around our environment and interact with objects in it. In actual fact, although at first sight it may appear counterintuitive, the structure of a perceptual space (acquired via a single or a combination of modalities) is typically dissimilar from the corresponding physical space. As a consequence, perceptual spatial judgments are generally non-veridical. This dissimilarity between perceptual and physical spaces was noted long ago. For instance, von Uexküll (1909) coined the term *Umwelt* to describe the subjective world that a living being perceives and experiences. According to him, the environment that living beings perceive is not an objective and veridical representation of the physical world, but is instead a product of particular sensory modalities that each living being has. More specifically, von Kries (1923) presupposed the existence of separate visual and haptic spatial representations that inevitably differ from the physical structure of space.

The main interest of the present research was to focus our attention on haptic perceptual space and, particularly, on the ability in dealing with the spatial concept of parallelity. Interestingly, von Uexküll (1928) took for granted that haptic perception of space is veridical, although the opposite would be inferable from his previous work mentioned earlier. As an example, he supposed that the task of haptically matching the orientations of two spatially separated bars while blindfolded is manifestly a very simple operation. This supposition was contradicted by Hammerschmidt (1934) who actually performed the aforementioned experiment. None of the participants was able to orient a bar physically parallel to a second bar. This was the first study to show that perceptual haptic parallelity

differs from physical parallelity (see Blumenfeld (1937) and von Skramlik (1937) for other studies with similar implications). This topic was later tackled by von Skramlik (1959) who confirmed the previous findings, albeit without proposing any theoretical explanation. Unfortunately, these studies merely observed and described the fact that what feels haptically parallel does not correspond to what is actually physically parallel.

Only recently have different studies started to focus on haptic perception of spatial relations with an emphasis on the perception of parallelity by directing their attention to the disentanglement of the underlying mechanisms. The haptic parallelity task was performed on the horizontal plane (Kappers 1999; Kappers and Koenderink 1999; Zuidhoek et al. 2003), and similarly on the midsagittal (Kappers 2002) and on the frontoparallel planes (Hermens et al. 2006; Volcic et al. 2007). Large and, more importantly, systematic deviations from veridicality were found to consistently occur on all the three main orthogonal planes, thus, over the whole region of space directly in front of the participant (i.e., frontal peripersonal space). The magnitude of the deviations was shown to be participant-dependent with the deviations varying between 10° and 90° (Kappers 2003).

The systematicity of the error patterns was the indicator that the processes subserving our haptic representation of space are tightly linked to the reference frames in which these internal representations are coded. Spatial knowledge may be stored in many ways and in many different formats, but it is quite straightforward that the spatial characteristics of an object have to be encoded with respect to some reference frame. Commonly, reference frames can be described in terms of two broad classes: egocentric reference frames, in which objects are represented relative to the perceiver, and allocentric reference frames, in which objects are represented relative to the environment that is extrinsic to the perceiver (for a review, see Soechting and Flanders 1992). The view that the brain constructs multiple spatial representations is supported by several studies in different research fields showing that we are biologically equipped to have multiple reference frames at the same time (e.g., Arbib 1991; Carrozzo et al. 2002; Colby and Duhamel 1996; Farah et al. 1990; Gross and Graziano 1995; Klatzky 1998; Paillard 1991). Besides, several different body parts have been defined to be the origin of the egocentric reference frame, for instance, just to mention those probably involved in haptic perception: the hand (Carrozzo and Lacquaniti 1994; Paillard 1991), the arm (Flanders and Soechting 1995; Soechting and Flanders 1992, 1993), and the body (Luyat et al. 2001; Millar and Al-Attar 2004). A question that has been frequently raised is whether the different frames of reference operate independently or mutually influence each other. The

preferential choice of one or the other reference frame could depend on the type of spatial problem to be solved. However, there is now abundant evidence that supports the hypothesis of synergistically operating spatial representations. The spatial characteristics of an object are thus coded neither in an allocentric reference frame nor in an egocentric one but in a frame that is intermediate to the two (Carrozzo and Lacquaniti 1994; Cohen and Andersen 2002; Flanders and Soechting 1995; Luyat et al. 2001; Paillard 1991; Soechting and Flanders 1992, 1993). In fact, the concrete existence of an intermediate reference frame is questionable; the weighted average of the two reference frames would provide an equally effective but a more parsimonious solution, but this issue lies beyond the scope of this paper. Although more than just two frames of reference could interact with each other, a single egocentric reference frame was usually identified as the primary biasing source on the allocentric reference frame. A systematic error pattern would therefore indicate the biasing influence of that specific egocentric frame of reference.

On the basis of the existence of multiple reference frames and their interactions, it has been hypothesized that the systematic patterns of errors occurring in the haptic parallelity task are a product of a weighted average of an allocentric and an egocentric frame of reference (Kappers 2004, 2005, 2007; Kappers and Viergever 2006; Volcic et al. 2007). Specifically, the participant-dependent magnitude of the deviations is determined by the degree to which the egocentric and the allocentric reference frames combine with each other. This model proved to be robust in describing the deviations on all of the three main orthogonal planes. Furthermore, it was able to predict an unchanged deviating behavior in a task in which participants were asked to set the bars perpendicular to each other, and, a disappearance of the deviations in a task in which participants were asked to mirror in the midsagittal plane the orientation of the reference bar (Kappers 2004). In the above mentioned studies, the hand, or more generically the forearm, was identified as the origin of the egocentric reference frame, although a contribution of an egocentric frame of reference linked to the body-midline could not be completely disregarded (Kaas and van Mier 2006; Kappers 2007). The indication that the hand-centered reference frame contributes most was shown by Kappers and Viergever (2006), who demonstrated a modulation of the magnitude of the deviations as a function of the relative orientations of the two hands. In other words, the deviations in perceived parallelity decreased when the hands were convergent, and increased when the hands were divergent. Since the bars were always in the same position relative to the participants' body, this modulation was certainly not caused by any reference frame fixed to the body, eyes or shoulders. Kappers (2007) has furthermore

quantified the biasing influence of the hand-centered reference frame. The contribution of this egocentric reference frame was about 25% on average. In other words, the deviations correspond approximately to a quarter of a given mismatch between the allocentric and the hand-centered egocentric frames of reference.

The primary purpose of our study is to explore haptic space perception of parallelity in three dimensions. Blindfolded participants had to match the orientation of a whole field of bars in such a way that they felt as if they were parallel to a reference bar. Participants had the freedom to orient the bars in three dimensions, as opposed to the constraint of orienting the bars in only one plane, which was incorporated in all the previous studies. Several questions were addressed in this study. The key question was whether the deviations (if any) participants make occur in a systematic manner also in the three-dimensional haptic parallelity task and if they are comparable in various aspects with the deviation patterns observed in the two-dimensional haptic parallelity task. If the processes underlying three-dimensional haptic perception of space also reflect the hypothesis of a weighted average model, then the systematic deviations should cluster along the direction of the mismatch between the involved reference frames. Therefore, what feels haptically parallel should lie in the plane defined by the allocentrically and the egocentrically parallel bars (see Fig. 1). Moreover, participant-dependent differences in the magnitude of the deviations would be expected to reveal the different contributions of the two reference frames. If, ad absurdum, the egocentric reference frame would completely dominate, the perceived parallelity would equal the egocentrically defined parallelity. The biasing influence of a specific egocentric reference frame would be expressed in participant-specific, but approximately stable, weighting factors. The final question concerned the choice and the validation of a specific model that would accurately describe the patterns of deviations. The comparison of models will especially try to discern the importance of either the body- or the hand-centered reference frame. In this respect, a deeper inspection of the different models is given in the following section.

Models

A vast variety of alternative reference frame-based models can be considered as best predictors of the results. To this end, however, we shall give careful consideration to a limited set of the most likely candidates. The main distinctive criterion is encapsulated in the typology of reference frames that are considered in each class of models; they can be built on a single allocentric frame of reference or on a combination of an allocentric and an egocentric frame of reference. The implication is that the geometrical concept of parallelity in the different reference frames can lead to different physical outcomes. Accordingly, some caveats should be noted. In the allocentric reference frame that corresponds to physical Euclidean space two bars with the same physical orientation are defined as parallel. Thus, the parallelity is independent of the relative locations of these bars. On the other hand, in the egocentric reference frame fixed to the body, or to some body part, two bars that are parallel within this frame can change their orientation with respect to the environment as a function of a spatial transformation (such as a translation, a rotation, or both) of the body part to which this frame is fixed. As a consequence, two bars that are parallel in an egocentric frame of reference can actually have different physical orientations.

Veridical model

The underlying idea that characterizes the *Veridical model* is that only an allocentric frame of reference subserves our perceptual representation of the surrounding space. The origin of the allocentric reference frame is considered to be independent of the actual position of the perceiver since it is anchored to the external space and defines spatial relations with respect to elements of the environment. We assume that the allocentric reference frame is derived from an internal construct built from extracting the stable covariant features of the environment. Therefore, the allocentric reference frame has to be inevitably internalized through egocentric experiences. Since the allocentric representation reflects the physical features of the surrounding space, the extent of the errors, if any, should be space-invariant. On this basis, the Veridical model assumes that the settings are physically correct, that is, all the bars are parallel in the allocentric reference frame. Deviations are expected to be minimally scattered and independent from the spatial location.

Descriptive models

These models serve the purpose of describing the general trend of the data by presupposing a systematic error pattern, but without any hypothesis about the origin of the error pattern. Two models are proposed, the second one being a more specialized version of the first model.

Systematic error model. This model presupposes that the deviations have a systematic directional error that is independent of the spatial location. The average deviation across participants is considered as the best predictor of the extent of the errors.

Participant-dependent systematic error model. This model surmises analogous deviations as the previous
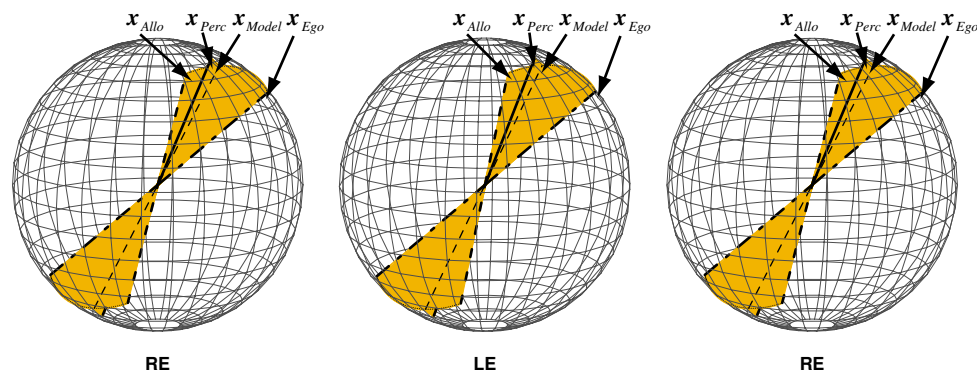
Fig. 1 Stereoscopic representation of a generic weighted average model. A three-dimensional picture can be seen by cross-fusing the left two images or divergently fusing the right two images (*RE* right eye, *LE* left eye). The vector $\mathbf{x}_{Allo}$ represents an allocentrically defined parallel bar and the vector $\mathbf{x}_{Ego}$ represents an egocentrically defined parallel bar. According to the weighted average model, what feels haptically parallel ($\mathbf{x}_{Model}$) should lie in the plane spanned by these two vectors. The vector $\mathbf{x}_{Perc}$ represents a haptically parallel bar that differs slightly from the model prediction. Generally, the angle between $\mathbf{x}_{Perc}$ and $\mathbf{x}_{Model}$ defines the out-of-plane deviation and the angle between $\mathbf{x}_{Allo}$ and $\mathbf{x}_{Model}$ defines the in-plane deviation from veridicality

model, that is, a systematic directional error independent of the spatial location, with the addition that the extent of the error is considered to be participant-dependent. As a consequence, the average deviation of each participant is considered as the best predictor of the extent of the errors.

Weighted average models

The weighted average models presuppose that the perceptual representation of space is based on the existence of an allocentric and an egocentric frame of reference and their mutual interaction. According to this presupposition, what feels haptically parallel is intermediate between the parallelity defined by the allocentric frame of reference and the parallelity defined by the egocentric frame of reference. Thus, haptic parallelity is determined by a biasing influence of the egocentric frame of reference, and the deviations from veridicality vary systematically across the space. Formally stated, what feels haptically parallel (vector $\mathbf{x}_{Model}$) should lie in the plane spanned by the two vectors $\mathbf{x}_{Allo}$ (allocentrically parallel) and $\mathbf{x}_{Ego}$ (egocentrically parallel), as can be seen in Fig. 1. Thus, the weighted average of the contributions of the allocentric and the egocentric frame of reference should determine the perceived parallelity:

$$\mathbf{x}_{Model} = (1 - w)\mathbf{x}_{Allo} + w\mathbf{x}_{Ego} \quad (0 \leq w \leq 1). \quad (1)$$

The size of the weighting factor (w) modulates the relative contributions of the two reference frames. A higher weighting factor causes a greater impact of the egocentric frame of reference and, consequently, larger deviations that are biased in the direction of the egocentric frame of reference. The participant-dependent component in this class of models is expressed by the variable weighting factor.

Obviously, the fundamental issue is the selection of the anchor point of the egocentric frame of reference. In the literature mentioned earlier, focus was restricted to a body-centered egocentric reference frame and a hand-centered egocentric reference frame. Hence the weighted average models are grounded on the combination of either one of the two egocentric reference frames and the allocentric reference frame. On this basis, the following two models were considered:

Body-centered weighted average model

The body-midline is defined as the anchor point of the egocentric frame of reference ($\mathbf{x}_{EgoBody}$). Thus, two bars that are parallel within this egocentric frame would have the same orientation with respect to concentric circles centered on the body-midline that are taken as reference lines (see Fig. 2a). Specifically, the orientation of the vector that would be defined as parallel to the reference orientation in this egocentric frame of reference is computed by taking into account the angle between the line connecting the reference bar to the body-midline and the line connecting the body-midline to a specific test bar. A change in the orientation of this vector would result in its rotation in the horizontal plane only. In this model, for each bar location two vectors ($\mathbf{x}_{Allo}$ and $\mathbf{x}_{EgoBody}$) define parallelity, one in the allocentric reference frame and one in the egocentric frame linked to the body-midline, respectively. The perceived parallelity would be determined by the weighting factor (w) calibrating the contributions of the two reference frames.

Hand-centered weighted average model

The egocentric frame of reference ($\mathbf{x}_{EgoHand}$) is anchored to the hand. Therefore, two bars that are parallel within this
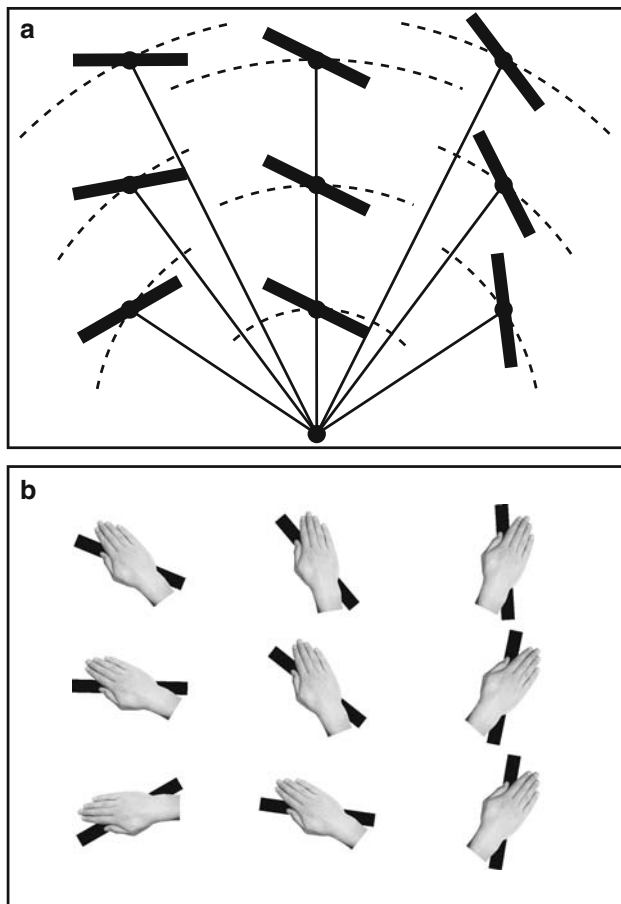
Fig. 2 Representations of *parallel bars* in the Body- and Hand-centered reference frames (top view of the set-up). **a** *Bars* that are parallel in the Body-centered reference frame have the same orientation with respect to concentric *circles* centered on the body-midline. **b** *Bars* that are parallel in the Hand-centered reference frame have the same orientation with respect to the hand. Note that *hand* orientation can change both in slant and tilt. Changes in tilt are not depicted in this two dimensional figure

frame of reference maintain the same orientation with respect to the hand, although their orientation with respect to the environment can change as a function of the hand displacement and its rotation (see Fig. 2b). Any change in the orientation of the hand induces a change in the orientation of the hand-centered egocentric reference frame. The orientation of the vector that would be defined as parallel to the reference orientation in this egocentric frame of reference is computed by taking into account the change in the measured hand orientation (see "Materials and methods") between each particular location of the test bar and the location of the reference bar. As a consequence, the orientation of this vector can vary both in the horizontal and in the vertical plane. As in the previous model, for each bar location two vectors (x_{Allo} and $x_{EgoHand}$) define parallelity, one in the allocentric reference frame and one in the ego-centric frame linked to the hand, respectively. The relative

contribution of each reference frame is determined by the weighting factor (w).

Materials and methods

Participants

Eight undergraduate students (six female and two male, 20–30 years of age) took part in this experiment and were remunerated for their effort. None of the participants had any prior knowledge of the experimental design and the task. The handedness of the participants was assessed by means of a standard questionnaire (Coren 1993). All participants were right-handed.

Apparatus

The set-up consisted of a table (150 × 75 × 75 cm) on which nine replaceable aluminum poles of variable height were fixed (for a schematic drawing see Fig. 3). If the middle of one of the two longest table edges is defined as the origin with coordinates (0, 0), then the poles were placed at the x-coordinates −30, 0, and 30 cm, and at the y-coordinates 10, 30, and 50 cm, forming a rectangular grid of locations centered along the longest table edge. The poles were 12, 36, or 60 cm high (three poles for each height). On the top of each pole a rotatable aluminum bar with a length of 20 cm and a diameter of 1.8 cm was attached (see Fig. 4). The rotation point of the bar was located in the middle of the bar's long axis. The bar could rotate in the vertical plane. Below each bar a half protractor was attached that allowed the bar orientation in the vertical plane to be read off with an accuracy of 0.5°. We define this orientation as tilt (θ). A 90° orientation corresponded to a horizontally oriented bar. By clockwise rotating the bar in the frontoparallel plane relative to the participant's viewpoint the orientation increases to its maximum at 170°. On the other hand, by counterclockwise rotating the bar in the frontoparallel plane the orientation decreases to its minimum at 10°. The poles could rotate along their vertical axis (360° range) and at the base of each pole a protractor was drawn that allowed the orientation in the horizontal plane to be read off with an accuracy of 0.5°. We define this orientation as slant (φ). A 0° orientation was parallel to the longest table edge with increasing angles in a counterclockwise direction. The three-dimensional orientation of the bar is defined by the tilt and the slant (elevation and azimuth are equivalent terms in use). For instance, a bar with a tilt of 90° and a slant of 90°, i.e. (90°, 90°), is horizontal, that is, parallel to the table plane, and perpendicular to the longest table edge. Bars were used both as test and reference bars; in the latter case a screw on the bar

protractor and another screw on the pole protractor were tightened to prevent accidental rotations of the bar.
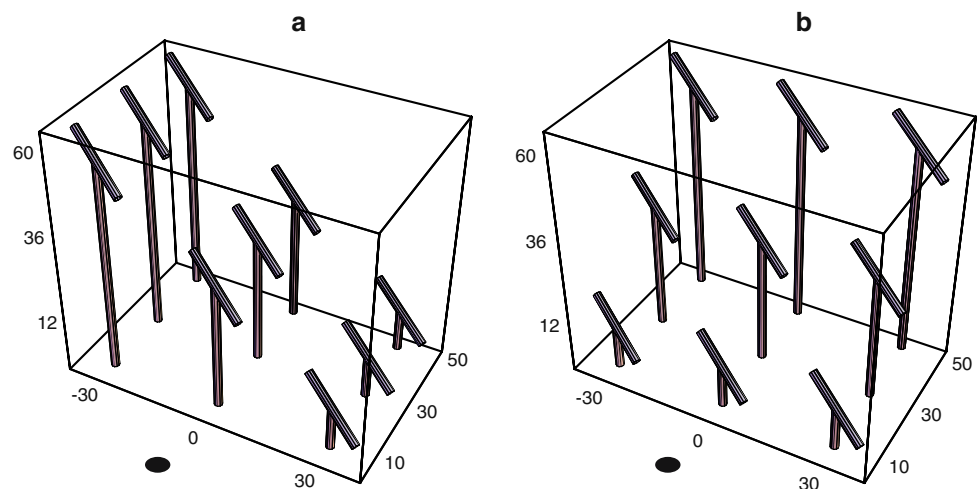
Design

The nine bars were arranged in two particular dispositions corresponding to different plane orientations and inclinations (see Fig. 3). In the left/right condition the bars with the 60 cm height were located at $x = -30$ cm, those with the 36 cm height at $x = 0$ cm, and those with the 12 cm height at $x = 30$ cm (see Fig. 3a). In the far/near condition the bars with the 12 cm height were located at $y = 10$ cm, those with the 36 cm height at $y = 30$ cm, and those with the 60 cm height at $y = 50$ cm (see Fig. 3b). In the first condition the rotation points of the nine bars define a plane that is inclined from left to right, whereas in the second condition the rotation points form a plane that is inclined from far to near. The far/near plane had a larger inclination than the left/right plane since the distances between the y-coordinates of the poles are shorter than the distances between the x-coordinates. In both conditions the reference bar was positioned at the location $(-30, 10)$, thus on the left side near the longest table edge. At all the other locations test bars were positioned. For each condition the reference bar was set at different orientations that can be divided into two categories, namely reference bar orientations that were lying in the planes defined by the rotation points of the bars (in-plane reference bars), and reference bar orientations that were at a certain angle with these planes (out-of-plane reference bars). No out-of-plane reference bar was normal to the plane. For the left/right condition the orientations $(120°, 45°)$ and $(60°, 135°)$ were given to the in-plane reference bars, whereas the orientations $(30°, 45°)$ and $(150°, 135°)$ were given to the out-of-plane reference bars. Similarly, for the far/near condition the orientations

Fig. 4 A close-up of the bar used in the experiment with the half protractor on the bottom of the bar indicating the tilt (θ) and with the protractor at the base of the pole indicating the slant (φ)

$(50°, 45°)$ and $(50°, 135°)$ were given to the in-plane reference bars, and the orientations $(140°, 45°)$ and $(140°, 135°)$ were given to the out-of-plane reference bars. The order of eight trials (2 planes × 2 reference bars relations with the plane × 2 reference bar orientations) was randomized for each participant. The block of eight trials was repeated three times with different randomizations,

Fig. 3 Representation of the spatial arrangement of the *bars* in the experiment. The reference bar was always positioned at the location $(-30, 10)$. The *black disks* indicate the location of the participants' body-midline with respect to the set-up. **a** Left/right condition. **b** Far/near condition

which amounted to 24 trials per participant and a total of 192 measurements per participant.

Procedure

Blindfolded participants had to perform the three-dimensional parallelity task unimanually. Participants were placed in front of the longest edge of the set-up. The floor in front of the set-up was marked specifying the locations on which the two participants' feet had to be positioned. Their body midline was aligned with respect to the mid-point of the set-up and was approximately 25 cm from the table edge (see the black disks in Fig. 3). From this position all the bars on the top of the poles were within easy reach; therefore no displacement of the body or bending of the upper body was either necessary or allowed.

Before the start of the experiment and before each trial the experimenter guided the right hand of blindfolded participants over the nine positions that defined the set of bars of the succeeding trial. In addition, the participants were encouraged to voluntarily explore the set of positions to acquire confidence in locating the bars without the help of vision. It should be noted that during this phase all nine bars were randomly oriented. Subsequently, the experimenter fixed the orientation of the reference bar and the right hand of the participants was placed on that bar. The participants were instructed to rotate all eight test bars in such a way that they felt all the bars were parallel to the reference bar. They could choose the order and, if needed, they could repeatedly switch between the same pair of bars. Importantly, it was never the case that two bars could be touched at the same time with their hand. Participants were allowed to use their fingers, palms and hands to touch the bars either statically or dynamically. However, one constraint was imposed on their exploratory behavior: they were permitted to approach the bars only from above. This limitation prevented them from exploring the bars from the side and simultaneously touching the poles on which the bars were attached, thereby giving them extra cues about their orientation. Neither during the trials nor between trials could the participants touch the table. To explore the bars and orient them they had 5 min, which appeared to be a more than adequate amount of time. An electronic digital timer signaled time when 2 min and 1 min of the trial were left and when the time had run out. Participants removed their hand from the set-up and the experimenter wrote down the orientations before starting with the next trial. No feedback was given on their performance. The experimental sessions ended after 1 h to prevent fatigue of the participants and were performed on separate days. They took on average 4 h to complete all sessions. Participants did not have the chance to see the set-up until all sessions were over, because it was covered before and after each session.

After the completion of the three-dimensional parallelity task one more experimental session was performed. In order to examine the influence of hand orientation, the orientation of the right hand was measured for each bar position employed in the three-dimensional parallelity task. This method enabled the orientation of the egocentric reference frame fixed to the hand to be calculated for each bar position. In previous studies on the haptic parallelity task conducted on the main orthogonal planes it was proven to be a valid method in demonstrating a correlation between deviations and hand orientations (Kappers 2005, in press; Volcic et al. 2007). Participants resumed their position in front of the set-up, this time without wearing the blindfold. The bars were distributed at the same locations as either in the left/right condition or in the far/near condition. They had to lay their right hand sequentially in a natural way (no radial or ulnar deviation) on the top of each of the bars including the reference bar that was then rotatable. Moreover, they were asked to hold their extended fingers close to each other (finger adduction). The participants' task was to align the bar to the middle finger, thus to the hand's major axis. The natural way of laying their hand on the bar closely corresponded to the orientation of the hand at the same location during the execution of the first experimental session. Several finger movements were certainly present in the first experimental session, but more importantly the orientation of the hands' major axis was quite stable. We assume that this hand orientation corresponds to the orientation of the egocentric reference frame at each bar location. The orientation of the hand was specified by the tilt and slant angles of the bar. The tilt angle refers to the up–down orientation of the hand, and the slant angle refers to the left–right orientation. The participants did not rotate the hand around its major axis during the three-dimensional parallelity task, because they had always to approach the bars from above. For this reason we limited the definition of the hand's orientation only to the tilt and the slant angle of the bar that the participants aligned to their hand. The hand orientations of each participant were measured for both the left/right condition and the far/near condition and repeated three times. Participants took on average twenty minutes to complete this session.

To estimate the variability of the hand orientation measurements we calculated the standard deviations for each bar location over the three repetitions. Standard deviations were rather small (on average 2°) and they did not vary for the different bar locations suggesting that the hand orientation measurements gave a good estimate of the orientation of the hand-centered egocentric reference frame.

Data analysis

The orientations of the bars are specified by the tilt (θ) and slant (φ) angles. Since the bars were all of equal length, we will treat them as unit vectors in $\mathbb{R}^3$ with the origin $(0, 0, 0)$ coinciding with the rotation point of each bar. The angular difference between two vector orientations can be expressed as a one-parameter angle, that is, the absolute angular difference between the vectors, or by several two-parameter angles. Our focus will be directed to three alternative methods for calculating the deviations from veridical. All three methods are based on two-parameter errors and they are interconnected with the different models employed in this study.

In the first method (Allo method) the errors are computed relative to the allocentric frame of reference. The *slant deviation* corresponds to the angular difference between the slant (φ) angle of the reference bar and the slant angle of the test bar. A positive sign is assigned to the deviations in the clockwise direction, whereas a negative sign is assigned to the deviations in the counterclockwise direction. The *tilt deviation* corresponds to the angular difference between the tilt (θ) angle of the reference bar and the tilt angle of the test bar. A positive sign is assigned to the deviations in the direction of the upward normal of the horizontal plane, and, conversely, a negative sign is assigned to the deviations in the opposite direction.

In the second method (Body method) the errors are computed in the context of the Body-centered weighted average model. Let $\mathbf{x}_{Perc}$ be a vector that corresponds to the orientation of a bar set by a participant, thus to the orientation that feels haptically parallel to the reference bar (see Fig. 1). If the haptic perception of parallelity were veridical the vector $\mathbf{x}_{Perc}$ would be aligned with $\mathbf{x}_{Allo}$. Otherwise, the vector $\mathbf{x}_{Perc}$ would point to some other direction. In this case, the deviation of the vector is defined with regard to the plane spanned by the vectors $\mathbf{x}_{Allo}$ and $\mathbf{x}_{EgoBody}$. The vector $\mathbf{x}_{EgoBody}$ coincides with the parallelity defined in the egocentric frame of reference linked to the body-midline. The *in-plane*$_{Body}$ *deviation* is defined as the angle between $\mathbf{x}_{Allo}$ and the projection of $\mathbf{x}_{Perc}$ on the plane. A positive sign is assigned to the deviations in the direction of $\mathbf{x}_{EgoBody}$, whereas a negative sign is assigned to the deviations in the opposite direction. Similarly, the *out-of-plane*$_{Body}$ *deviation* is defined as the angle between the vector $\mathbf{x}_{Perc}$ and its projection on the plane. The sign of the out-of-plane$_{Body}$ deviation is defined with respect to the normal of the plane calculated as $\mathbf{x}_{EgoBody} \times \mathbf{x}_{Allo}$. A positive sign is assigned to the deviations in the direction of the normal, and, conversely, a negative sign is assigned to the deviations in the opposite direction.

In the third method (Hand method) the errors are computed in the framework of the Hand-centered weighted average model. The reasoning regarding the computations of these errors is identical to the second method, with the only distinction being that the deviation of the vector is defined with regard to a different plane, namely the plane spanned by the vectors $\mathbf{x}_{Allo}$ and $\mathbf{x}_{EgoHand}$. In this case the vector $\mathbf{x}_{EgoHand}$ coincides with the parallelity defined in the egocentric frame of reference linked to the hand. As it was shown in the description of the previous method, the *in-plane*$_{Hand}$ *deviation* is defined as the angle between $\mathbf{x}_{Allo}$ and the projection of $\mathbf{x}_{Perc}$ on the plane. A positive sign is assigned to the deviations in the direction of $\mathbf{x}_{EgoHand}$, whereas a negative sign is assigned to the deviations in the opposite direction. Likewise, the *out-of-plane*$_{Hand}$ *deviation* is defined as the angle between the vector $\mathbf{x}_{Perc}$ and its projection on the plane. The sign of the out-of-plane$_{Hand}$ deviation is defined with respect to the normal of the plane calculated as $\mathbf{x}_{EgoHand} \times \mathbf{x}_{Allo}$. A positive sign is assigned to the deviations in the direction of the normal, and, conversely, a negative sign is assigned to the deviations in the opposite direction. It has to be noted that according to the weighted average models when $\mathbf{x}_{Allo}$ and $\mathbf{x}_{Ego}$ coincide the plane spanned by these vectors is not defined. Therefore, it is not possible to define the out-of-plane and in-plane deviations. However, this special case did not occur in our study.

The planes with respect to which we calculated the deviations (both Body and Hand) were computed as a function of the reference bar orientation and the position of the bar with respect to either the body-midline or the orientation of the hand (see Eq. 1). The planes in the Hand method were computed separately for each participant, since the hand orientations could vary between them.

To estimate the contributions of the allocentric and the egocentric frame of reference in the two weighted average models the least-square method was applied. The weighting factor (w) was computed by minimizing:

$$\sum_i \alpha_i^2(w), \tag{2}$$

with respect to w. α_i is the angle between the measured orientation $\mathbf{x}_{Perc}$ and $\mathbf{x}_{Model}(w)$ for a single bar. The index i refers to the eight measured orientations obtained in a single trial. Separate minimization procedures were performed for the Body-centered and Hand-centered weighted average models. Therefore, a total of 24 weighting factors per participant were computed for each egocentric reference frame (linked to the hand or to the body-midline). This measure specifies the biasing influence of the egocentric reference frame.

The different models were compared by means of two methods: first, an approximate estimate of the accuracy of each model was given by comparing the observed settings with the predictions of the models; second, the best-fitting model was selected on the basis of Akaike's information

criterion, which evaluates the complexity of a model against its accuracy in fitting the data (for details, see "Appendix").

Results

Our results showed that participants systematically misoriented the test bars with respect to veridicality, that is, with respect to a field of physically parallel bars. For all participants, a bar on the right side of the set-up has to be rotated clockwise in the horizontal plane to be perceived as parallel to a bar on the left side, and, simultaneously, a bar located lower has to be rotated clockwise in the sagittal plane (seen from the right side) to be perceived as parallel to a bar located higher. To explore the systematicity of the errors participants made the data were analyzed by converting them into the two-parameter angles according to the three methods explained in the Sect. "Data analysis".
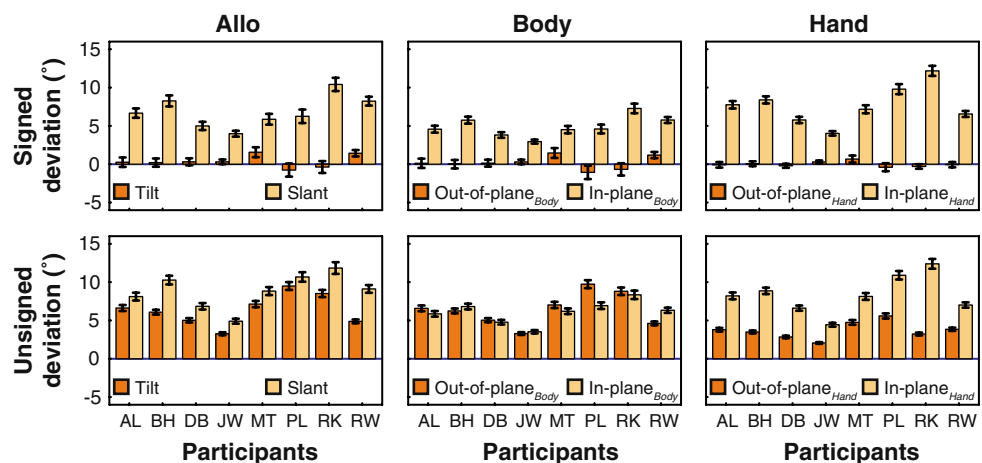
Comparison of the analyzing methods

The bar charts in Fig. 5 represent the mean slant, in-plane$_{Body}$, in-plane$_{Hand}$ deviations, and the mean tilt, out-of-plane$_{Body}$, out-of-plane$_{Hand}$ deviations, expressed both as signed and unsigned errors for each participant. The error bars indicate the standard errors of the mean. It should be noted that the signed deviations define the magnitude and the directionality of the errors, whereas the unsigned deviations combine the magnitude of the errors with the variable error component. By considering all the signed deviations, represented in the first row of Fig. 5, it is evident that the slant and in-plane deviations (Body, Hand) consistently point in the same direction, although the extent of the error is participant-dependent. On the other hand, all the signed tilt and out-of-plane deviations (Body, Hand) are scattered around zero. Simple t tests conducted separately

on the data of different participants and separately for the three analyzing methods were run to check if, on the one hand, the signed slant and in-plane deviations, and, on the other hand, the tilt and out-of-plane deviations differ from zero. For all participants, as is already clear from Fig. 5, the signed slant and in-plane deviations were significantly different from zero (Allo: $7.09 \leq t(191) \leq 14.24$, $P < 0.001$; Body: $8.01 \leq t(191) \leq 14.79$, $P < 0.001$; Hand: $13.65 \leq t(191) \leq 18.54$, $P < 0.001$). On the contrary, the differences between the signed tilt and out-of-plane deviations and zero proved to be mostly not significant. Specifically, for both Allo and Body analyzing methods, the out-of-plane deviations resulted to be significantly different from zero for participants MT (Allo: $t(191) = 2.4$, $P < 0.05$; Body: $t(191) = 2.27$, $P < 0.05$) and RW (Allo: $t(191) = 3.43$, $P < 0.001$; Body: $t(191) = 2.93$, $P < 0.005$). Only for the Hand analyzing method were the signed out-of-plane deviations not significantly different from zero for all participants.

In the second row of Fig. 5 the unsigned deviations are plotted. Since all the slant and in-plane deviations are strongly biased in one direction, the difference between the signed and the unsigned slant and in-plane deviations is almost unnoticeable, which means that only a few settings were actually in the opposite direction. This strong similarity between the signed and the unsigned slant and in-plane deviation underlines the strength of this bias. On the other hand, the unsigned tilt and out-of-plane deviations provide additional information about the magnitude of these deviations. If these deviations are compared among the three analyzing methods, it is clear that the unsigned out-of-plane$_{Hand}$ deviations are the smallest. This evidence is supported by paired t tests conducted separately on the data of different participants in which the three analyzing methods were compared. The unsigned out-of-plane$_{Hand}$ deviations were for all participants significantly smaller than both the unsigned tilt and out-of-plane$_{Body}$ deviations

Fig. 5 *Bar charts* that represent the deviations from veridicality for each participant according to the three analyzing methods. The mean slant and tilt deviations are presented in the *left panels*, the in-plane$_{Body}$ and out-of-plane$_{Body}$ deviations in the *middle panels*, and the in-plane$_{Hand}$ and the out-of-plane$_{Hand}$ deviations in the *right panels*. The *error bars* indicate the standard errors of the mean ($N = 192$). Signed deviations are shown in the *top panels* and unsigned deviations are shown in the *bottom panels*

(Allo versus Hand: $4.23 \leq t(191) \leq 10.94$, $P < 0.001$; Body versus Hand: $3.42 \leq t(191) \leq 11.19$, $P < 0.001$). The comparison of the unsigned tilt and out-of-plane$_{Body}$ deviations did not lead to any significant result. The minimal level of significance in these analyses was lowered to 0.017 (Bonferroni correction) because of multiple comparisons. In an overall view of the unsigned deviations it is also noteworthy to put alongside the two orthogonal error measures and consider their relative magnitudes. A series of paired t tests showed that the unsigned slant deviations were significantly larger than the unsigned tilt deviations with an average difference of $2.4°$ ($t(7) = 5.49$, $P < 0.001$). Similarly, the unsigned in-plane$_{Hand}$ deviations were significantly larger than the unsigned out-of-plane$_{Hand}$ deviations with an average difference of $4.6°$ ($t(7) = 6.19$, $P < 0.001$). On the contrary, the difference between unsigned in-plane$_{Body}$ deviations and unsigned out-of-plane$_{Body}$ deviations was found to be not significant.

Comparison of the models

One of the main purposes of the analysis was to select the model that best suits the gathered data. In this respect, first, the data were compared with the predictions of the models, and, second, Akaike's information criterion was applied to select the best-fitting model. The predictions of the weighted average models were based on the positions of the bars with respect to the body-midline or on the measured hand orientations. The weighting parameter was determined for each participant individually by averaging the weighting factors computed as explained in the Sect. "Data analysis".

In Fig. 6 the mean absolute deviations between the data and each model with the relative standard errors of the mean are shown, individually for each participant. The *absolute deviation* is a one-parameter error measure expressing the angular difference between a setting and the prediction of a model for that particular setting. From Fig. 6 it is evident that the Hand-centered weighted average model provides the smallest discrepancy with the data and it does so consistently for all participants. Moreover, the scatter of these deviations is rather low in contrast to that observed for the other models. The absolute deviations were constant for the different bar locations indicating no systematic error in the predictions of the model. The opposite was true for the other models that showed systematic absolute deviations as a function of the bar location. The Hand-centered weighted average model was thus able to better capture the participants' behavior over the whole set of bars.

The appropriateness of the set of models was evaluated using Akaike's information criterion (see "Appendix"). The relative probability of each model being correct among
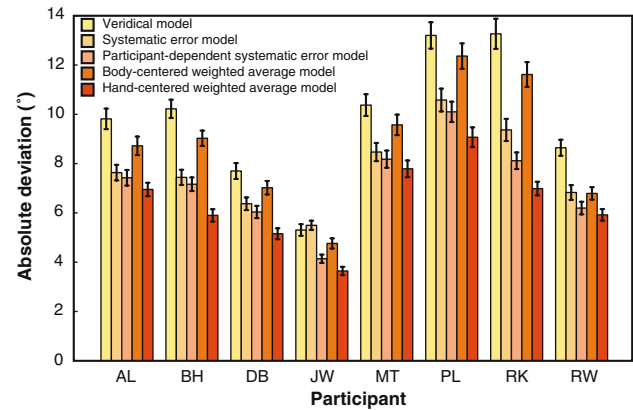

Fig. 6 Mean absolute deviations between the data and the five models for each participant. The absolute deviations of the Body- and Hand-centered weighted average models are computed using the average weight specific for each model and participant. The *error bars* indicate the standard errors of the mean ($N = 192$)

the set of candidate models was assessed by considering, on one side, the sum-of-squares of the errors between each model prediction and the set of data, and, on the other side, the different number of parameters that each model necessitates. The Veridical model and the Descriptive models do not have any free parameter, because they predict the same outcome for all bar locations. On the other hand, both the Body- and the Hand-centered weighted average models have one free parameter, namely the weighting factor (w) calibrating the contributions of the allocentric and the egocentric reference frames.[1] This procedure was executed separately for each participant and Akaike weights (w_A) that represent the relative probability of each model being correct were obtained. The Akaike weights indicated that for all participants the Hand-centered weighted average model proved to be better than all the other models with a probability close to one. In the set of alternative models the Participant-dependent systematic error model was ranked as the second best, followed by the Systematic error model and by the Body-centered weighted average model. The Veridical model resulted as the least likely model in explaining the data.

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[1] The comparison of models should be also considered in light of their overall complexity and not only on the basis of the number of free parameters. For instance, the Body-centered reference frame is defined as a cylindrical reference frame, whereas the Hand-centered reference frame is defined as a spherical reference frame. If we interpret these differences between models as additional parameters and we again apply the Akaike information criterion, the models' ranking remains unchanged with the Hand-centered weighted average model scoring best.

Hand-centered weighted average model

Given the fact that the Hand-centered weighted average model appears to account best for the data, subsequent steps will focus on more detailed analyses of the error patterns with respect to this model only. Figure 7 represents the signed in-plane$_{Hand}$ and the out-of-plane$_{Hand}$ deviations averaged over all participants and subdivided into the different conditions of plane (left/right plane versus far/near plane) and reference bar orientation (in-plane reference bars versus out-of-plane reference bars). A multivariate repeated measure analysis of variance (MANOVA) showed no effect either of the plane or of the reference bar orientation, but indicated a significant interaction between the two factors ($F(2,6) = 39.766$, $P < 0.001$). Furthermore, follow-up univariate repeated measures ANOVAs with the significance level α lowered to 0.025 using the Bonferroni correction were performed separately for the two dependent measures. In the case of in-plane$_{Hand}$ deviations, a significant main effect was found for the factor of plane ($F(1,7) = 36.227$, $P < 0.023$) and an interaction effect between plane and reference bar orientation conditions ($F(1,7) = 33.147$, $P < 0.001$). For the out-of-plane$_{Hand}$ deviations, none of the factors or their interaction reached significance. The tests of between-subjects effects led to an interesting result: while participants differed significantly in in-plane$_{Hand}$ deviations ($F(1,7) = 76.018$, $P < 0.001$), their performance did not differ in out-of-plane$_{Hand}$ deviations.

For each trial (that is, a set of eight bars that had to be oriented parallel to the reference bar) a weighting factor for the Hand-centered weighted average model was computed as explained in the Sect. "Data analysis". Thus, for each
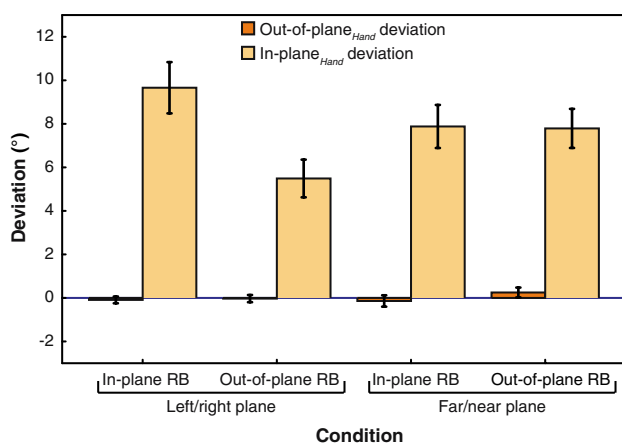
participant 24 weighting factors were obtained. The extents of the weighting factors sets' for each participant are displayed in Fig. 8 by means of a box-and-whisker plot. Each weighting factors set is represented by a box that spans the distance between the second and the third quartile surrounding the median. Whisker lines extending above and below indicate the non-outlying data points. Outliers are defined as points beyond 3/2 the interquartile range from the edge of the box and are represented by the black dots. It is worthwhile observing that the medians of the weighting factors distributions differ among participants indicating specific contributions of the egocentric frame of reference linked to the hand. Moreover, the individual interquartile ranges used as a measure of the statistical dispersion attest relatively small variations of the weighting factors estimates within each participant. Additionally, the three repetitions (in temporal order) of all the experimental conditions were compared with each other to detect any changes in the weighting factor due to practice. These multiple paired t tests were conducted on the data of each participant separately. The minimal level of significance retained was lowered to 0.017 (Bonferroni correction). No comparison led to a significant result ($P > 0.11$), thus, for every participant the average weighting factor stayed approximately stable over the three repetitions. Furthermore, the effects of the plane and reference bar orientation conditions on the weighting factor were tested by performing a repeated measures ANOVA. Similarly to the previous analysis no effect proved to be significant. These two analyses combined with the narrow interquantile
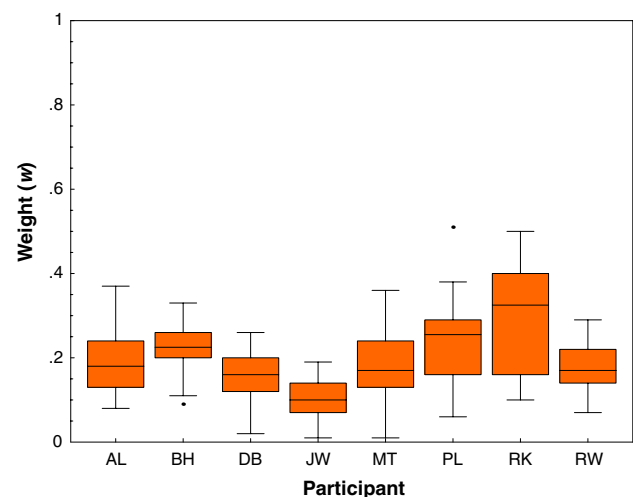

Fig. 7 A bar chart that represents the in-plane$_{Hand}$ and the out-of-plane$_{Hand}$ signed deviations averaged over all participants subdivided into the conditions of plane (left/right plane vs. far/near plane) and the conditions of reference bar (*RB*) orientation (in-plane RB vs. out-of-plane RB). The *error bars* indicate the standard errors of the mean ($N = 192$)

Fig. 8 Box-and-whisker plot representing the statistical dispersion of the weighting factor that indicates the contribution of the hand-centered egocentric reference frame for each participant ($N = 24$). The *boxes* represent the interquartile range and the whisker lines include the non-outlying data points. Outliers (*black dots*) are defined as points beyond 3/2 the interquartile range from the edge of the boxes

ranges observable in Fig. 8 provide fair evidence for the constancy of the weighting factor. It has to be noted that in a different analysis a single weight was obtained by fitting all the trials for each participant. These weights were almost identical to the average weights obtained in the previous analysis.

Discussion

In the present study, we researched haptic space perception of parallelity in three dimensions by considering different reference bar orientations and covering quite a large area of the frontal peripersonal space. Similar studies with a two-dimensional version of the parallelity matching task performed on the main orthogonal planes (horizontal, midsagittal, frontoparallel) have suggested that the deviations from veridicality are caused by a combined use of an allocentric and a biasing egocentric reference frame (Kappers 2004, 2005, 2007; Kappers and Viergever 2006; Volcic et al. 2007). These studies showed that a weighted average model that balanced the participant-dependent contributions of the two frames of reference efficiently described the experimental results. On the other hand, the identification of the origin of the egocentric reference frame was yet not conclusive. The findings of the present study extend the validity of the weighted average model to three-dimensional haptic perception of space and increase the evidence in support of a hand-centered egocentric reference frame.

We investigated the research question of whether systematic deviations occur also in three-dimensional haptic parallelity perception, by examining the errors under the three analyzing methods (Allo, Body and Hand methods). The extent of the errors made it evident that the participants' performance was physically unveridical, but the underlying structure of the deviations was undoubtedly characterized by a systematic error pattern. All the deviations occurred with regularity in specific directions and the sizes of the deviations were consistently scaled over the workspace reflecting the influence of a presumably unique mechanism. The three analyzing methods were adopted with the purpose of capturing these regularities in the deviations. On the basis of the hypothesis that presupposes a biasing influence of an egocentric frame of reference, the deviations were expected to cluster along the direction of the mismatch between the allocentric and the egocentric frame of reference. Specifically, the two-parameter analyzing method that best encapsulates the systematicity in the deviations should evince itself as the method that comprises almost the entirety of the total deviation in one parameter, and the contingent residual part in the second parameter orthogonal to the first one. In fact, the analyzing

method that assumed the hand as the origin of the egocentric reference frame convincingly satisfied these assumptions. The first error parameter, that is, the in-plane$_{Hand}$ deviation, accounted for most of the total deviation. The in-plane$_{Hand}$ deviations were characterized by a common direction and by a participant-dependent magnitude of the deviations in agreement with the hypothesis of a biasing hand-centered egocentric frame of reference. Regarding the second error parameter, the out-of-plane$_{Hand}$ deviation, the deviations were relatively small and the range of these deviations was centered on zero indicating that the out-of-plane$_{Hand}$ deviations were actually clustered around the plane defined by the mismatch between the allocentric and the hand-centered egocentric reference frame. On the contrary, the other two analyzing methods were less precise in capturing the directional systematicity in the deviations. This was mainly proven by the fact that the magnitudes of the unsigned deviations (tilt versus slant for the Allo analyzing method, and out-of-plane$_{Body}$ versus in-plane$_{Body}$ deviations for the Body analyzing method) were less differentiable than for the Hand analyzing method.

Given the fact that the aforementioned results gave a strong indication about the directionality of the deviations that is coherent with the hypothesis of a crucial involvement of a biasing hand-centered reference frame, it was of deep interest to validate the Hand-centered weighted average model also with respect to the expected extents of the deviations. For this purpose, the five considered models were compared by means of Akaike's information criterion and the average absolute deviations between each model and the data. Since Akaike's information criterion evaluates both the accuracy of a model and the costs of including extra parameters, it was advantageous to compare the different models through this method, as it determines the probability of each model being correct given the data. On the other hand, the analysis of the average absolute deviations evaluated the different models in a quantitative way by specifying the average discrepancy between a model and the data. The Hand-centered weighted average model proved to be the model with the highest probability of being correct among the considered models (despite the cost of additional parameters), and, at the same time, the model that most closely resembled the data. This means that the settings were actually biased towards the hand-centered egocentric frame of reference and the extent of the deviations was dependent on the amount of the contribution of the hand-centered egocentric frame of reference. The Hand-centered weighted average model, therefore, explained the direction and the magnitude of the deviations, and, moreover, accounted for the inter-participant variability. In contrast, each of the four alternative models was characterized by specific drawbacks. The Veridical

model failed to predict the systematic error patterns, because it was based on the assumption that no major deviation from the physically parallel settings would be observed. In the case of the Systematic error model, although the accuracy of the model improved, mainly because the general direction of the deviations was identified, the model was unable to capture the systematic variations in the magnitude of the deviations over the workspace and the inter-participant differences in the direction and in the magnitude of the deviations. The Participant-dependent systematic error model suffered from similar problems, although the accuracy was improved by the addition of a parameter that accounted for inter-participant heterogeneities. As for the Body-centered weighted average model, the inaccuracy was due to the fact that deviations were expected to occur in the plane perpendicular to the body-midline only and no prediction was made about any swerve from this plane. This characteristic of the model induced error in the predictions to such an extent that it proved to be even less accurate than the descriptive models predicting position-invariant deviations. A model that fixes the anchor point of the egocentric frame of reference to the body would probably gain in accuracy if, instead of defining the body-midline as the origin, it defined as the origin a specific point location on the body-midline. This problem was obviously not taken into consideration in the studies conducted on two-dimensional planes (Kaas and van Mier 2006; Kappers 2007) and any proposition about the location of the body-origin would be at this point highly speculative.

In light of the Hand-centered weighted average model being the most corroborated model, the deviations according to the Hand analyzing method were further analyzed with respect to the different conditions of plane and reference bar orientation. According to the model, some differences in the magnitude of the in-plane$_{Hand}$ deviations were expected to occur depending on the degree to which the reference bar orientation was aligned with respect to the direction of the mismatch between the allocentric and the hand-centered egocentric frame of reference. In the limit case, if the reference bar were orthogonal to the plane defined by the two reference frames, the magnitude of the in-plane$_{Hand}$ deviation would approach zero. On the other hand, we expected negligible fluctuations in the magnitude of the out-of-plane$_{Hand}$ deviations in all conditions. The comparison of the different conditions showed, in fact, minor variations in the magnitude of the in-plane$_{Hand}$ deviations in accordance with our expectations and no effect of the different condition on the out-of-plane$_{Hand}$ deviations. In addition, in an overall analysis of the conditions it was reconfirmed that whereas participants differed in in-plane$_{Hand}$ deviations, due to the participant-dependent contributions of the

egocentric reference frame, they all revealed the same average out-of-plane$_{Hand}$ deviations scattered around zero.

One of the assumptions of the Hand-centered weighted average model is that the inter-participant differences in performance reflect the strength of the biasing influence of the hand-centered egocentric reference frame. The model will gain in its descriptive capabilities if the weighting factor specific for each participant that expresses the biasing influence proves to be relatively stable in different conditions and over repetitions of the same trial. We have shown that the weighting factor could only vary in a limited range for each participant. Therefore, we can confidently assert that each participant was characterized by a specific weighting factor modulating the contributions of the allocentric and the hand-centered egocentric reference frame. Moreover, it is worth observing that although the average weighting factors differed among participants, they all fell in the range between 0.1 and 0.3. If we define a continuum between the reference frame fixed to the space and the one fixed to the hand, participants' performance shifted on average by 19.6% from the allocentric reference frame to the one fixed to the hand. This estimate is in agreement with the 23.8% shift towards the egocentric reference frame found by Kappers (2007) in the two-dimensional parallelity task. Moreover, in a slightly different task Flanders and Soechting (1995) showed that when participants were asked to orient the hand in a frame of reference fixed in space, they also showed a tendency of approximately 25% towards the use of a frame of reference fixed to the arm.

In general, we propose that a hand-centered and an allocentric reference frame operate synergistically in the construction of the haptic representation of space. Coding object's orientation with respect to the hand is of vital importance while grasping objects in everyday life and, therefore, an egocentric reference frame centered on the hand might have a central role in the interaction with objects. While it may seem restrictive to consider only an egocentric reference frame fixed to the hand, we have provided convincing evidence that this framework successfully accounts for the deviations observed in the three-dimensional haptic parallelity task. A more comprehensive model should certainly regard the hand-centered egocentric reference frame as part of a hierarchically organized structure of egocentric reference frames interconnected with an allocentric reference frame. The spatial processing therefore appears to be based on multiple spatial representations among which those that are relevant for a specific task emerge as the dominant representations. This view has its clear advantages since the maintenance of distributed representations of many reference frames can be available depending on the requirements of a specific behavior. A consequential limitation is given by the fact

that resulting behavior can be a product of different co-influencing representations that can bias the optimal solution for the required behavior. This hypothesis of multiple and interacting spatial representations is accordant with a more general framework in visuomotor literature (Carrozzo and Lacquaniti 1994; Carrozzo et al. 2002; Cohen and Andersen 2002; Soechting and Flanders 1992, 1993). The existence of multiple and coexisting levels of representation is thus supported by a plethora of psychophysical and neurophysiological studies (for a review, see Battaglia-Mayer et al. 2003). Therefore, we presume that the combination of different reference frames might be a general characteristic of spatial processing independent of the specific sensory modality.

In summary, we showed that participants systematically deviate from veridicality when asked to construct a field of parallel bars in three-dimensional space. The systematic patterns of deviations are efficiently captured by the Hand-centered weighted average model that presupposes a biasing, thus interfering, impact of an egocentric reference frame fixed to the hand on the allocentric frame of reference. The participant-specific weighting factor accounts for the inter-participant variability in the magnitude of the deviating behavior. Consequently, these results strengthen the hypothesis that haptic spatial processing bases its properties in the interaction of a plurality of reference frames.

Appendix

This appendix explains the method by which the different models were compared. The performance of the model was compared with those of alternative models by analyzing for each model the goodness-of-fit relative to the number of parameters by applying Akaike's information criterion (AIC) with sample-size correction (AIC_c). This method answers the question about which model best approximates reality given the set of measured data. This goal can be accomplished by minimizing the loss of information. Kullback and Leibler (1951) addressed this issue and developed a measure of loss that was later adopted by Akaike (1973). For details about this approach see Burnham and Anderson (2002). The measure of information loss comprises a term estimating the goodness-of-fit to a set of data (e.g., sum-of-squares) and a term estimating the effect

of the number of parameters (e.g., complexity) according to the principle of parsimony. Akaike's information criterion corrected for sample-size was evaluated as:

$$AIC_c = n \ln\left(\frac{SS}{n}\right) + 2k + \frac{2k(k+1)}{n-k-1}, \tag{3}$$

where n is the number of data, SS is the sum-of-squares, and k is the number of model parameters plus one. In general, the smaller the value of AIC_c the better the model performs. Different models (r) from a set of models (R) can be ranked on their performance by comparing AIC_c values for each ith model to a comparison model (superscript M):

$$\Delta AIC_c^i = AIC_c^i - AIC_c^M. \tag{4}$$

These ΔAIC_c values were then exponentially transformed to compute Akaike weights (w_A) that provide a measure of the strength of evidence for each model, and represent the relative probabilities of each model being correct among the whole set of R candidate models:

$$w_A^i = \frac{e^{-1/2\left(\Delta AIC_c^i\right)}}{\sum_{r=1}^{R} e^{-1/2\left(\Delta AIC_c^r\right)}}. \tag{5}$$

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Caski F (eds) Proceedings of the second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281

Arbib MA (1991) Interaction of multiple representations of space in the brain. In: Paillard J (ed) Brain and space. Oxford University Press, New York, pp 379–403

Battaglia-Mayer A, Caminiti R, Lacquaniti F, Zago M (2003) Multiple levels of representation of reaching in the parieto-frontal network. Cereb Cortex 13:1009–1022

Blumenfeld W (1937) The relationship between the optical and haptic construction of space. Acta Psychol 2:125–174

Burnham KP, Anderson DR (2002) Model selection and multi-modal inference: a practical information-theoretic approach. Springer, New York

Carrozzo M, Lacquaniti F (1994) A hybrid frame of reference for visuo-manual coordination. Neuroreport 5:453–456

Carrozzo M, Stratta F, McIntyre J, Lacquaniti F (2002) Cognitive allocentric representations of visual space shape pointing errors. Exp Brain Res 147:426–436

Colby CL, Duhamel J-R (1996) Spatial representations for action in parietal cortex. Cogn Brain Res 5:105–115

Cohen YE, Andersen RA (2002) A common reference frame for movement plans in the posterior parietal cortex. Nat Rev Neurosci 3:553–562

Coren S (1993) The left-hander syndrome. Vintage Books, New York

Farah MJ, Brunn JL, Wong AB, Wallace MA, Carpenter PA (1990) Frames of reference for allocating attention to space. Neuropsychologia 28:335–347

Flanders M, Soechting JF (1995) Frames of reference for hand orientation. J Cogn Neurosci 7:182–195

Gross CG, Graziano MSA (1995) Multiple representations of space in the brain. Neuroscientist 1:43–50

Hammerschmidt O (1934) Über die Genauigkeit der haptischen Verwirklichung geometrischer Grundbegriffe. B Sporn, Zeulenroda

Hermens F, Kappers AML, Gielen SCAM (2006) The structure of frontoparallel haptic space is task dependent. Percept Psychophys 68:62–75

Kaas AL, van Mier HI (2006) Haptic spatial matching in near peripersonal space. Exp Brain Res 170:403–413

Kappers AML (1999) Large systematic deviations in the haptic perception of parallelity. Perception 28:1001–1012

Kappers AML (2002) Haptic perception of parallelity in the midsagittal plane. Acta Psychol 109:25–40

Kappers AML (2003) Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. Acta Psychol 114:131–145

Kappers AML (2004) The contributions of egocentric and allocentric reference frames in haptic spatial tasks. Acta Psychol 117:333–340

Kappers AML (2005) Intermediate frames of reference in haptically perceived parallelity. In: World Haptics Conference (WHC 2005): First Joint Eurohaptics Conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems. IEEE Computer Society, Los Alamitos, pp 3–11

Kappers AML (2007) Haptic space processing: Allocentric and egocentric reference frames. C J Exp Psychol 61:208–218

Kappers AML, Koenderink JJ (1999) Haptic perception of spatial relations. Perception 28:781–795

Kappers AML, Viergever RF (2006) Hand orientation is insufficiently compensated for in haptic spatial perception. Exp Brain Res 173:407–414

Klatzky RL (1998) Allocentric and egocentric spatial representations: definitions, distinctions, and interconnections. In: Freksa C, Habel C, Wender KF (eds) Spatial cognition—an interdisciplinary approach to representation and processing of spatial knowledge. Springer, Berlin, pp 1–17

Kullback S, Leibler RA (1951) On information and sufficiency. Ann Math Stat 22:79–86

Luyat M, Gentaz E, Corte TR, Guerraz M (2001) Reference frames and haptic perception of orientation: body and head tilt effect on the oblique effect. Percept Psychophys 63:541–554

Millar S, Al-Attar Z (2004) External and body-centered frames of reference in spatial memory: evidence from touch. Percept Psychophys 66:51–59

Paillard J (1991) Motor and representational framing of space. In: Paillard J (ed) Brain and space. Oxford University Press, New York, pp 163–182

Soechting JF, Flanders M (1992) Moving in three-dimensional space: frames of reference, vectors, and coordinate systems. Annu Rev Neurosci 15:167–191

Soechting JF, Flanders M (1993) Parallel, interdependent channels for location and orientation in sensorimotor transformations for reaching and grasping. J Neurophysiol 70:1137–1150

Volcic R, Kappers AML, Koenderink JJ (2007) Haptic parallelity perception on the frontoparallel plane: the involvement of reference frames. Percept Psychophys 69:276–286

von Kries J (1923) Allgemeine Sinnesphysiologie. FCW Vogel, Leipzig

von Skramlik E (1937) Psychophysiologie der Tastsinne. Akademische Verlagsgesellschaft, Leipzig

von Skramlik E (1959) Über haptische Paralleleinstellung. Z Biol 111:81–98

von Uexküll J (1909) Umwelt und Innenwelt der Tiere. J Springer, Berlin

von Uexküll J (1928) Theoretische Biologie. J Springer, Berlin

Zuidhoek S, Kappers AML, van der Lubbe RHJ, Postma A (2003) Delay improves performance on a haptic spatial matching task. Exp Brain Res 149:320–330