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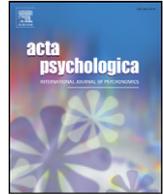
The perception and representation of orientations: A study in the haptic modality

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ABSTRACT

This research examines the haptic perception of orientations in the frontal plane in order to identify the nature of their representation. Blindfolded participants inserted the tip of the index finger into a thimble mounted on the extremity of a haptic interface and manually explored the orientation of a "virtual rod". After a short delay, participants had to reproduce the scanned orientation with the same hand without the guidance of the virtual rod. The analysis of the systematic errors showed that the recalled orientations were markedly biased toward the nearest diagonal in each quadrant with the exception of the orientations nearest to the vertical, which were biased toward the vertical. The variable error was greater for the oblique orientations than for the horizontal or vertical orientation. These results are interpreted with the Category-Adjustment model, which posits that orientations are categorically represented. We show that it is necessary to assume the existence of vertical and horizontal categories in addition to the previously postulated oblique categories to predict the error patterns observed in the present and former studies. The similarity of the error patterns in the visual and haptic modalities suggests that a common mechanism is at play in perceiving and reproducing orientations in both sensory modalities.

1. Introduction

Visual, vestibular and haptic systems provide information about orientation, which is a fundamental dimension of spatial cognition (Howard, 1982). However, the perception of this information is not always accurate, as demonstrated by numerous studies that have shown the presence of large perceptual errors when judging an orientation. For example, in the haptic modality, several studies have shown that blindfolded people can misalign two bars by as much 55° when the bars are widely separated (e.g., Kappers, 1999; Postma, Zuidhoek, Noordzij, & Kappers, 2008; Zuidhoek, Kappers, van der Lubbe, & Postma, 2003). Similar effects have also been observed in the visual modality, which has traditionally been studied more extensively than the haptic modality. In an influential review, Appelle (1972) coined the term "oblique effect" to refer to the pervasive observation that performance is generally better for vertical and horizontal stimuli than for oblique ones in a variety of tasks involving the processing of oriented stimuli. Later, Essock (1980) introduced the distinction between Class I oblique effects that have a low-level sensory origin and Class II oblique effects, which are related to the encoding or memory of orientation in the processing of stimulus orientation.

Many different tasks have been used to investigate the perception of orientations in the haptic modality. Moreover, previous studies on orientation perception have often focused on different measures of performance (e.g., systematic and variable errors) when reporting an oblique effect. In the haptic modality, the transfer of orientation information between two locations in space seems to be at the origin of the aforementioned large systematic errors observed in the parallelity or orientation-matching task. In contrast, much smaller systematic errors are observed in orientation (re)production tasks that do not involve a transfer of orientation information between two locations (Hermens, Kappers, & Gielen, 2006). In fact, the focus in the latter tasks has been on the variable error and, in this context, the term oblique effect usually refers to a decrease in precision at the oblique orientations relative to the cardinal (vertical or horizontal) orientations, which has been observed both in the visual (reviews in Gentaz & Ballaz, 2000; Gentaz & Junker-Tschopp, 2002) and haptic modalities (e.g. Appelle & Countryman, 1986; Gentaz & Hatwell, 1995, 1996, 1998, 1999; Lechelt, Eliuk, & Tanne, 1976; Lechelt & Verenka, 1980; Luyat, Gentaz, Corte, & Guerraz, 2001). Still, it is noteworthy that, in the visual modality, several studies have reported orientation-dependent biases in orientation tasks that don't involve the transfer of orientation information between two different positions (e.g. de Graaf, Sittig, & Denier van der Gon, 1994; Engebretson & Huttenlocher, 1996; Gourtzelidis, Smyrnis, Evdokimidis, & Balogh, 2001; Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Newcombe, & Hollister Sandberg, 1994;

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Smyrnis, Mantas, & Evdokimidis, 2007). In all these studies, the systematic errors were smallest at the vertical, horizontal and diagonal orientations and biased toward the nearest diagonal at the oblique orientations that lay between the cardinal and diagonal orientations (e.g., near 30° or 60°). In the haptic modality, some evidence for the existence of a similar orientation-specific bias can be found in orientation matching studies even if this bias is masked by the larger systematic errors induced by the transfer of the reference orientation between two positions in space in the parallelity task (Kappers, 2003, 2004; Postma et al., 2008; Zuidhoek, Kappers, & Postma, 2005). While these studies provide some hints that a bias toward the diagonals might be present within an egocentric frame of reference (see in particular Volcic, Kappers, & Koenderink, 2007), the effect of orientation on the pattern of systematic errors has yet to be investigated with a large set of orientations in a haptic orientation perception task that does not involve a shift of position.

This study has two main objectives. The first objective is to extend our knowledge of the orientation-dependent error patterns in the haptic modality by using a large number of orientations in the same spatial location. A large number of orientations is, in fact, crucial to prevent aliasing of complex error patterns. To our knowledge, it is not yet known whether the error patterns in the haptic modality present the same characteristics as the ones typically observed in the visual modality, i.e. a bias toward the diagonal accompanied with a decrease in precision away from the cardinal orientations.

The second objective is to present a model that can explain the origin of the observed distortions in orientation tasks that do not involve transfer of orientation information from one location to another in space. More precisely, the objective is to develop a model that can predict the two orientation-dependent patterns of systematic and variable errors observed in this orientation recall task. The model that we will develop is based on the Category-Adjustment (CA) model that was originally proposed by Huttenlocher et al. (1991) to model biases observed in position recall tasks. The gist of the model is that the recall of information is influenced by the way it is categorized. In their seminal study, Huttenlocher and colleagues observed a bias toward the diagonal of the recalled position and proposed that the orientation space is divided into four broad oblique categories that correspond to the four quadrants of a circle to explain this bias. In the present study, we show that it is necessary to postulate the existence of two additional narrow categories centered on the vertical and horizontal orientations to explain the pattern of systematic and variable errors observed in the present and former studies. The reason for the additional categories is that the CA model predicts an increase in the variable error at the category boundaries (see Section 3.1 Fitting the CA model), an observation that has been neglected in previous applications of the CA model (e.g., Engebretson & Huttenlocher, 1996; Haun, Allen, & Wedell, 2005; Huttenlocher, Hedges, & Corrigan, 2004; Huttenlocher et al., 1991). Finally, at the mathematical level, we reformulate the CA model in a way that takes better into account the fact that orientations are axial data (axial data are circular or angular data that have only a 180° range, see Mardia & Jupp, 2000).

2. Methods

2.1. Participants

Twelve right-handed adults (four women and eight men) participated in the experiment (mean age: 29.5 ± 8.1 years old). Participants were undergraduate and graduate students. All participants were naive with respect to the context and objective of this study.

2.2. Experimental procedure

The participant was blindfolded and wore a brace that limited wrist movement. The participant sat in front of a haptic device (PHANTOM

1.5, Sensable Technology) and put the tip of the right index finger into a thimble that was mounted at the extremity of the device. At the beginning of each trial (indicated by a beep), the device produced a central force field that guided the participant's finger to the center of the workspace 35 cm in front of the sternum. During the following exploratory phase (7.5 s), the haptic device generated an elastic force (stiffness of 1.5 N/mm) that maintained the freely moving fingertip near a 14 cm-long segment of line ("virtual rod") in the fronto-parallel plane. The midpoint of the virtual rod always coincided with the center of the workspace. Then, a central force field brought the fingertip back to the center of the workspace (5 s for this transition). Immediately after this transition period, a second beep indicated the beginning of the reproduction phase (7.5 s) during which the participant had to reproduce the exploratory to-and-fro movements as accurately as possible. During this phase, the device allowed free fingertip movements in the frontal plane by generating a force that was orthogonal to this plane. During both phases, the haptic device recorded fingertip position every 50 ms (20 Hz).

There were 16 target orientations in the frontal plane: 12 orientations were evenly spaced between 0° and 180° in 15° steps, plus two orientations on each side, 5° apart from the horizontal and vertical. Each orientation was presented five times yielding a total of 80 trials. The presentation order the 16 orientations was randomized within each of the five repetition blocks.

2.3. Data analysis

For each trial, we computed the systematic error (or bias) by computing the signed angular difference between the target orientation and the orientation of the line that best-fitted the fingertip trajectory during the reproduction phase. The best fitting line corresponded to the first eigenvector of the covariance matrix (Baud-Bovy & Gentaz, 2006). By definition, clockwise errors have a negative sign. The variability of the responses was estimated by computing the standard deviation of the bias. The use of standard estimators to compute the average and standard deviation of the biases is justified by the fact that the biases never spread over a large range of values and remained near zero. In this case, linear estimators give essentially the same results as the corresponding circular statistics based on the mean resultant vector (Mardia & Jupp, 2000). The effects of the orientation and repetition on the systematic and variable errors were tested with two-way repeated-measure full-factorial ANOVA. P values were adjusted by multiplying the degrees of freedom with Greenhouse and Geisser's epsilon to account for possible deviations from the sphericity condition.

2.4. The CA model

In the CA model, the stimulus is represented at two levels: a fine-grained value and a category. Formally, the recollection R is the weighted average of the fine-grained representation of the stimulus M and of a prototype P representing the category

$$R = \lambda M + (1-\lambda)P \qquad (1)$$

where λ is the weight of the fine grained representation (Huttenlocher et al., 1991). The fine-grained value is usually modeled by a gaussian random variable centered on the true position μ of the stimulus (the standard deviation σ_M represents the uncertainty about the position of the stimulus). The fine-grained representation M of the stimulus position is by definition veridical (i.e., unbiased: $E[M] = \mu$). The prototype is also modeled by a gaussian random variable with mean ρ and standard deviation σ_P where ρ corresponds to the center of the category and σ_P represents the uncertainty of the prototype location. Mathematically, the bias of the response corresponds to the expected value of the response minus the stimulus orientation. It is easily shown that the responses predicted by this model are biased toward the center of the category.

While the CA model was originally developed to model perceptual biases, it also makes predictions about the variability of the responses since both the stimulus and the prototypes are represented by random variables. Moreover, when the stimuli can be classified into different categories and the boundary between the categories is uncertain, the CA model predicts an increase in the variability at the category boundaries because orientations near the boundary might be classified into one category or another depending upon the trial. Thus, the response for these orientations will be pulled toward the center of different categories in different trials according to Eq. (1), which results in an increase in the variable error. To explain the decrease in the variable error at the vertical and horizontal orientations as well as the attraction toward the vertical of nearby orientations, we posit the following: two prototypes corresponding to the horizontal ($\rho_1 = 0°$) and vertical ($\rho_3 = 90°$) orientations in addition to the oblique prototypes corresponding to the diagonals ($\rho_2 = 45°$ and $\rho_4 = 135°$) assumed in Huttenlocher et al. (1991). We also adapt the mathematical expressions of the model to deal better with the fact that orientations are axial data (Mardia & Jupp, 2000).

In our reformulation of the CA model, the fine-grained representation of the orientation is a unit vector M oriented along the direction θ_M that follows a wrapped normal distribution WN(μ, σ_M) centered on the stimulus orientation μ. The categories are represented by unit vectors (prototypes) θ_i oriented along the directions θ_{Pi} that follow wrapped normal distributions WN(ρ_i, σ_{Pi}). The stimulus is classified in the category centered on the prototype θ_i with the greatest density of probability $f_{WN}(\mu|\theta_{Pi}, \sigma_{Pi})$ at the stimulus orientation μ

$$\text{argmax}_i \{f_{WN}(\mu|\theta_{Pi}, \sigma_{Pi})\} \qquad (2)$$

where $f_{WN}(\mu|\theta_{Pi}, \sigma_{Pi})$ is the probability density function of the wrapped normal distribution. Note that the variability σ_{Pi} of the prototype orientations θ_P causes stimuli near the boundaries to be classified into different categories depending upon the trial, which increases the variable error. The average position of the boundary between two adjacent categories is shifted toward low-variability prototypes. In other words, small categories have a less variable prototype than larger ones. The response was computed by taking the weighted average of the two unit vectors M and P_i according to Eq. (1):

$$R = \begin{pmatrix} R_x \\ R_y \end{pmatrix} = \lambda \begin{pmatrix} \cos\theta_M \\ \sin\theta_M \end{pmatrix} + (1-\lambda) \begin{pmatrix} \cos\theta_{Pi} \\ \sin\theta_{Pi} \end{pmatrix} = \lambda M + (1-\lambda)P_i \qquad (3)$$

where θ_M is the fine-grained representation of the stimulus orientation μ and θ_{Pi} is the center of the category in which the stimulus has been classified. Finally, to deal with the fact that the wrapped normal distribution is defined over a 360° interval while orientations are defined up to 180°, all angular values (i.e., the stimulus orientation μ, prototype values ρ_i, and corresponding standard deviations) are multiplied by two. The direction of the mean resultant vector R is then divided by two to yield the orientation response $\theta_R = 0.5 \, \text{atan2}(R_y, R_x) \mod 2\pi$ in the 0°–180° interval.[1]

The free parameters of the extended CA model are the weight λ and standard deviation σ_M of the fine-grained representation, the standard deviations $\sigma_H \equiv \sigma_{P1}$ and $\sigma_V \equiv \sigma_{P3}$ of the horizontal and vertical prototypes and the standard deviation $\sigma_O \equiv \sigma_{P2} \equiv \sigma_{P4}$ of the 45° and 135° prototypes. The free parameters of the model were fitted to the data by minimizing the mean square error (MSE):

$$\sum_i (m_i - m_{Ri})^2 + (s_i - s_{Ri})^2 \qquad (4)$$

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[1] The problem of computing the mean of axial data can be illustrated by two orientations, say 5° and 175°, the average of which is 0°, not 90°. The multiplication and successive division of angular values by two is a classical "trick" in modeling axial data, (Mardia & Jupp, 2000), where one needs to map the 0–180° range of possible orientations into the 0–360° range of angles to be able to used the wrapped circular distribution as well as to be able to add the vectors representing different orientations vectorially (see Eq. 3).

where m_i and s_i represent the observed bias and standard deviation at orientation μ_i (all participants and repetitions pooled together) while m_{Ri} and s_{Ri} correspond to the bias and standard deviation predicted by the model. The predictions were obtained by simulating a large number of presentations at each one of the tested orientations and by computing average and standard deviations of the predicted biases (Monte-Carlo method, N = 5000).

The original model with only the categories centered on the diagonals can be expressed and fitted in a similar way, the only difference being that it would not include the vertical or horizontal prototypes (the three free parameters of this model are λ, σ_O and σ_M).

3. Results

During the exploration phase, the participants explored the virtual rod several times making on average 7 ± 3 (standard deviation) movements. The participants produced a similar number of movements during the reproduction phase (7 ± 3 movements, with an average ranging from 4 to 11 movements depending on the participant). Reproduction movements were slightly longer than exploratory movements (17.9 ± 3.2 vs. 14.0 ± 0.1 cm) and deviated slightly from straightness (maximum deviation was $5.3 \pm 4.2\%$ of movement length). Visual inspection showed that reproduction movements passed near the center of the workspace and that the fitted lines represented the main direction of the trajectories well. The minimum distance between the fitted line and the center of the workspace was on average 0.8 ± 0.7 cm. The to and fro trajectories did not present any obvious differences.

The pattern of systematic errors can be described as the superposition of a large oscillation of period π centered on the vertical (mid-line) and two oscillations of period $\pi/2$ centered on 45° and 135° separated by a small oscillation centered on 90° (see Fig. 1A). As a preliminary approximation, we can model this pattern with a sum of several sines,

$$\beta_0 \sin(2\theta) + \beta_1 \sin(4\theta) + \beta_2 [\sin(\omega(\theta - \pi/2))] \qquad (5)$$

where $0 \leq \theta \leq \pi$ and $[\sin(\omega(\theta-\pi/2))] = 0$ if $|\theta - \pi/2| > 1/\omega$ π-periodic oscillation corresponds to a (counter-clockwise) overestimation of the orientations in the first quadrant (0°–90°) and to a (clockwise) underestimation of the orientations in the second quadrant (90°–180°), i.e., an attraction toward the vertical for all orientations. The $\pi/2$-periodic oscillations correspond to an attraction toward the closest diagonal (45° or 135°) for the orientations in each quadrant while the last term corresponds to a strong attraction toward the vertical for orientations near the vertical (90°). Finally, the last term in Eq. (5) corresponds to a single period of a $2\pi/omega$-periodic oscillation centered on the vertical. The value of $\omega = 15$ was adjusted to fit the data and corresponds to a basin of attraction that extends 12° on each side of the vertical. Fitting the parameters to the data shows that the amplitude ($\beta_1 = 3.68$, $t_{14} = 6.62$, $p < 0.001$) of the $\pi/2$-periodic oscillation that corresponds to an attraction toward the diagonals is larger than the amplitudes of the two other terms ($\beta_0 = 1.89$, $t_{14} = 62.87$, $p = 0.01$, and $\beta_2 = -2.76$, $t_{14} = -2.45$, $p = 0.03$). The systematic error was null at the orientations that correspond to the attractors (i.e., the 45° and 135° diagonals and the vertical) and at the limits between the corresponding basins of attraction (i.e., 0°, 80°, and 100°). A one-way repeated-measure ANOVA confirmed that systematic errors differed across orientations ($F(15,165) = 5.905$, $\varepsilon = 0.255$, $p = 0.001$).

Inspection of individual patterns revealed that the size of the basin of attraction for the bias toward the vertical could vary across subjects and that this bias could be absent in some subjects. To describe these differences, we fitted the above model (Eq. 5) without the third component ($\beta_2 = 0$) and with various values of ω ($\omega = 4$, 6, and 18, which correspond to a basin of attraction extending 45°, 30° and 10° on each side of the vertical respectively) for each participant. Then, we selected the model with the lowest Akaike information criterion (AIC) for
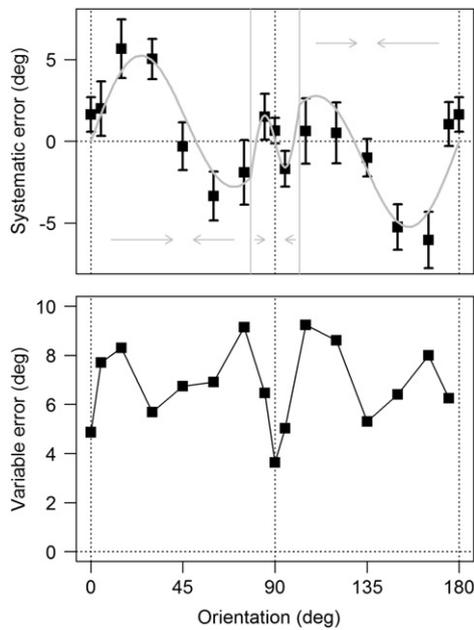
Fig. 1. Orientation-dependent error patterns. *Top*: average systematic error (*solid squares*) for each tested orientation (all responses from all participants are pooled together at each orientation). A positive error corresponds to a clockwise rotation while a negative error corresponds to a counterclockwise rotation. Vertical *error bars* correspond to 90% confidence intervals. The *arrows* indicate the direction of the bias and the *gray line* represents the prediction of the descriptive model (Eq. 5). *Bottom*: variability of the responses for each orientation (standard deviation of all responses from all participants).

each participant. This analysis confirmed that the strongest bias was the one (β_1) toward the diagonal, which was statistically significant for all but two subjects ($p < 0.05$). The best-fitting model also included a statistically significant attraction toward the vertical (β_2) for nearby orientations for seven out of twelve participants ($\omega = 4$, 6, and 18 for 2, 4 and 1 participants respectively). The first term of the model (β_0) was statistically significant only for three participants.

The variability of the responses was estimated by computing the standard deviations of all responses from all subjects (N = 60). This global estimate combines between- and within-subject variability. The variable error was smallest for the vertical (90°) and horizontal (0°) orientations, which delimit each quadrant (see bottom panel of Fig. 1). Inside each quadrant, the variability presented an M-shaped pattern with two peaks on each side of a local minimum close to mid-quadrant (45° or 135°). The differences across orientations were significant ($F(15,165) = 3.616$, $\varepsilon = 0.371$, $p = 0.005$). To analyze variable error in detail, we split the variability for each orientation into two components: a between-subject component, namely the standard deviation across participants (N = 12) of the across-repetition average of the angular error; and a within-subject component, namely the across-subject average of the standard deviation across repetitions (N = 5). The between-subject variability and, to a lesser degree, the within-subject variability also exhibited the same M-shaped pattern inside each quadrant. At the individual level, we compared the average standard deviation for the cardinal (horizontal and vertical) orientations to that of all other orientations with a one-sided one-sample *t* test for each subject. For all but two subjects, the precision for the cardinal orientation was greater than for the oblique ($p < 0.01$). Separate analyses for the vertical and horizontal orientations showed that the precision of the vertical was higher for all but one subject but that the precision of the horizontal was higher only for seven out of twelve subjects.

3.1. Fitting the CA model

The CA model with the vertical and horizontal categories was fitted by minimizing the mean square error (MSE = 79; see Methods). Fig. 2A

shows that the model accurately predicted the main features of the systematic error patterns such as the bias toward the vertical (90°) for nearby orientations and the larger biases toward the diagonals (see Fig. 2A). The model also predicted the M-shaped pattern of variable error in each quadrant well. The recall was based on about 80% of the fine-grained representation of the stimulus ($\lambda = 0.8$, $\sigma_M = 3.0°$) and on 20% of its categorical representation. The variability of the prototype was smaller for the vertical and horizontal categories than for the oblique one ($\sigma_V = 4.2°$, $\sigma_H = 2.9°$ versus $\sigma_O = 7.9°$).

For comparison's sake, we also fitted the CA model without the horizontal and vertical categories. The free parameters of this model, λ, σ_M and σ_O, were first fitted by minimizing the squared difference between the observed and predicted bias (the first term of Eq. 4) to predict the systematic error without taking into account the variable error ($\lambda = 0.83$, $\sigma_M = 6.0°$, $\sigma_O = 11.6°$; see Fig. 2 B). The result was a good fit of the large bias toward the diagonal but this model could obviously not predict the bias toward the vertical for nearby orientations in the absence of a vertical category. More importantly, the variable errors predicted by this model increase considerably at vertical and horizontal orientations, which correspond to category boundaries in this case. In fact, the fit of this model once the variability of the responses is taken into account is almost one order of magnitude larger than when the horizontal and vertical categories are included (MSE = 621 vs. 79).

The same model was also fitted by minimizing the mean square error (MSE = 186, see Fig. 2C). The set of parameters obtained in this manner ($\lambda = 0.99$, $\sigma_M = 0.2°$, $\sigma_O = 12.6°$) shows that the recall is based essentially on fine grained representation (λ is close to 1). In other words, a very small weight is given to the categorical representation so as to avoid an increase in the variable error at the category boundary. As a result, the
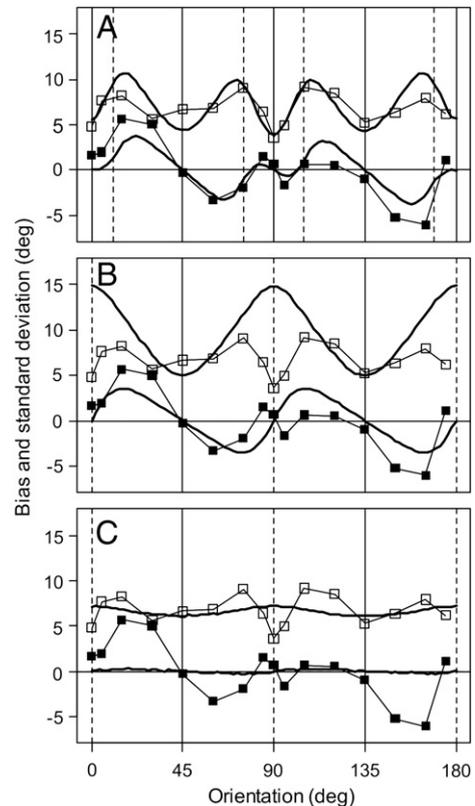

Fig. 2. CA model predictions. A: predictions of the extended CA model including the vertical and horizontal categories in addition of the oblique categories fitted to predict both the bias and the variable error by minimizing the MSE. B: original model CA including only the oblique categories fitted to predict the bias. C: original model fitted by minimizing MSE. For all panels, the *solid* and *empty squares* denote the average and standard deviation of the participants' responses respectively. The *thick lines* denote the model predictions. The vertical lines correspond to the prototypes (*dotted lines*) and category boundaries (*solid lines*).

original model no longer predicts the observed biases toward the diagonals. While this trade-off between variable and systematic errors leads to an improvement in the MSE, neither the bias nor the variability of the responses is well predicted. In particular, the model is still unable to predict a decrease in the variable error at the cardinal orientations. Additionally, the fit of this model is still considerably worse than the one obtained with the model including the vertical and horizontal categories (MSE = 186 vs. 79).

To summarize, these fits confirm the theoretical analysis of the model that it is impossible for the CA model to predict a decrease in the variable error at the category boundaries together with a bias toward the center of the categories. In other words, the CA model with only the four quadrants as categories is flawed not only because it fits the data badly but, more fundamentally, because it cannot predict a bias toward the diagonal without an increase of the variable error at the vertical and horizontal orientations. Our proposal to deal with this problem without rejecting outright the idea of categorization that constitutes the gist of the CA model is to assume the existence of additional categories around the vertical and horizontal orientations so that these orientations no longer correspond to category boundaries.

4. Discussion

We investigated the pattern of systematic and variable errors in the reproduction of haptically perceived orientations and found marked anisotropies in their processing. The pattern of systematic errors could be described as the combination of several biases: a strong bias toward the closest diagonal or toward the vertical for nearby orientations combined with a weak bias toward the vertical for all orientations. The variable error was smallest at the vertical and horizontal orientations. These results confirm the necessity to test a large number of orientations to avoid aliasing. For example, the bias toward the vertical would have been missed had we not tested the orientation 5° apart from the vertical. Also, our results clearly show the presence of a bias toward the center of the second quadrant even though the constant error is not null at 135°. In other words, it would have been mistaken to exclude such a pattern of errors on the basis of this single observation. The defining feature of this bias is rather its basin of attraction, which should correspond grosso modo to a quadrant with a center near but not necessarily at the diagonal.

We also showed in this study that the extended CA model can predict i) the decrease in the variable error at the vertical and horizontal orientations, and ii) the observed bias toward the main diagonals and toward the vertical for nearby orientations if one assumes the existence of vertical and horizontal categories in addition to the previously posited oblique categories (Huttenlocher et al., 1991). The fact that this model explains both the pattern of systematic and variable errors is one of its noteworthy characteristics. The existence of vertical and horizontal categories is well supported in the literature on orientation discrimination (e.g., Quinn & Bomba, 1986) and in good agreement with the widely-shared idea that these orientations correspond to the norm (e.g. Luyat & Gentaz, 2002; McIntyre, Stratta, & Lacquaniti, 1998; Spencer, Simmering, & Schutte, 2006). Admittedly, this model does not explain all features of the complex pattern of systematic errors observed in this study. In particular, it does not explain the tendency to overestimate orientations between 0° and 90°, and underestimate them between 90° and 180°. Additional factors might be at play such as the viewing angle in the visual modality (Hermens & Gielen, 2003; see also Dick & Hochstein, 1989; Keene, 1963) or a bias in the perceived orientation of the arm segments in the haptic modality (e.g., Baud-Bovy & Viviani, 2004).

4.1. External validity of the extended CA model

Although the error patterns found in this study are complex, our results resemble those observed in many different tasks involving processing axial or directional information. First, the most conspicuous aspect of

the systematic error, the bias of most oblique orientations toward the closest diagonal, has been observed in various visual tasks such as reproducing the location of a point in a circle (Huttenlocher et al., 1991; Huttenlocher et al., 2004) and perceiving oriented lines (de Graaf et al., 1994; Lennie, 1971; Smyrmis et al., 2007; Zlatkova, 1993) or random dot patterns (Yakimoff, Lansky, Mitrani, & Radil, 1989). A similar bias has also been observed in pointing tasks toward remembered targets presented in a circular arrangement in the kinesthetic (Baud-Bovy & Viviani, 2004) and visual modalities (e.g., Gordon, Ghilardi, & Ghez, 1995; Gourtzelidis et al., 2001; Smyrmis et al., 2007). Second, our results are also in line with the widespread observation that the reproduction of the vertical and horizontal orientations is more accurate than the reproduction of oblique orientations, which has also been cited in many different visual tasks (e.g., Appelle, 1972; Essock, 1980; Keene, 1963; Westheimer, 2003; Zlatkova, 1993). The lesser variability at the vertical and horizontal orientations relative to the main diagonals replicates results of previous haptic studies (review in Gentaz, Baud-Bovy, & Luyat, 2008). It should also be noted that the M-shaped pattern of the variable error within each quadrant, which involves not only a steep decrease in the variable error at the vertical and horizontal orientations but also a lesser decrease in the variable error at the diagonal, is consistent with some visual studies (e.g., Junker-Tshopp, Gentaz, & Viviani, 2010).

The similarities of the error patterns across tasks and sensory modalities suggest that a common mechanism is at play in the perception and reproduction of axial and/or directional information. In a recent review of the oblique effect (Gentaz et al., 2008), we proposed that the directional anisotropies in the perception and recall of orientations emerge at a late stage of processing, shared by the different sensory modalities, and thus correspond to Class II oblique effects (Essock, 1980). In this study, we advance the idea that categorical perception might be at the origin of these directional anisotropies (Harnard, 2003). This idea is supported by the fact that it was possible to adapt the CA model so that it could predict not only the biases but also the variable error pattern that has been observed in many studies on orientation perception.

To generalize the validity of the extended CA model to other studies, it is essential to note that the vertical and horizontal categories are not necessarily accompanied by biases toward these orientations (e.g., see the error pattern near the horizontal orientation in Fig. 2), since such biases are typically not observed in the visual modality. In fact, the extended CA model does not predict a bias toward the center of a category when the variability of the corresponding prototype is much smaller than the variability of the prototypes of the adjacent categories. We hypothesize that the variability of the vertical and horizontal prototypes could be related to the capacity of the observer to discriminate these orientations and, more generally, to the reliability of categorization processes. Accordingly, the biases toward the vertical and horizontal orientations would not be present in many studies involving the visual modality because these orientations could be identified more reliably in the visual than in the haptic modality (e.g., Gentaz et al., 2001). However, these categories are still necessary to explain the decrease in the variable error at the vertical and horizontal orientations observed in the visual modality (e.g., Haun et al., 2005). Additional research is needed to verify whether differences in the error patterns observed in the visual and haptic modalities can be explained within this theoretical framework by modality-specific changes of the extended CA model parameter values.

This theoretical framework might also help establish a better understanding of the effects of some experimental manipulation on the oblique effect. Studies on the oblique effect in the haptic modality have shown that the strength of this effect depends on gravitational cues and/or the cognitive resources available to process haptic information (Gentaz & Hatwell, 1999). Gentaz et al. (2008) proposed that the haptic oblique effect occurs when spatial information in the sensorimotor trace such as the orientation of an exploratory movement is

represented at the cognitive level and that this effect is more marked when the experimental conditions facilitate this encoding (e.g., presence of gravitational cues) or make the observer more reliant on this abstract representation (e.g.; interpolated tasks). In the theoretical framework of the extended CA model, one might assume that the storage of the fine-grained representation requires more resources than the storage of the categorical information. Thus, the observer should rely less on the fine-grained representation and more on the categorical representation (in other words, the parameter λ should decrease) when fewer resources are available, which should lead to an increase in the bias and variable error at the category boundaries.

4.2. Limits of the extended CA model

Spatial information is always specified with respect to some frame of reference (Howard, 1982) and many studies on the perception of orientations have focused on identifying it (Kappers, 1999, 2003, 2004; Luyat et al., 2001; Volcic & Kappers, 2008; Volcic, van Rheede, Postma, & Kappers, 2008; Volcic et al., 2007). However, the concept of reference frame per se does not explain why or how directional anisotropies occur within the possibly rotated subjective frame of reference since it fails to explain what might cause orientation-specific variations in the accuracy and precision of the responses such as the directional bias toward the diagonal. It might, however help to understand why these error patterns may be rotated. Conversely, the extended CA model does not explain why the perceived orientation changes in different regions of the peripersonal space or during the transfer of an orientation between two different regions.

The extended CA model is, however, compatible with the rotation of the whole pattern of errors observed in the parallelity task (Volcic et al., 2007) or when the head is tilted in the haptic and visual modalities (Luyat & Gentaz, 2002; Luyat et al., 2001; Van Beuzekom, Medendorp, & Van Gisbergen, 2001). This is explained in terms of a rotation of the underlying frame(s) of reference. For example, one might assume that both the fine-grained representations of the stimulus and the prototypes are defined in a subjective frame of reference that is influenced by ego-centric cues such as the position of the orientation relative to the body or the tilt of the body. Moreover, comparing the results of standard studies with those that involved the transfer of orientation between two locations suggests that different experimental factors might affect the underlying reference frame and the parameters of the extended CA model. For example, such a view would be in agreement with the observation that an unfilled delay leads a reduction of the systematic errors in the parallelity, which can be interpreted as a shift from the egocentric toward the allocentric reference during the delay period (Zuidhoek et al., 2003), but has no bearing on the oblique effect unless the delay is filled with an interpolated task (Gentaz & Hatwell, 1999). Still, this view does not exclude the possibility that the same factors affect both sets of processes. Additional research is needed to find out whether there is a link between increasing reliance on the allocentric frame of reference and, for example, the relative weight of the fine-grained and categorical representations.

In summary, the extended CA model is a theoretical framework that makes specific predictions about both the systematic and variable errors once a set of categories has been defined. Our study has shown that it is necessary to postulate the existence of additional categories to explain the decrease in the variable error at the vertical and horizontal orientations – a widespread observation – within the theoretical framework of the CA model. As noted previously, the prototypes that correspond to these categories must be narrow and have low variance and, thus, might be viewed as reference axes or norms. Orientations that would not be categorized as vertical or horizontal would be encoded as oblique with less precision as reflected in the model by the larger variability of the oblique prototypes.

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