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A phase dynamic model of systematic error in simple copying tasks

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Abstract A crucial insight into handwriting dynamics is embodied in the idea that stable, robust handwriting movements correspond to attractors of an oscillatory dynamical system. We present a phase dynamic model of visuomotor performance involved in copying simple oriented lines. Our studies on human performance in copying oriented lines revealed a systematic error pattern in orientation of drawn lines, i.e., lines at certain orientation are drawn more accurately than at other values. Furthermore, human subjects exhibit "flips" in direction at certain characteristic orientations. It is argued that this flipping behavior has its roots in the fact that copying process is inherently ambiguous—a line of given orientation may be drawn in two different (mutually opposite) directions producing the same end result. The systematic error patterns seen in human copying performance is probably a result of the attempt of our visuomotor system to cope with this ambiguity and still be able to produce accurate copying movements. The proposed nonlinear phase-dynamic model explains the experimentally observed copying error pattern and also the flipping behavior with remarkable accuracy.

Keywords Handwriting · Copying · Visuomotor transformation · Nonlinear oscillators · Phase dynamics

1 Introduction

Preferential stability in even simple handwriting strokes has been known for a long time. In a comparative analysis of strokes from several handwriting systems (including Arabic, Hebrew, Chinese, and English), van Sommers (1984) showed that bottom-right and bottom-left strokes are frequent, and that bottom-top and top-left strokes are nearly absent. Directional preferentiality is also observed in drawing simple closed curves. For example, van Sommers (1984) describes the "start rotation principle" that accounts for drawing patterns adopted by subjects drawing simple closed geometric curves. According to this principle, the preferred direction of drawing (clockwise or anticlockwise) is a function of the initial point on the curve. Stability of handwriting patterns seems to be shaped by two conflicting constraints: the need to simplify, and the need to have sufficient differentiation among various handwriting patterns. While simpler patterns are more stable, complex patterns aid differentiation. Influence of these constraints can be traced in the evolution of ancient Greek upper case letters to cursive script (Irigoin 1990). In a study involving copying elliptic patterns presented at different orientations, Athènes et al. (2003) found an interesting "two-peak" error pattern in orientation of ellipses. The authors suggest that ellipses that are more robustly and accurately reproduced correspond to stable attractors of handwriting coordination dynamics. However the authors do not provide a theoretical model to justify the claim (Athènes et al. 2003; Sallagoïty et al. 2004). Meulenbroek and Thomassen (1993) studied copying of three segment patterns consisting of three straight lines aligned to form two angles. They found that more pauses occurred at obtuse angle than at acute angle and at the second angle than at the first. Size overshoots occurred when acute angles were drawn. The above experiments were extended by Meulenbroek et al. (1998) for studying the exploitation of elasticity in copying three-segment geometrical patterns. Their study hypothesized that pauses between subsequent segments of a movement sequence were possibly due the

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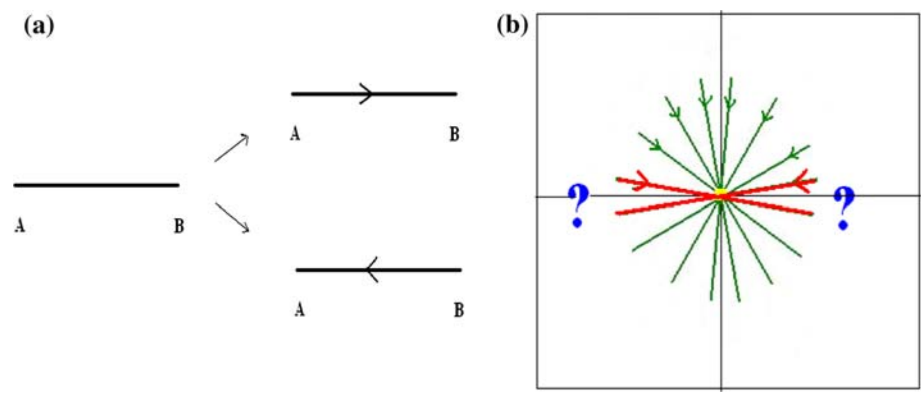

Fig. 1 Inherent ambiguity in copying: a given line AB can be drawn in two possible directions (from A to B or B to A (b) Ambiguity can be ameliorated by coupling orientation with direction, but ambiguity cannot be avoided at least at one orientation. Even when all lines are drawn in top-down direction, there is a conflict at the horizontal line, which can be drawn in two possible (opposite) directions

need of energy dissipation or due to the chunking strategies adopted. We had recently shown systematic error patterns in a variety of copying tasks involving simple line diagrams (Dubey et al. 2007). We have also described similar studies involving copying a wider variety of line diagrams, e.g., arcs and ellipses. In these cases too a systematic error pattern is observed. Analysis of data collected from school-going children of a range of ages (7–15) revealed that the systematic error is not present at a very early age (7–11 years); it develops and matures during early teens (12–15 years) (Dubey et al. 2007).

There have been several computational modeling approaches for understanding the mechanisms of copying. Grossberg and Paine (2000) proposed AVITEWRITE (Adaptive Vector Integration To Endpoint Write) model with the aim of describing how the complex sequence of movements involved in handwriting can be learned through imitation of previously drawn curves. This model describes the mechanism of movement initiation as a visual attention shift along the reference shape and the generation of vector movement using motor cortical cells. If the imitative movement deviates from an attentional focus around a shape to be imitated, the visual system shifts attention, and may make an eye movement, back to the shape, thereby providing corrective directional information to the arm movement system. This imitative movement cycle repeats until the cortico-cerebellar system can accurately drive the movement based solely on memory. The model also describes how cortico-cerebellar mechanisms control timing of various movement segments involved in handwriting. However this model does not address the problem of two-peak error in copying oriented line diagrams.

The idea that cursive handwriting movements are composed of resonant oscillations of hand-pen system inspired a whole different line of handwriting generation models (Hollerbach 1981). The network models of Schomaker (1991) and Kalveram (1998) had certain difficulties, which were addressed in the oscillatory neural network model of Gangadhar et al. (2007). The oscillatory neural network described in Gangadhar et al. (2007), Gangadhar and Chakravarthy (2005) had earlier been expanded as a model of copying also (Gangadhar et al. 2005). The studies noted above are examples of oscillatory network models of handwriting movements.

A much simpler, and perhaps more elegant, class of oscillatory models of movement are phase dynamic models (Kelso 1999). A pioneering example of modeling movement coordination in terms of phase dynamics is the Haken–Kelso–Bunz model for coordinated bimanual hand movements (Haken et al. 1985). This class of work laid foundations for study of motor coordination in terms of self-organized phase dynamics. It has been extended to dynamics of all four limbs (Kelso and Jeka 1992); to coordination between a pair of interacting individuals also (Schmidt et al. 1990); to modeling quadruped gaits and gait transitions (Schoner et al. 1990); and to speech generation and perception (Tuller and Kelso 1990). Therefore, though phase dynamic models have been proposed to explain a great range of rhythmic processes in nature, to our knowledge, there is no model of phase dynamics for copying of simple line diagrams.

Further, previous studies on copying seem not to have paid sufficient attention to an important aspect of copying performance viz., the inherent ambiguity in the visuomotor transformation involved in copying. Copying is a complex visuomotor task in which a static visual image is reconstructed using a sequence of well-planned motor movements of the hand/pen. An aspect of copying that is particularly emphasized in the present work is the inherent ambiguity involved in copying task (Fig. 1a). While copying a line segment AB, for example, a subject can draw the line in two possible directions (A to B or, B to A), both of which could be equally accurate visual reproductions of the presented line, though the motor movements involved in producing the stroke are considerably different. Therefore, if copying simple line diagrams (like lines, short curves, etc.) can be viewed as a mapping from a static image to a dynamic movement of the hand, the mapping is inherently ambiguous since it is one-to-many. The ambiguities are going to be more crucial in copying more complex patterns. How does the visuomotor system of the brain cope with these ambiguities and plan rapid, robust, and accurate copying movements?

One way of minimizing the ambiguity is to bind direction of movement with orientation of the pattern. Considering the case of copying line segments again, such binding amounts to drawing lines of a given orientation always in a certain direction. Ambiguity can be ameliorated by coupling orientation with direction, but ambiguity cannot be avoided at least at one orientation (Fig. 1b). Note that a line of orientation θ ($\theta \in [0, \pi)$) can be drawn as two possible strokes of direction, $\phi = \theta$ or $\phi = \theta + \pi$ ($\phi \in [0, 2\pi)$) respectively. Analysis of human data (Dubey et al. 2007) revealed that there is indeed a strong correlation between the orientation and direction of stroke: lines of a certain orientation are typically drawn only in a certain direction. (This is obviously valid only if the subjects draw the lines spontaneously and rapidly without any special intent to draw a line of given orientation in a consciously pre-chosen direction.) Such binding of orientation with direction seems to be essential to minimize the effects of ambiguity and produce robust strokes. However, such a strategy of binding orientation with direction cannot be extended to the full range of orientation angles. There must be an angle at which the ambiguity remains unresolved. This unresolved ambiguity at certain critical angles seems to correspond to the interesting phenomenon of "flipping", wherein the subject suddenly flips the stroke direction at certain characteristic orientations (see Sect. 2).[1]

In this paper we model human copying performance with simple oriented line diagrams. Human data reveals a systematic error performance with stable, multiple peaks. This systematic error pattern and the associated phenomenon of flipping is captured by a simple phase dynamic model that relates the orientation, θ, of the line image to be copied, with the direction angle, ϕ, of the stroke that is drawn. Section 2 describes experimental setup for collecting copying data. Statistical analysis of the data collected is also presented in the same section. Section 3 presents a phase dynamic model of the copying process studied in Sect. 2. The results of experimental data of Sect. 2 are compared with the theoretical estimates of Sect. 3. Finally the model predictions and a plausible interpretation in terms of relevant functional neuroanatomy are discussed.

[1] A different type of "flipping" was described by Rosenbaum et al. (1996) who studied the ways in which human subjects grasped objects with "handles." The subjects preferred to first hold the handle, which was "away," and subsequently "flip" the object into a more comfortable end-state. Though the two forms of flipping bear an interesting resemblance, it is difficult to perceive a deeper connection between them at the moment.

2 Copying experiments

Subjects were shown the image of an oriented line in one panel (the "display panel") on the computer monitor and were asked to reproduce the same inside another panel (the "writing panel") using an electronic pen device (*Graphire*^{TM}, Wacom Inc— Tablet Active area: $4'' \times 5''$, pen and mouse resolution: 1015 lines per inch, accuracy: 0.02 inch, 125 Hz sampling rate). The displayed line is 4.8 cm long. The subjects were seated comfortably on a chair (43 cm above ground) facing the computer and the monitor on the table in front of them was 40 cm away, and the electronic tablet placed on the table (of height 74 cm). The positions of the monitor, the tablet and the chair on which the subject is seated were fixed; some flexibility was allowed to the subject in the manner of holding the pen or placing the hand on the tablet. The data collection software is implemented in Visual Basic 6.0. Subjects were allowed to familiarize themselves with the setup by playing with it for a few minutes before the actual session begins. Each session consisted of a line presented at a full range of orientations (18 values of orientation: 0–170° in steps of 10°). Orientation of the displayed line was compared with the orientation of the drawn line and absolute orientation error distribution over orientation values was analyzed. Orientation of the drawn line is estimated by first fitting a straight line by least squares regression to the drawn line, and taking the orientation of the fitted line as the orientation of the drawn line. These experiments and results are now described.

2.1 Copying lines

Subjects were asked to reproduce line segments of different orientations displayed inside the "display panel" on the monitor (Fig. 2). The line segments were of fixed length (4.8 cm) and are centered at the origin (center) of a thin crosswire shown in the display panel. Subjects included 24 human adults (13 male, 11 female; aged 19–34 years). In a given session, input data was displayed in one of two possible orders ("anticlockwise" which refers to line images of increasing orientation presented in a sequence, and "random" order, which refers to random presentation of line images). The subjects were supposed to draw within a specific duration (inter-stimulus interval, ISI) after the presentation of input image. Three different ISIs (2, 3, and 4 s) are used. Thus every subject participated in 6 sessions corresponding to (1) two orders of presentation, and (2) three different ISIs. The absolute error at different input stroke orientations, averaged over all the subjects, is shown in Fig. 3. We notice that there are two very well-defined maxima in the orientation error profile as the input stroke angle is varied from 0 to 180° (Fig. 3a–f). A typical trend in these absolute error plots can be observed. Starting from a high error corresponding to input

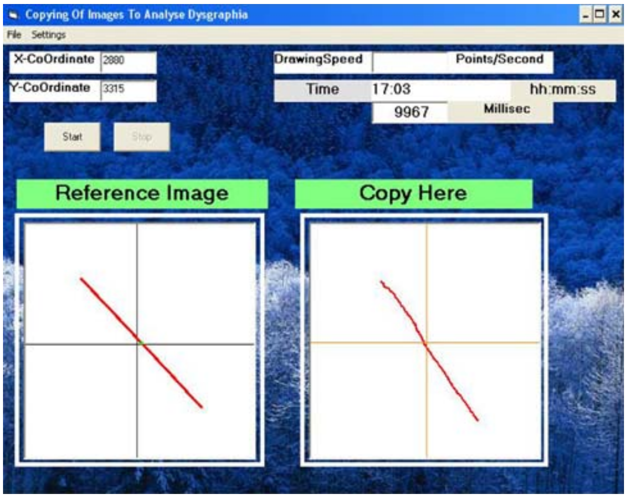

Fig. 2 User interface for copying lines. The image of the line to be copied is shown in the "display panel" on the left. The line is drawn inside the "writing panel" on the right

line orientation of 0°, the error dips to about 2–5°, and then increases gradually to a peak value of about 15–20°, drops rapidly to less than 5° again and climbs again to the second peak value of about 20–25° before falling rapidly.

2.2 Results from ANOVA analysis

We now perform statistical tests to investigate the relevance of various parameters in determining copying error performance. The software used for data analysis was Analyse-it® for Microsoft Excel® Version 1.73. Results from ANOVA analysis are given below:

The first question that may be verified is the dependence between the orientation of the line displayed (θ) and the orientation of the line drawn (ψ). The results from 1-way ANOVA with input orientation (in degrees) as factor and error, e, (in degrees) between displayed line orientation and drawn line orientation ($\mathrm{e} = |\theta - \psi|$) as variable shows that the dependence between orientations of displayed and drawn lines is highly significant ($F(17, 1494) = 34.54$, $P < 0.0001$).

We now consider the effect of varying ISI on copying performance. The results from 1-way ANOVA with ISI (in seconds) as factor and error, e, (in degrees) between displayed line orientation and drawn line orientation ($\mathrm{e} = |\theta - \psi|$) as variable were not significant. ($F(2, 1509) = 1.64$, $P = 0.1937$). It may be concluded that for the range of ISI values considered, there is no significant change in performance due to ISI variations. Similarly results from two-way ANOVA performed with displayed line orientation and ISI as factors and error as variable ($F(34, 1512) = 0.52$, $P = 0.9903$) also indicate a dependence that is not significant.

Similar analysis of the dependence of the order of presentation ((a) anticlockwise and (b) random order) on copying performance showed that the dependence is not significant. The results from 1-way ANOVA with Order as factor and error (in degrees) between displayed line orientation and drawn line orientation ($\mathrm{e} = |\theta - \psi|$) as variable were also not significant ($F(1, 1510) = 0.77$, $P = 0.3808$).

From the three statistical tests presented above we learn that the dependence between θ and e, is significant, while the dependence of output error, e, on ISI and order of presentation is not significant. These tests are done by way of confirming an intuition and are not very surprising. But there is a subtler aspect of copying lines, which will be addressed now.

We have noted earlier that a line, AB, can be drawn in two equivalent ways—from A to B, or from B to A. Therefore, unlike the displayed line which is characterized by a single angle parameter, viz. orientation, θ, the line drawn can be characterized by two angular parameters viz., orientation ψ, and direction, ϕ. Direction may be defined as the polar angle of the vector that connects initial point on the stroke drawn with the final point. Drawn line direction, ϕ and drawn line orientation, ψ, are related as,

$$\begin{array}{ll} \psi \approx \phi, & \text{or} \\ \approx \phi + \pi & \end{array} \tag{2.2.1}$$

Figure 5(c) shows the variation of direction angle, ϕ with respect to displayed line orientation, θ, averaged over all the cases of an individual subject's case (data from all 6 types of sessions are combined). As θ is increased, ϕ also changes gradually until there is a sharp increase in ϕ at about 110°, beyond which there is a gradual increase again. The angle by which ϕ increases when the sudden change occurs is about 180°. This is expected because a change of 180° (a "flip") in ϕ leaves ψ intact. We had earlier argued that due to the inherent ambiguity in copying, there must be one or more orientation values at which the mapping between ϕ and θ is discontinuous. In case of most people, the "flip" occurred only at one angle. Out of the combined 87 instances of total flips recorded, we had 73 cases of 1 flip, 13 instances of 2 flips, and 1 instance of 3 flips. A theoretical model that captures the relation between θ and ϕ and exhibits a single flip is now described.

3 A phase dynamic model of line copying performance

The proposed model relates the orientation, θ, of the line image shown, with the direction angle, ϕ of the stroke drawn in order to copy the shown image. The model essentially consists of a pair of coupled nonlinear oscillators driven by a pair of sinusoidal inputs. It is assumed that the frequency of the two oscillators is the same, and also equals the

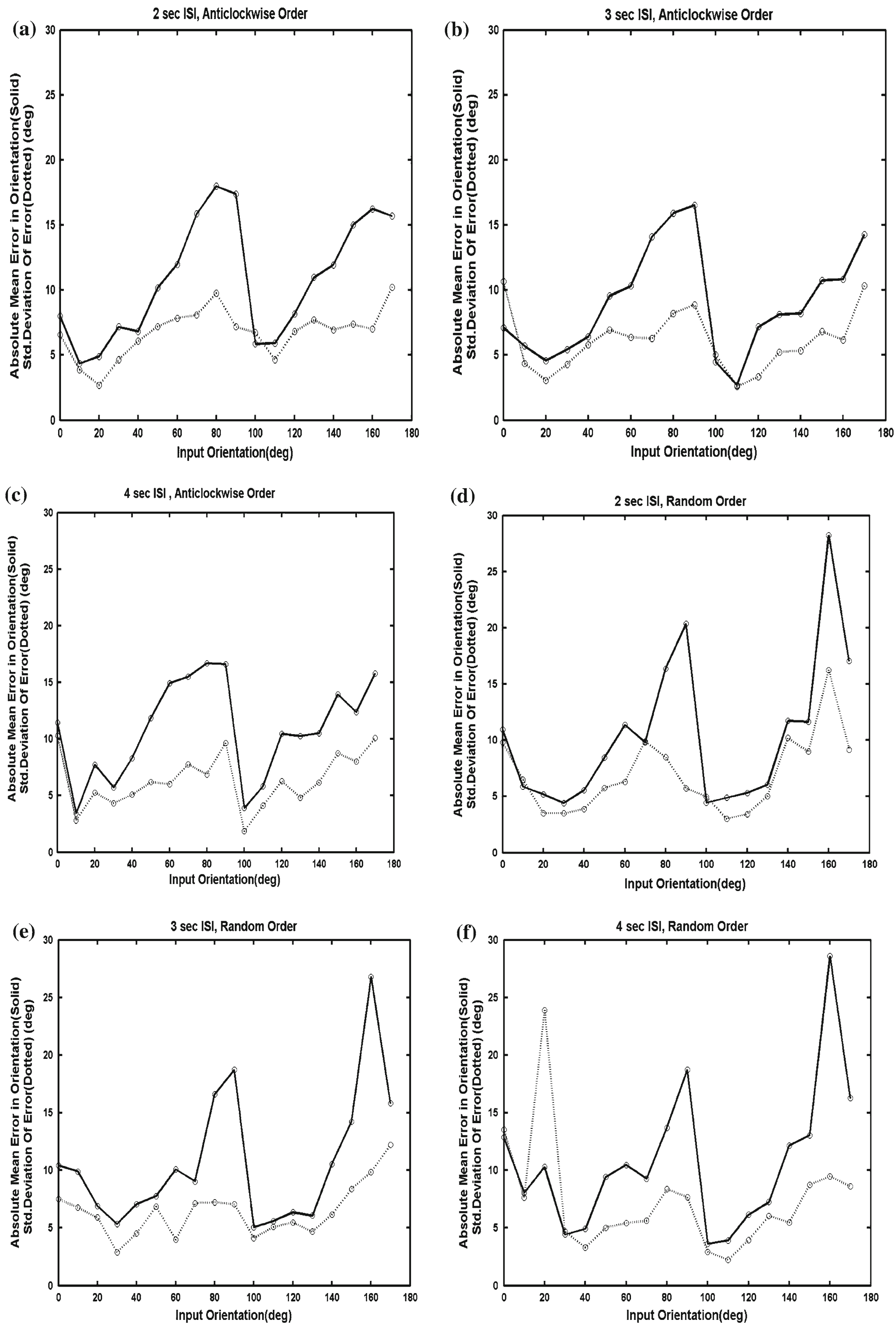

Fig. 3 Plots of mean error (in degrees) between displayed line orientation (θ) and drawn line orientation (ψ) (*solid line*) and standard deviation of mean error, e (in degrees) v/s orientation of line displayed (*dotted line*) for: **a** anticlockwise order, 2 s ISI, **b** anticlockwise order, 3 s ISI, **c** anticlockwise order, 4 s ISI, **d** random order, 2 s ISI, **e** random order, 3 s ISI, and **f** random order, 4 s ISI

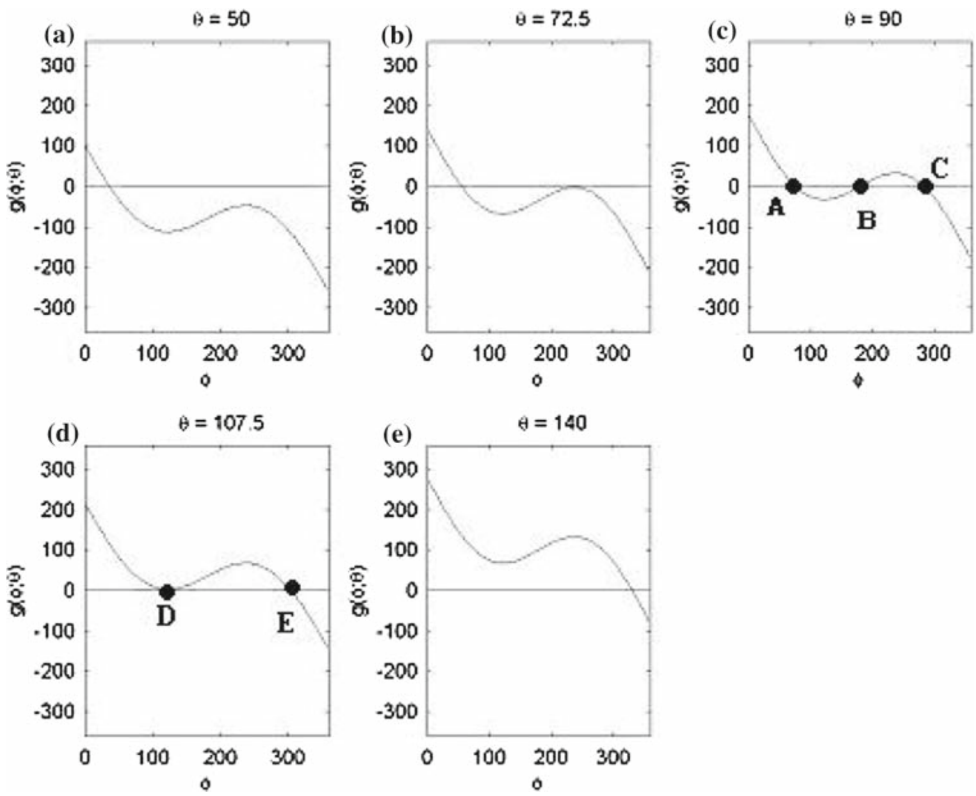

Fig. 4 The zeros of Eq. 3.2 as a function of θ. For smaller values of θ ($0 \leq \theta < \theta_1$), Eq. (3.2) has a single stable solution (Fig. 3a). For intermediate values of θ, ($\theta_1 \leq \theta < \theta_2$) there are three stationary states, with two stable states flanking an unstable state (Fig. 3b,3c). For ($\theta_2 \leq \theta < \pi$), again there is only a single stable state for ϕ. Note that $\theta_1 = 72.5°$ and $\theta_2 = 107.5°$

frequencies of the two sinusoidal inputs (Fig. A1). The phase difference between the two sinusoidal inputs represents twice the orientation angle, 2θ; the phase difference induced in the pair of oscillators by the effect of sinusoidal input represents direction angle, ϕ. Equation. 3.1 below describes the phase dynamics of such an oscillatory system (see Appendix-I).

A slight variation of Eq. (A1.5) is used to model the line data described in the previous section, as shown below.

$$\frac{d\phi}{dt} = -\phi - a\sin(\phi) + 2\theta \tag{3.1}$$

Note the slight difference between Eqs. (A1.5) and (3.1) (2θ instead of α). In Eq. (A1.5) both α and β vary over $[0, 2\pi)$. But in Eq. (3.1), θ (orientation) varies over $[0, \pi)$, while ϕ (direction) varies over $[0, 2\pi)$.

It is desirable that the relation between ϕ and θ resemble the experimental profile of Fig. 3. Now what is the condition on 'a' for a discontinuity to occur? Further, at what precise value of 'a' does the discontinuous change equal 180°?

Consider the zeroes of the following equation,

$$\frac{d\phi}{dt} = -\phi - a\sin(\phi) + 2\theta = 0 \tag{3.2}$$

for $\theta \in [0, \pi)$. For smaller values of θ ($0 \leq \theta < \theta_1$), Eq. (3.2) has a single stable solution (Fig. 4a). For intermediate values of θ, ($\theta_1 \leq \theta < \theta_2$) there are three stationary states, with two stable states flanking an unstable state (Fig. 4b). For ($\theta_2 \leq \theta < \pi$), again there is only a single stable state for ϕ.

As θ crosses θ_2 from below, the stable–unstable pair of solutions (A and B in Fig. 4c) annihilate each other (D in Fig. 4d) leaving a single stable state e (in Fig. 4d). Therefore, at this point ϕ jumps from D to E.

Let ϕ_1 be the value of ϕ corresponding to the point D in Fig. 4. Since the function $g(\phi)$ given as,

$$g(\phi) = -\phi - a\sin(\phi) \tag{3.3}$$

has a minimum at ϕ_1, we have,

$$-1 - a\cos(\phi_1) = 0$$

or,

$$\cos(\phi_1) = -\frac{1}{a} \tag{3.4}$$

There can be a real solution to the above equation only for $a > 1$ (for a positive). Thus, as θ is varied continuously, ϕ can exhibit a discontinuous change only for $a > 1$. This answers our first question. Let us investigate the second question now.

Let the stationary value of ϕ at E in Fig. 4 be ϕ_2. Since a flip occurs at D, we have,

$$\phi_2 = \phi_1 + \pi \tag{3.5}$$

Also, since the coordinates of D(ϕ_1, θ_2) and E (ϕ_2, θ_2) satisfy Eq. (3.2),

$$-\phi_1 - a\sin(\phi_1) + 2\theta_2 = 0, \quad \text{and}$$
$$-\phi_2 - a\sin(\phi_2) + 2\theta_2 = 0$$

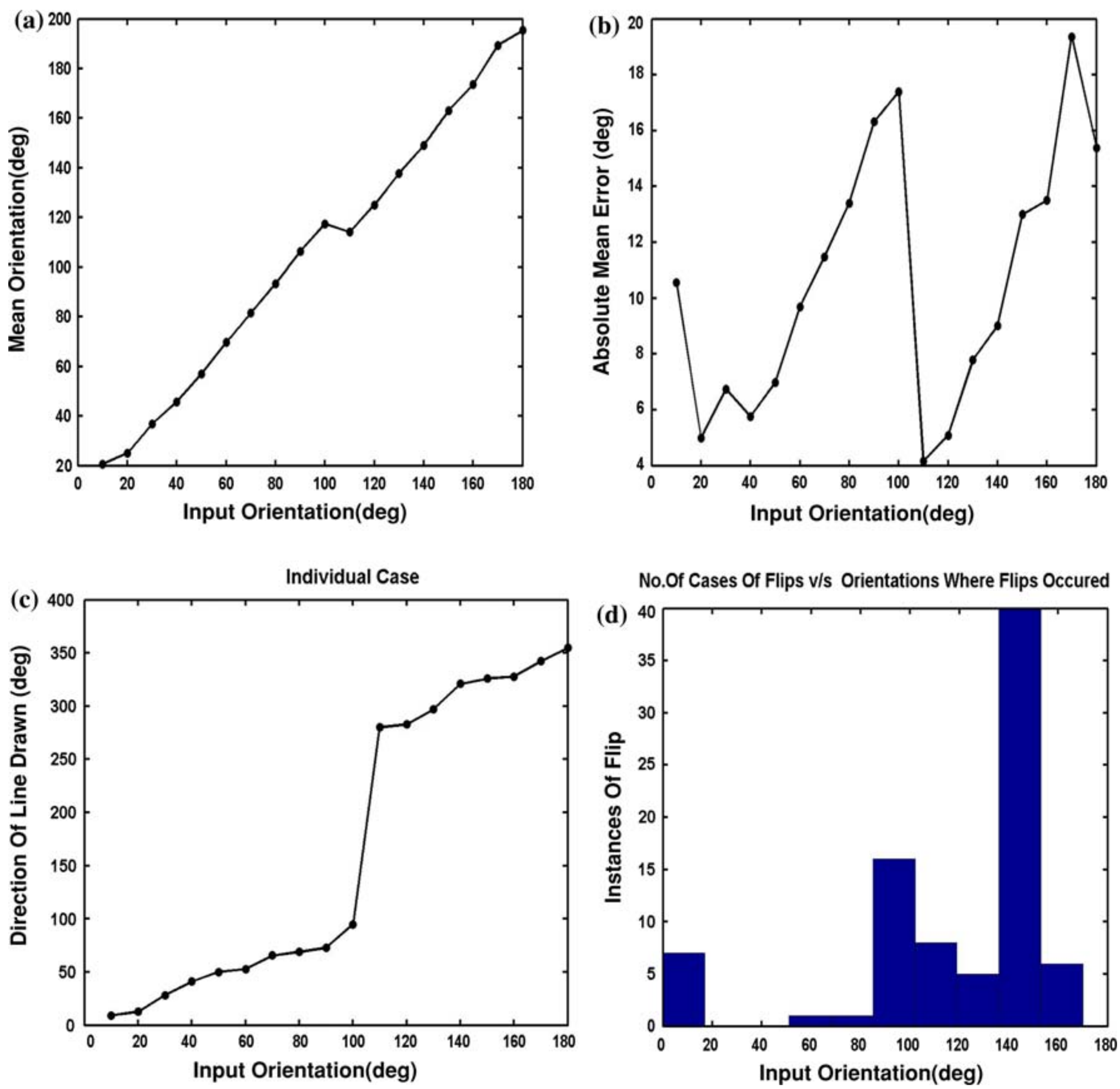

Fig. 5 Human Experiment Results (averaged over all ISI's and all orders of presentation for subjects with single flips which constituted the majority) **a** Shows mean of output or drawn orientation v/s Input Orientation shown to the subject as a reference. **b** Shows mean of absolute error in drawn orientation v/s input orientation shown to the subject **c** Depicts direction of output stroke v/s input orientation for an individual subject's case. Note the flip that occurs for input orientation of about 100°, at which point the drawn line direction angle jumps from about 100° to about 280°. **d** Shows a histogram of orientation values at which flip occurs for subjects who made a single flip

or

$$-\phi_2 - a\sin(\phi_2) = -\phi_1 - a\sin(\phi_1)$$

Using Eq. (3.5) here,

$$-\phi_1 - \pi + a\sin(\phi_1) = -\phi_1 - a\sin(\phi_1)$$

or,

$$\sin(\phi_1) = \frac{\pi}{2a} \tag{3.6}$$

Combining Eqs. (3.4) and (3.6),

$$a = \sqrt{1 + \frac{\pi^2}{4}} = 1.8621 \tag{3.7}$$

and $\phi_1 = 122.48°$

The value of θ at which the flip occurs is 107.5° and the corresponding value of $\phi = \phi_1 = 122.48°$ (Fig. 6). It is interesting that the flip occurs at 120.83° averaged over all cases of human data (Fig. 5c), which is remarkably close to $\phi_1 = 122.48°$. The absolute error in orientation taken from

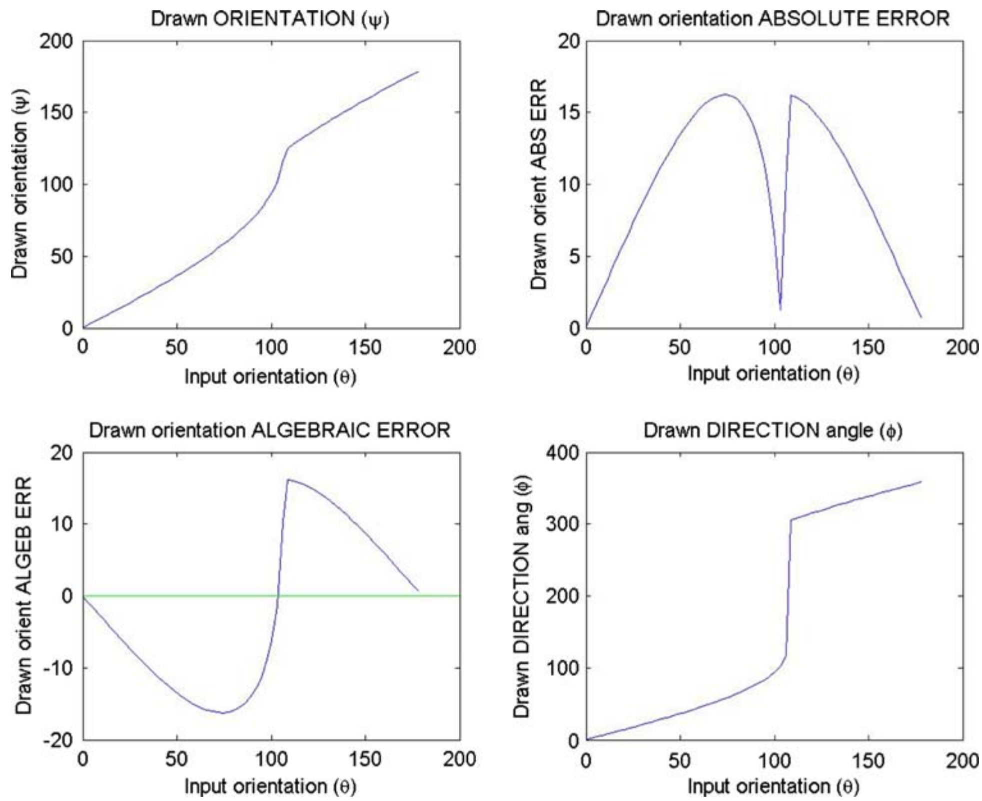

Fig. 6 Theoretical Results from the model of Line Copying Performance (using Eq. 3.2): Drawn orientation v/s input orientation (*top-left*), absolute error in Drawn Orientation v/s put Orientation (*top-right*), Algebraic Error in Drawn Orientation v/s Input Orientation (*bottom-left*), Drawn Direction v/s Input Orientation (*bottom-right*)

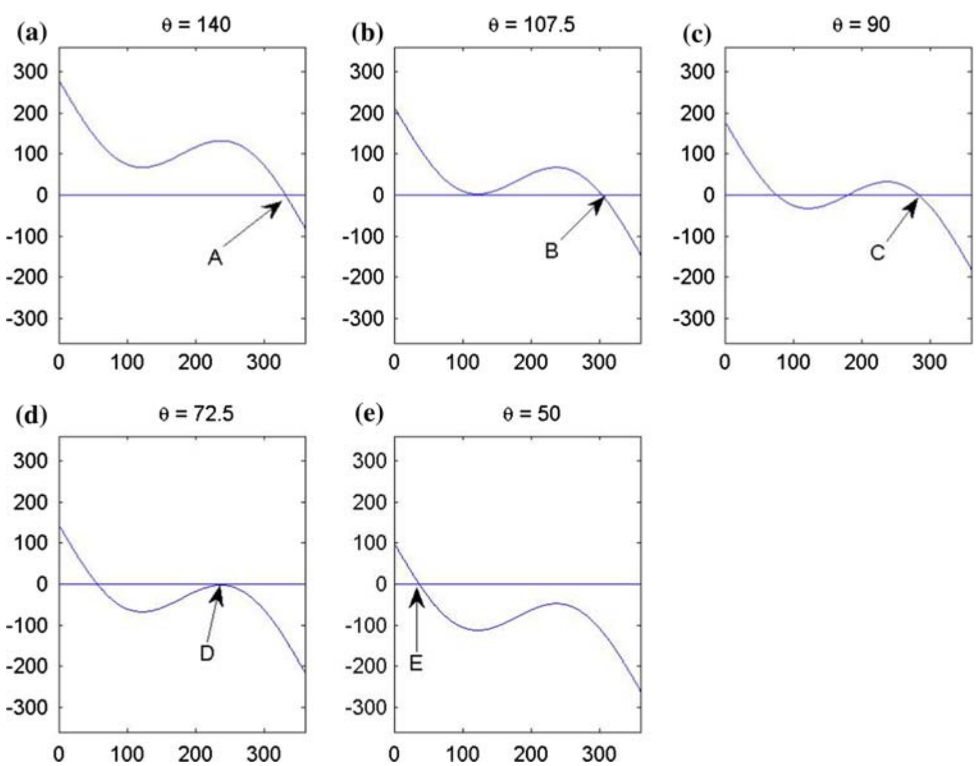

Fig. 7 Figure depicts how the drawn line direction varies as input orientation is varied in clockwise direction from 180°. In subfigures (**a**)–(**e**), points A to E depict the values of output orientation. Note the sudden drop in drawn line direction when input orientation is about 72.5°

human data is shown in Fig. 5b. Other parameters like minimum and maximum absolute error, flip angle etc. match well between human data (Fig. 5) and theoretical estimates (Figs. 6, 7) (see Table 1).

Thus, we have shown that the orientation variations involved in copying lines can be modeled approximately by a simple equation that represents a pair of oscillators driven by sinusoidal inputs.

Table 1 Comparison of Theoretical and Experimental Results from the model of Line Copying Performance (using Eq. 3.2)

Parameter	Experimental value (degrees)		Theoretical Value (degrees)	
Average absolute orientation error	10.88		10.09	
Local peaks in error (value)	Input orientation	Peak error value	Input orientation	Peak error value
	100	17	74.48	16.23 (max.)
	170	19	108.87	16.2
Orientation values at which error minima occur	Input orientation	Error Value at Minima	Input orientation	Error Value at Minima
	110	4	103.13	1.29
Average value of orientation at which flip occurs in single flip cases	120.83		122.48	
Average angle by which flip occurs in single flip cases	174.96		180	

4 Hysteresis study

In the phase dynamic model of the previous section, we used stable states of the model (Eq. (3.1)) to relate orientation of the displayed line with the direction of the drawn line. In this analysis only the zeros of Eq. (3.2) are used; dynamic aspects of Eq. (3.1) are not exploited. An interesting effect that emerges automatically out of a dynamic system with the stationary point structure like that of Fig. 4 is hysteresis. In Fig. 4, as input orientation is varied gradually, a sudden change is observed in output direction at a specific input orientation. Due to hysteresis, the point at which this sudden change occurs depends on the manner in which orientation is varied—clockwise or anticlockwise.

Figure 4 shows the pattern of variation of stationary points as input orientation is varied in anticlockwise (increasing from 0 to 180°) direction. Figure 8 shows corresponding results as input orientation is varied in clockwise direction (180 to 0°). With increasing orientation, flip occurs at a larger orientation ($\theta = 107.5°$) than in the case of decreasing orientation ($\theta = 72.5°$) (Fig. 8). This is a sign of hysteresis.

Hysteresis behavior is observed in human copying performance also (Fig. 9). In the studies of Sect. 2, we presented orientations in anticlockwise and random orders. We now present a study in which lines are presented with orientation gradually varying first in anticlockwise and then in clockwise directions. In this experiment 15 subjects were involved (total no. of subjects =15; males = 11; female = 4; right-handed = 14; left-handed = 1; ages = 22–26 yrs). Lines of orientation varying between 0 and 170° in steps of 10° were displayed – first in anticlockwise order immediately followed by presentation in clockwise order. Fig. 9 shows the direction angle w.r.t. input orientation averaged over the 15 subjects. With increasing input orientation, the "knee" (A in Fig. 9) on the lower part of the curve occurs at about 80.2°. With decreasing input orientation the "knee" (B in Fig. 9) again on the lower part of the curve occurs at about 69.9°. Note that

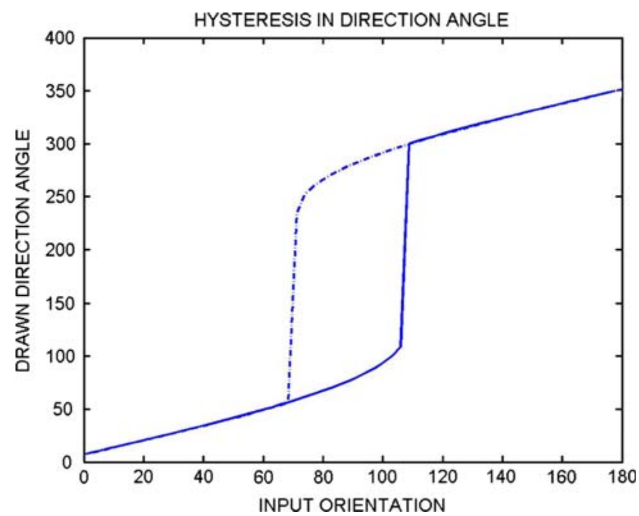

Fig. 8 Figure depicting hysteresis effect displayed by the model. The *solid line* indicates variation of direction angle with increasing input orientation. The *dashed line* indicates variation of direction angle with decreasing orientation

the orientation at which "knee" occurs in the reverse curve (dashed line in Fig. 8) according to the model is 72.5°, which is close to the human data. However, the corresponding value for increasing values of input orientation does not match significantly between human (80.2°) and model (107.5°) data.

5 Discussion

Human performance in copying oriented lines revealed systematic error pattern, a "two-peak" structure, consistently even when two independent parameters (a) order of presentation and (b) time delay, are varied. We argue that the systematic error profile has its roots in the inherent ambiguity involved in copying tasks. In a study involving copying elliptical patterns Athènes et al. (2003) found a two-peak structure in orientation error. However the authors do not

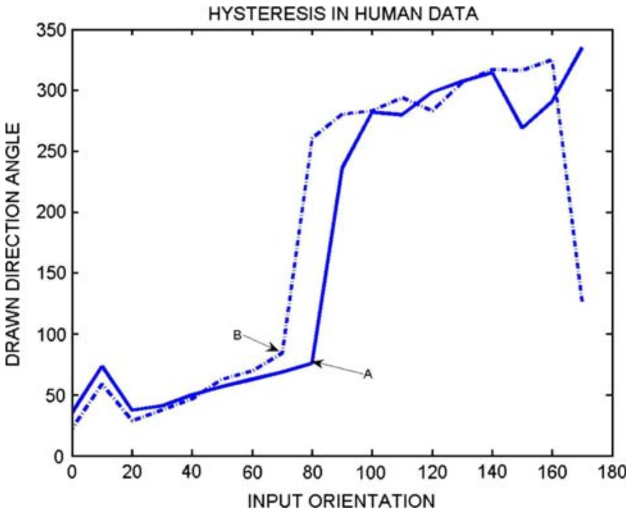

Fig. 9 Figure depicting hysteresis effect observed in human performance data. The *solid line* indicates variation of direction angle with increasing input orientation. The *dashed line* indicates variation of direction angle with decreasing orientation

provide a theoretical model to justify the claim (Athènes et al. 2003; Zanone et al. 2005). We designed a coupled oscillators model that explains the relation between input orientation and drawn line orientation in copying, which was supported by human experimental results.

An interesting phenomenon anticipated and captured by the proposed phase dynamic model is the hysteresis effect. In the proposed model, input orientation acts as a control parameter. As input orientation is varied gradually, the system (Eq. 3.1) exhibits a cusp bifurcation and a discontinuous change in output direction (the "flip") is observed. The flip occurs at a larger orientation value when the orientation is increased, than when orientation is decreased. This aspect of the model behavior is also reflected in human performance.

A novel aspect of our model is to use an oscillatory model to describe a movement that is apparently not oscillatory but discrete. Oscillatory dynamical models are usually used to describe oscillatory movements (Kelso 1999). Models that seek to describe both oscillatory and discrete movements tend to use limit cycle attractors for representing oscillatory dynamics, and fixed-point dynamics for discrete movements (Jirsa and Kelso 2005). However, though drawing of a line appears to be a discrete movement, it is embedded in a family of movements that is parametrized by a spatial phase. This spatial phase is represented as temporal phase of an oscillator in our work. Such an approach might appear rather unusual from a modeling perspective. However we argue that such a representation is neurobiologically more natural since in the brain all forms of information—static and dynamic, spatial and temporal—seem to be coded as oscillations. This viewpoint is further developed in the following paragraphs, quoting appropriate sources from neuroscience.

Coding spatial information as phase of cortical oscillation is not an entirely new notion in neuroscience. For example, it is known that certain neurons (the "place cells") in hippocampus of freely moving rat code for the location of the animal relative to its spatial environment. Further, frequency of the complex bursting pattern of these neurons is known to fall within the theta band (7–12 Hz) of electroencephalogram. Interestingly the phase of the theta wave when the place neuron fires is found to code for the animal's position. It has been observed that firing consistently begins at a particular phase when the rat enters a place field; the phase changes systematically as the rat crossed the place field (O'Keefe and Recce 1993). In other words, *spatial relative position is coded as temporal phase*. In human subjects also, cortical neural firing that is phase locked to theta and gamma frequency bands has been discovered (Jacobs et al. 2007). Ekstrom et al. (2005) investigated cortical oscillations in humans subjects engaged in spatial navigation tasks. In their studies, the subjects played Yellow Cab, a virtual taxi-driver game. The studies revealed that cells in the hippocampus respond at specific spatial locations, and cells in the parahippocampal region respond to views of landmarks (Ekstrom et al. 2003). However, it is not yet clear if the kind of phase-coding found in rodent hippocampus occurs in human hippocampus also. Cognitive significance of phase locking has been reported in human subjects engaged in a working memory task (Rizzuto et al. 2003). Stimulus-induced phase resetting has been reported by Makeig et al. (2002) and Rizzuto et al. (2003).

Oscillations have varied significances in the activity of motor cortex also. All the major cortical frequency bands in the Electroencephalogram (EEG)—theta (4–8 Hz), mu (8–12 Hz, also called sensorimotor alpha), sigma (12–15 Hz), beta (15-30 Hz) and gamma (>30 Hz) – exhibit movement dependent changes (MacKay 2005). Sigma band oscillations at about 14 Hz represent maintained active suppression of motor response. Event dependent desynchronization, which suggests power reduction in a given frequency band, is observed in mu and beta bands of EEG just before movement onset; these rhythms reappear on termination of movement (Rizzuto et al. 2003). The mu frequency of 10 Hz has been associated with physiological tremor for a long time. Increased movement-related activity in theta and gamma bands, was observed mainly over SMA, premotor, and parietal cortices; this increase occurred in sporadic bursts during the movement (Popivanov et al. 1999). Similarly gamma oscillations are related to vigorous muscle activity. Increased coherence between cortical and muscle activity in the gamma band is observed in such conditions (Brown 2000; Hari and Salenius 1999) It is noteworthy that the above-described motor cortical rhythms are present in all forms of movements—oscillatory or discrete.

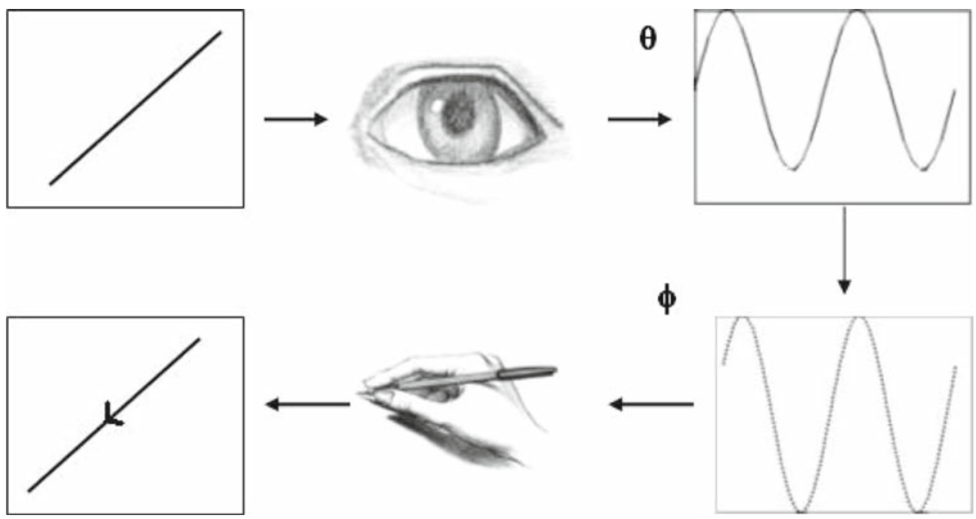

Fig. 10 A hypothetical schematic of stages of encoding involved in transforming a line image into a linear stroke

Based on the present work we speculate that the bias toward direction preferentiality lies deeper probably at the level of encodings in the visual and motor regions of the central nervous system. Thus, it is possible that the orientation angle of the line displayed is coded as phase of some central neural oscillators. Relative phase has been proved to be the "order parameter" in a variety of problems related to motor coordination (Kelso 1999). Information thus coded as oscillations is perhaps transmitted via a series of cortical areas viz., visual cortex → parietal cortex → premotor cortex → primary motor cortex, etc., before it is finally expressed by hand/pen movements. Figure 10 shows a hypothetical schematic of a series of encoding stages involved in transforming a line image into a motor movement that reconstructs the displayed line. The orientation of the line is coded as temporal phase, θ, (possibly of cortical rhythms in visuospatial regions of superior parietal cortex); further downstream the direction of movement is coded as temporal phase, ϕ, (possibly of motor cortical regions involved in handwriting generation).

On the whole, there is a renewed interest in brain rhythms in contemporary neuroscience. As attempts to match specific cognitive tasks with specific frequencies (e.g., matching theta waves with spatial processing) turned out to be inconclusive, the search is on to look for answers in both frequency and phase space (Kahana 2006). The present work proposes a simplified phase-oscillator model in which spatial information is encoded as temporal phase. In this regard, our model marks an interesting departure from phase dynamic models of motor coordination. In such models, typically, phase represents the temporal phase of an oscillatory movement. But in the present model the phase represents a spatial phase/angle i.e., the orientation of a line. This spatial phase is thought to be coded as a temporal phase of neural oscillators in the visuospatial regions of the brain. On the motor side, a similar phase may perhaps be related to the specific direction of hand movements. A fruitful line of future research will include looking for neurobiological evidence for appropriate forms of phase-encoding in EEG data taken from subjects involved in visuomotor tasks like copying line diagrams.

Mathematical appendix – I

In the experiments described in Sect. 2.1, a line displayed in one panel has to be copied onto another panel by the subject. Performance is based on error in orientation. Three angular quantities are involved in this calculation: orientation of the line displayed (θ), direction of the line drawn (ϕ) and orientation of the line drawn (ψ). ϕ and ψ are related simply as:

$$\phi = \psi \quad \text{or} \quad \phi = \psi + \pi \quad (\phi \in [0, 2\pi))$$

Our immediate objective is to model the relation between θ and ψ, and explain the systematic errors observed in human experiments (Fig. 3 a–f).

The desired model must essentially map one angular quantity onto another. We will show that a simple template model that can do so is a pair of coupled oscillators driven by sinusoidal input. Fig. 11 shows a schematic of a pair of coupled, identical oscillators, A and B, oscillating with phase difference β, driven by sinusoidal inputs I_1 (= $I_0 \cos(\omega t + \alpha)$) and I_2(=$I_0 \cos(\omega t)$) with phase difference α.

We describe the four oscillators of Fig. 11 as a chain of phase-coupled oscillator system following the formulation of (Sect. 10.4 in Murray (1989)). Since the phases of oscillators 1 and 4 are constant, we write down the phase dynamics of oscillators 2 and 3 only.

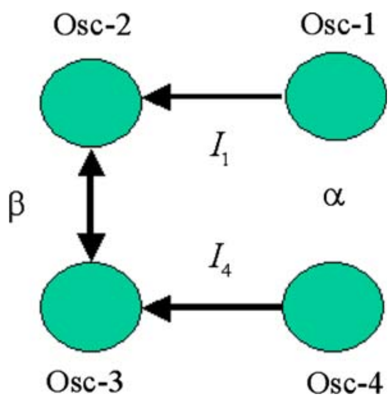

Fig. 11 The coupled oscillators model

$$\frac{d\phi_2}{dt} = \omega_2 + a_{21}\sin(\phi_1 - \phi_2) + a_{23}\sin(\phi_3 - \phi_2) \quad \text{(A1.1)}$$
$$\frac{d\phi_3}{dt} = \omega_3 + a_{32}\sin(\phi_2 - \phi_3) + a_{34}\sin(\phi_4 - \phi_3) \quad \text{(A1.2)}$$

where ϕ_1, ϕ_2, ϕ_3, and ϕ_4 are the phases of oscillators 1, 2, 3, and 4, respectively; ω_2 and ω_3 are intrinsic frequencies of oscillators 2 and 3, respectively. We assume that the inputs 1 and 4 are identical and the oscillators 2 and 3 are also identical, which implies that $a_{23} = a_{32}$, $a_{21} = a_{34}$ and $\omega_2 = \omega_3$. Since the phase difference between oscillators 2 and 3 is β (see Fig. 11), we have $\beta = \phi_2 - \phi_3$

Subtracting Eq. (A1.2) from Eq. (A1.1),

$$\frac{d\beta}{dt} = a_{21}(\sin(\phi_1 - \phi_2) - \sin(\phi_4 - \phi_3)) - 2a_{23}\sin(\beta) \quad \text{(A1.3)}$$

Since oscillator 2 is driven by oscillator 1, and oscillator 3 by oscillator 4, we assume that $|\phi_1 - \phi_2|$ and $|\phi_3 - \phi_4|$ are small enough to permit the approximations: $\sin(\phi_1 - \phi_2) \approx \phi_1 - \phi_2$ and $\sin(\phi_3 - \phi_4) \approx \phi_3 - \phi_4$. Substituting these approximations in Eq. (A1.3),

$$\frac{d\beta}{dt} = a_{21}((\phi_1 - \phi_2) - (\phi_4 - \phi_3)) - 2a_{23}\sin(\beta), \text{ or}$$
$$\frac{d\beta}{dt} = a_{21}((\phi_1 - \phi_4) - (\phi_2 - \phi_3)) - 2a_{23}\sin(\beta), \text{ or}$$
$$\frac{d\beta}{dt} = a_{21}(\alpha - \beta) - 2a_{23}\sin(\beta)$$
$$\frac{1}{a_{21}}\frac{d\beta}{dt} = -\beta - \frac{2a_{23}}{a_{21}}\sin(\beta) + \alpha \quad \text{(A1.4)}$$

Since we are only interested in equilibrium solutions of β for every α, Eq. (A1.4) may be replaced with:

$$\frac{d\beta}{dt} = -\beta - a\sin(\beta) + \alpha \quad \text{(A1.5)}$$

where $a = (2a_{23}/a_{21})$. In the above equation, for every value α, there is (are) one (or more) steady state values of β. The shape of the function $\beta = (f\alpha)$ depends on 'a'. Fig. 12 depicts the relation between β and α for various values of 'a'. Note that the discontinuity in the bottom right part of

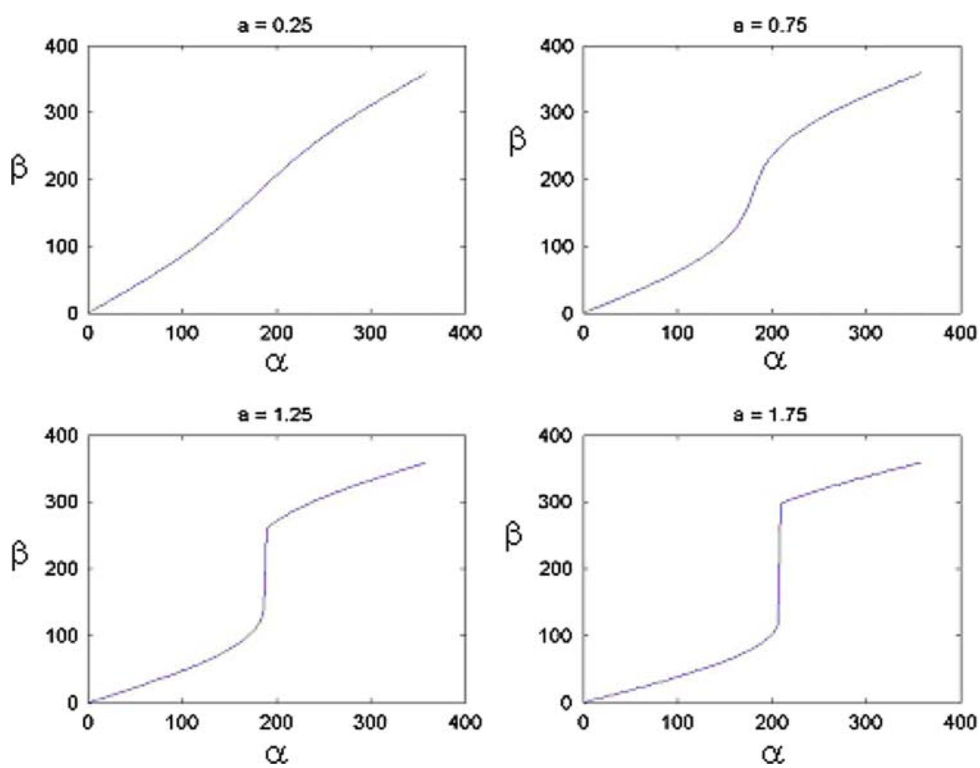

Fig. 12 Relation between β and α for various value of 'a'

Fig. 12 resemblances the "flip" observed in the direction angle of human data (see Sect. 2). Therefore, Eq. (A1.5) is used as a template to model the various experimental results of Sect. 2. It will be shown how a small variation of Eq. (A1.5) are adequate to explain the experimental copying results.

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