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Factors involved in the 'rotation' of the human embryonic stomach around its longitudinal axis: computer-assisted morphometric analysis

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ABSTRACT

The majority of studies as to whether gastric and nongastric factors are involved in the 'rotation' of the human embryonic stomach around its longitudinal axis have been morphological. The aim of this study was to analyse, with morphometric support, the influence on the angular modifications during gastric rotation of the simultaneous changes of the gastric walls and mesenteric growth, and the volumes of organs adjacent to the stomach (right, left and posterior groups). Computer imaging techniques were applied on cross sections of a graded series of 10 human embryos (from Carnegie stage (CS) 11) and 2 fetuses. A clockwise gastric rotation occurred during the embryonic period. The most rapid angular modifications took place from CS 11 to 16, after the rotation became oscillatory with angular changes in clockwise and anticlockwise directions, reaching the highest value at CS 18 (at the supraomental part of the stomach: 54.37°; at the omental part: 68.03°); after this period the angular values tended to stabilise. The predominant growth of the left gastric wall over the right and the changes in the width of the gastric mesentery were the most persistent factors involved in the modifications of the transverse gastric angle during the embryonic period although without relationship to their direction. During the increasing angular phases, clockwise rotation was promoted by the decrease of the volume of any group of organs adjacent to the stomach. When the volume of the left and posterior groups increased simultaneously, clockwise or anticlockwise angular directional change was related to the respective decrease or increase adjacent organ volume to the right. We conclude that the stomach of the human embryo undergoes heterogeneous and multifactorial rotation as a consequence of the overall increase in gastric wall growth to the left and the increase of gastric mobility produced by the previous mesenteric enlargement, and that the rotational direction results from the forces exerted on the stomach and the gastric mesenteries by the adjacent organs.

Key words: Embryology, stereology, gastric angles.

INTRODUCTION

It is generally believed that the stomach undergoes a rotation along its longitudinal and dorsoventral axes. Enbom (1939) was of the opinion that the rotation of the stomach was a more complex process that occurred along 3 axes.

The rotation around its dorsoventral axis, which accompanies the duodenal rotation, produces a final elevation of the pyloric part, which seems to be due to the pressure exerted by the enlarging of the liver on the freely movable cranial part of the stomach, whereas the caudal end is relatively firmly anchored by the short ventral mesogastrium and bile duct (Arey, 1966).

The 90° of clockwise rotation of the stomach from above along its longitudinal axis means that the right and left gastric walls are transformed into posterior and anterior gastric walls respectively, because the stomach changes from a sagittal to a frontal position. Different causal interpretations of this kind of gastric rotation have been proposed, but they can be

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synthesised into 2 theories. The theory which postulates that this rotation is real (Meckel, 1817; Pressler, 1911; Carey, 1920; Dott, 1932; Botha, 1959), is supported in the relative position of the gastric nerves and the gastric mesentery attachments at the gastric curvatures. The theory which postulates that this rotation is only apparent (Swaen, 1896; Broman, 1904; Gómez, 1956; Kanagasuntheram, 1957; Dankmeijer & Miete, 1959, Liebermann-Meffert, 1969; O'Rahilly & Müller, 1992), explains it from the morphological gastric changes basically secondary to 2 processes: by the extension of the omental bursa into the compound mesodermal anlage of the stomach and gastric mesenteries (Swaen, 1896; Broman, 1904; Gómez, 1956; Kanagasuntheram, 1957; García et al. 1974), and by the predominant growth of the left gastric wall over the right (Pernkopf, 1922; Kanagasunteram, 1957; Dankmeijer & Miete, 1959; Macarulla-Sanz et al. 1996). Other nongastric factors such as hepatic growth (Broman, 1904; Botha, 1959; Arey, 1966), unequal visceral growth (Dott, 1932) or differential thinning of the right side of the dorsal mesogastrium (Larsen, 1993), were proposed as determining factors in the positional changes of the embryonic stomach. Needham (1939) suggested that this dynamic vitality could be due to the influence of the intrinsic embryonic hormones.

However, few of these important embryological studies gave other morphometric information than angular values, lineal distances or areas. Lacking quantified global valuations obtained in every embryonic specimen which would allow us to relate the controversial rotation of the stomach around its long axis with gastric and nongastric factors, we proposed to analyse morphometrically the possible influence on the angular modifications that occur during this gastric rotation by the simultaneous changes in the degree of predominance of the left gastric wall growth over the right, the gastric mesentery width and the volumes of the organs adjacent to the stomach.

MATERIAL AND METHODS

The 'rotation' of the stomach around its longitudinal axis was assessed by means of the modifications in the mean transverse gastric angle (angular variable) during the embryonic and early fetal periods. As we determined gastric rotation only during the embryonic period, we analysed in each embryonic interval between 2 stages the effect on these angular changes of the simultaneous modifications of the gastric and nongastric hypothetical factors measured by means of their respective variables (nonangular variables). This effect was evaluated by means of the degree of proportionality between the angular change and each variable change (proportionality indices).

Specimen selection

The study was carried out on a graded series of normal human embryos and fetuses belonging to the Bellaterra Collection (Prof. Doménech Mateu). The embryos were classified (stage and postovulation age) according to O'Rahilly et al. (1981) and the fetuses (postovulation age) according to Patten (1976). Developmental data of the specimens are listed in Table 1. In order to allow a reliable comparison of the measures obtained on their histological sections, we only chose specimens subjected to the same histological process (fixed in 10% neutral buffered formalin; embedded in paraffin; serially sectioned at 10 μm in the transverse plane, and stained with haematoxylin and eosin).

Descriptive conventions

Reference planes. In order to obtain on the cross sections a coordinate projection of lines from some planes (see below) and to measure the transverse gastric angles we defined 2 reference planes (Fig. 1*A*). We considered the sagittal plane as that one which crossed both the notochord and the middle point of the ventral groove in the central canal of the neural tube, considering both landmarks in a stable position. The second reference plane was a coronal plane, perpendicular to the sagittal plane and crossing it at the level of the notochord.

Stomach. Descriptive conventions for gastric boundaries and walls were the same as in our previous study performed on the same graded series of specimens (Macarulla-Sanz et al. 1996). Briefly, in CS 11 and 12 we did not see a clear morphological distinction between the postpharyngeal foregut parts, and the supposed gastric primordium was determined as the foregut segment between the laryngotracheal groove and the hepatic diverticulum . Between CS 13 and 17, gastric dilatation allowed us to identify the gastric segment of the foregut. From CS 18 to 20 it was possible to identify the cardia and the pylorus respectively. In order to define the gastric walls, in every section 2 lines were drawn from the middle point of the gastric attachment of the dorsal and ventral gastric mesenteries to the geometric centre of the gastric area. In the caudal section in which the ventral

Table 1. *Transverse angles of the stomach of a graded series of human embryos and fetuses*

				Transverse gastric angles†					
Developmental data of the specimens*				Supraomental part			Omental part		
Specimen designation	CRL (mm)	CS	Postovulation age (d)	Maximum angle	Mean angle	Minimum angle	Maximum angle	Mean angle	Minimum angle
Embryo									
Ri.5‡	3.5	11	24	13.66	−4.90	−22.90	—	—	—
Mar‡	4	12	26	14.43	3.09	−5.65	—	—	—
SS.1	6	13	28	21.12	14.92	4.23	47.12	30.28	23.12
Bi.6	10	16	37	56.10	39.41	27.50	56.27	43.18	28.23
Mar.3	10.3	16	37	56.71	43.92	30.79	62.98	57.05	51.12
Gi-1	13	17	41	49.40	23.90	7.25	90.38	51.43	11.10
Re.1	15	18	44	74.99	54.37	−0.23	90.38	68.03	32.46
Ri.2	19	20	51	64.42	32.84	−18.53	90.03	67.28	31.10
Fu.11	24	21	54	70.37	46.57	36.37	90.80	67.52	43.66
Bi.1	30	23	57	65.63	34.67	21.33	90.02	62.47	34.02
Fetus			(wk)						
Gi.8	50		10	41.47	31.62	20.12	99.16	60.07	27.62
Llo	71		11.5	56.32	27.18	0.95	90.79	66.92	30.16

* According to the catalogue of the Bellaterra Collection (Prof. Doménech-Mateu). † Values of transverse gastric angle are given in degrees measured in every section between the greatest gastric diameter and the sagittal plane. Positive or negative sign shows the clockwise or anticlockwise direction of the angle. ‡ It is not possible to differentiate between supraomental and omental gastric parts because the pancreatico-enteric recess is not present. For explanations of abbreviations, see note to Table 3.

mesogastrium was not observed, we considered the equivalent point to the gastric attachment of this mesentery, the point to the furthest right among all the points that resulted from the intersection between the gastric outline and a straight line drawn on the most caudal section in which we could see the ventral mesogastrium. This line included the middle point of the hepatic and gastric attachments of this mesogastrium. Beginning from the formation of the pancreatico-enteric recess the gastric wall was defined in accordance with 2 options: in the first, gastric walls were delimited assuming the panceatico-enteric recess arose from an extension of the omental bursa into the compound mesodermal anlage of the stomach; in the second, gastric walls were delimited taking into consideration this omental recess resulting from a real rotation of the stomach (see fig. 1 in Macarulla-Sanz et al. 1996).

Organs adjacent to the stomach. In order to delimit the extension of the organs adjacent to the stomach, 2 spaces were defined: the gastric polyhedron and the retrogastric polyhedron (Fig. 1*A*). The gastric polyhedron was defined as the space delimited by 4 tangential planes at the most anterior, posterior, right and left gastric points, and by the planes of the furthest superior and inferior sections in the stomach. The anterior and posterior planes were perpendicular to the sagittal plane whereas the right and left planes were parallel to it. The tangential planes to the stomach were determined on all the sections by means of a coordinated projection of lines obtained from those where the extreme gastric points were located. The retrogastric polyhedron was the space between the gastric polyhedron and the coronal plane that crossed the sagittal plane at the level of the notochord. Three groups of organs adjacent to the stomach were considered (Fig. 1*B*). The right and left organs adjacent were those located inside the gastric polyhedron to the right or to the left of the stomach and gastric mesenteries respectively. In those histological sections where some gastric mesentery did not reach the gastric polyhedron walls, it was extended to them by means of a straight line perpendicular to the nongastric attachment of the mesogastrium, drawn from its middle point. The structures located in the retrogastric polyhedron were called posterior adjacent organs. In order to calculate the volumes of these 3 adjacent organ groups, the gastric mesenteries and the coelomic spaces were discarded.

Morphometry and data analysis

The angular and volumetric measures were carried out by PC-Draft Plus software on digitised photomicrographs taken from histological sections using a Wild photomacroscope M400. Calculations were done by the MUMPS software (Massachussets General Hospital Utility Multiprogramming System) which

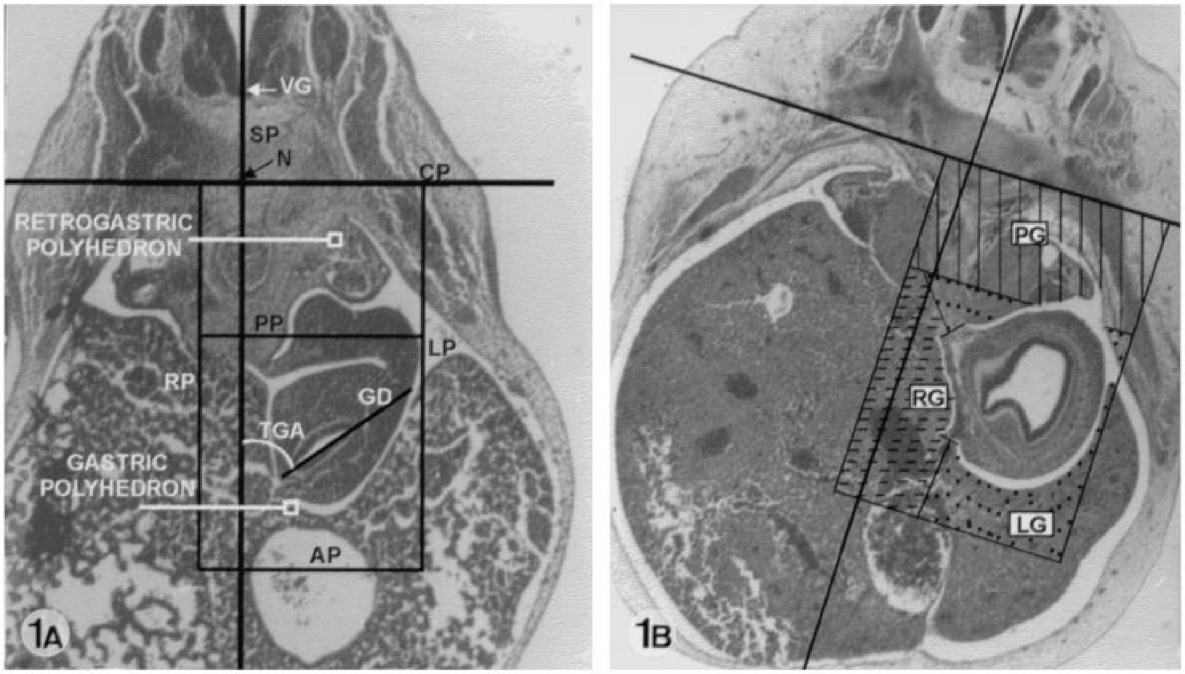

Fig. 1. Illustrations of the methods applied on cross sections of the stomach. (*A*) Cross section of the embryo Bi-6 (CS 16). The transverse gastric angle (TGA) is measured from the sagittal plane (SP) to the greatest gastric diameter (GD). The gastric polyhedron area is defined by 4 lines belonging to the tangential planes at the most anterior (AP), posterior (PP), right (RP) and left gastric (LP) points. The retrogastric polyhedron area is defined between the gastric polyhedron and the coronal plane (CP), that cross the sagittal plane at the notochord (N). VG, ventral groove in the central canal of the neural tube. ×48. (*B*) Cross section of the embryo Re-1 (CS 18). Location of the organ groups adjacent to the stomach: the areas of the right (RG) and left (LG) groups into the gastric polyhedron and the posterior group (PG) into the retrogastric polyhedron. ×29.

allowed us to import and analyse the data obtained with the PC-Draft Plus software. For the measurements of the width of the gastric mesentery an image analyser consisting of a microscope (Nikon, Optiphot-2), videocamera (Sony, CCD Iris), workstation with monitor (Silicongraphics) and suitable software (Visilog 5) were used. Calculations were done by Excel 5.0. The gastric cross section selection was done according to whether the crown-rump length was less than 10 mm (1 in 2), between 10 and 20 mm (1 in 4) or more than 20 mm (1 in 8). In every specimen the first section was randomly chosen from the superior boundary of the stomach.

Transverse gastric angles. On the cross section of the embryos and fetuses, the transverse gastric angle was measured from the sagittal plane to the greatest gastric diameter, with a positive or negative sign according to the clockwise or anticlockwise angular direction from above respectively (Fig. 1*A*). In every specimen the maximum and minimum transverse gastric angle values were identified and the mean transverse gastric angle (MTGA) was calculated. In order to determine maximum and minimum angles we considered the more positive or less negative the angular value the more the value attributed. Beginning from the pancreatico-enteric recess formation these angles were distinguished in the supraomental (above this omental recess) and omental (at the level of this recess) transverse gastric angles. According to different speeds in the changes of MTGAs, several phases were determined from the angular outlines. The MTGA was the angular variable used for comparative analysis.

Volumetric data. Volumetric measurements were carried out using the principle of Cavalieri (Gundersen & Jensen, 1987; Mayhew, 1992). In every selected specimen the volumes of organ groups adjacent to the stomach, gastric and retrogastric polyhedrons (mm^3) were calculated by adding together the corresponding cross-sectional areas (mm^2) and multiplying by the mean distance between the sections (mm). Data on the gastric wall volume were obtained from our previous study (Macarulla-Sanz et al. 1996) where the same method was applied. For comparative analysis the following variables were used. (1) Gastric wall volume ratio. In order to compare in every embryo the relationship between the volumes of the gastric walls, the left wall volume was divided by the right wall volume. Beginning from the pancreatico-enteric recess formation the gastric wall volume ratio was determined in accordance with each option considered in order to define the gastric walls: gastric wall (1st option) volume ratio and gastric wall (2nd option) volume ratio (see descriptive conventions for stomach). (2) Quotients between the volumes of the organs adjacent to the stomach and the reference polyhedrons. In order to have comparable results between the specimen, instead of the absolute value of the measurements, proportional changes in the volume of the organ groups adjacent to the stomach were considered. For this purpose the variable used was the result in each specimen of dividing the volume of each group of organs by the volume of the space where this was included. This comprises the gastric polyhedron for left and right organ groups and the retrogastric polyhedron for the posterior one.

Index of gastric mesentery width. In order to know the transverse dimension (width) of the dorsal and ventral gastric mesenteries, in each selected cross section skeletonisation of the gastric mesenteries was performed. The skeleton of a cross section of the mesogastrium was the line made up of those points for which the distance to the boundary of the mesogastrium was reached by at least 2 points. The final result of all the resulting line lengths of a mesogastrium was multiplied by the mean distance between 2 cross sections, so an area of a skeletonised mesogastrium was obtained. In order to obtain a measurement which was only in relation with the width of the mesogastrium, this area was divided by the length of the gastric insertion of the skeletonized mesogastrium, so an index of the mesogastrium width was obtained. The length of the gastric insertion of the mesogastrium was obtained by adding the distances between the gastric extreme points of the skeletonised lines in 2 consecutive sections. In each interval between 2 sections this distance (D) was calculated by means of the following equation:

$$D = \sqrt{d^2 + (X_s - X_i)^2 + (Y_s - Y_i)^2}$$

where d is the mean distance between 2 cross sections, X_s and Y_s were the coordinates of the gastric insertion of the upper skeletonised line and X_i and Y_i of the lower one (notochord: $X = 0$, $Y = 0$; sagittal plane: $X = 0$). The sum of both indices of the gastric mesentery width was the variable used for the comparative analysis as index of the gastric mesentery width.

Comparative unit. In order to correlate the simultaneous changes between nonangular variables (gastric wall volume ratio, organs adjacent volume quotients and index of the gastric mesentery width) and angular variable (MTGA), measured with different units, we used as a comparative unit the number of times that one variable increased (positive increment) or decreased (negative increment) from its previous value. This result was calculated by means of the following equation,

$$\Delta X = (X_{os} - X_{ys})/X_{ys}$$

where ΔX is the increment of variable in numbers of times, X_{os} is the value of variable at the older stage, and X_{ys} is the value of variable at the younger stage (each variable in its own units). At Carnegie stage (CS) 16 the values of variables were calculated as the mean value of the 2 embryos of this stage. Only as a comparative aim and in order to evaluate the width of the stomach rotation around its long axis, the modifications of MTGA during the embryonic period were recalculated after considering as value 0° the smallest transverse gastric angle obtained on the histological sections.

Proportionality indices. We have assumed that the more similar are the simultaneous values changes of a nonangular variable and the MTGA (angular variable) (see comparative unit), the more is the influence attributable to the former over the gastric rotation. The degree of similarity between both changes was evaluated by means of the proportionality indices of the increment of each nonangular variable. These indices were calculated by dividing the increment of the MTGA by the increment of each nonangular variable. If the absolute value was smaller than the unity, the inverse fraction was considered. The closer to 1 observed for the absolute value of the proportionality index, the more significance was attributable to the angle changes to the nonangular variable increment. The index sign showed us if the direction of the gastric angle and nonangular variable modifications were the same (positive value) or opposite (negative value).

RESULTS

Transverse gastric angles

Maximum, minimum and mean transverse gastric angles of each specimen are shown in Table 1. Mean transverse gastric angle curves are shown in Figure 2. From CS 13 the pancreatico-enteric recess appearance allowed us to distinguish supraomental and omental angles, and 2 options (see Material and Methods) were considered in order to define the gastric walls at the level of this omental recess.

Three phases in the modifications of the MTGAs were observed: the quick increase phase (CS 11–16); the oscillatory phase (at the supraomental part: CS 16–23; at the omental part: CS 16–18), and the stabilisation phase (at the supraomental part: CS 23 to early fetal period; at the omental part: CS 18 to

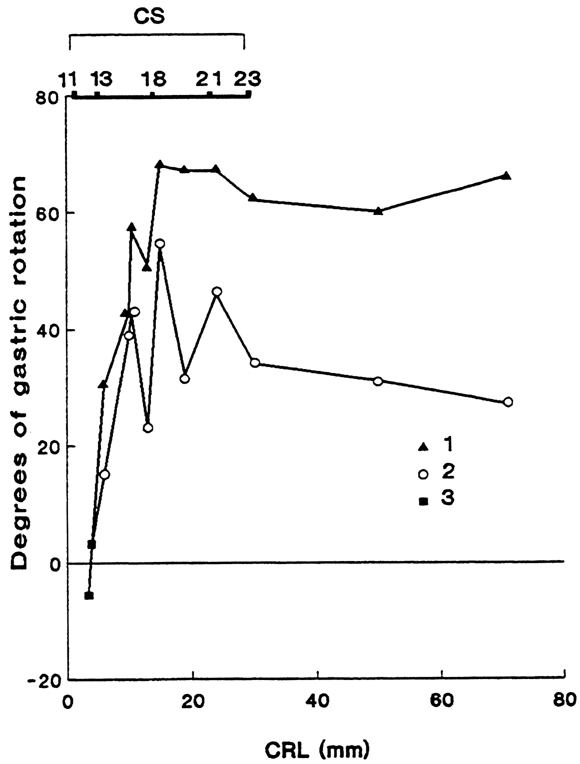

Fig. 2. MTGA curves. Note that from the formation of the pancreatico-enteric recess (CS 13) the values of the MTGA at the omental part of the stomach (curve 1) are higher than the MTGA at the supraomental part (curve 2). Before CS 13 (curve 3) is not possible to distinguish both gastric parts.

early fetal period). During the quick increase phase, the stomach underwent 7.1° and 9.1° of rotation in the clockwise direction at the respective supraomental and omental parts by each millimeter that the embryo increased its crown-rump length (CRL). After this phase, gastric rotation alternated in the clockwise and anticlockwise direction (oscillatory phase), and at CS 18, the MTGA reached the highest value: 54.37° and 68.03° at the supraomental and omental parts, respectively. During the oscillatory phase, by each millimeter of CRL increment the stomach underwent 0.3° of global rotation in the anticlockwise direction at the supraomental part, and 2.3° in the clockwise direction at the omental part. After the oscillatory phase, the stomach underwent a global anticlockwise rotation of 0.18° by each millimeter of CRL increment at the supraomental part, whereas at the omental part this rotation was 0.01° in the clockwise direction.

Growth of the gastric walls

In all the embryos the gastric wall volume ratio was greater than unity. This datum has demonstrated a predominant growth of the left gastric wall over the right.

Proportionality indices and significance of the factors analysed to the MTGA modifications

The proportionality indices between increments of MTGAs and increments of the nonangular variables which measured the factors whose influence over the angular modifications was analysed are given in Table 2. MTGA increment values are also shown.

Table 2. *Proportionality indices between the simultaneous increments of the mean transverse gastric angle (ΔMTGA) and the other variables**

Embryonic interval	Gastric part	ΔMTGA†	PIGWVR‡	PIGW1VR	PIGW2VR	PIIGMW	PIRAOVQ	PILAOVQ	PIPAOVQ
CS 11–12§		0.444	−5.41	—	—	−5.72	3.92	44.38	−5.55
CS 12–13	SO	0.455	—	1.05	2.28	1.45	−4.55	1.32	−1.23
	O	1.046	—	2.19	5.23	1.59	−10.46	1.74	−2.83
CS 13–16	SO	0.707	—	2.10	47.14	12.01	−7.07	1.36	1.08
	O	0.373	—	1.11	24.87	6.34	−3.73	1.40	2.04
CS 16–17	SO	−0.275	—	−2.19	−2.31	−1.23	−2.69	−2.18	−3.93
	O	0.018	—	33.30	6.58	18.86	41.67	33.30	3.89
CS 17–18	SO	0.651	—	20.35	3.27	1.87	−1.67	−2.33	32.55
	O	0.223	—	6.98	1.12	1.56	−1.75	−1.26	11.15
CS 18–20	SO	−0.279	—	2.24	11.61	−3.87	4.64	−13.93	−1.80
	O	−0.008	—	76.92	2.91	−134.96	7.52	−2.5	−62.50
CS 20–21	SO	0.246	—	3.00	−1.23	5.53	−2.27	1.05	−1.62
	O	0.003	—	31.25	−76.92	453.68	−200.00	83.33	−125.00
CS 21–23	SO	−0.171	—	−4.26	−1.26	3.21	−5.85	1.56	1.05
	O	−0.056	—	−12.99	−2.43	9.81	−17.86	1.96	3.22

*Angular and nonangular variable increments have been calculated as the number of times that one parameter increases or decreases its previous value during an embryonic interval. † Angular increments have been calculated by considering angle 0 to be the angle −22.90 which is the smallest value obtained (see Table 1). Positive or negative signs shows the clockwise or anticlockwise direction of the gastric rotation. ‡ The sign shows if the direction of the nonangular variable modification is the same (positive sign) or opposite (negative sign) to the ΔMTGA. § It is not possible to differentiate between supraomental and omental gastric parts and to consider the 2 options in the definition of the gastric walls, because the pancreatico-enteric recess is not present. For explanations of abbreviations, see footnote to Table 3.

Table 3. *Factors involved in the 'rotation' of the human embryonic stomach around its longitudinal axis: variables ordered in accordance with the significance of their modifications to the simultaneous MTGA changes*

Embryonic interval	Gastric part	Direction of the gastric rotation	Order of variables: the more to the left the variable, the closer to 1 the absolute value of the proportionality index between the ΔMTGA and the variable increment. The list includes only variables with an absolute value of the proportionality index between 1 and 10*					
CS 11–12†		CW	↑RAOVQ	↓GWVR	↓PAOVQ	↓IGMW	—	—
CS 12–13	SO	CW	↑GW1VR	↓PAOVQ	↑LAOVQ	↑IGMW	↑GW2VR	↓RAOVQ
	O	CW	↑IGMW	↑LAOVQ	↑GW1VR	↓PAOVQ	↑GW2VR	—
CS 13–16	SO	CW	↑PAOVQ	↑LAOVQ	↑GW1VR	↓RAOVQ	—	—
	O	CW	↑GW1VR	↑LAOVQ	↑PAOVQ	↓RAOVQ	↑IGMW	—
CS 16–17	SO	ACW	↑IGMW	↑LAOVQ	↑GW1VR	↑GW2VR	↑RAOVQ	↑PAOVQ
	O	CW	↑PAOVQ	↑GW2VR	—	—	—	—
CS 17–18	SO	CW	↓RAOVQ	↑IGMW	↓LAOVQ	↑GW2VR	—	—
	O	CW	↑GW2VR	↓LAOVQ	↑IGMW	↓RAOVQ	↓GW1VR	—
CS 18–20	SO	ACW	↑PAOVQ	↓GW1VR	↑IGMW	↓RAOVQ	—	—
	O	ACW	↑LAOVQ	↓GW2VR	↓RAOVQ	—	—	—
CS 20–21	SO	CW	↑LAOVQ	↓GW2VR	↓PAOVQ	↓RAOVQ	↑GW1VR	↑IGMW
	O	CW	—	—	—	—	—	—
CS 21–23	SO	ACW	↓PAOVQ	↑GW2VR	↓LAOVQ	↓IGMW	↑GW1VR	↑RAOVQ
	O	ACW	↓LAOVQ	↑GW2VR	↓PAOVQ	↓IGMW	—	—

* Arrow shows if the variable increases (↑) or decreases (↓). † See note (§) to Table 2.

Abbreviations (and for Tables 1, 2): ΔMTGA, increment of the mean transverse gastric angle; ACW, anticlockwise direction; CRL, crown-rump length; CS, Carnegie stage; CW, clockwise direction; GW1VR, gastric wall (1st option) volume ratio; GW2VR, gastric wall (2nd option) volume ratio; GWVR, gastric wall volume ratio; IGMW, index of gastric mesentery wideness; LAOVQ, left adjacent organ volume quotient; MTGA, mean transverse gastric angle; O, omental part; PAOVQ, posterior adjacent organ volume quotient; PIGW1VR, proportionality index of gastric wall (1st option) volume ratio increment; PIGW2VR, proportionality index of gastric wall (2nd option) volume ratio increment; PIGWVR, proportionality index of gastric wall volume ratio increment; PIIGMW, proportionality index of the increment of the index of gastric mesentery wideness; PILAOVQ, proportionality index of the increment of the left adjacent organ volume quotient; PIPAOVQ, proportionality index of the increment of the posterior adjacent organ volume quotient; PIRAOVQ, proportionality index of the increment of the right adjacent organ volume quotient; RAOVQ, right adjacent organ volume quotient; SO, supraomental part.

In Table 3 we show, according to their significance to the angle variations, those variables whose absolute value of the proportionality indices did not deviate more than 10 times from unity (maximum significant value) and in an ordered way. The direction of the gastric rotation and the nonangular variable variations are also shown in Table 3.

DISCUSSION

During the human embryonic period the transverse gastric angle increases its value in conformity with a clockwise rotation. We could not confirm a single angle value in every stomach analysed, but every gastric portion had its own rotation (Table 1). For this reason and in accordance with Pernkopf (1922) we think that the human embryonic stomach does not rotate around a fixed long axis. Thus, we used the mean value from all the analysed angles as a comparative angle.

From the appearance of the pancreatico-enteric recess at CS 13, we analysed the differences between the gastric rotation angle above this omental recess (supraomental transverse gastric angle) or at its level (omental transverse gastric angle). The angular differences between both portions were increased until CS 20 and became stable after this stage (Fig. 2, Table 1). The greater rotation at omental level could be related to the greater capacity for mobility depending on a longer dorsal mesogastrium at the level of the pancreatico-enteric recess. Two factors could explain the stabilisation of the angular differences between both gastric portions: firstly, related to the top growth of the pancreatico-enteric recess dorsally to the stomach in 17 mm CRL embryos, and secondly related to the fusion of the dorsal mesogastrium with the dorsal body wall from the early fetal period (Kanagasuntheram, 1957).

We observed that the tranverse gastric angle values in both gastric portions reached their highest mean values at CS 18 (15 mm CRL embryo) (Fig. 2, Table 1). Pernkopf (1922) located this highest gastric angle slightly before, in the 12 mm CRL embryo. Greater discrepancy existed with other authors who considered that the gastric rotation ended at the 7 mm CRL embryo (Swaen, 1896) or continued into the fetal period (Nieto, 1977). We observed that after the mean gastric angles reached their highest values, they slightly decreased their values which tended to become stable before the early fetal period (Fig. 2). In the same manner, Toldt (cited by Pernkopf, 1922), located the termination of the gastric rotation at the end of the third month.

We have studied the probable influence on the 'rotation' of the human embryonic stomach around its longitudinal axis, of the predominance of the left gastric wall over the right, the width of the gastric mesenteries and the volumes of the organs adjacent to the stomach, measured by means of the respective variables. In each interval between specimens staged as a graded series, these variables have been ordered in accordance with their influence on the angular changes (Table 3). Independent of the direction of the variable modifications, we attributed more significance to one factor instead of another over the angular gastric variation if the modification of its variable was numerically closer to the angular variation obtained in the same embryonic interval, because this meant that there existed a greater relationship between both modifications. In order to allow the comparison between variables measured with different units, we used, in each interval, as a comparative unit the number of times that a variable increased or decreased its previous value.

During the embryonic period, the changes on the gastric mesentery width and the predominant growth of the left gastric wall over the right were the factors which constantly showed an influence on the gastric angle modifications. However, modifications of the length of these factors were not always accompanied by variations in the same direction of the gastric angle (Table 3); this suggests the participation of other nongastric factors such as the shape and volume modifications of the organs adjacent to the stomach. We think that the mesenteric factor could be considered mainly as a passive factor, which facilitate gastric mobility, but also as an accumulative factor. This implies that increments of the mesenteric width during the earlier periods may facilitate the gastric angle modifications under the mechanical effect of the organs adjacent in later periods. The overall increase in the gastric wall growth to the left could be considered as an intrinsic factor involved in the changes of gastric morphology and thus in the orientation of the parts of the stomach, where the extrinsic forces can be exerted. After the appearance of the pancreatico-enteric recess at CS 13, the influence of the gastric parietal factor was independent of which theory about the formation of the pancreatico-enteric recess was considered for defining the gastric walls.

As during the embryonic period the relationship between the stomach and other organs was variable, the adjacent gastric organs were divided taking into consideration their position to the stomach (right, left and posterior groups), independent of which structures made up the group. Furthermore as the only volume modifications of organs adjacent to the stomach that could be an influence on gastric rotation were those that produced or permitted some gastric displacement, we only determined their volumes in restricted spaces related to the stomach (Fig. 1*A*, *B*) and used for comparison the volume of each group of organs adjacent per unit of volume of the space where they were measured. Predominant growth of some organs involved them in greater participation in the enlargement of each group of the organs adjacent to the stomach. In the right and left adjacent organ groups the predominant component was the liver (for embryological data see Hutchins & Moore, 1988); in the posterior group the adrenal, gonadal and mesonephric components could be outstanding by their own development and relationship to the stomach (Shikinami, 1926; O'Rahilly & Müller, 1992).

During the increasing phases of the transverse gastric angle (between CS 11 and 18), certain combinations of the volume of the organs adjacent to the stomach showed some influence on the direction of the gastric rotation (Table 3). Thus when the volumes of posterior and left organs adjacent increased, the clockwise or anticlockwise direction of the gastric rotation was related to the respective decrease or increase of the right adjacent organ volume. The clockwise direction of the gastric rotation was also in relation to the decrease of the volume of one or more groups of organs adjacent to the stomach. These results suggest that the different organ masses in growth act as forces over both sides of the stomach and its mesenteries, which are also growing; therefore, the direction of the gastric rotation is in relation to the growth ratio between them, and where these forces act in each period. Increasing of the volume of the posterior organs adjacent to the stomach may produce gastric displacement especially through pressure on the dorsal mesogastrium. Once the maximum values were reached, the transverse gastric angles only underwent only minor modifications which tended to stabilise the angular values (Fig. 2, Table 1). It is possible that either the closest gastric shape to the definitive one, or a greater degree of stability in the gastric relation to the adjacent organs, were the determining factors in understanding why the volume modifications of the organs adjacent to the stomach did not have the same effects on the gastric rotation that they showed in previous phases (Table 3).

In summary, the aim of this study was to consider again the old debate about the causes of the gastric 'rotation' in the human embryo around its longitudinal axis, but with a new strategy, quantifying the degree of relationship between the modification of the MTGA, and the simultaneous changes of the dimension of those structures which had been proposed as factors for explaining the gastric rotation. Our results allowed us to determine in each phase of the gastric embryonic development, what factors are implied and their degree of implication. The final analysis of these results suggested the following conclusions: the stomach of the human embryo undergoes a heterogeneous and multifactorial rotation in a transverse direction; this rotation is a consequence of the overall increasing gastric wall growth to the left and the increase of gastric mobility facilitated by the previous mesenteric enlargement, whereas the direction of the rotation results from the forces exerted on the stomach and its mesenteries by its adjacent organs.

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