

Developmental Changes in Line Bisection: A Result of Callosal Maturation?

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Normal adults tend to bisect horizontal lines to the left of the objective middle, especially when using the left hand. This bias has been attributed to the dominance of the right hemisphere in spatial attention. The authors investigated the effect of hand use and line position in visual line bisection in right-handed children and adults, classified into 4 different age groups: 10–12, 13–15, 18–21, and 24–53 years ($N = 98$). All 4 groups showed the characteristic leftward bias when using the left hand. When using the right hand, the youngest group showed a rightward bias, whereas the other 3 groups all showed a leftward bias. This suggests a shift from contralateral to right-hemispheric control during puberty and may reflect maturation of the corpus callosum.

Most studies investigating visual and tactile line bisection have shown that normal right-handed adults tend to bisect horizontal lines and rods to the left of the center, a phenomenon that is often called *pseudoneglect* (Bowers & Heilman, 1980). One prominent interpretation for this phenomenon is that the two hemispheres differ with respect to the allocation of spatial attention. The left hemisphere is concerned almost exclusively with attention to the contralateral right hemisphere, whereas the right hemisphere is capable of directing attention to both sides of space, although it tends to favor the contralateral left side (Heilman & Valenstein, 1979; Heilman & Van Den Abell, 1980; Mesulam, 1981). Clinical studies support the idea that the right hemisphere plays a special role in spatial attention and thus in bisecting horizontal lines. Typically, patients with lesions to the right posterior parietal lobe show a lack of awareness of stimuli, objects, persons, or events in particularly the left hemisphere. However, this hemispatial neglect has also been reported in patients with right frontal lobe or right-sided subcortical damage. Consequently, these patients systematically bisect lines to the right of the objective middle, a pattern referred to as left-sided contralateral neglect. Recent studies (Karnath, Ferber, & Himmelbach, 2001; Karnath, Himmelbach, & Rorden, 2002) suggest that spatial awareness might also be a function of the superior temporal cortex, although again it is the right side that is dominant.

As noted, the right hemisphere is dominant for spatial awareness and is capable of directing attention to both sides of space, whereas the left hemisphere is concerned almost exclusively with attention to the right (Kinsbourne, 1970).

The dominance of the right hemisphere nevertheless results in a slightly biased representation, which is manifest in pseudoneglect. Because the left hand is controlled by the right hemisphere, we might expect pseudoneglect to be especially pronounced with the left hand. This has been confirmed by several studies (Brodie & Pettigrew, 1996; Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Luh, 1995; Scarisbrick, Tweedy, & Kuslansky, 1987; see Jewell & McCourt, 2000, for a review). However, Nicholls, Bradshaw, and Mattingley (2001) found that unilateral hemispheric activation triggered by movements (unrelated to the task) did not affect free-viewing perceptual asymmetries. This suggests that pseudoneglect is not simply a matter of motor activation but is rather a consequence of hemispheric control. The left bias is still present, although typically somewhat reduced, if the right hand is used. For this dominance to persist when the right hand is used implies the interhemispheric transfer of the attention-biased perceptual representation from the right hemisphere to the motor cortex of the left hemisphere. This transfer probably involves the corpus callosum.

The relevance of the corpus callosum is supported by evidence of hemispatial neglect in patients with callosal infarction (Heilman, Bowers, & Watson, 1984; Kashiwagi, Kashiwagi, Nishikawa, Tanabe, & Okuda, 1990) and in patients with complete forebrain commissurotomy (Corballis, 1995), who show significant deviation to the right of the objective middle, particularly when the right hand is used. Moreover, there is evidence that the effect of hand in line bisection differs between men and women (Hausmann et al., 2002) and between left- and right-handed individuals (e.g., Scarisbrick et al., 1987), perhaps reflecting differences in the size of the subdivisions of the corpus callosum (e.g., Driesen & Raz, 1995). For example, Hausmann et al. (2002) found that women showed similar degrees of left bias with either hand, whereas men showed the bias predominantly with the left hand. This might reflect stronger interhemispheric connectivity in women that is due to larger cross-sections of the posterior corpus callosum (DeLacoste-Utamsing & Holloway, 1982; Holloway, Anderson, Defendini, &

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Harper, 1993; Oka et al., 1999; Steinmetz et al., 1992; for a review, see Driesen & Raz, 1995).

The size of the corpus callosum also changes with age. The human corpus callosum contains at least 200 million fiber's (Aboitiz, Scheibel, Fischer, & Zaidel, 1992; Tomasch, 1954), which are mostly topographically organized (DeLacoste, Kirkpatrick, & Ross, 1985) and connect homotopic areas of the left and the right hemisphere. The size of the corpus callosum is approximately proportional to the size of the neocortex, suggesting that the two structures evolved in parallel in many species (LaMantia & Rakic, 1984; Rapoport, 1990). Although the number of callosal fibers reaches its maximum in utero (LaMantia & Rakic, 1984), quantitative magnetic resonance imaging (MRI) has clearly shown that the total midsagittal callosal area increases in size up to the age of 18 years, particularly in the regions of the midbody and splenium (Giedd et al., 1996). In contrast, the anterior (rostrum and genu) regions reach adult size during the preschool years, indicating an anterior-to-posterior gradient of maturational changes. The relationship between age and the total area (or subregions) of the corpus callosum is linear, with no higher order polynomial components (Giedd et al., 1996). Electrophysiological, MRI, and postmortem evidence suggests that the increase in callosal size is the result of myelogenesis throughout childhood (Fleischauer & Wartenberg, 1967; Waxman & Swadlow, 1976).

If callosal connectivity is critical for the integration of motor and perceptual processes, the left-sided bias in line bisection should also change as a function of age. This is supported by studies showing that neurologically normal young children tend to bisect the lines to the left with the left hand and to the right with the right hand (Bradshaw, Spataro, Harris, Nettleton, & Bradshaw, 1988; Dellatolas, Coutin, & De Agostini, 1996; Dobler et al., 2001). This *symmetrical neglect* has been attributed to callosal immaturity (Bradshaw et al., 1988; Dobler et al., 2001; Roeltgen & Roeltgen, 1989). A similar hand effect has been reported in an adult patient with partial callosal disconnection (Heilman et al., 1984).

Few studies systematically investigating age effects in line bisection have controlled for the effect of hand use. For example, Van Vugt, Fransen, Creten, & Paquier (2000) investigated line bisection in 650 normal children aged between 7 and 12 years, but only with their preferred hand. Although the authors concede that their data were "far from ideal in view of the assessment of hand effects" (p. 892), it is important to note that all left-handed participants (i.e., left-hand bisectors) showed a significant leftward bias, whereas all right-handed participants (i.e., right-hand bisectors) showed a significant rightward bias when the lines were positioned to the right of the page. No bias was found for the right-handed group when the lines were placed in the center of the page, whereas a leftward bias was found when lines were located to left. The position of the presented line (left, center, or right) is therefore a further important influence (Hausmann et al., 2002; Luh, 1995; see Jewell & McCourt, 2000, for a review). Although Luh (1995) maintained that adults show a leftward bias irrespective of line position, the leftward bias is stronger when lines are located

in the left hemispace rather than in the center or in the right hemispace (Hausmann et al., 2002; Luh, 1995).

Studies investigating age-related changes in pseudoneglect have typically included samples of children ranging in age from 4 to 12 years (e.g., Bradshaw, Nettleton, Wilson, & Bradshaw, 1987; Bradshaw et al., 1988; Dellatolas et al., 1996; Dobler et al., 2001; Van Vugt et al., 2000). Although it is assumed that the *symmetrical bias* just described is shown by young children up to an age of 7 or 8 years (Bradshaw et al., 1988; Dobler et al., 2001), it remains unclear precisely when the symmetrical neglect pattern changes to the adult pattern of left-sided pseudoneglect. Clarification would involve assessing and comparing line-bisection performance in preadolescents to that in adolescents and adults. One might expect the transformation from symmetrical neglect to left-sided pseudoneglect to parallel the maturational changes that occur in the callosal area (Giedd et al., 1996).

On these grounds, we investigated line bisection in a cross-section of four age groups: 10–12 years, 13–15 years, 18–21 years, and 24–53 years. We predicted a strong age-related change of pseudoneglect during childhood and mid-adolescence. Specifically, line bisections with the right hand should shift from a right bias to a strong left bias with increasing age, whereas left-handed line bisections should show a developmentally stable leftward bias. No difference in line-bisection performance was expected between the two older groups (18–21 years and 24–53 years), because the maturational changes to the size of the corpus callosum are thought to be complete by the age of 18.

Method

Participants

Ninety-eight neurologically normal right-handed volunteer students (5th, 8th, and 13th grade) and teachers from a comprehensive school in Hagen, Germany, took part. The mean age of the 5th-grade participants was 10.91 years ($SD = 0.75$; range = 10–12 years; $n = 22$), for the 8th-grade participants it was 14.08 years ($SD = 0.65$; range = 13–15 years; $n = 24$), for the 13th-grade participants it was 18.96 years ($SD = 0.93$; range = 18–21 years; $n = 25$), and for the teachers it was 43.11 years ($SD = 7.39$; range = 24–53 years; $n = 27$). The handedness of all participants was determined with the Edinburgh Handedness Inventory (Oldfield, 1971). The laterality quotient (LQ) provided by this test is calculated as $[(R - L)/(R + L)] \times 100$, resulting in values between -100 and 100 . Positive values indicate dexterity, and negative values indicate sinistrality. The mean LQ for 5th-grade participants was 80.0 ($SD = 18.26$; range = 40–100), for 8th-grade participants it was 73.75 ($SD = 13.45$; range = 50–100), for 13th-grade participants it was 82.22 ($SD = 24.49$; range = 30–100), and for the teachers it was 77.55 ($SD = 18.78$; range = 40–100). The reading direction of all participants was left to right. Those who had used any medication affecting the central nervous system during the last 6 months were excluded. The children were recommended by the teacher as potential participants on the basis of a list of stringent criteria that included (a) no known neurological or attention concerns, (b) normal or corrected-to-normal vision and hearing, and (c) no cognitive dysfunction, including difficulties with language reception or reading. All participants were naive to the study's hypothesis.

Procedure and Materials

The line-bisection task was identical to that used in a previous study (Hausmann et al., 2002). It comprised 17 horizontal black lines of 1-mm width on a white sheet of paper (21 × 30 cm). The lines ranged from 100 to 260 mm in their length in steps of 20 mm. The mean length was 183.5 mm. They were pseudorandomly positioned so that 7 lines appeared in the middle of the sheet, 5 lines appeared near the left margin, and 5 lines appeared near the right margin. The lateralized lines were 13 mm away from the margin. The line lengths for the 7 centered lines were 12 cm (1), 18 cm (2), 22 cm (2), and 24 cm (2; $M = 20$ cm), and the line lengths for the 5 left- and 5 right-lateralized lines were 10 cm, 14 cm, 16 cm, 20 cm, and 26 cm ($M = 17.2$ cm). The sheet was laid in front of the participant's midline. Participants were instructed to bisect all lines into two parts of equal length by marking the subjective midpoint of each line with a fine pencil. All participants completed the task with one hand and then repeated it with the other in a balanced order. The experimenter covered each line after it was marked to ensure that the participants were not biased by their previous choices. There were no time restrictions. The deviations to the left or to the right of each marked line were carefully measured to 0.5-mm accuracy. The percentage of deviation for each line was computed as [(measured left half – true half)/true half] × 100. This procedure is comparable with that used in other studies (Scarisbrick et al., 1987; Shuren, Wertman, & Heilman, 1994) and takes individual line length into account. We then computed the mean score for all lines separately for each hand used. Negative values would indicate a left bias, and positive values would indicate a right bias. The absolute directional bias (in millimeters) was also calculated, and again, negative absolute scores would indicate a leftward bias, whereas positive absolute scores would indicate a rightward bias.

Preliminary analysis revealed no significant differences in line bisection between participants who were consistently right-handed (LQ = 100; $n = 24$) relative to those who were less strongly right-handed (LQ < 100; $n = 74$).

Results

To explore the age effect, we subjected the percentages of deviation to a Group (4) × Sex (2) × Hand Use (2) × Line Position (3) split-plot analysis of variance, with hand use and line position as repeated measures. Descriptive statistics (including absolute directional deviations) are presented in Table 1 for each age group, hand use, and line position.

As expected, there was a strong leftward bias, which was indicated by the intercept effect, $F(1, 94) = 23.79, p < .01$. The leftward bias was significantly more pronounced when the left rather than the right hand was used, $F(1, 94) = 46.94, p < .01$. A significant main effect of line position, $F(2, 188) = 9.96, p < .01$, also showed that the bias was more pronounced when the lines were positioned to the left (-1.95 ± 0.33) relative to both the center (-1.06 ± 0.26), $t(97) = -2.90, p < .01$, and the right ($-0.36 \pm .34$), $t(97) = -3.67, p < .01$, of the page.

The Hand Use × Age Group interaction approached significance, $F(3, 90) = 2.58, p = .06$, with the leftward bias significantly more robust with the left than with the right hand for each age group ($ps < .01$). This interaction did reach statistical significance, $F(3, 90) = 2.86, p = .04$, when the absolute rather than the relative directional deviations were analyzed. However, differences between groups were significant only with the right hand, $F(3, 94) = 3.86$,

Table 1
Mean Relative and Absolute Directional Deviations (With Mean Standard Errors) for Visual Line Bisection as a Function of Age Group, Hand Use, and Line Position

Line position and deviation	Ages 10–12 years ($n = 22$)		Ages 13–15 years ($n = 24$)		Ages 18–21 years ($n = 25$)		Ages 24–53 years ($n = 27$)	
	Left hand	Right hand	Left hand	Right hand	Left hand	Right hand	Left hand	Right hand
Left								
Relative (%)	-3.04 (1.12)	-0.09 (0.96)	-2.72 (0.66)	-1.18 (0.62)	-2.68 (0.78)	-1.41 (0.68)	-3.18 (0.62)	-1.34 (0.50)
Absolute (mm)	-2.15 (0.91)	0.35 (0.72)	-1.85 (0.64)	-0.52 (0.57)	-2.02 (0.68)	-0.92 (0.61)	-2.46 (0.52)	-1.16 (0.42)
Center								
Relative (%)	-2.10 (0.81)	2.16 (0.93)	-2.52 (0.55)	0.10 (0.81)	-2.16 (0.72)	-0.89 (0.46)	-2.32 (0.57)	-0.65 (0.38)
Absolute (mm)	-2.13 (0.83)	2.16 (0.91)	-2.55 (0.55)	0.04 (0.80)	-2.16 (0.73)	-0.92 (0.47)	-2.31 (0.57)	-0.68 (0.38)
Right								
Relative (%)	-1.79 (1.08)	2.57 (1.08)	-2.02 (0.71)	-0.57 (0.83)	-1.04 (0.82)	1.55 (0.76)	-1.33 (0.54)	-0.29 (0.68)
Absolute (mm)	-2.01 (0.83)	1.85 (0.87)	-2.44 (0.60)	-0.75 (0.67)	-1.16 (0.67)	1.04 (0.62)	-1.20 (0.45)	-0.38 (0.55)
All								
Relative (%)	-2.28 (0.73)	1.62 (0.67)	-2.44 (0.48)	-0.48 (0.60)	-1.98 (0.66)	-0.33 (0.48)	-2.28 (0.51)	-0.74 (0.39)
Absolute (mm)	-2.11 (0.63)	1.53 (0.65)	-2.31 (0.47)	-0.35 (0.56)	-1.82 (0.61)	-0.34 (0.43)	-2.02 (0.46)	-0.73 (0.33)

Note. Negative values indicate a deviation to the left; positive values indicate a deviation to the right.

$p = .01$. As shown in Figure 1, for all groups except for the age group ranging from 10–12 years, right-handed line bisections were made to the left of the veridical center. In contrast and of importance, the youngest group (mean age = 10.91 years, $SD = 0.75$) showed a marked right-handed rightward bias, which was particularly deviant relative to the oldest age group, $t(47) = 3.12$, $p < .01$. One-sample t tests further confirmed that the left hand was significantly biased leftward from the objective middle for all age groups ($ps < .01$). When using the right hand to bisect lines, however, only the three older groups showed a (nonsignificant) leftward bias. The youngest group, in contrast, showed a significant rightward deviation from center ($M = 1.45 \text{ mm} \pm 0.57$), $t(21) = 2.41$, $p = .03$.

No other main or interaction effect was significant involving the percentages of deviation. However, the Hand Use \times Line Position interaction was significant when the absolute directional deviation scores were analyzed, $F(2, 180) = 3.21$, $p = .04$. Analysis of simple effects revealed that only when the right hand was used were there any significant differences (with Bonferroni adjustment) in line position, with the leftward bias stronger when the line was positioned to the left relative to the right of the page, $t(97) = -2.40$, $p = .02$.

The interaction between age, gender, and hand use was not significant. The interaction was also not significant when only the two younger groups were included in the analysis, $F(1, 42) = 0.03$, *ns*. However, consistent with earlier evidence derived from adults only (Hausmann et al., 2002), when the two oldest groups were combined, there was a highly significant difference in leftward bisection between left ($M = -2.78$, $SD = 3.38$) and right ($M = -0.54$, $SD = 2.62$) hands in men, $F(1, 24) = 18.50$, $p < .01$. In contrast, the differences between the left and the right hands ($M = -1.55$, $SD = 2.41$, and $M = -0.55$, $SD = 1.79$, respectively) did not reach significance in women, $F(1, 26) = 3.60$, *ns*.

Discussion

Overall, the left bias in line bisection that is typically observed in neurologically normal individuals was found in

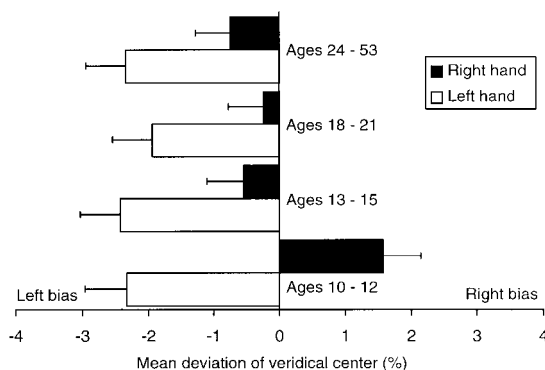


Figure 1. Mean deviations from the true center during line bisection according to age group and hand used. Data are collapsed across gender and line position. Error bars represent mean standard errors.

the present study and was particularly pronounced when the left hand was used. More important, however, was the finding of a strong hand-contingent age effect. Line bisection with the left hand, which may be assumed to be under the control of the attention-dominant right hemisphere, did not change as a function of age. In contrast, age-related changes in line bisection performance appeared with the right hand. Although the size of the corpus callosum increases linearly up to about age 18 (Giedd et al., 1996; Pujol, Vendrell, Junque, Marti-Vilalta, & Capdevila, 1993), the change in the directional bias of the right hand did not appear to be linear. The children in the youngest group (10–12 years) showed symmetrical neglect—a left bias with the left hand and a right bias with the right hand. This might be taken as evidence for lack of callosal transfer. All other age groups, comprising ages 13–53 years, showed the typical pseudoneglect (i.e., a left-sided bias in line bisection for both hands), suggesting that both hands were influenced by a bias emanating from the right hemisphere and implying callosal transfer in the case of responses with the right hand.

The symmetrical neglect observed in young children has also been found in previous studies (Bradshaw et al., 1987, 1988; Dellatolas et al., 1996; Dobler et al., 2001) and is assumed to be present up to the ages of 7 or 8 years (Bradshaw et al., 1987; Dobler et al., 2001). However, the results of this study indicate that this pattern persists through the ages of 10–12 years and that there is a dramatic developmental step to the adult pattern of pseudoneglect between the ages of 10–12 and 13–15 years. We assume that this change is related to the maturation of the corpus callosum.

Because line bisection appears to change in stepwise fashion, however, it is unlikely that it is related in simple fashion to the size of the corpus callosum, which changes linearly. The critical event that distinguishes the 10- to 12-year-old group from the 13- to 15-year old group is puberty, the transition from childhood to adolescence. Physiologically, this time is accompanied by dramatic hormonal changes in both sexes. In boys, testosterone levels increase dramatically, and in girls, hormonal changes, especially of estradiol and progesterone, are related to the onset of the menstrual cycle. It has been found that for healthy boys, testosterone is positively related to morphological changes in the posterior body of the corpus callosum (Moffat, Hampson, Wickett, Vernon, & Lee, 1997). Although organizing effects of testosterone in callosal development occur already during the pre- and neonatal period, they are still sensitive into adulthood in rats (Bimonte, Fitch, & Denenberg, 2000). Recent morphological evidence in humans (Giedd et al., 1996; Pujol et al., 1993) indicates that callosal development, particularly the posterior part as well as the midbody, does not end in the neonatal period but continues to develop and increase in size throughout childhood to young adulthood. Histological studies in animals have shown that biologically active metabolites of testosterone are highly concentrated in white matter structures, including the corpus callosum (Celotti, Melcangi, Negri-Cesi, Ballabio, & Martini, 1987; and in the purified myelin sheaths of central nervous system axons), suggesting an androgenic influence on the process of myelination (Melcangi et al., 1988). Moreover, Stocker,

Guttinger, and Herth (1994) found that the administration of testosterone in canaries early in development triggered neuronal growth, whereas testosterone administration later in development promoted an increase in myelin formation.

Although neither Giedd et al. (1996) nor Pujol et al. (1993) found sex differences in the midsagittal subdivisions or total size of the corpus callosum, Pujol et al. reported a greater growth rate in boys from teenage years onward. They suggested that the corpus callosum in girls matures earlier. A recent study by Achiron, Lipitz, and Achiron (2001) showed that sex differences in the development of the human corpus callosum morphology appear in utero, with female fetuses showing a thicker corpus callosum than males. These findings support previous evidence of sexual dimorphism of the human corpus callosum. The nature of this dimorphism remains controversial, although most studies have shown the hemispheres to be anatomically and functionally more connected in women than in men (Clarke & Zaidel, 1994; DeLacoste-Utamsing & Holloway, 1982; Holloway et al., 1993; Oka et al., 1999; Steinmetz et al., 1992; for a review, see Driesen & Raz, 1995; but see also Bishop & Wahlsten, 1997). This might explain why men showed a significant difference in left bias between hands, whereas women did not, both in the present study and in that of Hausmann et al. (2002).

As in other studies (see Jewell & McCourt, 2000, for a review), including that of Hausmann et al. (2002), we found a strong effect of line position. The leftward bias, overall, was increased when participants viewed lines in the left position and was decreased when lines were located to the right. This effect may be explicable in perceptual terms, such that the line located to the left leads to a greater right-hemisphere engagement and hence greater attentional bias to the left (Kinsbourne, 1970). However, this effect did not interact robustly with hand use, as it did in the study by Hausmann et al. (2002), and was significant only when the absolute measurements were analyzed. Moreover, the effect of line position did not interact with age. That is, all age groups showed a leftward bias when the lines were positioned to the left of the page rather than to the right. Even the youngest group showed this shift in pseudoneglect as a function of line position, shifting from a strong right bias with the right hand when the lines were located on the right to a small left bias with the right hand when the lines were located to the left. This effect supports MacLeod and Turnbull's (1999) suggestion that "perceptual factors might be the predominant cause of (pseudo)neglect" (p. 707).

It is, however, clear from the effect of hand use on line bisection that the hemispatial effect in neurologically healthy participants is due to the interaction between perceptual and perceptual-motor judgments. In a series of reports, Goodale and colleagues (Goodale & Humphrey, 1998; Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991) have provided convincing evidence that there are separate but interacting systems for the perception of objects (the *ventral* visual pathway projecting to the inferotemporal cortex) and the control of actions directed at those objects (the *dorsal* pathway projecting to the posterior parietal cortex). Both visual streams are thought to be modulated by attention. As such, processes in the right- (pri-

marily) and left-hemisphere dorsal pathways would be used when performing a motor line-bisection task (again assuming callosal transfer of information), whereas mainly the ventral pathway would be invoked for purely perceptual line-judgement tasks.

In summary, this study supports the idea of developmental changes in visual line bisection. All four age groups showed the characteristic leftward bias when using the left hand, indicating that performance with the left hand (and thus right-hemisphere predominance for spatial awareness) remains stable across time. When using the right hand, the youngest group (ages 10–12 years) showed a rightward bias, whereas the other groups all showed a bias to the left. The findings suggest a shift from contralateral (left hemisphere) to right-hemispheric control during puberty and may reflect maturation of the corpus callosum.

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