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The role of the corpus callosum in the perception of reversible figures in children

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ABSTRACT

To test the role of interhemispheric competition through the corpus callosum in the perceptual alternation of reversible figures, we compared children with callosal pathology and typically developing children on a bistable stimulus task. The children with corpus callosum pathology reported significantly less changes of percepts per minute than the age-matched typically developing children. In addition, older typically developing children reported significantly more changes of percepts than the younger ones. These results support the hypothesis that the rate of reversal between two interpretations of a bistable stimulus may be partly mediated by the corpus callosum.

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1. Introduction

Perceptual bistability may arise when a stimulus is not only ambiguous but also reversible. Ambiguity refers to the fact that the stimulus can *a priori* be interpreted in two distinct ways, whereas reversibility refers to the ability of the observer to experience these two interpretations. When the reversible figure is continuously presented, the viewer spontaneously alternates between opposite interpretations of the stimulus as he inspects it. Perceptual bistability may also arise when a stimulus is reversible but not ambiguous, for instance in the case of binocular rivalry where the two eyes are looking at incompatible images (Mamassian & Goutcher, 2005). Bottom-up,[1] top-down, and mixed explanations have been called upon to explain perceptual reversibility (Long & Toppino, 2004). Another, rather orthogonal, explanation suggests that subcortical interhemispheric competition underlies the perceptual alternation (Miller et al., 2000). The objective of the study presented here was to explore the role of the corpus callosum (CC) in alternation during perception of reversible figures by comparing children with pathology of the CC with typically developing children.

There has been an enduring interest in perceptual ambiguity. Dozens of reversible figures have been described in the literature, with perceptual instability arising from different processes, such as reversals in figure-ground organization, fluctuations in perspective (depth), or changes in meanings. There are several explanations of the processes involved in reversible perception. Some early explanations of perceptual bistability involved peripheral (related to the sense organ itself) processes. Other early explanations involved central processes (from the brain mostly cortical mechanisms), such as attention, or imagination (see Long & Toppino, 2004, for a review).

With the Gestaltists, the notion of satiation was used as a dynamical brain process explaining that the second percept arises after a gradual build up of resistance in the brain to the field flow underlying the first percept. A more contemporary approach used the concept of neural adaptation to explain alternation. According to this bottom-up or sensory view, figure reversals would depend on relatively automatic brain processes largely independent of the observer's higher order cognitive processes.

This view contrasts with another mainstream contemporary approach, a top-down hypothesis that favors the role of more cognitive processes such as learning or attention. In fact, a pure bottom-up approach to the perception of ambiguous figures fails to account for the conditions necessary for this phenomenon to occur, such as expectations, world-knowledge, and the direction of attention (Long & Toppino, 2004). Finally, in their long review of results that indicate that neither sensory nor cognitive

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[1] Bottom-up and top-down mechanisms refer here coarsely to both the primary level of representation, i.e., sensory (low-level) vs. cognitive (high-level), and the primary flow of processing, i.e., from low-level to high-level vs. from high- to low-level (Long & Toppino, 2004).

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processes can explain the reversible phenomenon alone, Long and Toppino offer an hybrid model that incorporates both bottom-up and top-down processes in a conceptual approach (Long & Toppino, 2004).

A few studies have examined the age at which perceptual alternation arise. Findings indicate that children are unable to perform uninformed perceptual switching before the age of 5 years, and that only some of the 3- and 4-year-olds do so even when informed; furthermore, those that reverse do so only once or twice over a 60-s inspection period (Doherty & Wimmer, 2005; Gopnik & Rosati, 2001; Rock, Gopnik, & Hall, 1994). Some developmental data on bistable perception indicate high-level modulation of the phenomenon. For instance, with a duck–rabbit image, children tested on Easter Sunday are more likely to see the figure as a rabbit; if tested on a Sunday in October, they tend to see it as a duck or similar bird (Brugger & Brugger, 1993).

Recent fMRI studies looking for neural correlates of binocular rivalry support the notion that the right frontoparietal cortex may be implicated in transitions between competing stimuli (see Blake & Logothetis, 2002, for a review). An alternative theory of binocular rivalry promoted by Pettigrew and colleagues (Miller et al., 2000; Pettigrew & Miller, 1998) proposes another neural basis for switching between competing stimuli. They suggested the involvement of interhemispheric competition to explain the alternation of competing stimuli. According to this theory, each hemisphere adopts one interpretation arbitrarily and competition between hemispheres results in alternating perceptual dominance of one interpretation and simultaneous suppression of the other. To test this model, Miller et al. (2000) investigated the effects of unihemispheric activation and disruption during viewing of a binocular rivalry task, in which horizontal lines were presented to one eye and vertical lines to the other. Unihemisperic activation was obtained by cooling down the contralateral ear with cold water to see whether this would imbalance the relative frequency of report of the two stimuli compared to the controls. Pettigrew and colleagues observed a bias with the cold water and also observed a change in the rate of alternation of the two stimuli, both results being consistent with their interhemispheric switch model of binocular rivalry.

Although the CC is the main structure connecting the two hemispheres, Pettigrew and colleagues do not assume that it is involved in their hypothesized interhemispheric switching, since, for instance, bistable oscillators have been observed in the brain of animals lacking a corpus callosum (Miller et al., 2000). Instead, they favor subcortical bistable oscillator to explain interhemispheric switching. Such an interhemispheric switch model has been tested in a series of studies by O'Shea and Corbalis (2001, 2003, 2005) on one or two split-brain patients. These authors found that the split-brain patients did alternate between two percepts and that the alternation rate was not different when the stimulus was presented to the left or right hemisphere. However, a closer look at the results in these three studies indicates that the split-brain patients were between two and three times slower to alternate between percepts in comparison to the control observers. Therefore, these studies on split-brain patients are inconclusive regarding the absence of implication of the CC in the alternance of reversible figures. Thus, the study of children who lack, partially or totally, a CC may provide a useful test of the role of the corpus callosum (and of the interhemispheric switch hypothesis) in switching between two percepts. This study is, to our knowledge, the first developmental one to report on such a test so far.

The CC represents the major pathway of associative fibers connecting the cerebral hemispheres. It connects mainly the homotopic areas of the hemispheres, and the secondary areas more than the primary areas. The first fibers appear *in utero* around the 12th week, as the splenium and the body develop first, followed by the genu and the rostrum, and the number of fibers is complete by the 20th week of gestation. The post-natal period of development of the CC size concerns mainly the splenium. The CC reaches a size comparable to the adult by 2 years of age, but it is one of the last structures to complete myelination, a process which starts at the fourth month of pregnancy and continues throughout adulthood (Giedd et al., 1999; Knyazeva & Farber, 1991; Pujol, Vendrell, Junqué, Larti-Vilalta, & Capdevila, 1993; Yakovlev & Lecours, 1967). A key role for the CC has been asserted for transfer of information during bimanual learning, or during visual depth judgement in the child split brain (Lassonde, Sauerwein, Geoffroy, & Décarie, 1986), and in children born with agenesis of the CC (ACC) (Lassonde & Sauerwein, 2003; Rivest, Cavanagh, & Lassonde, 1994; Sauerwein & Lassonde, 1994). The role of the CC is not only to permit the transfer of information from one hemisphere to the other, but also to permit activity in one hemisphere to inhibit activity in the other, and to distribute attention between the hemispheres (Cook, 1986; Meyer, Röricht, Gräfin von Einsiedel, Kruggel, & Weindl, 1995; Schnitzler, Kessler, & Benecke, 1996).

Before the generalization of ultrasound recordings during pregnancy, ACC was often discovered by chance, when brain investigation was needed for some associated pathology. Thus, it was difficult to observe subjects with isolated ACC. It is now possible to diagnose isolated callosum agenesis in fetuses. About 1.3 children in 1000 are born without a CC, and agenesis can be total or partial, depending on the time of brain damage. When diagnosed before birth, infants with ACC can be followed during their development (Moutard et al., 2003). If the children with an isolated ACC report less change in their percepts when viewing a reversible figure than children with intact corpus callosum, then this would argue in favor of a role of the corpus callosum in switching between the two figures and it would support Pettigrew's hypothesis of interhemispheric switching, although through a different mechanism from that he hypothesized.

Other pathologies involve corpus callosus dysgenesis. For instance, the CC is frequently affected following prenatal alcohol exposure. All or parts of the CC are often thinner than normal in children exposed to alcohol prenatally, whether these children have the physical features of fetal alcohol syndrome (FAS), or not (they are then categorized as children with fetal alcohol effect or FAE) (Riley et al., 1995). In some cases, the agenesis can be total (Roebuck-Spencer, Mattson, Marion, Brown, & Riley, 2004). Assuming that the FAS or FAE children are most often associated with a dysgenesis of the CC, we also tested two children with prenatal exposure to alcohol (one FAS and one FAE).

Finally, the CC matures late during the first decade of life, and it has been shown that progress in bimanual coordination requiring interhemispheric transfer occurs during the end of the first decade of life (Fagard, Morioka, & Wolff, 1985; Fagard & Pezé, 1992). We could then also test the role of the corpus callosum in the perceptual alternation of reversible figures by comparing children with assumed different stages of maturation of the CC. If the corpus callosum plays a role in alternation, then we should observe that the frequency of perceptual alternation increases with age in typically developing children. Although it has been shown already that young children cannot perform uninformed perceptual switching before the age of 5 (Rock et al., 1994), nothing is known, to our knowledge, on the change in the rate of switching once it is acquired.

Thus, we decided to compare the perception of reversible figures between typically developing children and children with a pathology of the CC (agenesis or dysgenesis), and between younger (before full maturation of the CC) and older children.

2. Experiment

2.1. Subjects

A group of 10 children with ACC was observed in two French hospitals: Hôpital Trousseau in Paris and Institut Gustave Roussy in Villejuif. There were five boys and five girls, between 5 and 9 years of age (mean age: 7 years 6 months, *SD*: 1.6), nine of them right-handed and one left-handed. The pathology of the CC was detected with prenatal ultrasound recording, and the agenesis was categorized as total or partial on the basis of MRI after birth (see Table 1). The children that we have seen had an isolated agenesis of the corpus callosum, and all but one were in the normal range of IQ (one girl had an IQ of 68). This girl and three other children presented some language-related perturbations, for talking or reading. We considered that it did not influence the results directly because, first we kept asking the children what animal they were seeing in case they did not report a change in perception, so that the number of reported names could be comparable for all children; secondly, we checked that all children were at ease in naming the duck and the rabbit on the non-ambiguous pre-test images. Finally, we also checked whether the difference in rate of alternation between CC pathology children and age-matched controls were not due to these four slightly language-impaired children.

The two children suffering from prenatal exposure to alcohol (two girls, one left-handed and one right-handed, aged 5 and 9, respectively) were observed in Rennes (Hôpital Sud). For the FAS child, the diagnostic was suspected prenatally from the mother's behavior during pregnancy and later confirmed by the typical facial abnormalities of the girl. For the FAE child the exposure to alcohol had been observed during pregnancy, but the girl did not show the typical facial abnormalities. The two children were following a normal scholar *cursus* at the time of testing, and had, according to the neuropediatrician following them, an impressive verbal fluency.

The control group consisted of 11 children with typical development observed in their regular school. There were five boys and six girls. Their age range was between 5 and 9 years (mean age: 7 years 2 months, *SD*: 1.5).

In addition, a second group of typically developing children, older than the control group for the children with pathology of the CC, was tested. There were 14 children aged between 10 and 11 (mean age: 10 years 4 months, *SD*: .51). For all children, prior parental consent was required before testing.

2.2. Procedure

To test for the perception of reversible figures we used the same ambiguous stimuli used by Sobel and collaborators (Sobel, Capps, & Gopnik, 2005). The test comprised three duck–rabbit images: one slightly ambiguous image more on the rabbit side ("rabbit-like"), one slightly ambiguous image more on the duck side ("duck-like"), and a reversible duck–rabbit image (see Fig. 1). All children were given first two unambiguous images, one of a rabbit, and one of a duck, to be sure that they knew these two animals and that they reported only one percept for these unambiguous stimuli. These images were presented only once, half of the children starting with the duck, half of them starting with the rabbit. The first two phases of the experiment itself were familiarization phases: the first phase consisted of the first presentation of the two slightly ambiguous figures, shown five times each in alternation. The first phase lasted 2 min. For the second phase we presented the reversible duck–rabbit image for 2 min. Finally, in the third phase, the test itself, the three images were presented in succession and for 1 min each time, in the following order: rabbit-like, duck-like, reversible duck–rabbit. This was done twice so that the total duration of the third phase was 6 min. All three ambiguous and reversible images were presented on a computer, using *E-prime* software to pilot the study. We decided to use only one set of stimuli, since the children showed fatigue by the end of the testing session and it was not possible to ask all ACC children to come back to the hospital, usually far from their home.

The children were told that they would be shown images in which they could see different animals. They were informed that they would have to report verbally which animal they saw in the images. They were told that even when the image did not change, they could see a different animal after a while and they had to tell every time they saw something different.

Given the relationships between handedness and interhemispheric connections, we also evaluated the possible influence of handedness in our results. To this end, we asked the child to perform or pretend to perform 15 items (e.g., hand used to brush hair, throw a ball). All these items were borrowed from the main questionnaires for lateral preferences (Coren, 1993; Corey, Hurley, & Foundas, 2001; Oldfield, 1971). For each item, the experimenter coded one of three answers: "left", "right", or "either left or right". A laterality index (LI) was calculated for hand preference, using the

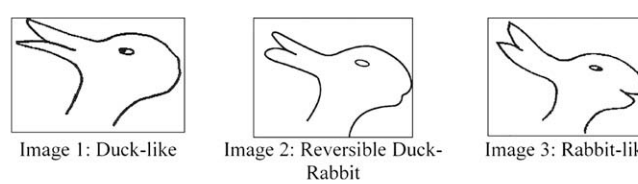

Fig. 1. Test images.

Table 1
Characteristics of the ACC children (and their CPM for reversible stimulus as compared with FAE and FAS children and age-matched control children)

Child	Group	Gender	Age	CC pathology	Associated cognitive problems	CPM for reversible stimulus
1	ACC	Boy	6	Total agenesis	No	0
2	ACC	Boy	6	Total agenesis	Language deficit	0
3	ACC	Girl	8	Total agenesis	IQ = 68 dyslexia	1
4	ACC	Boy	8	Partial (no beak, no splenium, thin central part)	No	0
5	ACC	Girl	8	Total agenesis	Language deficit	0.5
6	ACC	Girl	8	Total agenesis	No	3.5
7	ACC	Boy	8	Total agenesis	Language deficit	5
8	ACC	Boy	8	Total agenesis	No	0
9	ACC	Girl	9	Partial (no beak, no splenium)	No	4
10	ACC	Girl	9	Total agenesis	No	5
	FAE	Girl	5			3
	FAS	Girl	9			2.5
	Control group		5–9			2.5–14 (mean = 6.8)

classic formula: [(number of right − number of left)/(number of right + number of left + number of "either hand"] × 100.

2.3. Data analysis

We did not code the first report of an animal. Every time the child reported seeing a different animal, we coded it as one change in perception. We then calculated the number of changes for each of the three stimuli. Since the first two phases were aimed at familiarizing the children with the stimuli, only the third phase was analyzed. We report the number of changes per minute (CPM) for each of the three stimuli. Since each was presented twice for 1 min each time, the CPM = total number of changes/2.

2.4. Results

There were no changes reported by any children for the non-ambiguous stimuli (pre-test images). We found very little difference between the number of changes per minute (CPM) for the two slightly ambiguous stimuli. Therefore, we decided to pool them. We could then compare the number of changes when there was a slight ambiguity (mean of duck-like and rabbit-like), and when the image was most ambiguous (reversible duck–rabbit). We hypothesized that the children would indicate more changes as the figure became more ambiguous, that the callosal pathology group would switch perception less often than the control group, and that the younger typically developing children would switch perception less often than the older children.

As one can see in Fig. 2 there were occasional changes for the slightly ambiguous stimuli, and even more for the reversible stimulus. The children in all groups showed an increase in CPM over these two stimulus types although the magnitude of the increase differed between groups.

We first evaluated the effect of the pathology of the CC on the CPM. An ANOVA for group (× 2; CC pathology vs. their control matched group) and image (× 2; slightly ambiguous vs. reversible), with image as repeated measures, showed a significant effect for group ($F(1,23) = 12.5$, $p < .01$), a significant effect for image ($F(1,23) = 30.8$, $p < .0001$), and a significant group × image interaction ($F(1,23) = 18.8$, $p < .01$). Thus, on average, children had a higher CPM when looking at the reversible image than when looking at the slightly ambiguous images. The children with CC pathology showed a lower CPM than the control children with typical development, especially on the reversible figure, although the interaction might be due to a floor effect. As one can see on Table 1, the two children exposed prenatally to alcohol reported more alternations that most of the ACC children, and the results of the ACC children were quite homogenous. When we compared only the 10 ACC and the age-matched control group, the difference was still highly significant between the two groups ($p < .001$).

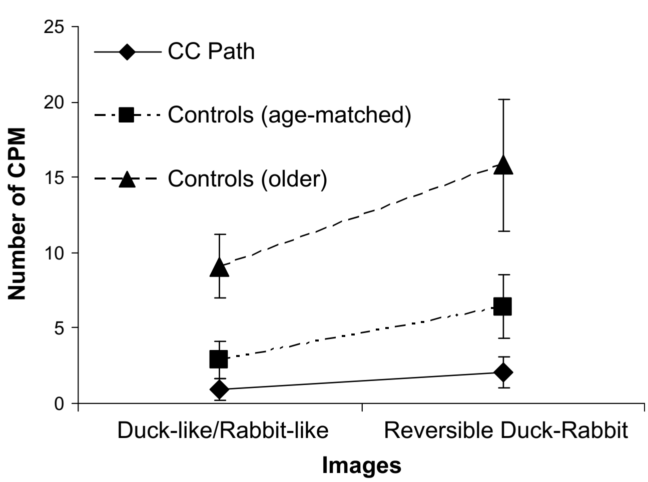

Fig. 2. Number of changes per minute (CPM) as a function of images (slightly ambiguous vs. reversible) and groups.

To test for the age effect in the group of children with typical development, we applied an ANOVA for age group (× 2; typical 5–9-year-olds vs. typical 10–11-year-olds) and for image (× 2; slightly ambiguous vs. reversible), with image as repeated measures. It showed a significant effect for age group ($F(1,23) = 12.5$, $p < .01$), a significant effect for image ($F(1,23) = 30.8$, $p < .0001$), but no significant group × image interaction. Thus, on average, children had a higher CPM when looking at the reversible image than when looking at the slightly ambiguous images. The younger children showed a lower CPM than older children on both types of image.

Handedness had no significant effect on the results. The two left-handers from the CC pathology group tended to have a lower CPM when looking at the slightly ambiguous stimuli and a higher CPM when looking at the reversible image, as compared with the right-handed children from the same group. However, the difference was far from significance. In addition, across groups, we observed no difference in CPM between the consistent right-handers (LI = 100) and the less consistent right-handers (LI < 100).

3. Discussion

These results show that the more ambiguous the image, the more often the children switch between the two interpretations of the image. The children with pathology of the CC showed significantly less changes in percepts than typically developing children. The behavior of these children with CC pathology is closer to that of younger children who do not reverse often (Rock et al., 1994), than to their age-matched peers. We did not find any significant difference regarding the number of reversals between the ACC children depending on whether they were totally exempt of associated cognitive problems or not. We thus think that the CC pathology is likely to be responsible for the difference between age-matched groups.

We also observed an influence of age in the rate of switches between interpretations in typically developing children. The older children showed more changes per minute than the younger ones, and the difference was significant for the slightly ambiguous stimuli as well as for the reversible stimulus. These results are in line with previous results showing an increase in the rate of switching between interpretations of an ambiguous figure with age. However, previous studies mostly concerned younger children (Doherty & Wimmer, 2005; Gopnik & Rosati, 2001; Rock et al., 1994), or, when applied to children older than 4 years of age, did not focus on the rate of switching but rather on the likelihood of switching interpretations when non-informed. In our study, the children were informed of the possibility of seeing different animals, all of them could see the two alternatives and we recorded the rate of changes between interpretations. Even though many other explanations cannot be excluded, this age difference could be due to the maturation of the CC. It has been shown, for instance, that tasks sensitive to the integrity of the CC improve particularly between 7 and 10 years of age (Fagard & Pezé, 1992).

Our results indicate that an intact CC is not necessary for driving alternations of percepts when looking at a reversible figure because children with pathology of the CC still presented some alternations. However, these children showed a significant reduction in their alternation rate, and these results are consistent with those recorded in adult split-brain patients who also showed a reduction of the number of alternations (O'Shea and Corballis, 2001, 2003, 2005). Overall, the results indicate that the CC plays some role in bistability. This role might be attentional since the CC is known to be involved in the regulation of attention between the two hemispheres (Cook, 1984). Given that the corpus callosum is the main structure involved in interhemispheric connections, these results are supportive of the interhemispheric switch model (Miller et al., 2000; Pettigrew & Miller, 1998). However, Pettigrew and colleagues favored subcortical bistable oscillator to explain interhemispheric switching. Our results support the emphasis put by Pettigrew on interhemispheric communication, but not the exclusive reliance on subcortical structures. Because the CC connects mainly associative and secondary cortical areas (Selnes, 1974), we believe that the interhemispheric communication involved in bistability occurs not only at low levels but also high levels of processing.

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