3 Cognitive Abilities Before Birth: Learning and Long-Lasting Memory in a Chimpanzee Fetus

NOBUYUKI KAWAI

1 Introduction: The Dawn of Research on Prenatal Cognition

Everyone has a naive question about ontogenesis ("the ontogenetic origin") of our intelligence. When do we start to learn about events and memorize them? To address this question, two species have been intensively investigated: rats (Rattus norvegicus) and humans (Homo sapiens). In this chapter, I briefly review the literature of prenatal and postnatal learning of the two species. Then, I discuss our recent research on learning and memory by a chimpanzee fetus.

Once not only laymen but also researchers believed that neonates did not have most of the cognitive abilities of adults (Douglas 1975) because the immature brains of atricial infants are under development for some years or even until adolescent years (Paus et al. 1999). This notion corresponded with general behavioral development, especially in humans. It takes almost 12 months before a human infant begins bipedal locomotion and 6 months or more before an infant utters a meaningful word. Therefore, it is not surprising that it was long believed that a neonate is not yet prepared for many physical and cognitive abilities.

In the late 1970s, however, the journal *Science* reported unexpected behavioral and cognitive capabilities of rat and human newborns in succession: (1) infant imitation (Melzoff and Moore 1977), (2) instrumental conditioning in 1-day-old rats (Johanson and Hall 1979), (3) instrumental conditioning in human newborns (DeCasper and Fifer 1980), and (4) instrumental conditioning and its memory in human newborns (Rovee-Collier et al. 1980). A curtain was opened for research on cognition during infancy by these studies.

2 Learning Abilities in Prenatal and Postnatal Animals

2.1 Learning in Postnatal Animals

Although Pavlovian conditioning in newborn rats had been demonstrated in the 1960s (Caldwell and Werboff 1962), the obtained levels of performance were weak. Caldwell and Werboff (1962) trained 1-day-old rat pups by giving a pair of vibrotactile stimuli to the rat's chest as the conditioned stimulus (CS) and an electric shock (the unconditioned stimulus; US) to the forelimb 80 times. The highest level of conditioned response (leg flexion by the CS) attained was only 32% for the two best groups. This level of performance was significantly below that traditionally reported in the literature of Pavlovian conditioning of adult rats (Hilgard and Marquis 1961).

Later, it found that newborn rats are ready to associate events when olfactory and/or gustatory stimuli are employed. For instance, Rudy and Cleahtle (1977) found that 2-day-old rat pups exposed to a single paired presentation of lemon scent and nausea induced by lithium chloride (LiCl) displayed a reduced preference for the lemon scent after 6 days of testing. Subsequent studies demonstrated that even 1-day-old pups could readily establish conditioned odor aversions (Cleatle and Rudy 1978). Even more, 1-day-old rat pups learned to probe upward into a puddle when they were rewarded with small infusions of milk into their mouths, namely, instrumental learning (Johanson and Hall 1979). These results strongly suggest that newborn rats are born equipped with the ability to recognize events and learn from them.

2.2 Prenatal Learning in Animals

There is no reason to distinguish cognitive ability between before and after birth. It should be plausible to assume that the ability is available before birth. Smotherman (1982) revealed that fetal rats are capable of rapidly acquiring olfactory aversions. In that study, the flavor of apple juice introduced into the amniotic fluid was paired with injections of LiCl into fetuses 2 days before the normal end of gestation. When these infant rats were tested 10 days after birth, they demonstrated marked aversion to the odor of apple juice (Smotherman and Robinson 1991). Appetitive conditioning has also been reported in the same species (Robinson et al. 1993). Robinson et al. (1993) demonstrated that rat fetuses exposed to chemosensory stimuli are capable of retaining associations after birth. These studies indicate that the rat fetus seems well prepared to process chemical stimuli (e.g., amniotic fluid and milk) that are critical to its survival.
2.3 Some Restrictions to Prenatal and Postnatal Associative Learning in Rats: Limited Abilities in Early Visual and Auditory Senses

Nevertheless, there seem to be some constraints in learning even during infancy. In the early period of development, not all the stimulations establish learning. Although significant odor aversion was produced in 2-day-old rats by both LiCl and intraperitoneal shock US, foot shock was not effective until pups were 14 days old (Haroutunian and Campbell 1979).

Rats are born with immature sensory organs. Through quick development, weaning in rats occurs at about postnatal day 21. The rat’s auditory and visual systems, however, start to function after about postnatal day 14. The external meatus opens the ear canal to sound at about 13 days of age (Kelly et al. 1987), and the eyes open at 15 days (Spear and Rudy 1991). These completions of organic maturation do not mean that rats are ready to learn by these sensory systems. Learning by these systems is delayed a few days after functioning of these sensory systems has begun. Hyson and Rudy (1984) report that it was not until the rat pups were 14 days old that they were conditioned to that tone, whereas pups 12 days old were able to detect the 2,000 Hz tone used as the CS. Moye and Rudy (1985) found that even though the 15-day-old rat pups could detect the flashing light CS, the light paired with shock did not elicit a conditioned freezing response until the pups were 17 days old. This finding cannot be attributed to the ineffectiveness of the shock in reinforcing the conditioning because 15-day-old rats were conditioned to both auditory and olfactory stimuli paired with the same shock. Therefore, the learning ability of perinatal rats relies on the chemical (olfactory and/or gustatory) stimulation for which the mammalian fetus appears to be prepared. This result is not surprising, because the fetus and newborn need to process chemical stimuli (amniotic fluid and milk, etc.) in their intrauterine and perinatal life (Papini 2002) (Table 1).

### Table 1. The onset of sensory modalities and its availability in learning in rats

<table>
<thead>
<tr>
<th>Sensation</th>
<th>Cognitive function</th>
<th>Perinatal fetus</th>
<th>Birth</th>
<th>12 days</th>
<th>14 days</th>
<th>17 days</th>
</tr>
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<tbody>
<tr>
<td>Olfaction</td>
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<td>Yes</td>
<td>Yes</td>
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<tr>
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</tr>
<tr>
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<td>Learning</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

3 Cognitive Abilities in Human Fetuses

3.1 The Human Newborn Is Sensitive to the Mother’s Voice and Learns by Hearing the Voice

The human fetus and newborn are unique because they are sensitive to visual and auditory stimuli from just after birth. Among all, newborns selectively respond to the stimuli produced by humans (Melzoff and Moore 1977). Not only are they sensitive, but also they can change their own behavior to listen to the voice, namely, instrumental learning. Infants younger than 3 days can rapidly be conditioned using sucking as the instrumental response and tape recordings of the mother’s voice as the reinforcement (DeCasper and Fifer 1980). Not only do very young infants have the ability to learn, but they are also able to distinguish the sound of a human voice from other kinds of sounds, and they seem to prefer this sound (Butterfield and Siperstein 1974). Human neonates readily display a preference for their mother's voice as opposed to an unfamiliar female voice, whereas they show no significant preference for their fathers' voice (DeCasper and Prescott 1984). These results suggest that the prenatal auditory experience of the human infant influences postnatal auditory preferences.

3.2 The Human Fetus Shows Habitation to Acoustic Stimuli

In fact, human newborns prefer the sound of a passage recited over the last 6 weeks of gestation to the sound of a passage from a novel (DeCasper and Spence 1986). Prenatal auditory experience exerts a change in fetal response perse (Birnholz and Benacerraf 1983; Murphy and Smyth 1982). Typically, human fetuses decrease their response when a sound or vibration is repeatedly presented to them (Lecanuet et al. 1986). Such a decrement in response has been interpreted to reflect habituation rather than receptor fatigue (Madison et al. 1985) and implies that the human fetus also has a simple form of learning ability.

3.3 Can the Human Fetus Learn Within the Uterus?

This result does not imply, however, that human fetuses are capable of more complex learning, such as associative and moreover discriminative learning. Associative learning can be distinguished from habituation, because habituation is a behavioral and/or attentional change to a single stimulus, whereas associative learning requires the ability to associate more than two events that are characterized in terms of a relationship between two or more environmental events. In addition, habituation does not persist for a long period. For instance, a recent study (van Heteren et al. 2000) reported that human fetuses demonstrated habituation to vibroacoustic stimulation (VAS) in the uterus, but it was only main-
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tained for 24 h. Further, although the auditory system of human fetuses already functions so that they can distinguish a slight difference between syllables (Lacam et al. 1992), hearing ability does necessarily mean that the fetus is ready to form auditory associations.

As already mentioned, although rat pups that were 10 and 12 days old could detect a 2,000-Hz tone that served as the CS, they did not become conditioned to that tone until they were 14 days old (Rudy and Hyson 1984). During the development of a particular sensory system, there seems to be a period when the system can detect and respond reflexively to a relevant stimulus source and yet be unable to mediate associative learning involving that stimulus (Moyle and Rudy 1985; Rudy and Hyson 1984). Therefore, it is still unclear whether a human fetus can form an association between events originating from outside the uterus.

3.4 Does the High Sensitivity to Acoustic Stimuli by Human Fetuses Evolve in the Human Lineage?

As mentioned, the human fetus responds to various sounds from outside the uterus. Behavioral (Ramus et al. 2000) and neurophysiological (Peña et al. 2003) studies report that newborns already distinguish their own language from unfamiliar ones. Is this advanced auditory sensitivity related to our greater vocal communication after birth and only limited to the human fetus?

Other than humans, evidence that prenatal auditory experience can exert a heavy influence on postnatal behavior has been limited to precocial mammals (Vince 1979) and birds (Gottlieb 1976). So far, we have no information on whether this well-developed auditory sensitivity is shared with other fetal primates. If a chimpanzee fetus can establish associative learning mediated by its auditory system, then we can infer that our closest relative, the chimpanzee, shares the superior auditory sensitivity of the human fetus. In other words, we can infer that the advanced auditory sensitivity of human fetuses and newborns has not evolved in the H. sapiens lineage for our rich vocal communication.

3.5 Toward Decisive Evidence of Prenatal Learning in a Natural Situation

To our knowledge, there has been no decisive evidence demonstrating fetal associative learning in primates, including humans. Although substantial evidence on associative learning capacity has been provided by studies on rat fetuses, these involved directly stimulating the rat fetus via an incision in the maternal abdomen. Of special interest here is whether a fetus that remains untouched within the uterus can form an association between stimuli presented from an extraterrestrial environment. To address this, we employed the fetus within a captive chimpanzee as the subject. These particular primates not only afford many opportunities for daily experiments but allow a close comparison with humans.

The primary purpose of the present study was to assess whether a chimpanzee fetus could undergo associative learning. Because chimpanzees have long life spans and it is not easy to increase their numbers in captivity, for practical reasons our treatment had to be limited to a single fetal subject. For this limited number of subjects, we employed differential conditioning as the control procedure. We compared responsiveness to two tones, one of which was paired with an unconditioned stimulus of VAS, which produces exaggerated responses in fetuses, whereas the other tone was never paired with VAS. We hypothesized that if an association were formed between a tone and the VAS, the subject would demonstrate active movement to the tone, because fetal responses to the VAS are essentially unconditioned. Two other chimpanzee infants served as the control subjects to assess their unconditioned potential to respond to the tones employed in the conditioning.

4 Associative Learning and Long-Lasting Memory Before Birth in a Chimpanzee

4.1 Conditioning with a Chimpanzee Fetus

We investigated whether a chimpanzee fetus can form associations between external stimuli by using Pavlovian conditioning (Kawai et al. 2004). The conditioning was initiated at 201 days gestational age (GA). An experimenter (MT) well known to the chimpanzee mother (Pan) came into the same booth (cf. Kawai and Matsuzawa 2000), and, after calming the pregnant chimpanzee, was able to position the equipment on her lower abdomen. Before each conditioning, another experimenter (NK) outside the booth monitored the fetus ultrasonically through the mother's abdominal wall and confirmed the fetus was behaviorally active. Activity was defined as any substantial movement of the arms, legs, or whole body for 1 min before each trial. If the fetus was not active, conditioning was postponed until activity resumed. Once activity was confirmed, the speaker and stimulator were placed on the lower maternal abdomen, then differential conditioning was applied to the fetus (Fig. 1). Two pure 1-s tones were employed as conditioned stimuli (110 db), with one tone (500 Hz; CS+) always followed by a VAS of 80 Hz (110 Gal) applied near the fetus, while another (1,000 Hz; CS-) was never followed by the VAS. The conditioning was conducted for 156 trials in total until labor on 233 days GA.

The conditioned fetus was born as a result of natural delivery and reared by her own mother. The tests were done on the 33rd and 58th days after birth along with various other kinds of behavioral, cognitive, and developmental experiments and observations (see other chapters in this volume). In the test session, the conditioned infant (Pal) was taken by anesthetizing her mother and was placed supine on a wide white bed in another room. She was then presented with
4.2 Data Analysis for the Test

4.2.1 Behavioral Measures: Body Movements

The degree of body movement was calculated graphically by subtracting adjacent frames at 100-ms intervals for the first 5 s after each stimulus was presented (Fig. 2). The original images were captured on digital video and saved in 256-step gray-scale mode. We arbitrarily established a rectangular region of interest (see Fig. 2) to cover the whole body of the infant for each session. We calculated the absolute difference in brightness for corresponding pixels between adjacent frames. If this value exceeded a predetermined threshold of 20, a black dot was placed on the white background to establish an image of subtracted brightness. The body movement index for each of these brightness-subtracted images was the proportion of black dots to the total region of interest. The mean body movement index for each trial was the average of ten brightness-subtracted images.

4.2.2 Behavioral Measures: Observer Rating

In addition, the video tape recording was edited into silent video clips of the first 5 s after the CS so that observers could evaluate the activity of subjects. Five experimentally blind observers rated the subjects' activity according to a five-point Likert scale (1 being "completely inactive" and 5 "very active"). These ratings for behavioral activity were averaged. The observers were unfamiliar with the chimpanzees and could not distinguish among the three subjects. The clips were presented in random order with 7-s intervals.

4.3 Evidence of Fetal Learning by the Chimpanzee

Pal (the conditioned subject) was activated by the CS+, but not by the CS−, in which the conditioned infant went through frenzied movements and cries (i.e., surprised) for CS+ but not for CS− presentations. This behavior was observed in both tests at 33 and 58 days old. However, Pico and Cleo (the two chimpanzee infants), who experienced no conditioning, did not show any response to either CS.

These differences are evident in the two indices. Figure 3, which shows the mean body-movement indices calculated graphically, shows that Pal (the conditioned subject) demonstrated greater activity after the CS+ than the CS−,
Fig. 3. Mean body movement of the conditioned (left panel) and control (middle and right panels) infants calculated graphically by subtraction between adjacent pictures for each 100 ms of the first second after stimulus presentations.

whereas the body movements of the control subjects were limited and indistinguishable between the two trials. Statistical analysis on body-movement indices revealed that the conditioned infant reacted significantly more after CS+ than after CS− presentations \( F(1, 2) = 75.24, P < 0.05 \). The effects of age \( F(1, 2) = 1.62, \text{n.s.} \) and interaction \( F(1, 2) = 1.71, \text{n.s.} \) were, however, not significant. The activity of Pico (the control infant of the same age) was lower and indistinguishable between CSs \( F(1, 2) < 1, \text{n.s.} \). The effects of age \( F(1, 2) = 2.54, \text{n.s.} \) and interaction \( F(1, 2) < 1, \text{n.s.} \) were also not significant. The activity level of Cleo (the unconditioned 120-day-old chimpanzee infant) was also lower and indistinguishable between CSs \( t(4) = 0.12 \).

Exactly the same picture can be drawn by the behavior scores rated by experimentally naive observers. Scores on the behavior of Pal (the conditioned subject) after the CS+ period were evaluated as being more active than those after the CS−, but Pico’s and Cleo’s behaviors (the control subjects) were rated as less active and indistinguishable (Table 2). Pal’s mean CS+ and CS− scores were 1.8 and 2.1, respectively, at 33 days, and 2.0 and 3.5 at 58 days. Those of Pico (the same age control infant) were 2.2 and 2.3 at 34 days, for the CS+ and CS−, respectively, and 2.9 and 2.7 at 57 days. Those of Cleo (the 121-day-old infant) were 1.2 and 1.1 for the CS+ and CS−, respectively. Statistical analysis confirms that only Pal’s behavior after the CS+ was active.

These results can be summarized as follows: (a) a chimpanzee fetus is capable of associative learning mediated by its auditory system, and (b) its memory persists for at least 2 months. This learning was assessed by comparing responses to two CS. The conditioned chimpanzee demonstrated greater response to the 500-Hz tone, which had been paired with VAS during the prenatal period, than to the 1000-Hz tone that had never been paired with VAS. These differential responses to the two tones suggest that the chimpanzee fetus distinguished them in utero and was already capable to inhibit responding to the CS−.

One may argue that the fetus could only detect the 500-Hz tone. Although the present study cannot exclude this possibility, intrauterine recordings indicate...
that sound frequencies below 1,000 Hz, which hardly attenuate acoustic energy, are detected by the fetus (Armitage et al. 1986; Querlier and Renard 1981). Furthermore, some studies have reported that human fetuses respond to a 2,000-Hz tone at 100 dB (Dwornicka et al. 1964) and 110 dB (Gelman et al. 1982). Regardless of the stimulus control tone of 1,000 Hz, it is certain that the 500-Hz tone activated the conditioned infant. The exaggerated responses to the 500-Hz tone by the conditioned infant cannot be attributed to any unconditioned potential because it did not elicit any response in the unconditioned control infants. So far, there have been no reports on fetal associative learning mediated by the auditory system. The present demonstration of associative learning by a chimpanzee fetus suggests that its auditory system is already functioning and ready for associative learning. We expect that a near-term human fetus, which is sensitive to auditory stimulation, would also demonstrate the ability to form associations if the same procedure as used in the present study were followed.

4.4 Long-Lasting Memory in the Chimpanzee Infant

Interestingly, the associative learning demonstrated in our experiment (Kawai et al. 2004) remained for at least 58 days. Such retention seems surprising, given that studies with human infants report less persistent memory during infancy (Fagen and Rovee-Collier 1983; Rovee-Collier et al. 1980). In the case of the human fetus, the longest retention interval of habituation is just 24 h (van Tueren et al. 2000). Nevertheless, the relatively long-term memory noted in our study may be the result of the biological significance of reinforcement. Reinforcement used in studies on human infant memory seems to be biologically less significant than that used in associative learning by animals. In most studies on human infant memory (cf. Grossel et al. 2002), visual stimuli used as reinforcers did not elicit unconditional responses. In contrast, the VAS we used in our study usually evoked greater activity in the fetus within the uterus. Other studies on nonhuman infant learning have also employed biologically significant stimuli as reinforcers, such as milk (Johanson and Hall 1975, 1982), LIC (Rudy and Cheutte 1977), and electric shock (Caldwell and Werboff 1962). Smotherman (1982) reports that infant rats tested postnatally at 10 days maintained an association acquired 2 days before the end of gestation. Consequently, it appears that the more biologically significant the reinforcement, the longer the retention span.

It is worth to mention that Pal might retain the conditioning for a longer time. We conducted extinction training at the age of 8 months. Pal came into the experimental booth along with her mother, Pan, for the behavioral and cognitive tests. The CS were presented from outside the booth. In the beginning, Pal rushed back to her mother when the CS+ was presented. This result does not mean that Pal was merely surprised by the loud sound because this kind of behavior was not observed when the CS− (the same intensity) was presented. In the latter trials, Pal paid attention to the CS without overt behavior. Then, she came to ignore the CS. Although the purpose of the extinction was to extinguish the potential association and we did not expect her memory, behavioral changes by the CS+ presentation suggest she retained the memory for 8 months.

4.5 Long-Term Effects of Early Experience in Other Animals

So far, long-term effects of early experience have been documented for insects (Alloway 1972) and amphibians (Hepper and Waldman 1992). For instance, injecting orange extract into the eggs of frog embryos resulted in a preference for locations doused with that odor in both tadpoles and adult frogs (Hepper and Waldman 1992). More-complex learning can be trained in larvae of the crested newt in a visual discrimination task by food reward (Herakowitz and Samuel 1973). The newt as adults responded to the visual stimulus previously followed by food (which were now non-rewarded). Similarly, Miller and Berk (1977) trained both tadpoles and frogs in a one-way avoidance situation. After completion of the learning, a retention interval of 35 days was inserted, in which period the tadpoles became adult. The learning was preserved regardless of the biological status at the time of acquisition. These results suggest behavioral habits induced by conditioning in immature amphibians can exert an effect on behavior of adults, even after metamorphosis.

4.6 Infantile Amnesia and Brain Development: Limits of Long-Term Effects of Early Memory

Nevertheless, we can hardly remember our own experiences in early life. This phenomenon is known as "infantile amnesia." Comparative-developmental studies suggest this phenomenon is caused by the immature brain. Campbell et al. (1974) trained rats, an arid species, and guinea pigs, a precocial species, in an escape-from-shock situation. In the case of rats ranging from 15 to 35 days of age, the performance was the same as the original training after a 1-day retention interval. However, with a 14-day retention interval, performance was degraded substantially for the young unwarranted infants (less than 20 days of age). In contrast, 35-day-old and 100-day-old guinea pigs learned rapidly, and behavioral levels after a 75-day-long retention interval were well preserved when original training had many trials and were indistinguishable between the two age groups.

Infantile amnesia, however, does not necessarily mean that the forgotten information is irreparably lost. It is possible, within certain limits, to reactivate early memories otherwise forgotten (cf. Springer and Miller 1972). For instance, human infants at the age of 3 months can learn to activate an overhead crib mobile by operant foot kicking; however, forgetting had occurred after 1 week. Nonreinforced exposure to a visual reminder of the event that existed in the training session (i.e., mobile, etc.) reactivates their memory (Fagen and Rovee-Collier 1983).
This recovery by reactivation treatments suggests that forgetting in the early period of life may not necessarily involve the destruction of relevant memories. Rather, it may be caused by retrieval failure. The neural network responsible for retrieving (and/or storing) memories may be overlaid by networks that develop subsequently.

4.7 Brain Development and Cognitive Abilities in the Fetus

Brain development correlates not only with memory but also with learning ability in humans. Our recent study showed that the chronological age of human fetuses determines the habituation ability to the VAS presented from a maternal abdomen. Morokuma et al. (2004) divided 26 fetuses at 32 to 37 weeks of gestation into three groups using combined criteria of gestational age (GA) and behavioral indicators. First, based on GA at the time of testing, the fetuses were divided into two groups, 32 to 34 weeks and 35 to 37 weeks of GA, because it is known that the neurologically normal fetus shows RRM (repetitive mouthing movement) at or above 35 weeks of gestation. Then, the fetuses less than 34 weeks of GA were divided in terms of the positive or negative of three behavioral indicators: EM/NEM (alternation of the eye movement/no eye movement periods), REM/SEM (rapid and slow eye movement patterns), and RMM. Group II (younger age) showed RMM (positive), but Group I in the same age group did not show RMM. This difference between the same-age groups was regarded as reflecting a difference in CNS development. As results, fetuses showed habituation from at least 32 weeks of gestation. Nevertheless, fetuses less developed (Group I) from the behavioral standpoint took significantly more trials to achieve habituation than developed fetuses even in the same gestational age. These findings strongly suggest a relationship between brain development measured by behavior scores and habituation ability.

5 Conclusion: Toward Comparative and Physiological Analysis of Cognitive Ability by Fetuses

The prenatal learning capacity of mammals has been documented, particularly in rats and human. Our study adds a decisive evidence of prenatal learning in the closest primate to humans, namely, the chimpanzee. The fact that the chimpanzee fetus can distinguish the two tones provided from the maternal abdomen and form an association within uterus indicates that the advanced auditory sense in the human fetus has not evolved in human lineage. This result, however, does not always mean early acoustic experience is not a prerequisite to human rich vocal communication. Early experience (even a mere exposure) exerts an obvious effect on adult behaviors, even when the brain is undergoing substan-

tial changes in maturation during early development. The best evidence for this is provided by human language acquisition.

The question is no longer whether fetal learning occurs, but how complex prenatal learning abilities are and how much early experiences influence adult behavior. Furthermore, we have to assess the time at which the fetus begins to acquire information. Our treatment of conditioning was initiated at 201 days GA and continued until labor at 233 days GA. It is not certain that the fetus at 201 days GA was mature enough to establish learning or whether it was formed in the later prenatal age. Obviously, more detailed information ranging from rodents to primates including human fetuses is needed to address the question of the ontogenetic and phylogenetic origins of our cognition.

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