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Normal Development of Prefrontal Cortex from Birth to Young Adulthood: Cognitive Functions, Anatomy, and Biochemistry

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Dorsolateral prefrontal cortex (DL-PFC) is needed when concentration is required, as when a task is novel or complicated or when you must switch tasks. An example would be when you need to guide your actions by information that you are holding in mind, and must pay close attention so that you act according to that information and not to your natural inclination. While it is difficult to resist a natural inclination or inhibit a dominant response, after awhile such inhibition no longer requires DL-PFC action so long as you consistently do that without interruption. For example, on the classic Stroop task (Stroop, 1935; MacLeod, 1991, 1992), color words often appear in the ink of another color (for example, the word *blue* might be printed in green ink). It is difficult to report the color of the ink, ignoring the words, but it is far easier to do that over many trials than to switch back and forth between reporting the ink color and reporting the word, even though many trials in the latter condition are purportedly easy because the correct response on those trials is to make the prepotent response (that is, read the word). Task-switching paradigms (Jersild, 1927; Shaffer, 1965; Allport et al., 1994; Rogers & Monsell, 1995; Meiran, 1996; Goschke, 2000; Mayr, 2001) epitomize the twin needs of active maintenance (working memory) and inhibition, which are the hallmarks of when DL-PFC is most clearly needed. The antithesis of when DL-PFC is required is when you can go on "automatic pilot" (Reason & Mycielska, 1982; Norman & Shallice, 1986).

PFC undergoes one of the longest periods of development of any brain region, taking over two decades to reach full maturity in humans (Kostovic et al., 1988; Sowell et al., 1999a). Even during the first year of life, however, significant maturational changes occur in PFC that help to make possible important cognitive advances by 1 year of age. Other periods of life when marked changes occur in the abilities associated with prefrontal cortex are the periods from 3 to 6 years and 7 to 11 years. In this chapter I will focus on normal development, dividing it into the following epochs: 0–1 years, 1–3 years, 3–7 years, and 7 years through early adulthood. For each epoch I will try to summarize some of what is known about *(a)* the development of the working memory and inhibitory control functions that depend on PFC and *(b)* the anatomical and biochemical developmental changes in PFC during that period. First, however, I will briefly indicate where PFC is located.

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LOCATING PREFRONTAL CORTEX GEOGRAPHICALLY

All of the cortex in front of the central sulcus is frontal cortex. The area just in front of the central sulcus, between it and the precentral sulcus, is primary motor cortex (Brodmann's area 4). In front of that is premotor cortex and the supplementary motor area (SMA), both subregions of Brodmann's area 6. All of the cortex in front of that is PFC (areas 8, 9, 10, 12, 44, 45, 46, 47, and 9/46). It is an extremely large area, about 25% of all the cerebral cortex in the human brain. While the brain as a whole has increased in size during evolution, the size of PFC is disproportionately large in humans (Blinkov & Glezer, 1968; Preuss, 2000). DL-PFC extends over the superior and middle frontal gyri. Areas 9, 46, and 9/46 comprise the core of DL-PFC (*mid-dorsolateral* PFC; Petrides & Pandya, 1999), with area 8 constituting the posterior portion of DL-PFC and area 10, the anterior portion. Areas 44, 45, and 47/12, all of which lie on the inferior frontal gyrus, comprise ventrolateral PFC.

DEVELOPMENT DURING THE FIRST YEAR OF LIFE

IMPROVEMENTS IN COGNITIVE FUNCTIONS THAT DEPEND ON PREFRONTAL CORTEX

The *A-not-B task* (introduced by Piaget, 1954, [1936]) has been used worldwide to study infant cognitive development (Wellman et al., 1987). Under the name *delayed response*, the almost-identical task has been widely used to study the functions of the DL-PFC subregion of PFC in rhesus monkeys since Jacobsen first introduced it for that purpose in 1935. In the A-not-B/delayed-response task, a participant watches as a desired object is hidden in one of two hiding places that differ only in left–right location. A few seconds later the participant is encouraged to find the hidden object. He or she must hold in mind over those few seconds where the object was hidden. Over trials, the participant must keep this mental record to reflect where the reward was hidden most recently. The participant is rewarded for reaching correctly by being allowed to retrieve the hidden object, thus reinforcing the behavior of reaching to that location. Hence the tendency to emit that response is strengthened. When the reward is hidden at the other location, the participant must inhibit the tendency to repeat the rewarded response and instead respond according to the representation held in mind of where the reward was hidden most recently. This task thus requires an aspect of working memory (holding information in mind), resistance to proactive interference, and inhibition of a prepotent action tendency (the tendency to repeat a positively reinforced response).

By roughly 7½ to 8 months of age, infants reach correctly at the first hiding location with delays as long as 2–3 seconds (Gratch & Landers, 1971; Diamond, 1985; see Fig. 29–1). When the reward is hidden at the other hiding location, however, infants err by reaching back to the first location (the *A-not-B error*). Infants show marked improvements in their performance on the A-not-B/delayed response task between 7½ and 12 months of age. For example, each month they can withstand delays approximately 2 seconds longer, so that by 12 months of age they can succeed with delays almost 10 seconds long (Diamond, 1985; Diamond & Doar, 1989).

In a transparent barrier detour task called "object retrieval" (Diamond, 1988, 1990, 1991), a toy is placed in a clear box, open on one side. Difficulties arise when the infant sees the toy through one of the closed sides of the box. Here, the infant must integrate seeing the toy through one side of the box with reaching through a different side. There is a strong pull to try to reach straight for the toy; that prepotent response must be inhibited when another side of the box is open. Infants progress through a well-demarcated series of five stages in performance of this task between 6 and 12 months of age (see Fig. 29–2). Infants of 6–8 months reach only at the side through which they are looking. They must look through the opening and continue to do so to reach in and retrieve the toy. As they get

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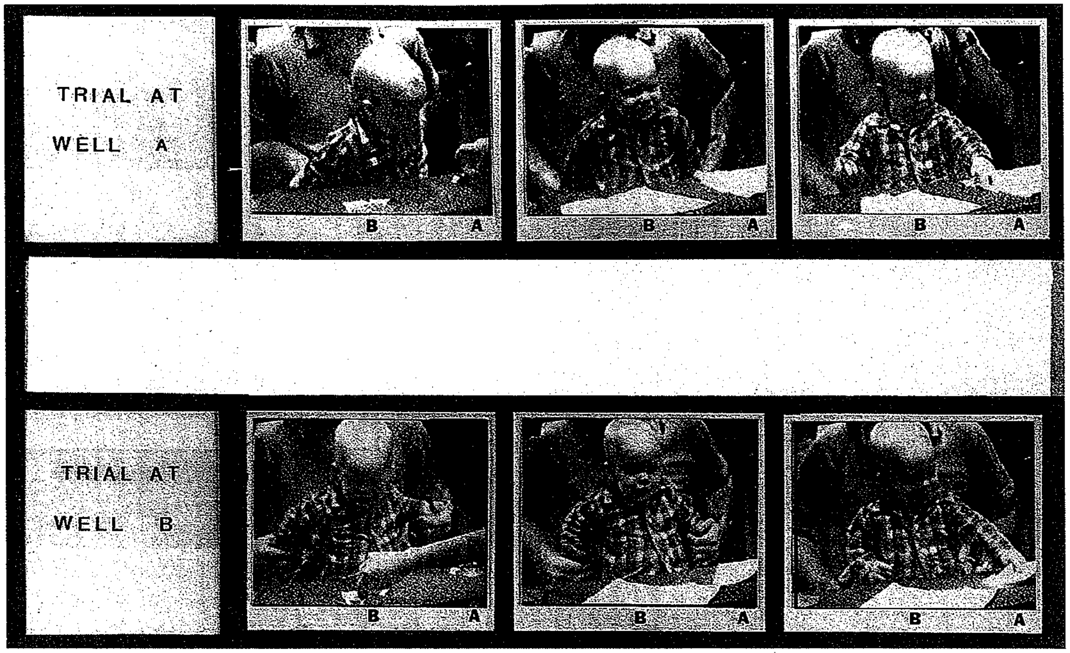


Figure 29–1. *A*: Illustration of the A-not-B task, showing an infant making the A-not-B error. The first frame (*top* and *bottom*) illustrates the experimenter hiding the desired object as the infant watches. Notice that the infant sees where the desired object is placed. The second frame of both rows illustrates the delay period. The delay begins immediately after both wells are covered. During the delay, the parent restrains the infant's arms, and the experimenter calls to the infant to break the infant's visual fixation on the correct well. The third frame of both rows illustrates the infant's response. The infant uncovers a well to search for the desired object. The infant reaches correctly during the trial at the A location, but on the trial at well B the infant incorrectly searches again at well A.

(*continued*)

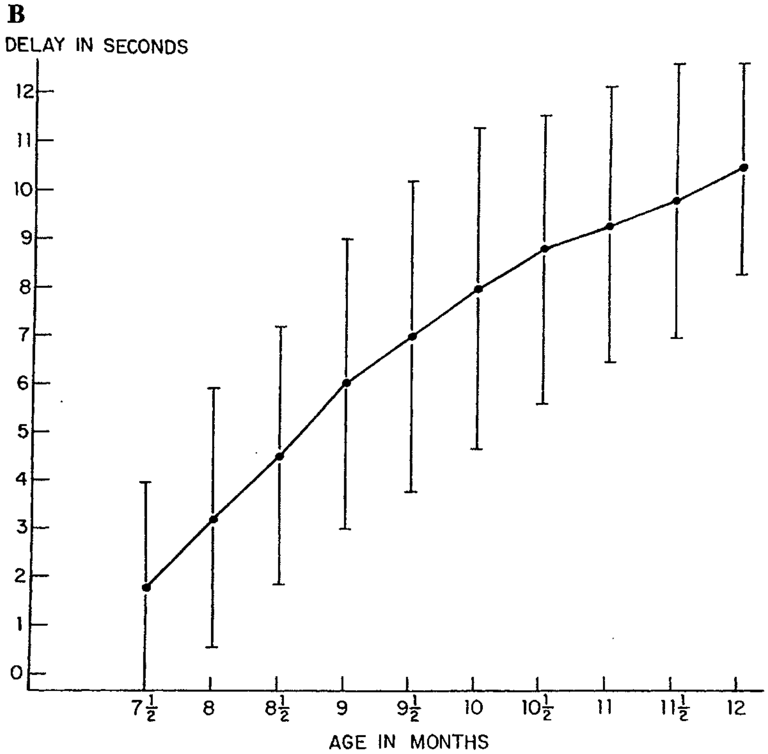
older, the memory of having looked through the opening is enough; infants can look through the opening, sit up, and reach in while looking through a closed side. By 11–12 months, infants do not need to look along the line of reach at all (Diamond, 1988, 1991).

Although the A-not-B/delayed response and object retrieval tasks share few surface similarities, human infants improve on these tasks during the same age period (6–12 months; Diamond, 1988, 1991) as do infant rhesus monkeys (1½–4 months; Diamond & Goldman-Rakic, 1986; Diamond, 1988, 1991). Despite marked variation among infants in the rate at which they improve on each of these tasks, the age at which a given infant reaches phase 1B on the object retrieval task is remarkably close to the age at which that same infant can first uncover a hidden object in the A-not-B/delayed response paradigm (Diamond, 1991; see Table 29–1).

There is no behavioral task more firmly linked to DL-PFC than the A-not-B/delayed response task (e.g., in ablation studies; see Butters et al., 1969; Goldman & Rosvold, 1970; Diamond & Goldman-Rakic, 1989; electrophysiology studies; see Fuster & Alexander, 1971; Fuster, 1973; Niki, 1974; localized cooling studies; see Fuster & Alexander, 1970; Bauer & Fuster, 1976; and localized injection of dopamine receptor antagonists; see Sawaguchi & Goldman-Rakic, 1991). This is one of the strongest brain–behavior relations in all of cognitive neuroscience.

Lesions of DL-PFC also disrupt performance on the object retrieval task (Diamond & Goldman-Rakic, 1985; Diamond, 1991). Injections of 1-methyl-4-phenyl-1,2,3,6-tetrahy-

Figure 29–1 (*continued*)
B: Developmental progression in the ability to withstand longer and longer delays on the A-not-B task as infants get older (based on 25 infants tested longitudinally every 2 weeks). The graph shows that as infants get older, increasingly, longer delays are required to elicit the A-not-B error. (*Source:* Reprinted with permission from Diamond, 1985)



dropyridine (MPTP), which reduce the level of dopamine in PFC, also produce deficits in object retrieval task performance (Taylor et al., 1990a,b; Schneider & Roeltgen, 1993). (MPTP also affects the level of dopamine in the striatum, but lesions of the striatum do not impair performance on the object retrieval task [Crofts et al., 1999].)

Human infants of 7½ to 9 months, infant monkeys of 1½ to 2½ months, adult monkeys in whom DL-PFC has been ablated, infant monkeys of 5 months in whom DL-PFC was ablated at 4 months, and adult monkeys who have received MPTP injections to disrupt the prefrontal dopamine system fail the A-not-B/delayed response and object retrieval tasks under the same conditions and in the same ways (Diamond, 1988, 1991). Developmental improvements on the A-not-B/delayed response and object retrieval tasks in human infants are related to changes in the pattern of electrical activity detected by electroencephalogram (EEG) over frontal cortex and in the coherence of electrical activity detected by EEG over frontal cortex and parietal cortex (re: the A-not-B task, see Fox & Bell, 1990; Bell & Fox, 1992, 1997; re: the object retrieval, N.A. Fox, personal communication). This does not prove that maturational changes in DL-PFC during infancy are one of the prerequisites for the age-related improvements in performance of these tasks, but it is consistent with that hypothesis.

ANATOMICAL AND BIOCHEMICAL EVIDENCE OF PREFRONTAL CORTEX MATURATION DURING THE FIRST YEAR OF LIFE

In humans the period of marked growth of the length and extent of the dendritic branches of pyramidal neurons in layer III of DL-PFC is 7½ to 12 months (Koenderink et al., 1994), coinciding exactly with the period when human infants are improving on the A-not-B/delayed response and object retrieval tasks. Pyramidal neurons in DL-PFC have a relatively short dendritic extent in 7½-month-old infants. By 12 months of age, their dendrites have reached their full mature extension.

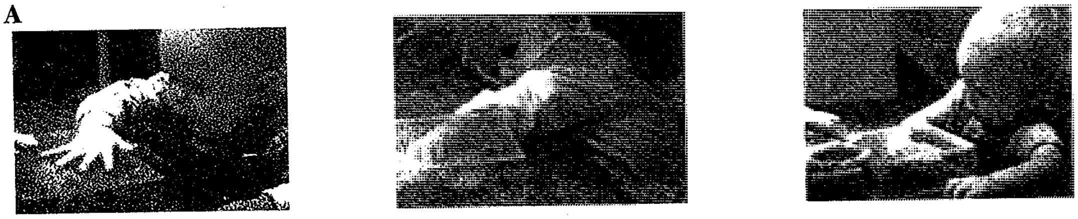


Figure 29–2. *A*: Examples of the typical performance of infants at 6–8 months, 8½ to 9 months, and 10½ to 12 months on the object retrieval task. In each frame the same transparent box is shown with a desired toy visible inside. *Frame 1* shows performance typical of Phases 1 and 1B. Here the front of the box is open, but the infant sees the toy through the closed top of the box. This 6½-month-old infant tries to retrieve the toy by reaching directly for it through the side he is looking through, as do all infants at that age. Although his hand hits the solid, impenetrable surface of the box's top, and although he may touch the top edge of the box's opening and even grasp the opening's edge, the infant tries only, though persistently, to reach through the side through which he is looking. *Frame 2* shows performance typical of Phase 2. This 8½-month-old infant still needs to look through the side she is reaching. Sitting straight up, she sees the toy through the top, and perhaps through the front of the box, but it is the right side of the box that is open. Infants at this age come up with a very creative solution to their need to match up the side through which they are looking and reaching. They lean over to look through the open side. In that position, their arm ipsilateral to the box opening is somewhat trapped under their body, so infants recruit the contralateral arm, whose movement into the box they can monitor from start to finish. This "awkward reach" may look inelegant, but it is a very creative way to get the job done, given infants' strong pull to reach through the side through which they are looking. *Frame 3* illustrates performance typical of Phase 4. This infant, now 11 months old, is the same infant pictured in Frame 1. Now the infant can sit up straight, look through the closed top of the box, and reach into the open right side of the box to retrieve the toy. No longer does the infant need to look through the box opening to retrieve the toy. Note the complex mental calculation needed to coordinate a direct line of sight to the toy through the top of the box and a circuitous detour reach through the box's right side. *(continued)*

These dendritic branches reach a plateau—in total length, in length of uncut terminal segments, and in radial distance—at around 1 year of age, a plateau that extends at least through 27 years of age. The surface of the cell bodies of these neurons also increases between 7½ and 12 months of age (Koenderink et al., 1994). The level of glucose metabolism in DL-PFC increases during this period as well, and reaches approximately adult levels by 1 year of age (Chugani & Phelps, 1986; Chugani et al., 1987).

Dopamine is an important neurotransmitter in PFC. During the period when infant rhesus monkeys are improving on the A-not-B/delayed response and object retrieval tasks (1½–4 months), the level of dopamine increases in their brain (Brown & Goldman, 1977; Brown et al., 1979), the density of dopamine receptors increases in their PFC (Lidow & Rakic, 1992), and the distribution within their DL-PFC of axons containing the rate-limiting enzyme (tyrosine hydroxylase) for production of dopamine markedly changes (Lewis & Harris, 1991; Rosenberg & Lewis, 1995).

Indeed, even as early as the first year of life, the dopamine projection to PFC is already critical for the cognitive functions subserved by DL-PFC. Thus, if infants 6–12 months old (as well as in older children) have reduced dopamine in PFC while in other respects their central nervous systems appear to be normal, they show a selective deficit in holding information in mind and simultaneously inhibiting a prepotent response (as, for example, on the A-not-B and object retrieval tasks) while other cognitive functions appear to be spared (Diamond et al., 1997; Diamond, 2001).

Acetylcholinesterase (AChE) is an enzyme essential for metabolizing another neurotransmitter, acetylcholine. The pattern of AChE staining in various layers of DL-PFC changes dramatically during the first year of life in humans (Kostovic et al., 1988; Kostovic, 1990).

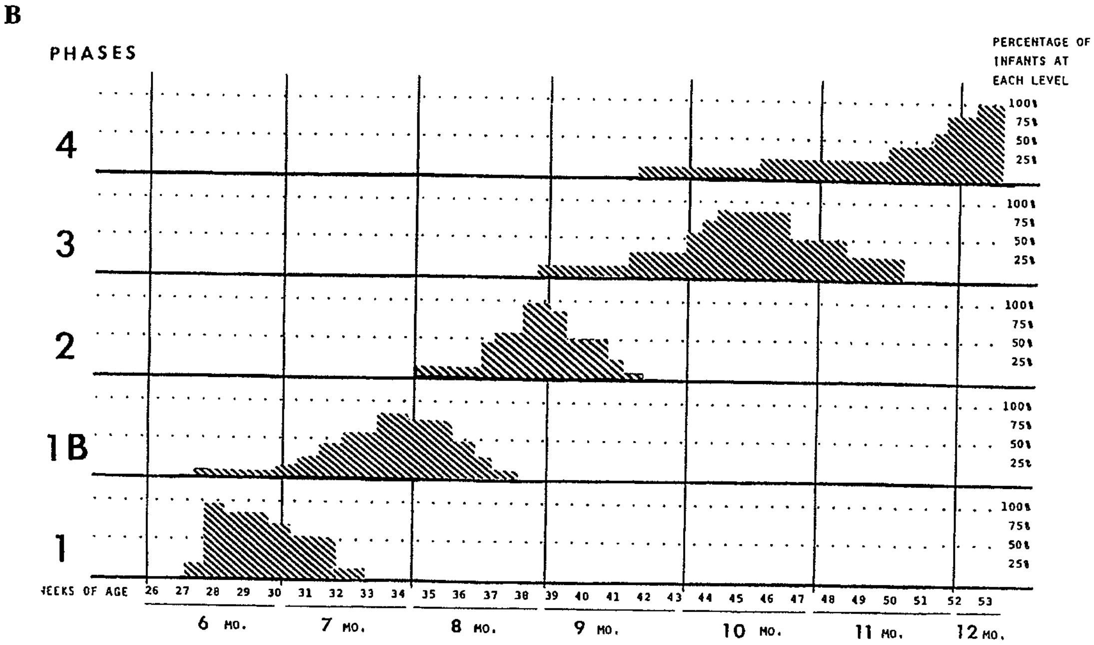


Figure 29–2 (*continued*) *B*: Illustration of the developmental progression on the object retrieval task. These histograms indicate the percentage, at each age, of 25 infants tested longitudinally every 2 weeks (Diamond, 1990) who were performing at each level of competence with transparent boxes on the object retrieval task. (Source: reprinted with permission from Diamond, 1988.)

DEVELOPMENT AT 1 TO 3 YEARS OF AGE

IMPROVEMENTS IN COGNITIVE FUNCTIONS THAT DEPEND ON PREFRONTAL CORTEX

Less is known about changes during this period in the cognitive functions dependent on PFC or in PFC anatomy and biochemistry than during any other period of life. It is area ripe for further investigation.

Koslowski and Bruner (1972) charted the developmental progression between the ages of 12 and 24 months in the ability to use a lazy Susan to bring a toy within reach. This task requires relating the lazy Susan and its movement to the toy and its movement. It also requires inhibition of trying to reach on a direct line of sight (as the younger children try to do) and inhibition of the tendency to push the lazy Susan in the direction one wants the toy to go (one must push left to make the toy approach on the right). Case (1985; Marini & Case, 1989) similarly reports marked improvements in performance of a simple balance beam problem by children between 1½ and 2½ years of age.

Using a battery of tasks, Kochanska and colleagues (2000) found that the ability to inhibit a prepotent response in order to perform a modulated or different response improved markedly from 22 to 33 months of age and that consistency in performance across the various measures also increased from 22 to 33 months of age. In a spatial-incompatibility task appropriate for children 24 to 36 months old, Gerardi-Caulton (2000) instructed the children to press the button that matched the stimulus. For each pair of stimuli, a stimulus might appear on the same side as its associated button (spatially compatible trial) or on the side opposite its button. Thus, on roughly half the trials, children had to inhibit the prepotent tendency to respond on the same side as the stimulus. Although the location of the stimulus is irrelevant to the task, even adults perform worse on trials in which a stimulus and its associated response are on opposite sides (*the Simon effect*; e.g., Simon, 1969;

Table 29–1. Age at which 25 infants studied longitudinally entered Phase 1B of object retrieval and could first uncover a hidden object°

	Age (in weeks [and days]) of First Appearance of:		
Infant	Phase 1B, Object Retrieval Task	Able to Uncover a Hidden Object, One Hiding Location	A-not-B Error
Brian	28 (3) =	28 (3)	
James	28 (5)	28 (5)	30 (5)
Erin	30 (3)		32 (4)
Nina	31		29
Jennine	31 (4) =	31 (4)	33 (2)
Kate	31 (6)		33 (5)
Rachel	32 (4)		30 (6)
Isabel	32 (5) =		32 (5)
Chrissy	32 (6) =	32 (6)	34 (4)
Ryan	33 (1) =		33 (1)
Bobby	33 (2) =		33 (2)
Julia	33 (2) =		33 (2)
Lyndsey	33 (2) =		33 (2)
Jamie	34 =		34
Mariama	34		36 (3)
Michael	34		36 (4)
Emily	34 (2) =		34 (2)
Graham	34 (2) =		34 (2)
Jane	34 (5) =		34 (5)
Sarah	34 (6) =		34 (6)
Jack	35 (3) =	35 (3)	37 (5)
Blair	35 (4) =	35 (4)	37 (3)
Rusty	35 (6)		33 (5)
Tyler	36 (2)		38 (4)
Todd	39 (4) =		35 (1)

°Five infants were not yet ready for A-not-B testing with two wells when they could first uncover a hidden object. Note the striking similarity in age of entering object retrieval phase 1B and age of onset of the A-not-B error.

Simon et al., 1976; Lu & Proctor, 1995). By 2½ years of age, children were able to inhibit the prepotent tendency well enough to perform above chance on the spatially incompatible trials and by 3 years they were correct 90% of the time, though they (like adults) continued to be faster on the compatible than the incompatible trials.

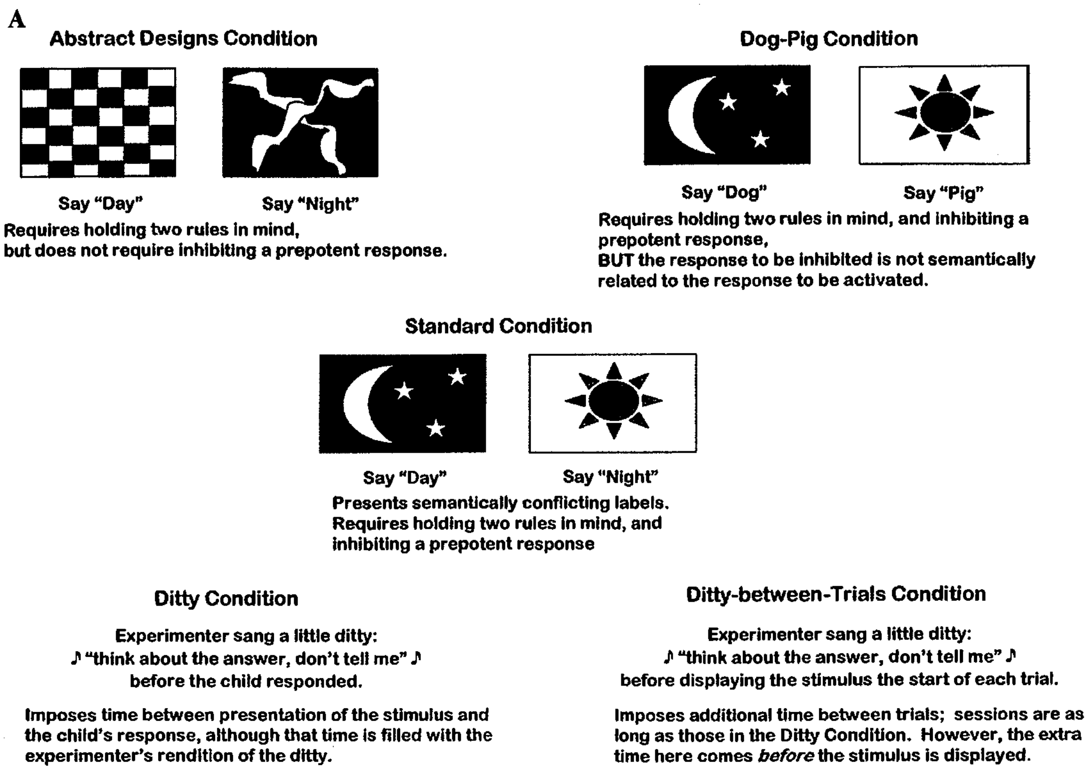
ANATOMICAL AND BIOCHEMICAL EVIDENCE OF PREFRONTAL CORTEX MATURATION BETWEEN 1 AND 3 YEARS OF AGE

Almost nothing is known about changes in PFC during this period. One of the few things we do know is that the AChE reactivity of layer III pyramidal neurons begins to develop during this period (Kostovic, 1990), but that is surely not the only change in PFC between 1 and 3 years of age.

DEVELOPMENT AT 3 TO 7 YEARS OF AGE

IMPROVEMENTS IN COGNITIVE FUNCTIONS THAT DEPEND ON PREFRONTAL CORTEX

The period of 3–7 years of age, and especially 3–5 years, is a time of marked improvements on a great many cognitive tasks that require holding information in mind plus inhibition (tasks such as day–night, tapping, card sorting, go/no-go, conditional discrimination, appear-



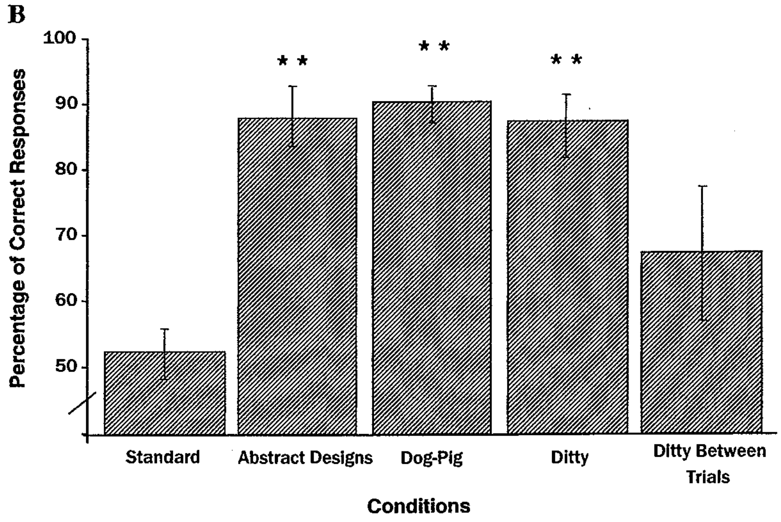


Figure 29–3. *A:* Illustration of the standard day–night task (center) and of some variants of it. *B:* Performance of 4-year-old children on the day–night task. Children perform at chance in the standard condition, but succeed when the demands on inhibition are reduced (the abstract designs and dog-pig conditions) and when forced to allow themselves more time to compute their answers (the ditty condition). °°Performance significantly better than that on the standard condition at $P < 0.001$.

ance–reality, theory of mind, false belief, liquid conservation, and delay of gratification). On the *day–night task* (Gerstadt et al., 1994; Diamond et al., 2002; Fig. 29–3) a child must hold two rules in mind, inhibit saying what the stimuli really represent, and instead say the opposite ("Say 'night' when shown a white card with a picture of the sun, and say 'day' when shown a black card with a the moon and stars"). Children 3½ to 4½ years of age find the task very difficult; by the age of 6–7 years it is trivially easy. Improvement in responding correctly is relatively continuous from 3½ to 7 years of age (see Fig. 29–4), while the im-

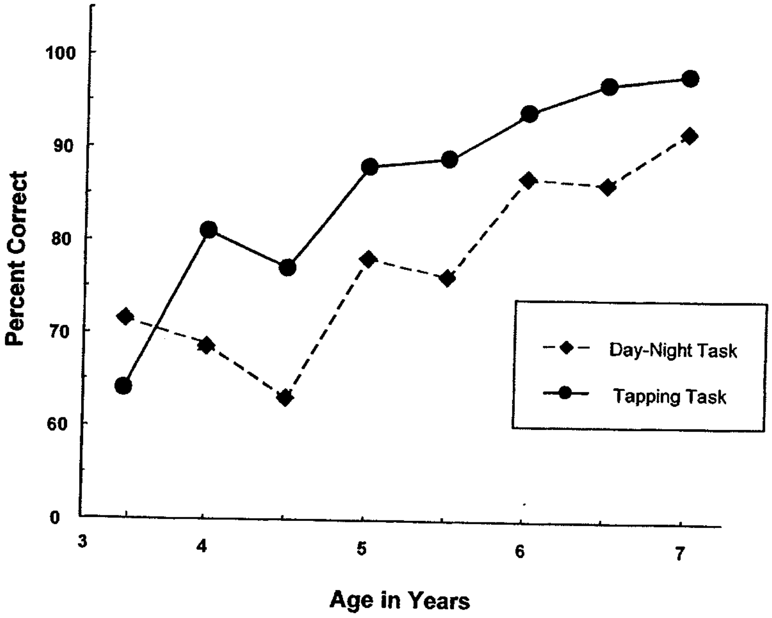


Figure 29–4. Illustration of the developmental progression of children on the day–night and tapping tasks (Source: reprinted with permission from Diamond & Taylor, 1996, Fig. 5)

provement in speed of responding occurs primarily from 3½ to 4½ years.

If abstract designs are used as the stimuli, even the youngest children have no difficulty correctly saying 'day' to one and 'night' to the other (Gerstadt et al., 1994; see Fig. 29–3). Hence, the need to learn and remember two rules is not in itself sufficient to account for the poor performance of young children. If the words to be said to the white-sun and black-moon cards are "dog" and "pig" or "dog" and "cat," even the youngest children have no difficulty (Diamond et al., 2002; see Fig. 29–3). Hence, young children can remember two rules and inhibit saying what the images on the cards represent *unless* what the children are supposed to say is semantically related to what they are not supposed to say.

Comparisons across different trials of the same child and comparisons on the same trials across different children show that when younger children take longer to respond they perform better (Gerstadt et al., 1994). Apparently, it is sufficiently difficult for them to compute the answer of saying "day" to the black-moon card or "night" to the white-sun card that it takes them quite a long time to generate the correct answer. When they rush or answer impulsively, they err. If a delay between presentation of the stimulus and when the child is able to respond is imposed by chanting a little ditty to the child ("think about the answer, don't tell me"); even young children of 4 years are able to succeed despite the potential interference from the experimenter's chanting (see Fig. 29–3). Slowing down the session by inserting the experimenter's chanting is not what helps the children because if the chanting comes before the stimulus is presented, it does not help the children (see Fig. 29–3).

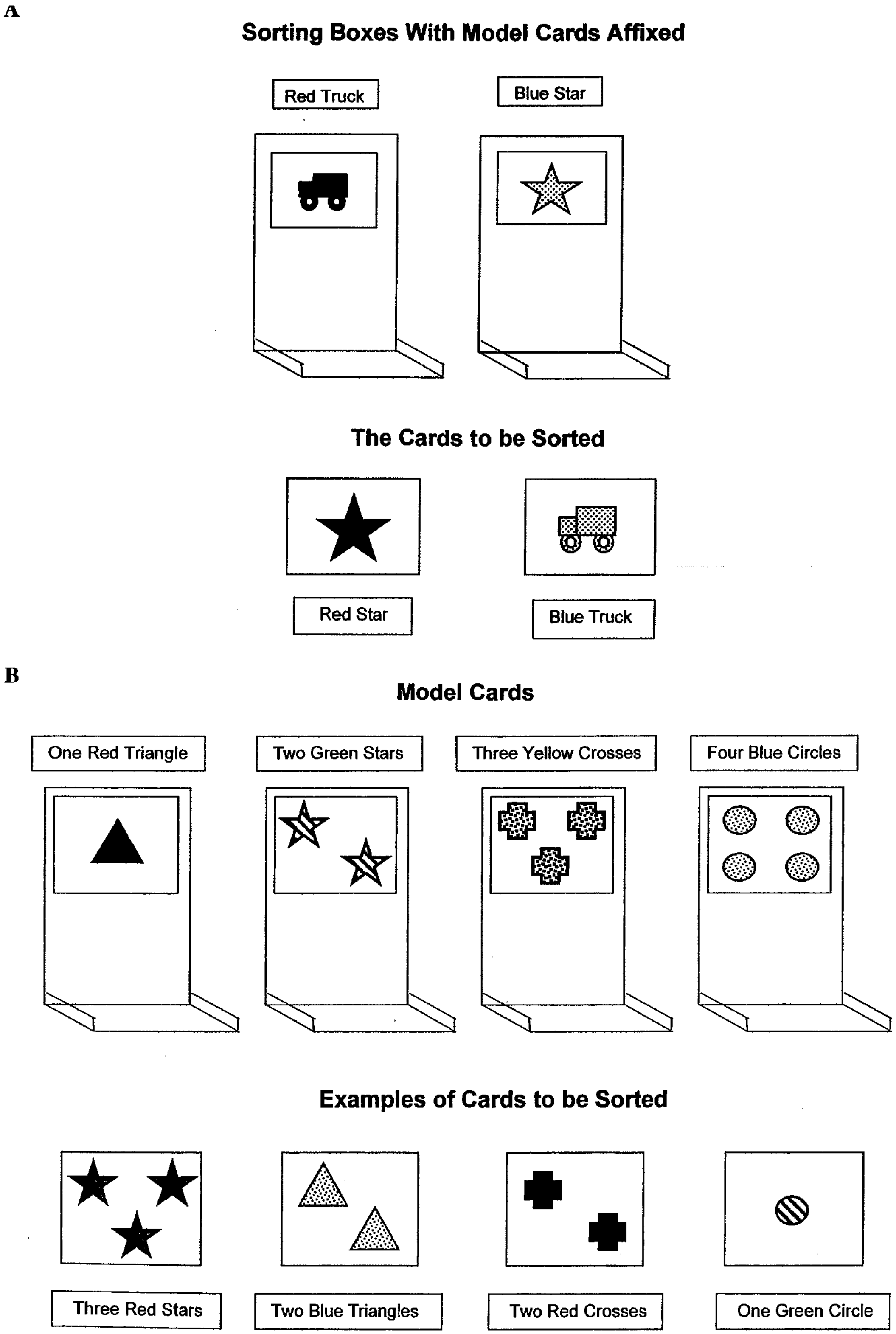
Luria's *tapping test* (Luria, 1966) also requires *(a)* remembering two rules and *(b)* inhibiting a prepotent response to make the opposite response instead. Here, one needs to remember the rules, "tap once when the experimenter taps twice, and tap twice when the experimenter taps once," and inhibit the tendency to mimic what the experimenter does. Adults with large frontal lobe lesions fail this task (Luria, 1966). Performance of this task has been shown to increase activation in DL-PFC in normal adults, in comparison with mimicking the experimenter's tapping response (Brass et al., 2001). The greatest improvement in correct responding on this task occurs between 3½ and 4 years of age, and the greatest improvement in speed of responding occurs between 4½ and 5 years (Passler et al., 1985; Becker et al., 1987; Diamond & Taylor, 1996; see Fig. 29–4).

Performance on the day–night and tapping tasks is correlated, so that children whose performance on the day–night task is delayed or accelerated show a corresponding delay or acceleration in their performance of the tapping task (Diamond et al., 1997; Diamond, 2001). Indirect evidence on the neural system underlying successful performance on these tasks comes from the finding that children treated early and continuously for phenylketonuria (PKU) and who are thought to have reduced levels of dopamine in PFC are impaired in their performance of both the day–night and tapping tasks but not on an array of unrelated cognitive tasks (Diamond et al., 1997; Diamond, 2001).

Three-year-olds make an error reminiscent of infants' A-not-B error, but on a more difficult task. On this task, 3-year-olds sort cards correctly by the first criterion (regardless of whether that criterion is color or shape; see Zelazo et al., 1995, 1996; Fig. 29–5), just as infants and prefrontally-lesioned monkeys are correct at the first hiding place, and adults with PFC damage sort cards correctly according to the first criterion on the Wisconsin Card Sort Test (WCST; Milner, 1964; Drewe, 1974; Stuss et al., 2000; Fig. 29–5). Three-year-olds err when they must switch to a new sorting criterion, e.g., when cards previously sorted by color must now be sorted by shape. This error is similar to that of infants of 7½ to 9 months and prefrontally lesioned monkeys when the reward is switched to a new hiding location, and to that of adults with PFC damage when they are required to switch to a new sorting criterion. Although 3-year-old children fail to sort by the new sorting criterion, they can correctly state the new criterion (Zelazo et al., 1996), as is sometimes seen with adult patients who have sustained damage to PFC (Luria & Homskaya, 1964; Milner, 1964). Infants, too, occasionally indicate that they know the correct answer on the A-not-B task, by looking at the correct well, although they reach back incorrectly to the well that was previously correct (Diamond, 1991; Hofstadter & Reznick, 1996). By 4 years of age, most children succeed on the simple card sorting task with two dimensions, two values per dimension, and a single switch between dimensions; by 5 years of age, all succeed (Zelazo et al., 1995, 1996; Kirkham et al., 2002).

Zelazo's card sort task can be thought of as perhaps the simplest possible test of task switching. Children must first sort the cards by one dimension (e.g., color, task 1) and then switch to sorting them by the other dimension (e.g., shape, task 2). The single switch between tasks occurs between the block of trials for task 1 and the block of task 2 trials. Errors occur because of difficulty in inhibiting or overcoming what might be termed *attentional inertia*, the tendency to continue to focus on what had been initially relevant (Kirkham et al., *submitted*). For example, once a child of 3 years has focused on the "redness" of a red truck, it is difficult for the child to switch mind-sets and focus on its "truckness." The child gets stuck in thinking about a stimulus in the initially appropriate way.

That tendency never completely disappears. Traces of it can be seen in the heightened reaction times of even healthy, young adults when they are required to switch and respond on the basis of another dimension (e.g., Rogers & Monsell, 1995; Monsell & Driver, 2000; Diamond & Kirkham, 2001). No matter how much warning adults are given about which dimension will be relevant on the upcoming trial, and no matter how long the period between the forewarning and when the stimulus appears or how long the period between trials, adults are still slower to respond on trials in which the relevant dimension switches than on non-switch trials (Allport et al., 1994; Rogers & Monsell, 1995; Meiran, 1996). Remnants of attentional inertia can also be seen in the difficulty adults have in representing more than one interpretation of an ambiguous figure at a time (Chambers & Reisberg, 1985). Even when informed of the alternatives in an ambiguous figure, 3-year-old children remain stuck in their initial way of perceiving the figure; they cannot reverse (Gopnick & Rosati, 2001). By 5 years of age, most children can reverse. Seeing a stimulus in the card sort task


A
Sorting Boxes With Model Cards Affixed
Red Truck
Blue Star
The Cards to be Sorted
Red Star
Blue Truck
B
Model Cards
One Red Triangle
Two Green Stars
Three Yellow Crosses
Four Blue Circles
Examples of Cards to be Sorted
Three Red Stars
Two Blue Triangles
Two Red Crosses
One Green Circle

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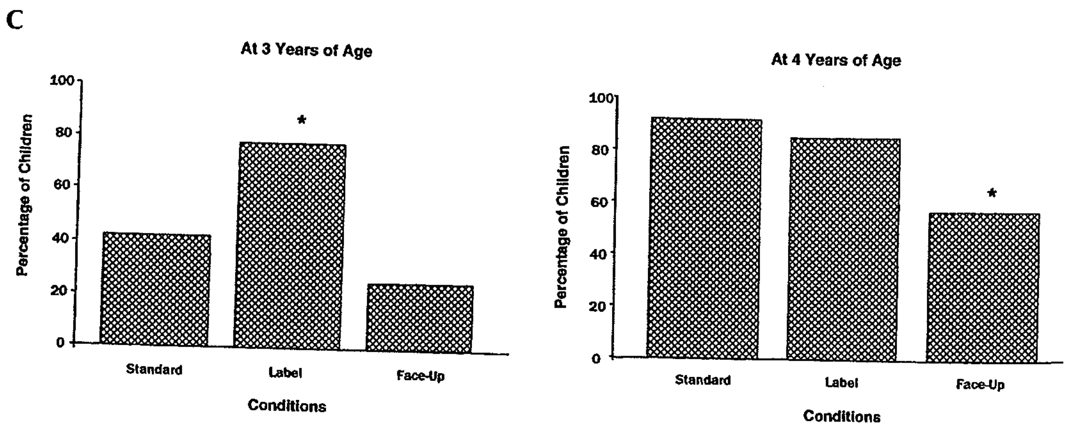


Figure 29–5. *A*: Illustration of the Kirkham et al. (submitted) version of Zelazo's card sorting task for preschoolers. When sorting by color, for example, the blue truck card should go in the bin under the blue star card. When sorting by shape, the blue truck card should go in the bin under the red truck card. *B*: Illustration of the Wisconsin Card Sorting Test (WCST), one of the classic tests for studying prefrontal cortex function in adults (Milner, 1964; Drewe, 1974; Stuss et al., 2000). Each card in this test can be sorted by color, shape, or number. The task for the participant is to deduce the correct sorting criterion on the basis of feedback and to flexibly change the manner of sorting when the experimenter changes the sorting criterion without warning. Zelazo's card sort task and the WCST are similar in that participants are to sort each of the cards in a deck under a model card, first by one dimension and then by another. There are also differences between the tasks, however, in addition to the obvious ones of two dimensions and two levels per condition in Zelazo's task and three dimensions and four levels per dimension in the WCST. For the WCST, the participant must deduce the correct sorting criterion based on feedback; in Zelazo's task, children are told what the correct criterion is and when the criterion switches. Feedback is given after each sorting response in the WCST, whereas no feedback is given after any card is sorted on Zelazo's task. Zelazo's task involves only one switch of sorting criteria; the WCST involves several. Memory load is intentionally minimized on Zelazo's card sort task by the experimenter reminding the child of the current sorting criterion on every trial; in the standard version of the WCST, no such memory aid is provided. *C*: Percentage of children who currently switched dimensions on Kirkham et al.'s (submitted) version of Zelazo's card sort task. An asterisk above a histogram indicates significantly different performance from that of children of the same age on the standard condition at $P < 0.05$.

relevant in incompatible ways to the previously relevant dimension and the newly relevant dimension (e.g., according to its color, one response would be correct, but according to its shape the other response is correct) creates a problem. There is a pull to focus on the previously relevant dimension and to respond on that basis, which must be inhibited before the correct response can be made—despite knowing full well which dimension is currently relevant and which responses are appropriate for each value along that dimension.

Similarly, children 3 years of age have difficulty with *appearance–reality tasks* (Flavell, 1986, 1993) in which they are presented, for example, with a sponge that looks like a rock. Three-year-olds typically report that it looks like a rock and really is a rock, whereas children 4–5 years of age correctly answer that it looks like a rock but really is a sponge. The problem for the younger children is in relating two conflicting identities of the same object (e.g., Rice et al., 1997) and in inhibiting the response that matches their perception. When Heberle and colleagues (1999) reduced perceptual salience in the appearance–reality task (by removing the object during questioning), they found significantly better performance by children 3–4 years of age.

Theory-of-mind and *false-belief tasks* are other tasks that require holding two things in mind about the same situation (the true state of affairs and the false belief of another person) and inhibiting the impulse to give the veridical answer. For example, the child must keep in mind where the hidden object is now and where another person saw it placed before, and must inhibit the inclination to say where the object really is, saying instead where the other person (who is mistaken) would think it is (see Fig. 29–6). Manipulations that reduce the perceptual salience of the true state of affairs aid children 3–4 years of age (e.g., telling the children where the object is really hidden but never actually showing them [Zaitchik, 1991]), as do manipulations that reduce the inhibitory demand in other ways. For example, Carlson et al. (1998) reasoned that pointing veridically is likely to be a well-practiced and reinforced response in young children, and that children of 3–4 years have trouble inhibiting that tendency when they should point to the false location on false-belief tasks. Carlson et al. (1998) found that 3- to 4-year-old children performed better when given a novel response by which to indicate the false location.

Increasing the perceptual salience of the previous dimension impairs performance. For example, cards are normally sorted face-down in Zelazo's card sort task. If they are sorted face-up and color was the previous dimension, a red-star card would be under the red-truck model and a blue-truck card would be under the blue-star model. This emphasizes the salience of the color dimension. While almost all 4-year-olds succeed in the standard (face-down) condition, almost 50% of 4-year-olds fail the face-up condition (Kirkham et al., submitted; see Fig. 29–5C). Similarly, the cards are normally sorted face-up in the WCST. If they are sorted face down, adults perform better and adults with frontal lobe damage are especially helped. Manipu-

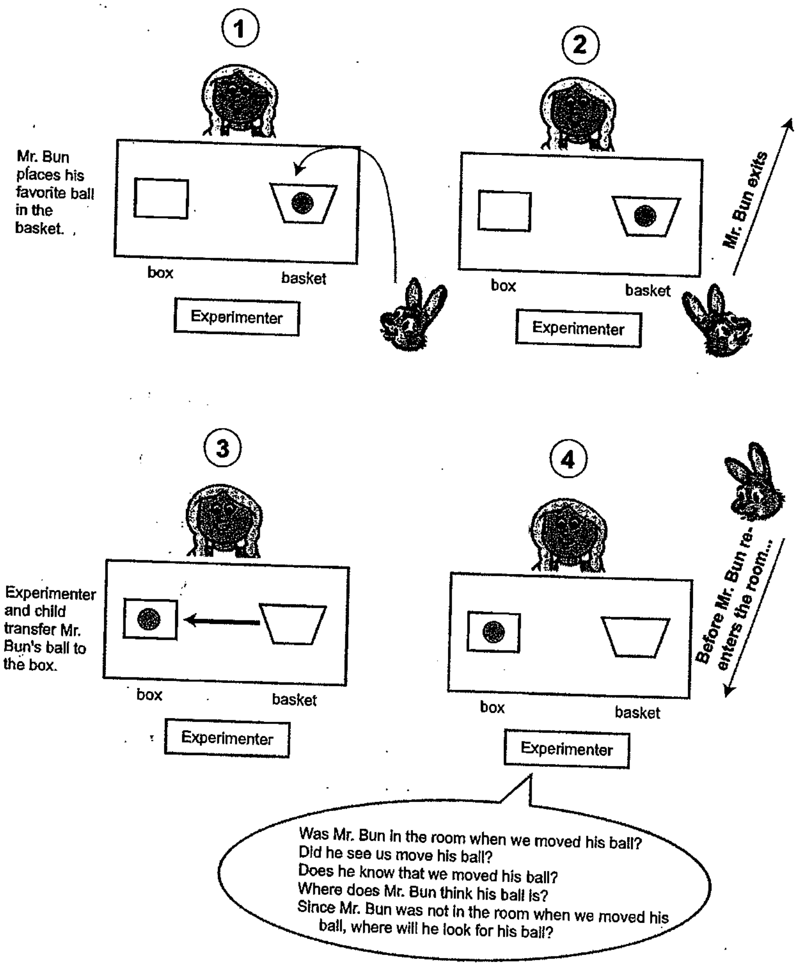


Figure 29–6. Illustration of a typical theory-of-mind task.

lations that *reduce* perceptual salience on appearance–reality tasks, by removing the object during questioning, enable children of 3–4 years to perform much better (e.g., Heberle et al., 1999).

Redirecting attention to the currently relevant dimension improves performance. At the outset of each trial in Zelazo's card sort task, the experimenter labels the new card for the child according to the relevant dimension (e.g., "Here is a truck" or "Here is a blue one"). Despite that, most 3-year-olds continue to sort by the previously correct dimension. One small change—having the child, rather than the experimenter, label the card to be sorted—enables most 3-year-olds to succeed on the switch trial. Thus, if the experimenter asks the child to label each new card (by asking on the first trial of a dimension, "What color (shape) is this?" and on the following trials, simply, "What is this?"), almost twice as many 3-year-olds are able to succeed when the sorting criterion changes (Towse et al., 2000; Kirkham et al., submitted; see Fig. 29–5C [Label Condition]). Children 3 years of age find it extremely difficult to redirect their attention to a newly relevant sorting dimension when the values of the dimension they had been using are still present; they appear to get stuck in a mind-set (a way of thinking about the stimuli) that is no longer relevant. Perhaps their own labeling of the relevant dimension gives 3-year-old children a way to use verbal mediation to help themselves (Luria, 1959; Vygotsky, 1978) inhibit the mental set that is no longer correct and refocus their attention.

Patients with frontal cortex damage are much worse at switching to sort by a different dimension and at switching tasks than are patients with damage elsewhere in the brain or normal controls. It is now fairly firmly established that being able to switch criteria on the WCST test and to resist perseverating on the previously correct dimension selectively recruits lateral prefrontal cortex, perhaps especially dorsolateral prefrontal cortex, and is particularly vulnerable to damage to DL-PFC compared with damage elsewhere in the brain, including other prefrontal regions (Milner, 1964, 1971; Stuss et al., 2000). There is also broad consensus that patients with frontal cortex damage in the left hemisphere, in contrast with patients with damage to other areas of the brain, are impaired at switching between tasks (e.g., switching between dimensions; Shallice & Burgess, 1991; Owen et al., 1993; Rogers et al., 1998; Diedrichsen et al., 2000; Keele & Rafal, 2000). They are impaired under the same conditions as those under which children 3 years of age fail (i.e., when the stimuli are relevant to both tasks), and they fail in the same way as do 3-year-old children (by perseverating on the previously relevant dimension). Like children of 3 years, their deficit in switching to the newly relevant dimension persists over several consecutive trials (Keele & Rafal, 2000).

Neuroimaging studies of brain activity in healthy, young adults yield similar results. Activity in lateral PFC (both dorsolateral [Brodmann areas 9 & 46] and ventrolateral [areas 44 & 45]) is consistently found to be increased when people must switch between tasks, compared to when they continue doing the same task (Meyer et al., 1998; Postle & D'Esposito, 1998; Omori et al., 1999; Badre et al., 2000; Dove et al., 2000; Sohn et al., 2000; Wylie et al., 2000; Braver et al., 2001; Dreher et al., 2001; Landau et al., 2001). Similar results have been found using the WCST (for analysis with position emission tomography [PET] neuroimaging, see Berman et al., 1995; Nagahama et al., 1996; with single-photon emission computed tomograph [SPECT] neuroimaging, see Marenco et al., 1993; Rezai et al., 1993; with functional magnetic resonance imaging [fMRI] see Konishi et al., 1998, 1999a; Monchi et al., 2001). Konishi et al. (1998, 1999a) found increased activation in a posterior portion of the inferior frontal sulcus (dorsal Brodmann areas 45/44) that was time-locked to when the sorting dimension changed. This occurred even when participants were explicitly informed of the new sorting dimension (Konishi et al., 1999a; much as children are explicitly informed of the new sorting dimension on Zelazo's card sort task). Monchi et al. (2001) found that activity in area 47/12 of ventrolateral prefrontal cortex increased specifically when feedback signaled a switch in the sorting dimension on the WCST.

Zelazo's card sort task can be thought of as a conditional discrimination task (e.g., if it is a color game, blue truck goes with blue star; if it is a shape game, blue truck goes with red truck). Indeed, the cognitive complexity and control theory espoused by Zelazo and Frye (1997) emphasizes the conditional, hierarchical rule structure implicit in the card sort task. In classic conditional discrimination paradigms participants first learn that responding to one member of a pair of stimuli is rewarded (analogous to the pre-switch block in the card sort task). Testing conditions might be as follows: Stimuli are always a circle and triangle; both are shown on every trial, always against a black background; right–left positions of the stimuli are randomly varied over trials; and choice of the circle is always rewarded. After participants reach a high level of accuracy, the stimuli are presented against a different background (say, white) and the reward contingencies are reversed (analogous to the post-switch block in the card sort task). Hence, the conditional rules for this illustration would be if the background is white, choose triangle; if the background is black, choose circle. After passing criterion on the second subtask, trials with each background are alternated or randomly intermixed (analogous to the mixed-task block in task-switching paradigms). Participants receive feedback on every trial about whether their response is correct or not (unlike the standard procedures in Zelazo's card sort task or task-switching paradigms).

When children are tested with procedures similar to those used with monkeys (minimal instruction so that the participant must deduce the rules), children cannot succeed at the task until they are 4½ to 5½ years old (Heidbreder, 1928; Jeffrey, 1961; Gollin & Liss, 1962; Gollin, 1964; 1965; Doan & Cooper, 1971). When told the rule, children younger than 4½ do much better, but perfect performance is not seen until about age 5 (Shepard, 1957; Osler & Kofsky, 1965; Gollin, 1966; Campione & Brown, 1974). Children younger than 3½ years cannot do this at all, even with explicit instruction. For example, when Gollin (1966) gave reminder trials with feedback before the mixed-task block, he found that 3½-year-olds (43–48 months) performed better, but children of 3 years still failed. Note again the transition between the ages of 3 and 5 years.

While conditional discrimination tasks involve two relevant dimensions and participants must relate two separate things (background color and foreground shape) to one another, *only* two rules apply: if there is a black background, choose circle; if white, choose triangle. There are half as many rules as on the card sort task, yet success appears at the same age. Similarly, the day–night and tapping tasks involve only two rules (e.g., when the tester taps once, you tap twice, when the tester taps twice, you tap once), but they also require inhibition of strong stimulus–response mappings, and children of 3 years fail them miserably (Gerstadt et al., 1994; Diamond & Taylor, 1995).

Conversely, when children need to hold four rules in mind, but no inhibition or shifting of attention is required, children 3 years of age succeed. Zelazo et al. (1995) presented 3-year-old children with two manipulations of the card sort task that required memory of four rules (the same number as in the standard version) but did not require switching between two dimensions (unlike the standard version). In one condition, children were presented with four target cards of different shapes and told four rules: "If it is a plane, it goes here; if it is a car, it goes here; if it is a bus, it goes here; and if it is a boat, it goes here." Three-year-olds performed better there than on the standard version of the task, even though they were required to keep the same number of rules in mind.

Recently Brooks and colleagues (2001) and Perner and Lang (2002) independently tested children on conditional discrimination reversal tasks where the relevant dimension never changed. Their tasks contained the same number of rules (four) and the same hierarchical embedding as Zelazo's card sort task (two games, two rules each), but unlike the card sort task, the tasks of Brooks et al. and Perner and Lang contained no switch of dimensions. The same, single dimension was relevant throughout. (Indeed, being black-and-white line drawings, the stimuli contained only one dimension [shape, object identity].) In Brooks et al.'s "same" game, children were to sort airplanes with the airplane model card and dogs with the dog model card. In the "silly" game, children were to sort dogs with the airplane model card and planes with the dog model card. Similarly, in Perner and Lang's pre-switch "normal" shape game, children were to put cars with the car target card and suns with the sun target card. In the post-switch "reversed" shape game, children were to put cars with the sun target card and suns with the car target card. If the problem for children on the card sort task is its hierarchical rule structure (as the theory of Zelazo and Frye (1997) purports), 3-year-old children should fail here, for these tasks involve the same logical structure. Yet, children of 3 years succeed at these tasks. In contrast to Zelazo's card sort and conditional discrimination tasks (each of which have two relevant dimensions), 99% of 3½-year-olds succeeded in Brooks et al.'s study, as did 73% of 3-year-olds. Similarly, children of 3 and 3½ years succeeded on roughly 90% of the post-switch trials in the Perner and Lang study. When young children did not have to switch their attentional focus—i.e., did not have to shift from focusing on one dimension to another—they were able to succeed. This is true despite the fact that during the "silly" or "reversed" games, children had to sort to the opposite item, to a model card that matched the stimulus on no feature, resisting the pull to go to the model card that matched the stimulus exactly.

In these experiments, Brooks et al. and Perner and Lang used black-and-white line drawings. In a second experiment, Brooks et al. (2001) used pictures of socks and cups as the stimuli, with half of each being green and the other half yellow. Thus, a second dimension (color) was introduced, but it was irrelevant to the task throughout testing. The task was formally identical to that in Experiment 1. Under these conditions, 3-year-olds failed the task. Thus, when a second dimension was introduced, increasing the demand on attentional inhibition to avoid distraction by the irrelevant dimension, 3-year-olds failed the same task on which they succeeded in Experiment 1.

Meyer et al. (1998) found that DL-PFC activity was not increased for within-dimension switches, even though these required changing stimulus–response mappings (paralleling the success of 3-year-old children on that condition [Brooks et al., 2001; Perner & Lang, 2002]). Dorsolateral prefrontal cortex activity was only required when participants needed to refocus their attention (i.e., overcome attentional inertia) and switch to a different dimension. Similarly, Pollman (2001) found that when only stimulus–response mappings needed to switch (attentional focus remained unchanged), activity did not increase in DL-PFC. (There is some suggestion from the Meyer et al. [1998] and Pollman [2001] studies that premotor cortex, in Brodmann's area 6, may be particularly important for inhibiting acting according to the previously relevant rules and switching to different stimulus–response mappings.) Conditional discriminations appear to require the frontal cortex regions which, in the monkey, border the arcuate sulcus (premotor cortex and the frontal eye fields in areas 6 and 8; see Goldman & Rosvold, 1970; Petrides, 1982, 1985, 1986; 1988; Halsband & Passingham, 1985; Lawler & Cowey, 1987; Passingham, 1988). For example, Petrides (1985) found that monkeys with lesions of the periarcuate region could learn a simple discrimination (choose the lit over the the unlit box) but they could not learn the conditional discrimination (choose the lit box in the presence of one stimulus object, and choose the unlit box in the presence of a different stimulus).

Another example of apparently knowing the correct answer but not being able to act in accord with it is provided by work with *go/no-go tasks*. Here, the child is to respond to one stimulus but do nothing when shown another. Children who are 3–4 years old can correctly restate the instructions, but they cannot get themselves to act accordingly (Tikhomirov, 1978; Bell & Livesey, 1985; Livesey & Morgan, 1991). They respond even to the no-go stimulus. Studies of go/no-go performance consistently find that children cannot succeed at the task until they are roughly 4½ years old because of inhibitory failures (errors of commission to the no-go stimulus; see Jeffrey, 1961; Luria, 1961; Birch, 1967; Beiswanger, 1968; Garber & Ross, 1968; Miller et al., 1970; Norton et al., 1971; Bronckart, 1973; Tikhomirov, 1978; Bell & Livesey, 1985; Livesey & Morgan, 1991; van der Meere & Stemerdink, 1999; Dowsett & Livesey, 2000).

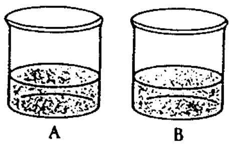
Note again the transition between 3 and 5 years of age.

This is not to say that continued improvements cannot be seen with age, especially when more rapid responding is required and/or the ratio of go to no-go responses is increased. For example, Garber and Ross (1968) report that children 4¾ years of age perform significantly worse than children of 7¾ years. van der Meere and Stemerdink (1999) report more errors by 8-year-old children than by children of 10 or 12 years, and Casey et al. (1997) report more errors by 9-year-old children than by young adults of 22 years. Even adults are rarely at ceiling on the variant of the go/no-go task known as *Simon Says*. Conversely, with a slightly easier variant of the task, children of 3¾ to 4 years have been reported to perform at better than 90% correct (Jones et al., in press).

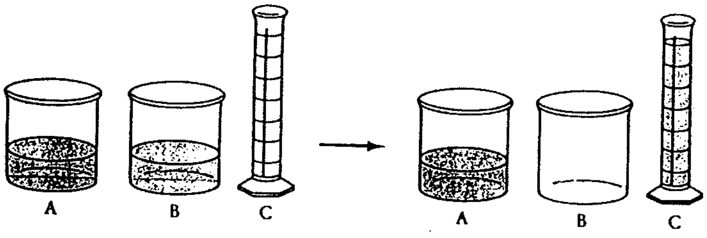
Neuroimaging studies indicate the importance of dorsolateral and ventrolateral PFC for performance of go/no-go tasks. Tsujimoto et al. (1997) report increased regional cerebral blood flow in the principal sulcus (DL-PFC) and frontal pole of macaques during performance of a go/no-go task. Konishi et al. (1998, 1999) report increased activation in the inferior frontal sulcus (ventrolateral PFC) on no-go trials compared with that on go trials. Liddle et al. (2001) report increased activity in dorsolateral and ventrolateral PFC during no-go trials. Casey et al. (1997) report increased activity in the inferior frontal gyrus (ventrolateral PFC), middle frontal gyrus (DL-PFC), and orbital frontal gyrus on no-go trials compared with that on go trials.

Many of the advances of Piaget's "concrete operational" child, who is 5–7 years old, over a "preoperational" child, who is 3–4 years of age, also reflect the development of the abilities to hold more than one thing in mind and

Step 1: Present two beakers with
equal amounts of liquid.



Step 2: Present taller, thinner
beaker, and pour contents of B
into it.



**Step 3: Ask: "Which beaker has more
liquid, A or C—or do they
contain the same amount?"**

Figure 29–7. Illustration of the procedure used for testing conservation of liquid quantity. (Source: Reprinted with permission from Cole & Cole, 1989) inhibit the strongest response of the moment (Flavell, 1963). For example, children of 3 or 4 years fail tests of liquid conservation (they do not attend to both height and width, attending only to the more perceptually salient of the two dimensions; Fig. 29–7) and they fail tests of perspective-taking in which they must mentally manipulate a scene to indicate what it would look like from another perspective and must inhibit the tendency to give the most salient response (their current perspective). By 5 or 6 years of age, they can do these things. Since part of the difficulty posed by Piaget's liquid conservation task is the salience of the visual perception that the tall, thin container contains more liquid, placing an opaque screen between the child and the containers before the child answers enables younger children to perform the task better (Bruner, 1964).

In the *delay-of-gratification paradigm*, when faced with the choice of a smaller, immediate reward or a later, larger reward, many 3- to 4-year-old children are unable to inhibit going for the immediate reward, although they would prefer the larger one (Mischel & Mischel, 1983). If they cannot see the rewards or can see only pictures of the rewards, they perform much better than if the smaller reward is sitting right in front of them. On the *windows task*, in which children are rewarded for pointing to a box that is visibly empty and are not rewarded for pointing to a box in which they can see candy, many 3-year-olds fail to inhibit the tendency to point to the baited box (Russell et al., 1991). Children of 5–6 years perform well on both tasks.

ANATOMICAL AND BIOCHEMICAL EVIDENCE OF PREFRONTAL CORTEX MATURATION FROM 3 TO 7 YEARS

The density of neurons in human DL-PFC is highest at birth and declines thereafter. At 2 years of age, the density is 55% above the adult mean, but by age 7 years it is only 10% above adult levels (Huttenlocher, 1990). Thus there is a dramatic change in neuronal density in DL-PFC between 2 and 7 years of age. The synaptic density of layer III pyramidal cells in DL-PFC increases after birth and reaches its maximum at about 1 year of age; by 7 years of age the decrease in synaptic density is significant, though not yet down to adult levels (Huttenlocher, 1979). Another change during this period is a marked expansion in the dendritic trees of layer III pyramidal cells in human DL-PFC between 2 and 5 years of age (Mrzlijak et al., 1990). In addition, the density of neuropeptide Y-immunoreactive neurons in human DL-PFC increases between the ages of 2–4 years and 6–7 years (DeLalle et al., 1997). (Neuropeptide Y–immunoreactive neurons are a class of local circuit intrinsic neurons [Hendry et al., 1984; Hendry, 1993].)

DEVELOPMENT FROM 7 YEARS OF AGE THROUGH EARLY ADULTHOOD

IMPROVEMENTS IN THE COGNITIVE FUNCTIONS THAT DEPEND ON PREFRONTAL CORTEX

Aspects of memory that do not depend on PFC, such as the ability to recognize or recall what one has previously seen, even after a long delay, or the ability to hold information in mind (without an added requirement of manipulating that information or exercising inhibition), develop very early, are robust by the preschool years, and show little improvement with age (Brown, 1975; Dempster, 1985; Diamond, 1995). Where improvements with age, even after 7 years, and in most cases even until early adulthood, are seen are in *(1)* speed of processing, *(2)* the ability to use strategies, *(3)* the ability to hold information in mind *and* work with it (manipulating, monitoring, or transforming it), and *(4)* the ability to hold information in mind and exercise inhibition (resisting interference, resisting attentional inertia, or resisting a prepotent response tendency). Interestingly, each of these four classes of abilities appears to be tied to the PFC, especially DL-PFC.

Speed of Processing

Speed of processing increases markedly until early adolescence and continues improving, though more gradually, until early adulthood (Kail, 1988, 1991a,b; Hale, 1990; Kail & Park, 1992; Fry & Hale, 1996; Miller & Vernon, 1997). There is a strong, well-replicated relation between speed of processing and performance on tasks either known or hypothesized to tap DL-PFC functions (Case et al., 1982; Fry & Hale, 1986; Salthouse, 1992; Kail & Salthouse, 1994; Duncan et al., 1995), although the reason for this association is not yet fully understood.

Improvements in speed of processing with age account for a good deal of what has been taken to be age-related improvements in the ability to hold information in mind. For example, Case et al. (1982) found that the faster people were able to repeat back the word they had just heard, the more words they could hold in mind, and as the speed of word repetition improved with age so too did word span. When Case et al. equated the speed at which adults and 6-year-olds could repeat back words (by presenting adults with unfamiliar words), they found equivalent word spans in adults and children. Similarly, when they equated adults and children in the speed at which they could count (by requiring adults to count in a foreign language), they found equivalent counting spans in adults and 6-year-olds.

Speed of encoding is another aspect of speed of processing. Item recognition time decreases with age (e.g., Samuels, et al., 1975–1976; Chi, 1977) and speed of item identification is related to the number of items (span) that can be held in mind and retrieved (Dempster, 1981). Individuals who have shorter naming times (within and between ages) have larger memory spans. For example, people generally have larger spans for digits than for words and people can generally name a digit faster than a word; people generally have larger spans for words than pictures, and words are identified faster than pictures (Mackworth, 1963). Chi (1977) found that when adults were only allowed to view picture stimuli for half as long as 5-year-olds (to offset the faster encoding speed of adults), the age difference in the number of pictures that could be held in mind was dramatically reduced. Similarly, Zald and Iacono (1998) found that, given the same amount of time for encoding, 20-year-olds were significantly more accurate than 14-year-olds at indicating, from memory, the location of an object in space, even after a brief delay of only 500 ms. Although they found little difference among age-groups in the rate of degradation of the internal representation, they did find a developmental improvement in how accurately the information could be encoded in a given amount of time.

Use of Strategies

As children get older they are more likely to use strategies and to improve in their use of strategies. Rehearsal strategies as a memory aid generally emerge around the age of 7 years and are rarely seen in younger children, even when overt attempts are made to try to encourage their use (Flavell, et al., 1966; Johnston, et al., 1987; Gathercole & Hitch, 1993; Gathercole, 1998). Patients with DL-PFC damage are notorious for being unsystematic and for failing to avail themselves of strategies to aid their performance (e.g., Owen et al., 1996; Mangels, 1997; Baldo & Shimamura, 1998). When the material does not lend itself to use of any particular strategy, age differences in memory span are greatly reduced (Ross, 1969; Dempster, 1978; Hess & Radke, 1981), as are performance differences between frontal patients and controls and as is the difference in degree of PFC activation (Bor et al., 2001).

The Ability to Hold Information in Mind and Work with it (Manipulating, Monitoring, or Transforming it)

Piaget (1958) proposed that beginning at about 7 years of age, children begin to be able to simultaneously take into account more than one perspective and to simultaneously think about two aspects of something. Beginning at this age, according to Piaget, children become able to mentally combine, separate, order, and reorder. They become more flexible in their thinking, and can think about alternatives when solving problems.

Baddeley, who coined the term *working*

memory, defined it as involving both temporarily maintaining information in mind and manipulating that information (Baddeley, 1992). This definition of working memory—"temporary storage + manipulation of information"—has received widespread acceptance. Neuroimaging studies have repeatedly demonstrated that activation of DL-PFC is far greater when information must be both held in mind and manipulated than when it must only be held in mind (e.g., D'Esposito et al., 1995, 1998; Petrides, 1995; Cohen et al., 1997; Owen, 1997; Smith et al., 1998; Smith & Jonides, 1999).

Thus, for example, the forward digit span task (recalling numbers in the order in which they are heard) requires less DL-PFC involvement, and performance of this task is less impaired in patients with PFC damage than that of backward digit span (repeating back numbers in the order opposite that in which they were presented), which requires not only holding the information in mind but also manipulating it (Hoshi et al., 2000). Similarly, there is much less improvement with age in performing forward digit span than there is with backward digit span. From ages 7 to 13 years, the number of digits that can be held in mind for forward digit span increases by little more than 1.5 digits (Dempster, 1981). Over the same age period, it increases by twice that for backward digit span (3 digits). Indeed, from ages 6 to 13 years there is a fivefold increase in backward digit span.

Moreover, involvement of DL-PFC and marked improvements in performance of a variety of tasks over the school-age years appear to be found regardless of how the information held in mind is to be manipulated—e.g., ordering randomly presented information (in alphabetical or numerical order) or mentally adding or multiplying numbers. This is true whether monitoring a list of randomly presented numbers to determine which one was omitted, generating all the numbers from 1 to 10 in random order without repeating any (Petrides et al., 1993; Jahanshahi et al., 2000), trying to remember which stimuli were already chosen so that each one is choosen once and none more than once (Petrides, 1995; 2000), or keeping in mind a main goal while performing concurrent subgoals (Koechlin et al., 1999). Developmental differences are consistently greatest on those tasks that require some (or any) kind of transformation of information held in mind (Dempster, 1985). These findings may describe the limited capacity system independently hypothesized by Daneman and Carpenter (1980, coming from a cognitive science perspective) and by Case et al. (1982, coming from a developmental psychology perspective) that subserves both processing (i.e., manipulation) and storage such that the more information that must be held in mind the fewer resources there are for acting on that information, and the more extensive the processing needed the fewer items of information that can be maintained in mind.

Ability to Hold Information in Mind While Exercising Inhibition (Resisting Interference, Resisting Attentional Inertia, or Resisting a Prepotent Response Tendency)

Engle and Kane have defined working memory slightly differently from Baddeley. They define it as the ability to *(a)* maintain selected information in an active, easily retrievable form while *(b)* blocking or inhibiting other information from entering that active state (Conway & Engle, 1994; Kane & Engle, 2000; 2002; see Hasher and Zacks [1988] for a somewhat similar perspective on the role of inhibition in working memory).

Task-switching paradigms epitomize the twin needs of activate maintenance and inhibition captured by this perspective on working memory, as such paradigms require that one activate the information and rules relevant for the current task and inhibit the mind-set relevant to the other task. Children 4 years of age can begin to perform such switching paradigms, but only poorly. Improvement on task-switching paradigms occurs throughout childhood and into adulthood. On one simple paradigm devised by Meiran (1996; see Fig. 29–8), by age age 11 years children are correct on virtually all non-switch trials but on only 80% of the switch trials, and by age 11 years children are still not performing at adult levels (Cohen et al., 2001). As noted in the section Development at 3 to 7 Years of Age (above), switching tasks elicits increased activation of

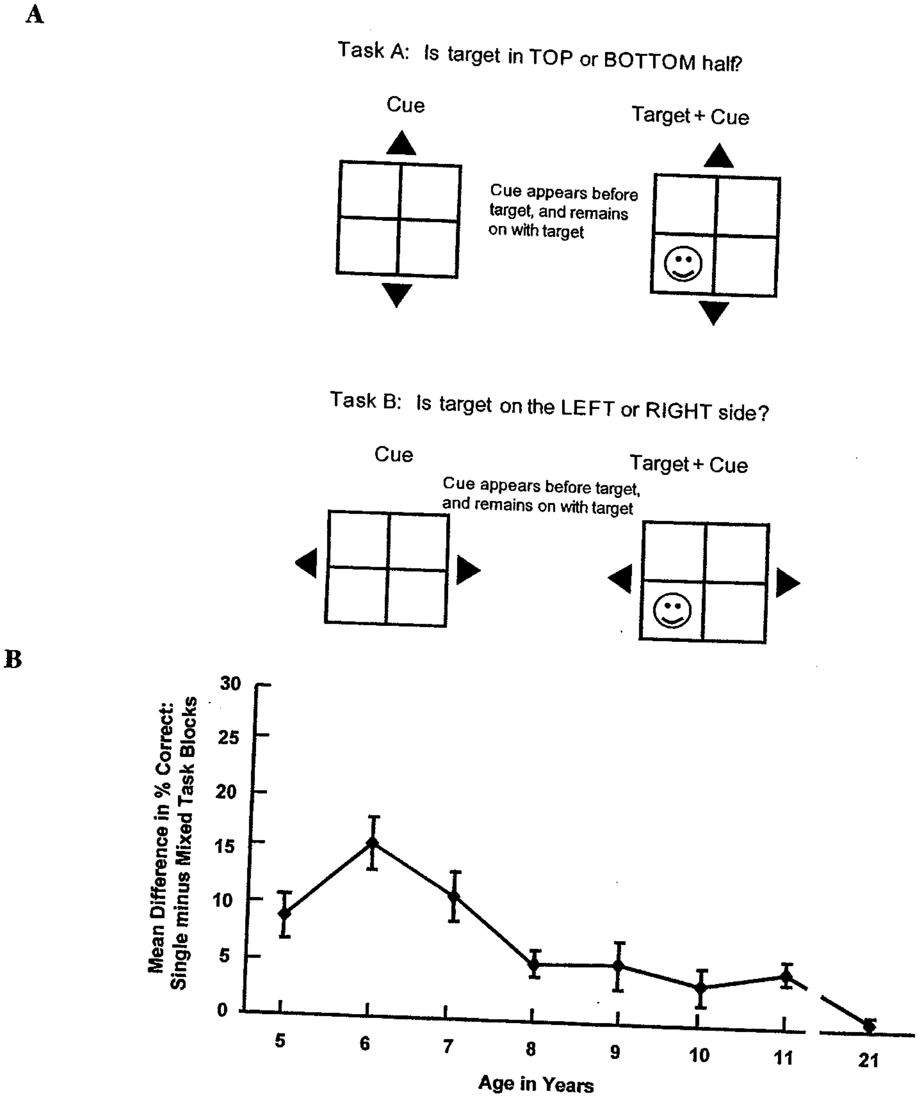
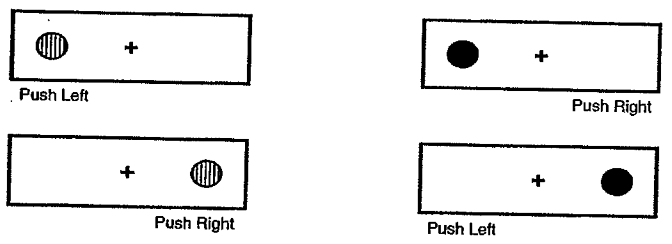


Figure 29–8. *A*: Illustration of Meiran's task-switching paradigm. Participants are to press the "3" key on the keyboard number pad to indicate a response of "down" or "right" and are to press the "7" key to indicate a response of "up" or "left." *B*: Difference in percentage of correct responses on mixed-task blocks versus single-task blocks. Children were significantly less accurate on switch than on nonswitch trials at every age, and on both kinds of trials in mixed-task blocks than on trials in single-task blocks. Indeed, children were correct on significantly fewer non-switch trials in mixed-task blocks than on exactly the same type of trials (non-switch trials) in single-task blocks. Just knowing that sometimes they would have to switch tasks impaired their performance on all trials in the block. Although the difference in accuracy decreased continuously with age, even 11-year-old children showed a significantly larger difference in accuracy (a significantly larger "switch cost") than did adults.

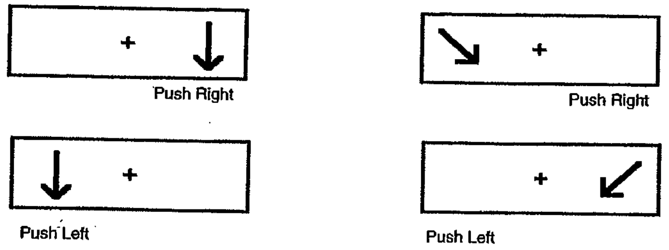
PFC, and task switching is impaired in patients with PFC damage.

Several bodies of work indicate that the ability to exercise inhibitory control continues to improve until early adulthood. In the *directed-forgetting paradigm*, participants are directed to forget some of the words they are shown and to remember others. Even children 11 years of age show more intrusions of the to-be-forgotten words than do adults (e.g., Harnishfeger & Pope, 1996; Lehman et al., submitted). The *anti-saccade task* requires participants to suppress the tendency to reflexively look at (saccade to) a visual stimulus in the periphery, and instead look away in the opposite direction. Performance of this task depends especially on the frontal eye fields (Brodmann's area 8; Guitton et al., 1985; O'Driscoll et al., 1995) as well as on the supplementary eye fields and DL-PFC (Luna et al., 2001). Performance of the task improves continuously from 8 through 20–25 years of age (Fischer et al., 1997; Munoz et al., 1998; Luna et al., 2001). Luna et al. (2001) report that while activation in the frontal eye fields, supplementary eye fields, and DL-PFC increased during anti-saccade performance in participants of all ages, increased activation of the thalamus, striatum, and cerebellum was seen only in adults, suggesting perhaps late maturation of the circuit connecting PFC with subcortical regions.

Further evidence of the very protracted developmental progression of the ability to exercise inhibitory control comes from testing with the *directional Stroop task* (Diamond et al., 1998; Davidson et al., 1999; see Fig. 29–9), in which participants are given a response box with two buttons (one for the left thumb and one for the right). When stimulus A appears to the left or right, the participant is to press the button on the same side as the stimulus. When stimulus B appears, the participant is to press the button on the side opposite the stimulus, which requires inhibition of the tendency to respond on the same side as the stimulus. (The tendency to respond on the same side as a stimulus is well documented. People are slower and less accurate to respond on the side opposite a stimulus than they are to respond on the same side. This type of response is called "spatial incompatibility" or the "Simon effect" [Simon, 1969; Craft & Simon, 1970; Simon & Berbaum, 1990; Hommel,


Dots Variant (Congruent Condition)

Dots Variant (Opposite Condition)


Arrows Variant (Congruent Condition)

Arrows Variant (Opposite Condition)

Figure 29–9. Illustration of two of the conditions in the directional Stroop task. In the *dots variant,* when a striped dot appears, the participant is to press the response button on the same side as the stimulus. When a gray dot appears, the participant is to press the button on the side opposite the stimulus. Similarly, in the *arrows variant,* when the arrow points straight down, the participant is to press the button on that side, and when the arrow points diagonally to the opposite side, the participant is to press the button on the side opposite the arrow. The dots-variant requires holding two rules in mind and, when the dot is gray, inhibiting the tendency to respond on the same side as the stimulus. The arrows-variant also requires inhibiting that tendency (when the arrow is diagonal), but it requires little memory because the stimulus itself points to where the participant should respond.

1995; Lu & Proctor, 1995].) The two kinds of stimuli are randomly intermixed over trials. In a comparison of the percentage of correct answers, or reaction time, on trials in which participants are to respond on the same side as the stimulus versus on the opposite side, one finds that the cost (in accuracy and speed) of inhibiting the natural tendency to respond on the same side as the stimulus shows a protracted developmental course, improving linearly from 4 to 26 years of age (Davidson et al., 1999; see Fig. 29–10).

Most tests of working memory require both *(a)* manipulation of information held in mind and *(b)* inhibition of potentially competing information from intruding and potentially competing responses from being made. Indeed, one perspective on the reason for speed of item identification being so highly correlated with memory span is that both are usually tested under high-interference conditions requiring inhibition (Dempster, 1981), as, for example, in the counting span and spatial span tasks (see Fig. 29–11). On each trial of the counting span task (Case et al., 1982), the participant is asked to count a set of blue dots embedded in a field of yellow dots, touching each blue dot and enumerating it. Immediately thereafter, the participant is to give the answer for that display and the answers for all preceding displays in correct serial order. Thus, this task requires *(1)* selective attention (inhibiting attention to the yellow dots), *(2)* holding of information in mind while execut-

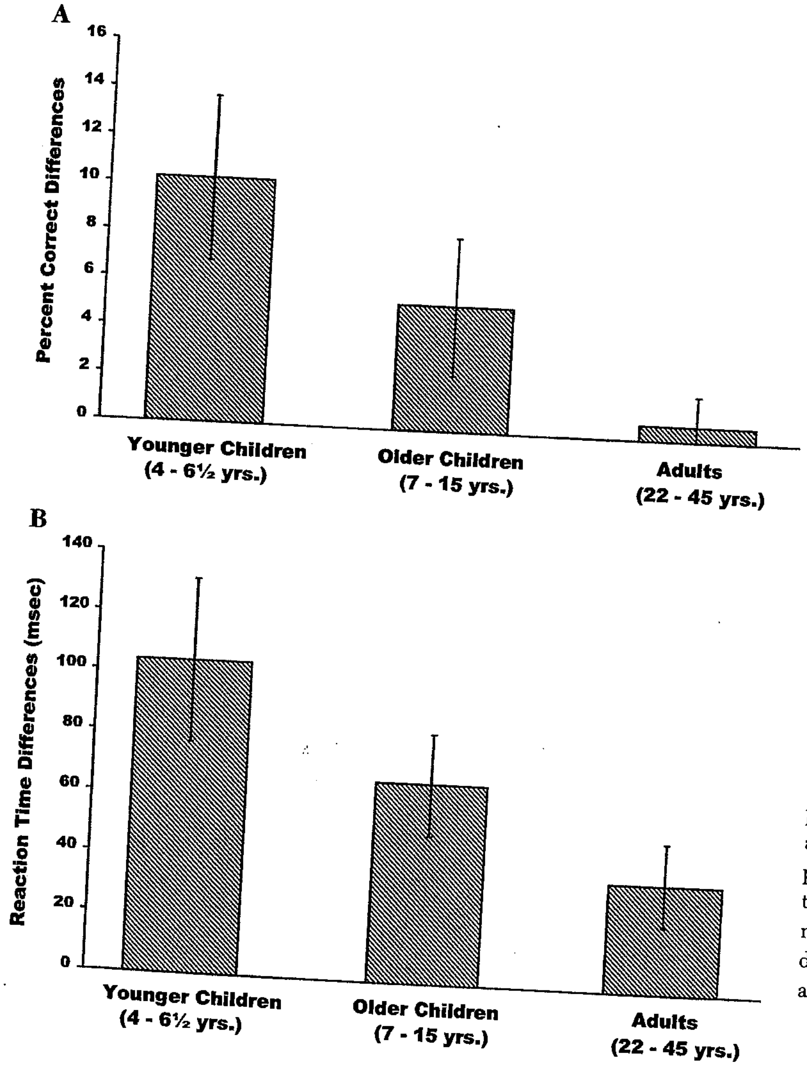
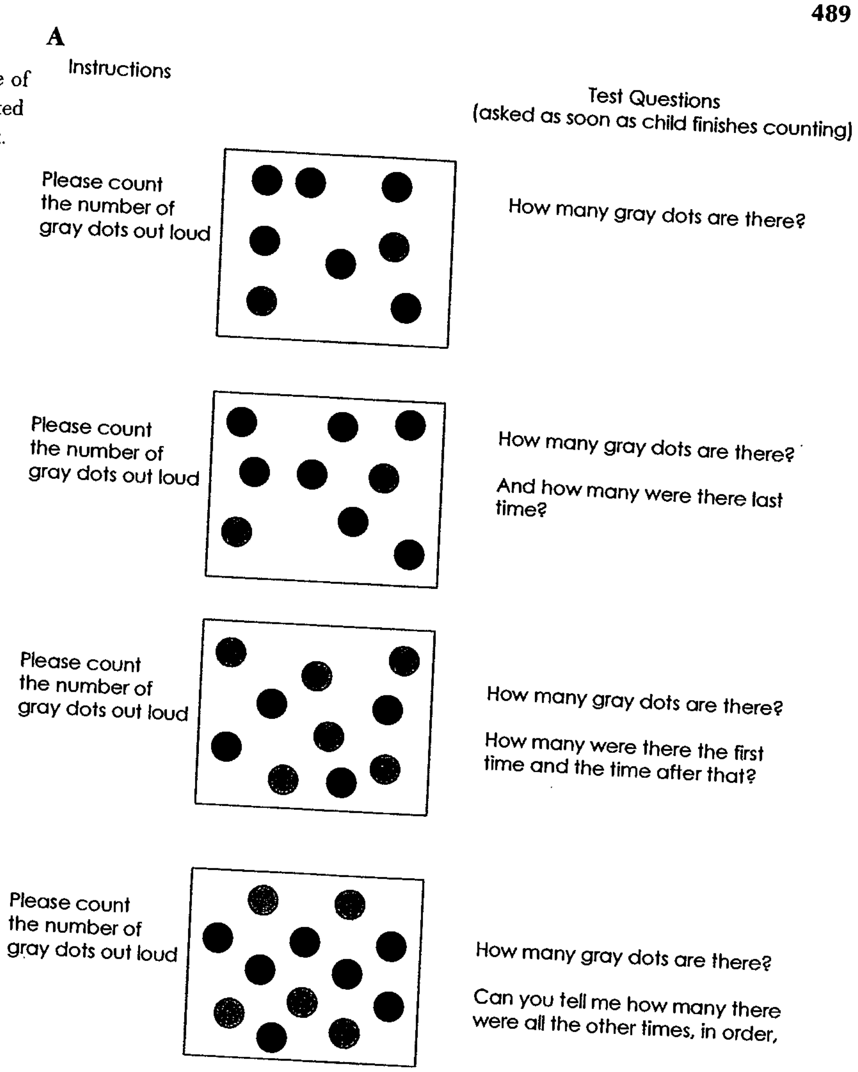


Figure 29–10. *A:* Accuracy when inhibitory control was not required (congruent trials [spatial conflict absent]) minus accuracy when inhibitory control was required (opposite or incongruent trials [spatial conflict present]) on both the dots and arrows variants. *B:* Reaction time when inhibitory control was required (opposite or incongruent trials [spatial conflict present]) minus when inhibitory control was *not* required (congruent trials [spatial conflict absent]) on both the dots and arrows variants. It was sufficiently difficult for children to inhibit responding on the same side as the stimulus that their performance on trials requiring such inhibition was significantly worse (as indexed by either accuracy or speed) at every age (4 through 15 years) than their performance on congruent trials. Even 15-year-olds did not perform at adult levels, although the difference in performance on these two trial types decreased continuously with age.

Figure 29–11. *A*: Sample of the kinds of trials presented on the counting span task. (*continued*)



ing another mental operation (counting), *(3)* updating of the information held in mind on each trial, and *(4)* temporal order memory (keeping track of the order of the totals computed across trials).

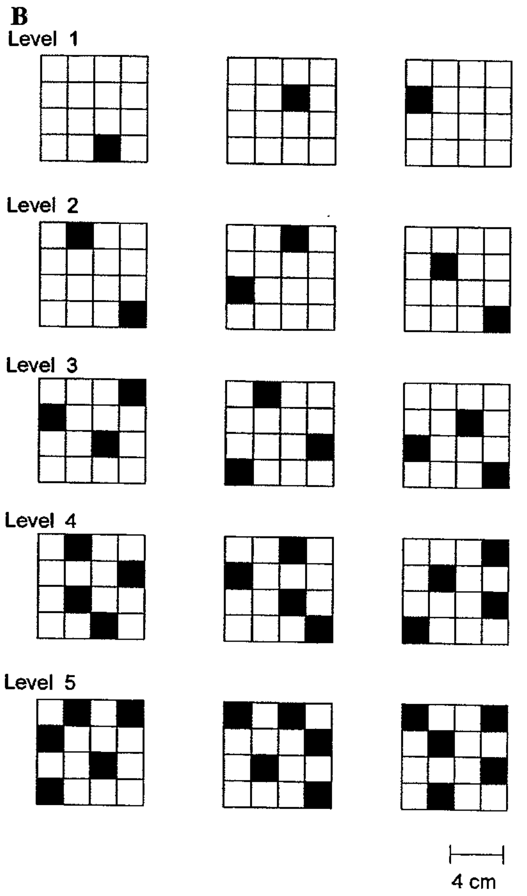
In the spatial span task (Case, 1992a; b) the participant inspects a 4 × 4 matrix on each trial, noting which cell is shaded in. A filler pattern is then shown, and then a second 4 × 4 grid. The second grid is empty; the participant is to point to the cell that had been shaded in on that trial. Several blocks of trials are presented. The number of shaded cells increases by 1 for each subsequent block. Interference from prior trials and from the filler pattern is very high.

A meta-analysis by Case (1992a; b) of 12 cross-sectional studies showed remarkably similar developmental progressions on both of these tasks (see Fig. 29–11). Continuous and marked improvements are seen on both tasks from 4½ to 8 years of age, and continued, more gradual improvement is seen until performance asymptotes on both tasks at around 10–11 years of age.

Quite parallel developmental progressions have also been seen on the compound stimulus visual information (CSVI) task, the pattern span task, and the WCST. In the *CSVI task* (Pascual-Leone, 1970), the participant is taught a different novel response (e.g., raise your hand, clap your hands) for each of several different visual cues (e.g., a square shape or red color). After learning these to criteria, compound stimuli (e.g., red square) are presented, each for 5 seconds, and the participant is to "decode the message" by producing every response called for by the stimuli. The number of correct responses increases until about age 11 (Case, 1972, 1995).

The *pattern span task* is similar to the spatial span task except that several cells are filled in. First, the participant gets a quick look at the pattern. At test, one of the cells that had been filled-in is now unfilled and the participant must point to that cell. The number of filled-in cells increases until the participant's accuracy falls below criterion. Performance on this task also improves greatly between 5 and 11 years of age, when it reaches roughly adult levels (Wilson et al., 1987; Miles et al., 1996).

On the WCST, one of the classic tests of PFC function in adults, the participant must deduce the rule for sorting cards, which can be sorted by color, shape, or number, and must flexibly switch sorting rules, without warning, on the basis of feedback of whether each response is correct or not. Children begin to reach adult levels of performance on this task at about 10–11 years old (Chelune & Baer, 1986; Welsh et al., 1991).



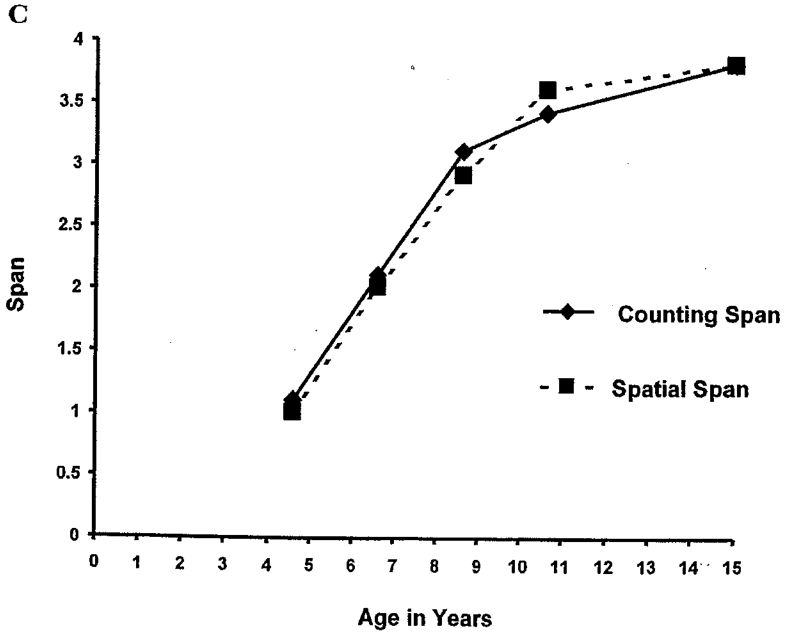


Figure 29-11 (*continued*) *B*: Sample of the kinds of trials presented on the spatial span task. *C*: Developmental progression in the number of items that could be held in mind (span) on the counting span and spatial span tasks. The data for the counting span task are from Crammond (1992), and for the spatial span task, are from Menna (1989).

On the *listening span task* (Daneman & Carpenter, 1980) the participant needs to process incoming information (auditorially presented sentences) while retaining, in correct temporal sequence, the final words of each of the preceding sentences he or she heard. Performance on this task improves from 6 years until at least 15 years of age (Siegel, 1994).

ANATOMICAL AND BIOCHEMICAL EVIDENCE OF PREFRONTAL CORTEX MATURATION FROM AGE 7 UNTIL EARLY ADULTHOOD

Myelination of PFC is protracted and does not reach adult levels until adolescence (Yakovlev & LeCours, 1967; Huttenlocher, 1970; Giedd et al., 1999). For example, using MRI and following the same children longitudinally, Giedd et al. (1999) were able to show that the amount of white matter (i.e., myelinated axons) increased linearly in frontal cortex from 4 to 13 years of age.

Portions of the neuron that are unmyelinated, such as the cell body, have a gray appearance. In their longitudinal study, Giedd et al. (1999) found that gray matter in frontal cortex increased until adolescence, reaching its maximum size at age 12 for males and age 11 for females. However, in cross-sectional volumetric studies, Jernigan et al. (1991) and Sowell et al. (1999a) report *reductions* in gray matter volume between childhood and adolescence, with the most dramatic changes occurring in dorsal frontal and parietal cortex. Sowell et al. (2001) related these gray matter changes to cognitive performance and found that, between 7 and 16 years of age, gray matter in frontal cortex (which included in their analyses not only PFC but also motor cortex, the supplementary motor area, and premotor cortex) decreased in size and the ability to accurately remember which words had and had not been presented earlier (i.e., the ability to remember which words had been seen in the present context and to discriminate them from other familiar words) improved. More impressively, gray matter thinning in frontal cortex was significantly correlated with this source memory, independent of chronological age. Indeed, whereas the relation between frontal cortex gray matter thinning and this ability remained significant even while controlling for age, the relation between age and source memory was no longer significant when controlling for frontal gray matter changes.

Synaptogenesis occurs concurrently with myelination. Huttenlocher (1979) reported that the synaptic density of layer III pyramidal cells in DL-PFC increases until about the age of 1 year, and then decreases, finally reaching adult levels at about 16 years of age. Huttenlocher and Dabholkar (1997) reported that the formation of synaptic contacts in DL-PFC reaches its maximum after 15 months of age, and synapse elimination occurs late in childhood, extending to mid-adolescence for DL-PFC.

Developmental changes in PFC continue on into adulthood. Sowell et al. (1999b) reported a reduction in the density of gray matter in frontal cortex between adolescence (12–16 years) and adulthood (23–30 years). They also reported a reduction in the striatum (primarily in the putamen and globus pallidus) over five times greater in size during this period. Kostovic et al. (1988) reported that AChE reactivity of layer III pyramidal cells in DL-PFC, which begins to develop after the first postnatal year, finally reaches its peak intensity in young adults.

CONCLUSIONS AND UNANSWERED QUESTIONS

Clearly, the ability to exercise inhibitory control over one's thoughts, attention, and action and the ability to interrelate, reorder, and play with information held in mind both show a protracted developmental progression that is matched by the protracted maturation of DL-PFC into early adulthood. Yet, advances in these abilities, as well as maturational changes in DL-PFC, are evident even during the first year of life. While this chapter has generally focused on memory and inhibition rather than on attention, clearly the abilities discussed here are critical for focused, selective, divided, and sustained attention. Indeed, can attention and working memory really be distinguished from one another? The difference is, in part, merely semantic—one can say that information is held in working memory for several seconds or that focused attention on the information was sustained for several seconds; they mean the same thing. The same PFC system that enables us to selectively keep our mind focused on the information we want to hold in mind also helps us to selectively attend to stimuli in our environment (tuning out irrelevant stimuli; e.g., Awh et al., 2000; Awh & Jonides, 2001; Casey et al., 2001). Awh and colleagues (Awh et al., 1998; Awh & Jonides, 2001) have shown, for example, that people are quicker to see, and respond to, stimuli in a location they are holding in working memory; if forced to orient their attention away from a memorized location, their memory accuracy declines. Individual differences in working memory capacity (using the Engle and Kane definition of working memory, see Ability to Hold Information in Mind While Exercising Inhibition, above) correspond to individual differences in selective attention (Conway et al., 1999).

What is the relation between the ability to hold information in mind and inhibition? Is inhibition necessary to keep the relevant information, and only the relevant information, on the stage of one's mind? How can one know what to inhibit unless one is holding the information on what is relevant in mind? Are the abilities to hold information in mind and to exercise inhibitory control, then, fundamentally intertwined? Certainly individuals who perform better on tests of working memory are better at blocking out, or inhibiting, distracting information (Hasher & Zacks, 1988; Gernsbacher, 1993; Conway & Engle, 1994; Rosen & Engle, 1997; Conway et al., 1999). Individuals with better working memory perform better on tasks that tax inhibition, but have minimal memory demands, such as the anti-saccade task (Kane et al., 2001). Vulnerability to proactive interference may determine working memory span scores (May et al., 1999). Conversely, taxing working memory can impair one's ability to resist distractors (de Fockert et al., 2001) and to perform tasks that demand inhibition of prepotent response tendencies, such as the anti-saccade task (Roberts et al., 1994). One view is that working memory and inhibition depend on the same limited capacity system so that increasing the demand on either affects one's ability to do the other (e.g., Kane & Engle, 2002). Another view is that working memory is primary and inhibition is derivative (Goldman-Rakic, 1987; Kimberg & Farah, 1993; Munakata, 2000).

Are inhibition and working memory separable, and if so, under what circumstances? Evidence has been presented in this chapter that these abilities can be dissociated during development (e.g., Davidson et al., 1999). There is also evidence that they can be dissociated neurally (e.g., Bunge et al., 2001). If they are separable, are holding information in mind + manipulating it and holding information in mind + exercising inhibition separable? What are the relations between self-control (or its inverse, compulsions or addictions) and working memory or attention? For example, impairments in the executive functions discussed in this chapter, especially inhibition, are prominent problems in obsessive–compulsive disorder (OCD; see, e.g., Cox, 1997; Hartston & Swerdlow, 1999; Rosenberg, et. al., 1997). What is the role of PFC in compulsive behavior and do all addictions share a common neural substrate? There is a burgeoning literature on this (see, e.g., Lyvers, 2000; Goldstein et al. 2001; Schroeder et al. 2001).

Are the different aspects of inhibitory control dissociable from one another? For example, is the same neural system required to resist internal and external distractions? Is the neural system that subserves inhibition in attention (selective attention [inhibiting attention to distractors], switching the focus of one's attention) the same neural system that subserves inhibition in action (inhibiting a prepotent response tendency, switching stimulus–response mappings)? There is some evidence that inhibition in attention, memory, or cognition may require anterior portions of dorsolateral and ventrolateral PFC, whereas switching stimulus–response mappings may require posterior DL-PFC and the premotor cortex immediately behind it (e.g., Goldman & Rosvold, 1970; Petrides, 1982; Halsband &

Passingham, 1985; Meyer et al., 1998; Wylie et al., 2000; Pollman, 2001). Might developments in inhibition and in working memory appear earlier at the behavioral level and then later at the cognitive level? If so, would behavioral inhibition appear before cognitive inhibition, and might the ability to hold information in mind + exercise inhibitory control appear earlier than the ability to hold information in mind + mentally manipulate it?

Is the neural system required to inhibit an action and not act at all (e.g., on no-go trials) the same as the system required to inhibit one action to do another? The work of Petrides (1986) and de Jong and colleagues (1995) suggests it is not. Is the neural system that underlies the ability to inhibit an unwanted action the same system as that which underlies the ability to check a desired action (e.g., as in not swinging at a poorly pitched ball or as on the stop-signal task [Logan, 1994])? Do all of these forms of inhibition develop concurrently and are they equally susceptible to disruption because of a particular genetic abnormality or environmental insult during development? If they are separable, how are we to divide them into components (see, e.g., Nigg, 2000; Casey, 2001)?

In this chapter I have discussed the ability to simultaneously hold information in mind plus manipulate it in a host of different ways, monitor it, or inhibit prepotent thoughts, stimuli, or action tendencies. This ability requires DL-PFC and develops during the course of the first two decades of life as DL-PFC develops. Is DL-PFC to be understood as some sort of general, all-purpose central executive? If so, how is that possible at the neural level? The most consistent finding across all neuroimaging studies is that activity in DL-PFC is greater when a task—any task—is more difficult (e.g., D'Esposito et al., 1998; Diamond et al., 1998; Duncan & Owen, 2000)—when the task demands greater concentration, for example, when it is new and unfamiliar, and when small changes in the neural or mental signal-to-noise ratio are most likely to result in significant consequences for performance. How are we to understand the seemingly pervasive involvement of DL-PFC in so many different functions and behavioral tasks? Can differential developmental profiles in these functions and/or in performance on these tasks provide a clue? Are the developmental profiles of these dissociable?

Is the close relation between developmental improvements in speed of processing and developmental improvements in holding information in mind + manipulating it or + inhibiting intruding perceptions, thoughts, or actions just a coincidence? Is the close relation between the degradation of each of these abilities with advancing old age (e.g., Hasher & Zacks, 1988; Salthouse, 1990, 1993; Salthouse & Meinz, 1995) also a coincidence? Is it simply that faster, more efficient processing is helpful to the development of any cognitive functions, including those dependent on DL-PFC but by no means limited to them? Might the functions dependent on DL-PFC be particularly sensitive to system-wide improvements (and impairments) in the tuning of signal-to-noise ratios, and is speed an index of that? Or, could it be that speed measures are also sensitive to distraction and interference, and so the relation between measures of speed and those of working memory consists in their both requiring the exercise of inhibition? Might it be that a more mature, better functioning DL-PFC is able to reduce signal-to-noise ratios in diverse neural regions, permitting faster and more efficient cognitive functioning?

This chapter has been concerned with the development of working memory and inhibitory functions, and the focus has been on how maturation of DL-PFC may be one of the factors contributing to the development of those cognitive functions. However, the anterior cingulate cortex has also been linked to many of these same cognitive functions (e.g., Posner & Rothbart, 1998; Carter et al., 1999; Bush et al., 2000; Cohen et al., 2000). How are the differences between the functions of DL-PFC and those of the anterior cingulate, or the interdependence between DL-PFC and the anterior cingulate in subserving common functions, to be understood? Similarly, the cerebellum is consistently activated during any cognitive task in which DL-PFC is activated (independent of any motor requirements of the task), and cerebellar and DL-PFC activation is remarkably closely linked, such that when activation of one increases (or decreases) so does activation of the other (for review, see Diamond, 2000). Moreover, the cerebellum shows the same protracted developmental progression as does DL-PFC and it has undergone the same explosion in size during primate evolution (Leiner et al., 1987; 1994–95). How is the interrelation between DL-PFC and the cerebellum in subserving cognitive functions to be understood? Does the cerebellum (traditionally thought of as being important for motor functions) play a role in the working memory and inhibitory functions linked to DL-PFC?

Certainly, PFC does not subserve any of its functions in isolation from other neural regions. We are only beginning to understand the components of the neural systems through which the functions associated with DL-PFC are realized. DL-PFC sends a heavy projection to the caudate nucleus. What roles do the basal ganglia play in the cognitive functions discussed in this chapter? The caudate matures much earlier than DL-PFC. Might maturational changes involving the caudate be responsible for any of the developmental changes during the first years of life that I have attributed to maturational changes in DL-PFC? DL-PFC, posterior parietal cortex, and the superior temporal cortex send reciprocal projections to one another, and send intricately interdigitated projections *throughout* the brain, providing multiple opportunities for these neural regions to communicate with, and influence, one another (Goldman-Rakic & Schwartz, 1982; Schwartz & Goldman-Rakic, 1984; Selemon & Goldman-Rakic, 1985, 1988; Johnson et al., 1989). What roles do those neural regions play in the cognitive functions discussed here? Since DL-PFC, posterior parietal cortex, and superior temporal cortex communicate directly with one another, why has the brain evolved in such a way that these neural regions are also able to communicate with one another at so many different levels throughout the brain and to *simultaneously* influence those diverse neural regions?

What are the developmental changes in the prefrontal neural system that underlie improvements in the cognitive functions it subserves? We still know little about that. What is the developmental timetable in the functional connectivity between PFC and the other neural regions with which it is interconnected? What is the relation between that timetable and the age-related cognitive advances discussed in this chapter? If DL-PFC subserves inhibitory control functions, what is the wiring diagram and neurochemical basis by which it does that? What roles do pruning and increased arborization in PFC play in cognitive advances discussed here? What roles do hormones play in PFC development? What role does exposure to stress play in PFC development? What roles do changes in various neurotransmitter systems in the PFC play in prefrontal maturation and in the development of the cognitive functions dependent on DL-PFC? Little is known about the roles of neurotransmitters other than dopamine and norepinephrine in DL-PFC, although we know that serotonin, acetylcholine, and other neurotransmitters are present there (Goldman-Rakic et al., 1990; Kritzer & Kohama, 1999; Lambe et al., 2000; Passetti et al., 2000). Indeed, the region that is source of the dopamine projection to PFC (the ventral tegmental area) sends a much heavier projection of GABA to PFC than of dopamine (Carr & Sesack, 2000). What roles do changes in these neurotransmitter systems play in developmental changes in the cognitive functions subserved by PFC? The neurotransmitters in PFC interact. What are the mechanisms and consequences of those interactions in adults and during development?

We share with even simple creatures such as worms and sea slugs the ability to be conditioned (to be affected by our experience) and, like them, we come into the world with certain biological predispositions. Even in humans, these are by far the two strongest influences on behavior. However, because having PFC enables us to hold in mind things we cannot see and to inhibit our predispositions and conditioned responses—however fragile and incomplete those abilities may be—we have the possibility to exercise choice and control over what we do. This is important not just for cognitive development but for social and emotional development as well. Now is an exciting time in front lobe research because finally we have the tools to begin to answer many of the still unanswered questions about the development of PFC and the abilities it subserves. Finding the answers to these questions is particularly pressing because PFC is important for so many diverse cognitive functions and for so much of what makes us proud to be human.

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