ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Volume 608

THE DEVELOPMENT AND NEURAL BASES OF HIGHER COGNITIVE FUNCTIONS

Edited by Adele Diamond

The New York Academy of Sciences
New York, New York
1990

PART VII. INHIBITION AND EXECUTIVE CONTROL

Developmental Time Course in Human Infants and Infant Monkeys, and the Neural Bases of, Inhibitory Control in Reaching[a]

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Development appears to proceed by destruction and inhibition, as well as by construction and acquisition. For example, neural development involves, in part, pruning back an oversupply of neurons and an exuberance of axonal projections (see, e.g., Frost, this volume; Innocenti & Clarke, 1984). There are more nerve cells at birth in the neocortex of monkeys and humans than at any time thereafter (e.g., Rakic, 1974; 1985). Motor development and cognitive development, likewise, are made possible, in part, by the inhibition of reflexive and automatic reactions (e.g., Diamond & Gilbert, 1989). More and more regions of frontal cortex are being found to play a role in inhibition, although various subdivisions of frontal cortex appear to participate in different aspects of inhibition.

Frontal cortex is by far the largest area of cortex in the human brain, it has increased the most in size (and in the proportion of brain mass devoted to it) over the course of evolution, and it takes longer to reach maturity than any other area of the brain (frontal cortex only becomes fully mature around puberty [e.g., Diamond, in press, a]). There is general agreement that the most anterior regions of frontal cortex (i.e., prefrontal cortex) subserve the highest cognitive abilities, the crowning intellectual achievements of the human race. The role of frontal cortex in inhibition is probably critical to its ability to subserve complex cognitive operations.

Take, for example, the importance of prefrontal cortex for focusing attention. The role of frontal cortex in aiding attention appears to depend on the inhibitory functions of frontal cortex. Frontal cortex activity is critical to reduce distractibility

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[a] The work discussed here was carried out at: (a) Harvard University, in the laboratory of Jerome Kagan, with funding from the National Science Foundation (Doctoral Dissertation Grant BNS-8013-447) and the National Institute of Child Health and Human Development (HD-10094), and support to the author from NSF and Danforth Graduate Fellowships; (b) Yale University School of Medicine, in the laboratory of Patricia Goldman-Rakic, with funding from the National Institute of Mental Health (MH-00298 & MH-38456), and support to the author from a Sloan Foundation award and NIMH Postdoctoral Fellowship (MH-09007); (c) University of California, San Diego, in the laboratory of Stuart Zola-Morgan, with funding from the Medical Research Service of the Veterans Administration, the National Institutes of Health, and the Office of Naval Research, and support to the author from a grant from Washington University; and (d) Washington University, St. Louis, and the University of Pennsylvania, Philadelphia, in the laboratories of the author, with funding from the McDonnell Center for Studies of Higher Brain Function at Washington University School of Medicine, NIMH (MH-41842), and BRSG (RR07054 & RR07083).

(to inhibit the tendency to be pulled by this or that compelling or interesting stimulus, and to sharpen the signal-to-noise ratio, see e.g., Arnsten, Neville, Hillyard, Janowsky & Segal, 1984; Guitton, Buchtel & Douglas, 1985). Thus, patients with damage to frontal cortex have difficulty concentrating on a conversation in a noisy room or in giving a simple personal history (they wander off on tangents as one memory awakens other associations). When given instructions to perform a task, frontal patients usually "begin to perform the task set, but as soon as a stranger enters the ward, or the person in the next bed whispers to the nurse, the patient ceases to perform the task and transfers his gaze to the newcomer or joins in conversation with his neighbor" (Luria, 1973: 275). A classic test of the ability to focus attention on a usually ignored stimulus dimension, and to inhibit attention to the usually salient dimension, is the Stroop Test. Here, the names of colors are printed in the ink of another color (e.g., the word "blue" is printed in red ink). Subjects are instructed to report the color of the ink as they look through the list of words. The customary response when reading, however, is to ignore the color of ink and attend to the meaning of the word. Frontal patients fail the Stroop Test; they recite the words and not the color of the ink (Perret, 1974).

Lack of inhibitory control can also cause the opposite of distractibility in frontal patients: They can become so captured by a salient stimulus that they fail to take into account the larger picture or other stimuli (e.g., Luria, 1973). A single cause (insufficient inhibitory control) can, thus, lead to two very different outcomes—inability to focus on just one thing, and inability to expand one's attention beyond one thing. Both skills are crucial for planning, problem solving, and sound critical judgment in general.

One of the first instances of inhibition one sees in development is inhibition of the neonatal reflexes. When infants begin to reach for objects, they sometimes encounter problems because of difficulty inhibiting the reflexes of the hand (the grasp and avoidance reactions first described by Twitchell, 1965; 1970). For example, if infants of 5–7 months accidentally touch a neighboring object en route to their goal, they often reflexively grasp the neighboring object (grasp reaction) or reflexively pull their hand back (avoidance reaction). After 7½ months of age or so, reflex inhibition is less of a problem, but inhibition of predominant response tendencies (such as behavior tendencies built up through reinforcement experience or behavior tendencies that are inherently strong, e.g., reaching straight for a visible goal or being distracted by a compelling stimulus) still remains to be mastered. Significant progress is made in this regard by the end of the first year.

Inhibition of the grasp reflex probably depends upon maturation of an area of frontal cortex called the supplementary motor area (SMA). Inhibition of prepotent response tendencies depends upon maturation of the dorsolateral region of prefrontal cortex. Dorsolateral prefrontal cortex borders SMA and is immediately anterior to it. Thus, major strides in inhibition at the level of reaching behavior occur in human infants between 5–12 months of age. These strides are probably made possible by maturational changes in frontal cortex. Those maturational changes probably begin more posteriorally in SMA and progress toward the frontal pole over these months.

Neither SMA nor dorsolateral prefrontal cortex are fully mature by 12 months, and neither is inhibitory control fully developed, but significant strides are made during the first year. These strides reveal the presence of cognitive competencies that appear to have been present much earlier, but could not be behaviorally demonstrated because of lack of ability to inhibit more automatic responses. Inhibition of reflexive and predominant response tendencies, then, allows knowledge already present in the infant to finally be demonstrated, and enables the infant to succeed at complex tasks hitherto failed.

INHIBITION OF REFLEXES OF THE HAND: 5–7½ MONTHS OF AGE

Retrieval of a Contiguous Object, Direct Line of Reach

Piaget observed that infants of 5–6 months, while able to retrieve a free-standing object, often fail to retrieve that same object when it is placed upon another, slightly larger object. For example:

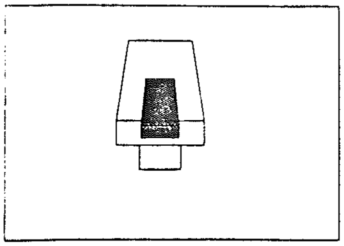
> Laurent tries to grasp a box of matches. When he is at the point of reaching it I place it on a book; he immediately withdraws his hand, then grasps the book itself. (Piaget, 1954 [1937]: 177)

Piaget attributed this difficulty to a lack of understanding of the concept of contiguity. Infants of 5–6 months, according to Piaget, did not realize that two objects could be independent of one another when the first was placed upon the second. Piaget also noted exceptions to this, however:

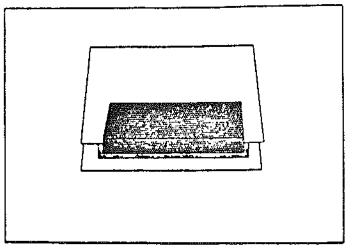
> On the other hand, when I place upon the book a narrow and deep goblet which stands out from its support, Laurent takes possession of it directly. . . .
>
> The child tries directly to grasp the object on cushions, coverlets, etc., in short, supports which have a surface large enough to be likened to simple neutral bases. On very small bodies, on the contrary, the object ceases to be perceived as directly accessible and the child grasps the support itself. (Piaget, 1954 [1937]: 177–178)

Recently, we have investigated the difficulty infants of 5 months have in retrieving one object placed upon another. We tested Piaget's interpretation against an alternative possibility: that the problem for infants is not in understanding contiguity, but in getting their hand to the object without touching the edge of the support, for when they touch an edge they react reflexively by grasping it or withdrawing their hand. Thus, according to this alternative interpretation, infants who are not yet precise in their reaching and often reach with their hand wide open in preparation for grasping, are likely to touch an edge of the support (and hence fail) when the support is only slightly larger than the object (as in Piaget's observation with a matchbox on a book) but not when the support has no edges (as when Piaget used a cushion as the support) or when the object stands well out from the support (as when Piaget placed a goblet on a book).

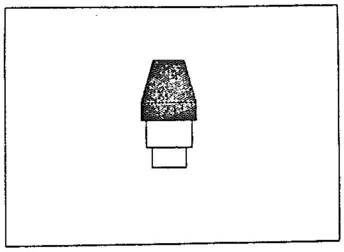
We tested 12 infants of 5 months and 12 infants of 7 months on 15 trials (see test conditions, FIG. 1A,B). In one condition, for example, we placed an object on a slightly smaller support. Since the object and support were close in size, we reasoned that if infants did not understand the concept of contiguity they should fail. However,



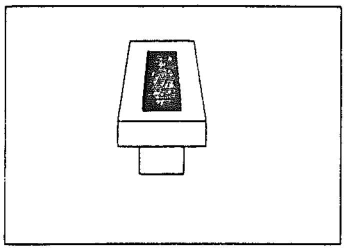
Trial 4: Object A extending over front of base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Success



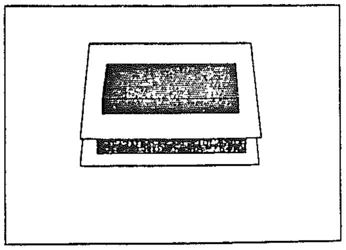
Trial 6: Object B extending over front of base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Success



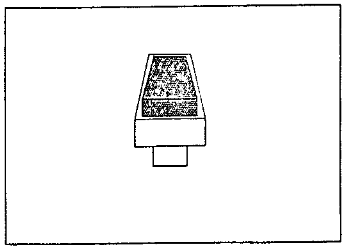
Trial 12: Object C on slightly smaller base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Success



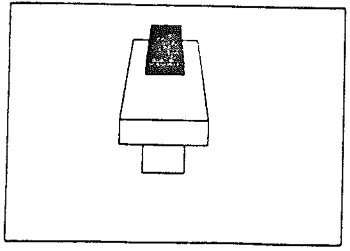
Trial 3: Object A centered on base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Failure



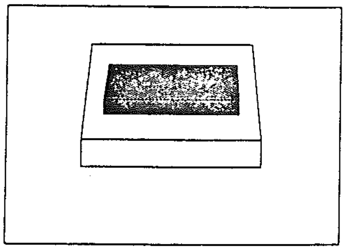
Trial 7: Object B centered on base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Failure



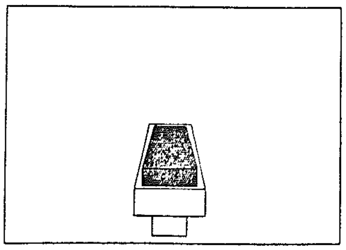
Trial 10: Object C on slightly larger base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Failure



Trial 14: Object A extending over back of base
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Failure

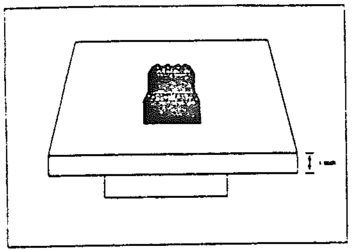


Trial 15: Obj B centered on base, binding toward S
Understanding Contiguity Predicts = Trial 7
Reflex Inhibition Predicts easier than Trial 7

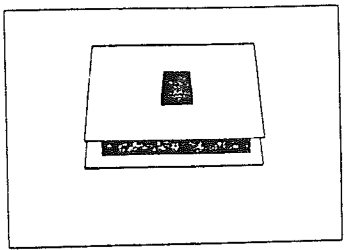


Trial 9: Obj C on slightly smaller base, closer to S
Understanding Contiguity Predicts Failure
Reflex Inhibition Predicts Success

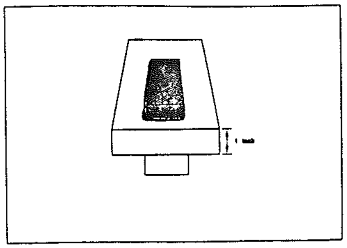
FIGURE 1. Illustration of the conditions under which infants were tested with one object on top of another object (for a more detailed description see Diamond, in prep).



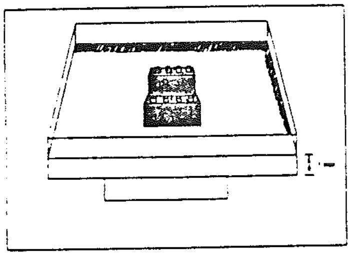
Trial 1: Tall obj D centered on larger base, no rim
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Success



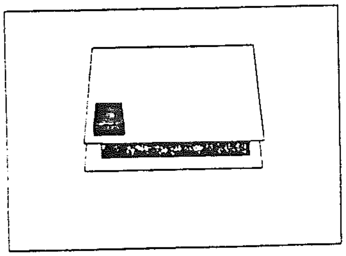
Trial 8: Object E centered on larger base
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Success



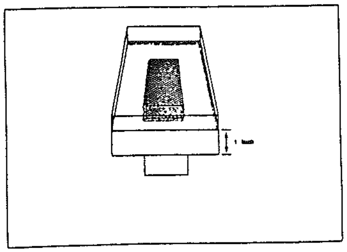
Trial 16: Object F centered .5 inches above base
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Success



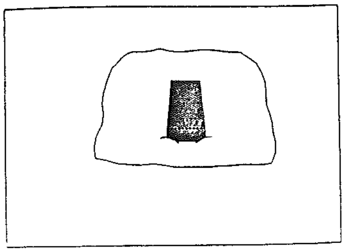
Trial 2: Tall obj D centered on larger base w/ rim
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Failure



Trial 5: Obj E near front corner of much larger base
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Failure



Trial 13: Object F centered .5 in above base w/ rim
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Failure



Trial 11: Object F centered on cushion
Understanding Contiguity Predicts Success
Reflex Inhibition Predicts Success

FIGURE 1. Continued

since the object was larger than the support and should have been contacted first, we reasoned that if the problem for infants is getting to the object without first touching the support, they should succeed. In another condition we placed a small object on a much larger support near the front, left, or right corner of the support. Since the support was much larger than the object, we reasoned that Piaget would have said the support would be treated as a neutral base, and the infants should succeed. However, since the object was near two edges of the support, we reasoned that infants might touch these edges en route to the object and hence fail.

Our predictions concerning the likelihood of the support being touched in the different conditions were confirmed (TABLE 1). More important, infants at both ages succeeded in those conditions where the edge of the support was rarely touched en route to the goal object, even when the goal object and support were close in size (see TABLE 1). However, even when the goal object and support differed considerably in size, when the object stood out from the support, or the object was not even touching the "support," infants of 5 months failed when contact with the edge of the support was likely. They failed because their reach was not yet accurate enough for them to obtain the object without accidentally touching the support. They reacted to touching the support by reflexively grasping it or reflexively withdrawing their hand. Infants of 7 months succeeded easily on all trials and almost never touched the support as the precision of their reaching along a simple, direct route to an object was quite good.

Thus, even infants as young as 5 months appear to understand contiguity sufficiently well to know that an object continues to exist independently even when placed upon another. Infants of 5 months, however, have difficulty retrieving the top object if the edges of the support are close to, and extend just beyond, the top object. Five-month-old infants fail because their hand touches the support's edge as they are reaching for the goal object, and they react to these touches reflexively, by grasping the edge or pulling their hand back. Their inability to inhibit these reflexes interferes with their ability to retrieve the object, even though they know the object is there and are reaching for it. Their problem consists, then, not of lack of conceptual understanding, but of lack of skill in precisely aiming their reach and lack of ability to inhibit reflexive reactions to touch. These problems get in the way of the infants' demonstrating the conceptual understanding that is already present.

Retrieval of an Object Just behind the Opening of a Barrier, Direct Line of Reach

Much of my work has been with a transparent box open on one side. A toy is placed in the box and the infant's task is to retrieve the toy. I call the task "object retrieval" (Diamond, submitted). As soon as infants can retrieve a free-standing object, they can retrieve a toy that extends partially out of the box. Infants of 5–6 months (22–27 weeks) fail, however, as soon as the toy is totally inside the box, even if the toy is just inside the opening, the opening is facing the infant, and the infant is looking through the opening at the toy. The results are quite dramatic: 93% success rate with the toy extending partly out of the front of the box; 4% success rate when the same toy is moved a half-inch back so that it is just behind the front opening.

Infants of 5–6 months try to reach for the toy in the box but have difficulty aiming

TABLE 1. Percent of Infants Succeeding under Various Conditions of One Object on Top of Another Object

Conditions	Age of Infants 5 months (N = 12)	 7 months (N = 12)
Understanding Contiguity Explanation Predicts Failure Reflex Inhibition Explanation Predicts Success		
(T4)[a] object A (4 × 1.5 × 1.5)[b] extending over front of support (5 × 3 × 1.75)	75	83
(T6) object B (5 × 3 × 0.5) extending over front of support (6.25 × 5 × 1)	100	92
(T12) object C (3.5 × 1.5 × 0.63) on slightly smaller support (3.25 × 1.25 × 1.25)	75	100
(T9) object C (3.5 × 1.5 × 0.63) on slightly larger support (3.75 × 2 × 1.25), closer to infant	83	83
Understanding Contiguity Explanation Predicts Failure Reflex Inhibition Explanation Predicts Failure		
(T3) object A (4 × 1.5 × 1.5) centered on support (5 × 3 × 1.75)	25	100
(T7) object B (5 × 3 × 0.5) centered on support (6.25 × 5 × 1)	25	92
(T10) object C (3.5 × 1.5 × 0.63) on slightly larger support (3.75 × 2 × 1.25)	50	92
(T14) object A (4 × 1.5 × 1.5) extending over back edge of support (5 × 3 × 1.75)	0	67
Understanding Contiguity Explanation Predicts Success Reflex Inhibition Explanation Predicts Failure		
(T2) object D (2.5 × 1.25 × 1.5) on much larger support w/rim (9 × 5 × 1.5; ht. of rim: 0.75)	75	100
(T5) object E (1.5 × 1.5 × 1.5) near edge of much larger support (6.25 × 5 × 1)	25	100
(T13) object C (3.5 × 1.5 × 0.63) not touching (0.5 above) support w/rim (7 × 3.5 × 1; ht. of rim: 1.0)	25	92
Understanding Contiguity Explanation Predicts Success Reflex Inhibition Explanation Predicts Success		
(T1) object D (2.5 × 1.25 × 1.5) on much larger flat support (9 × 1.5)	100	100
(T8) object E (1.5 × 1.5 × 1.5) centered on much larger support (6.25 × 5 × 1)	50	100
(T11) object C (3.5 × 1.5 × 0.63) on cushion (7 × 6.5 × 1.25)	100	100

[a] (T #) = trial number.
[b] Measurements are given in inches; length × width × height.

their hand so that it clears the opening. Upon touching the edge of the opening, they reflexively grasp the edge or reflexively withdraw their hands. Here the toy is not in contact with the box at all as the box has no bottom and the toy is touching none of the walls, so the problem is not one of failure to understand contiguity. The problems 5- to 6-month-old infants have here appear to be the same as the ones they have when one object is placed on top of another: the imprecision of their reaching and their inability to inhibit the reflexes of the hand. By 6½–7 months, infants are able to reach more precisely and clear the opening, easily retrieving the toy when they can see it just inside the opening.

Similar findings are reported by Schonen and Bresson (1984) who found that even when infants saw a toy just behind the opening of an opaque screen, fully visible, 6-month-olds did not enter the opening. They stared at the toy, reached for it, but stopped at the opening. When the same toy was placed in the opening, extending partially out, infants of 6 months retrieved it immediately.

Retrieval of a Contiguous Object, Indirect Line of Reach

Although infants of 7 months successfully retrieve an object from on top of another object, they often fail to retrieve an object from behind another object. Bower (1974) was the first to comment on this, noting success when a small object was placed several inches behind a screen, but failure when the same object was directly behind the screen. Bower's interpretation of this echoed the earlier interpretation of Piaget:

> It seems that what the baby doesn't understand is that two objects can be in a spatial relationship to one another, so that they share a common boundary. Evidently it is the common boundary that is critical. (Bower, 1977: 116–117)

Jeanne Gilbert and I suspected that the problem here was similar to that at 5 months, an inability to inhibit reflexive reactions if the neighboring object was touched en route to the goal object. We reasoned that although by 7 months infants could reach with precision when a simple, straight reach to the goal was possible, they still had difficulty when a more complicated, 2-directional reach was required. They would be likely to touch the neighboring object when required to execute a reach that changed direction, and their reflexive reactions to this contact would interrupt the reach.

We investigated this (Diamond & Gilbert, 1989) in 60 infants (12 each at 7, 8, 9, 10, and 11 months of age), and in a second experiment with 16 infants of 7 months and 8 infants of 10 months using the object retrieval boxes (opening at the top) and rectangular Lego building blocks. We started with a simple observation: If infants reached over the front wall of the box and continued without changing direction, their hand would land in the center of the box, a few inches behind the front wall. From this we reasoned that if the building block were in the center of the box (similar to Bower's condition of object several inches behind a screen) infants could reach over the front wall of the box and then continue to retrieve the object without changing direction and hence would succeed. If, however, the building block were directly behind the front wall of the box (similar to Bower's condition of object directly behind a screen), infants would have to reach over the front wall and then reverse direction to retrieve the object and hence would fail. We tested this in several conditions where contiguity with the front wall of the box was varied independently of whether or not a direct line of reach to the building block was possible. For example, we placed the block directly in front of the front wall of the box (contiguous, but accessible by a straight line of reach), and we placed a thinner block one-half inch behind the front wall of the box (not contiguous, but requiring a 2-directional reach) (see FIG. 2).

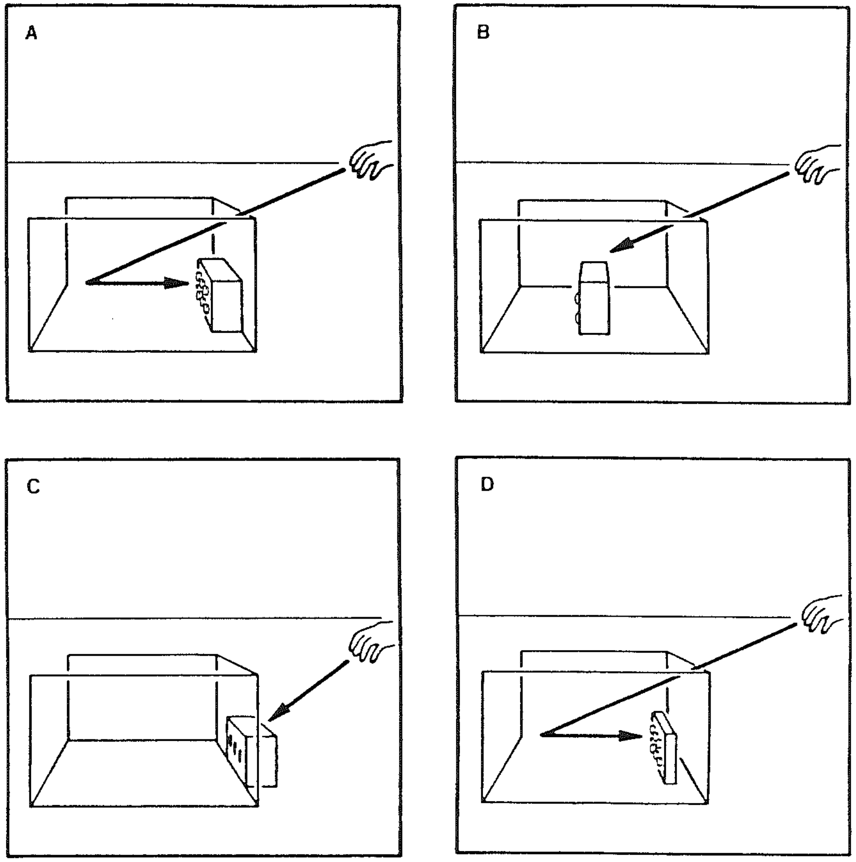


FIGURE 2. Diagram of a few testing conditions to illustrate how contiguity with the front wall of the box was varied independently of whether infants could reach on a straight line for the toy.

Panel A (toy directly behind front wall of box): The Lego block is *contiguous with the front wall* of the box and a *2-directional reach is required* (infant must first reach over the front wall and then change direction and reach back for the block). This is similar to Bower's condition of an object directly behind a screen.

Panel B (toy in center of box): The Lego block *does not border the front wall* of the box and can be retrieved by a *straight line of reach.* This is similar to Bower's condition of an object several inches behind a screen.

Panel C (toy directly in front of front wall of box): The Lego block is *contiguous with the front wall* of the box but it can be retrieved by a *straight line of reach.*

Panel D (thinner toy one-half inch behind front wall of box): The Lego block *does not border the front wall of the box* but a *2-directional reach is required* to retrieve it.

We replicated Bower's findings: success when the toy was in the center of the box, and failure when the toy was directly behind the front wall. Moreover, 7-month-old infants succeeded in retrieving the toy when it was outside the box bordering the front wall, but failed when the thinner toy was a half-inch behind the front wall, even though they successfully retrieved the thinner toy when it was in the center of the box. Thus, they succeeded in a condition of contiguity ("in front of") but failed in a condition where the wall and toy shared no common boundary (thin toy a half-inch from the wall). Similarly, they performed better when the box was closer to them (so that they could reach straight down for the toy), when the walls of the box were lower, when the toy was placed vertically so that it was as tall as the box, or when the toy was placed perpendicular to the wall (so that although a side of the toy still bordered the wall, the toy extended into the middle of the box and could be appoached by a straight line of reach) (see FIG. 3).

The infants gave clear evidence of reaching for the toy, rather than the box (for example, they did not reach for the box when it was presented without the toy, though they reached for the toy when presented alone), and they never failed for not trying. Frame-by-frame analyses indicated that 7-month-old infants touched the edge of the front wall much more often in conditions requiring a two-directional reach than in conditions permitting a direct reach. They reacted to these touches, especially if their palm touched, by reflexively grasping the box or reflexively withdrawing their hand in the manner of the grasp and avoidance reactions. Grasping the edge or withdrawing the hand was followed by another attempt to reach, and another, each ending in failure. Infants of 7 months were much more likely to touch the box en route to the toy and much more likely to react to this by grasping the box than were infants of 10 months, who succeeded easily on all trials (see FIG. 4).

Piaget and Bower proposed that infants fail to retrieve an object when it shares a boundary with another object because infants have not yet acquired the concept of contiguity. Instead, we have seen that infants understand that the object is still there when it shares a boundary with another object but are unable to inhibit reactions that get in the way of demonstrating this understanding. At 5–7 months of age, they cannot inhibit reflexive reactions to touch (the grasp and avoidance reactions) if their hand grazes the neighboring object en route to the goal. As early as 8 months, these reflexive reactions are much less in evidence.

Reflexive grasping such as is seen here is released in adults by lesions in anterior medial portions of Brodmann's Area 6 of frontal cortex (SMA). No other cortical area, besides Area 6,[b] has been implicated in the release of this reflexive behavior. The effect of Area 6 lesions on reflexive grasping was noted in monkeys by Richter and Hines (1932) and has been confirmed by Fulton, Jacobsen, and Kennard (1932); Penfield and Welch (1951); Travis (1955); Denny-Brown (1966); and Goldberger (1972). Observations of this in human patients are abundant (Addie & Critchley, 1927; Freeman & Crosby, 1929; Davis & Currier, 1931; Walshe, Robertson & Graeme, 1933; Kennard, Viets & Fulton, 1934; Penfield & Jasper, 1954; Luria, 1973).

SMA is also essential for executing a sequence of movements (Orgogozo & Larsen, 1979; Roland, Larsen, Larsen & Skinhoj, 1980; Halsband, 1982). Direct responses do not require linking two actions together, but indirect responses (such as reaching over a barrier and then changing direction to obtain the goal) do. Similarly, retrieving a hidden object, which also comes in at around 8 months, requires a sequence of actions too (removing the barrier and then reaching for the goal). The

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[b] Area 6 includes both SMA and premotor cortex. Many of the reports of release of reflexive grasping are older and the lesions were not limited solely to SMA.

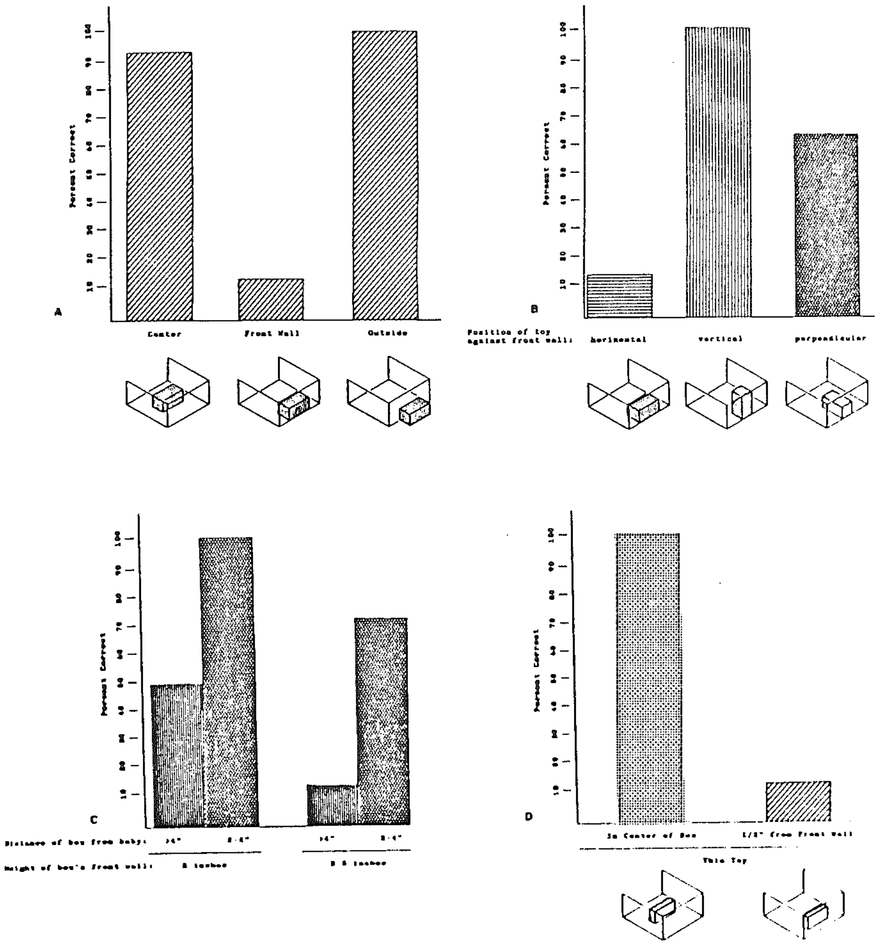

FIGURE 3. (A) Percent correct with the toy in the center of the box, directly behind the front wall, and outside directly in front of the front wall. (B) Percent correct with the toy horizontal, vertical, or perpendicular to the front wall. Toy was directly behind front wall in all conditions. (C) Percent correct by distance of box from the infant and height of the front wall of the box. Note that percent correct is lowest when the taller box is farther away, and percent correct is highest when the shorter box is closer. (D) Percent correct for the thin toy with the toy in the center of the box and one-half inch from the front wall.

Box is drawn with front of box toward the lower right-hand corner of the page. Top and back of box are open. (From Diamond & Gilbert, 1989. Used with permission.)

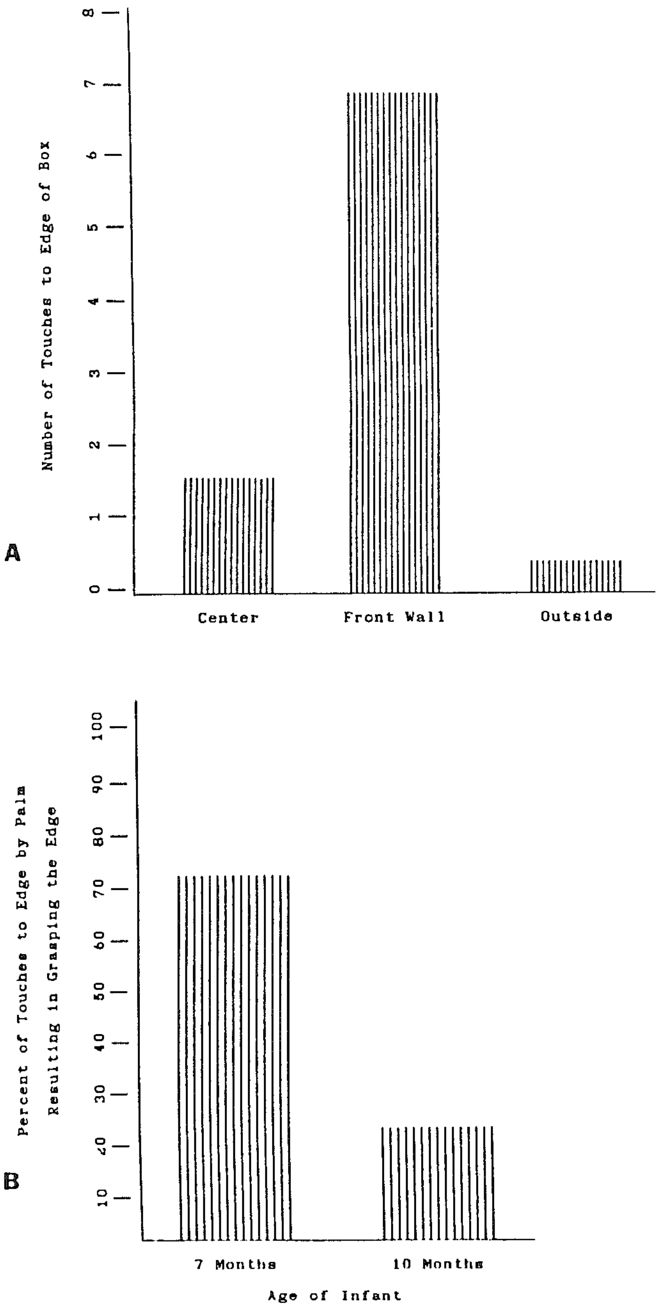

FIGURE 4. (A) Number of instances of touching the edge of the box when the toy was in the center of the box, directly behind the front wall, and outside directly in front of the front wall. (B) Percent of times 7-month-olds and 10-month-olds reacted to touching the edge of the box by grasping the edge. (From Diamond & Gilbert, 1989. Used with permission.)

role of maturation of SMA in the development of the ability to execute sequences of actions (e.g., means–end behavior) is discussed elsewhere (Diamond, in press, a).

From the time infant monkeys are first able to reach for a free-standing object (about 1½ months), they have no difficulty retrieving an object from on top of another object or an object extending partly out of the front opening of the object retrieval box. They are able to succeed here at the outset. They have not been tested with one object directly behind another to my knowledge. The same is true for monkeys with lesions of dorsolateral prefrontal cortex: They have no difficulty retrieving an object from on top of another or extending outside the box opening. They have not been tested with one object directly behind another. Monkeys with lesions of SMA have not been tested on any of these conditions so far as I know.

INHIBITION OF PREPOTENT RESPONSE TENDENCIES: AT 7½ TO 12 MONTHS OF AGE

The Object Retrieval Task

Between 6 to 12 months, human infants show a clear developmental progression in their ability to retrieve an object from inside a clear, open box. Here, the problem for the infants is not inhibiting a reflex, but inhibiting the natural tendency to reach straight for what they want. When the object is seen through one of the closed sides of the box, the infant must inhibit the impulse to reach directly for the object, and instead detour around to the opening. Infant monkeys show a similar developmental progression between 1½ and 4 months. Adult monkeys with lesions of dorsolateral prefrontal cortex or with dopamine depletion due to MPTP injections show the same errors on the task as do younger infants.

The object retrieval task is usually administered with a transparent box (4.5 × 4.5 × 2 inches or 6 × 6 × 2 inches in size). Performance is also assessed with a white opaque box (4.5 × 4.5 × 2 inches) for comparison. Each box is constructed of Plexiglas, and the opening is sufficiently large for an infant's hand to enter easily. All boxes have 4 closed sides. With a box placed so the front, left, or right is open, the box has no bottom. With a box placed so that the top is open, the box has no back.

Experimental variables include: (a) which side of the box is open (front, top, left, or right), (b) distance of the object from the box opening (ranging from partially outside the box to deep inside the box), and (c) position of the box on the testing surface (near the front edge of table or far, far to the left, midline, or far to the right). The object inside the box is always visible when the box is transparent, but the experimental variables jointly determine whether the object is seen through a closed side of the box or through the opening.

Developmental Progression in Human Infants

Twenty-five infants (11 male, 14 female) were tested longitudinally every 2 weeks from roughly 6 months through 12 months of age. Another 84 children were tested once to control for the effect of repeated testings (6 male and 6 female subjects at

TABLE 2. Progression of Performance on the Object Retrieval Task over Age[a]

Age in Months	Percent of Reaches to a Side Other Than the One Infant Is Looking Through: Front-Open Trials	Percent of Reaches to a Side Other Than the One Infant Is Looking Through: Side-Open Trials	Percent of Trials Where Infant Succeeds Without Ever Looking in Opening on That Trial: Front-Open Trials	Percent of Trials Where Infant Succeeds Without Ever Looking in Opening on That Trial: Side-Open Trials	Average Duration of Trials Where Infant Cannot See Through Opening at Outset (in sec): Front-Open Trials	Average Duration of Trials Where Infant Cannot See Through Opening at Outset (in sec): Side-Open Trials
6½	12	5	0	0	22.9	44.8
7	17	28	0	0	18.8	28.9
7½	11	21	2	0	6.5	26.8
8	28	27	2	2	7.2	20.8
8½	23	21	4	4	10.8	24.8
9	49	28	18	4	9.8	13.8
9½	72	47	33	12	10.8	15.0
10	70	49	50	6	7.5	13.6
10½	83	55	67	13	4.2	9.0
11	81	70	77	38	4.2	7.2
11½	80	82	73	60	5.0	4.8
12	75	78	80	80	2.6	4.9

[a] Based on 25 infants tested longitudinally every 2 weeks (from Diamond, submitted).

each of the following ages: 6, 7, 8, 9, 10, and 11 months; and 3 male and 3 female subjects at 5 and 12 months of age) (Diamond, submitted).

A trial began with the experimenter placing a much desired toy in one of the boxes. The infant had simply to retrieve the toy. No time limit was imposed. A trial ended with retrieval or when the infant refused to try any longer. Considerable freedom of movement was permitted and if an infant became distracted, the experimenter tapped the box or toy to regain attention. The experimenter held the back of the box throughout each trial to prevent the infant from simply lifting the box off the toy.

Not until 6½ months could infants retrieve the toy when it was totally inside the box. However, infants of 6½–8 months succeeded only when they happened to see the toy through the opening of the box. They were unable to retrieve the toy if they saw it through a closed side (see TABLE 2). They banged and scratched with considerable effort and persistence, but if their line of sight did not change they tried no other route to the toy.

Infants of 7½–8 months actively tried to change the side through which they saw the toy by moving their bodies or the box (although they, like younger infants, reached only at the side they happened to be looking through at the time of the reach). Infants of 6½–7 months not only reached exclusively at the side through which they were looking, but made no attempt to change which side this was. Hence, the conditions specifying the side infants would look through at the outset of the trial determined with remarkable accuracy whether infants of 6½–7 months would succeed or fail. For example, when (a) the front of the 4.5 × 4.5 × 2 inch transparent box was open, (b) the box was placed no closer than 3 inches from the front edge of the table, and (c) the toy was placed within 0.75 inches from the front of the box, infants of 6½ and 7 months succeeded on 91% and 96% of the trials, respectively. On the other hand, when the same side of the same box was open, but the box was placed within 1.5 inches from the front edge of the table, and the toy was placed at least 1.5 inches from the front edge of the box, infants of 6½ and 7 months succeeded on 0 or only 14% of the trials, respectively.

Failure could be turned into success if the experimenter moved the box so that the infant saw the toy through the box opening. On 90% of such experimenter interventions, infants of 6½–7 months succeeded in retrieving the toy as soon as the box was moved (see TABLE 3, columns 4 & 7). The sight of the toy through the opening had a dramatic, immediate effect. Infants who were crying or fussing stopped abruptly. All straightaway zoomed in the opening for the toy.

On the other hand, if the experimenter moved the box so that the infant could see the toy through the box opening, but then returned the box to its original position as the infant began to reach ("show and return"), only 15% of these experimenter interventions enabled infants of 6½–7 months to succeed (TABLE 3, columns 3 & 6).

TABLE 3. Percent Correct on Trials in Which Infants Could Not See the Toy Through the Box Opening at the Outset of the Trial: Without Assistance from the Experimenter, with the Box Moved Momentarily so Infant Could See the Toy Through the Opening, and with the Box Permanently Moved So Infant Could See the Toy Through the Opening

Age in Months	Opening at Front of Box: Infant Sees Toy Through a Closed Side	Opening at Front of Box: "Show & Return"	Opening at Front of Box: E Moves Box So Infant Sees Toy Through Box Opening	Opening at Side of Box: Infant Sees Toy Through a Closed Side	Opening at Side of Box: "Show & Return"	Opening at Side of Box: E Moves Box So Infant Sees Toy Through Box Opening
6½	00	09	88	07	14	79
7	13	15	91	00	09	89

NOTE: Based on 25 children studied longitudinally every 2 weeks (see Diamond, submitted).

Percent of infants succeeding when the box is moved momentarily so they can see in the opening and then returned to place ("show and return"; columns 3 & 6) is never significantly different from the percent of infants succeeding when the box is not moved at all (columns 2 & 5).

However, the percent of infants succeeding when the box is moved so that the infant can see in the opening and the box is left in that position (columns 4 & 7) is significantly greater than the percent of infants succeeding when the box is moved in this way but then returned to place (columns 3 & 6) at both ages and for both orientations of the box opening:

6½ months, front of box open: $t = 12.91$, $p = 0.001$; 6½ months, side open: $t = 6.97$, $p = 0.0004$; 7 months, front of box open: $t = 12.13$, $p = 0.0001$; 7 months, side open: $t = 12.91$, $p = 0.0001$.

Typically, infants immediately reached into the opening when they could see in, but deserted the opening just as quickly when their line of sight to the toy was again through a closed side.

Lack of inhibitory control is often confused with perseveration. Because the prepotent response is often the response the subject has been making, a failure to inhibit the prepotent response is often manifest as perseveration. In the object retrieval task, however, perseveration and lack of inhibition can be distinguished because the dominant response is the product, not of reinforcement history, but of the tremendously strong pull that the sight of the goal exerts on behavior.[c] Consider the performance of 6½–7-month-old infants on the following sequence of 5 trials with the opening of the box at the front: On trial 1, the box was positioned so that the toy inside was seen through the closed top of the box; all infants failed. For trials 2–4 the box was moved back 1 inch, and the toy forward one-half inch (so that the toy was now visible through the open front); the infants succeeded on all 3 trials. On the final trial, the conditions of trial 1 were again presented. Despite the 3 success experiences of retrieving the toy through the front opening, infants did not repeat this response on the last trial, but reached instead to the side they were now looking through, the top. They would have succeeded had they perseverated in the response of the previous 3 trials. However, they deserted the opening as soon as they no longer saw the toy through the opening. Here, a lack of inhibitory control (in resisting the pull to reach to the side through which they were looking) led to a change in behavior rather than to perseverative repetition.

The lure of the line of sight was so powerful that even the tactile information provided by the infant pushing the toy inside the box him- or herself was ignored when the infant no longer saw the toy through the opening. All children, at all ages, quickly reached directly to the toy if it was partly (even slightly) out of the box, regardless of whether the opening was on the top, front, or side. Being a bit clumsy, however, infants sometimes accidentally pushed the toy back inside the box in trying to grasp it. Rather than pursue the toy through the opening (which would usually have meant extending their hand another inch or so), 6½–8 month old infants often deserted the opening and tried to reach instead at the side of the box through which they were looking.

At 8½–9 months, the first separation of line of sight from line of reach was seen. Infants bent down and looked through the front of the box, sat up, and then reached into the front while looking through the top of the box. Performance when the left or right side of the box was open, however, always lagged behind performance with the front opening. Hence, while infants bent down to see into the front opening at 7½–8 months, they did not try to lean and look into the side opening until 8½–9 months. Just as at 7½–8 months they needed to continue to look in the front if they were to reach in the front opening, so at 8½–9 months they needed to continue to look in the side opening if they were to reach in. When leaning all the way over to look in the opening, the hand ipsilateral to the opening is tucked under the body, indeed there is a tendency to want to extend it downward to stop oneself from falling. Hence, leaning and looking in the side was almost always accompanied by a reach with the hand contralateral to the opening, which though easier from this position than reaching with the ipsilateral hand, looks very contorted and is therefore termed an "awkward reach." The awkward reach is not the result of a hand preference, as it is seen on both sides of the box, and it has been observed in several other laboratories as well (Bruner, Kaye & Lyons, 1969; Gaiter, 1973; Schonen & Bresson, 1984).

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[c] It should be noted that it is probably not simply the sight of the goal, but the sight of the goal seemingly within reach. The farther away the goal, the weaker the pull it exerts on behavior. Thus, when the top of the object retrieval box is open, infants of 8–9 months will pull the box closer to themselves to retrieve the toy—if the toy is initially clearly out of reach. If, however, the toy is positioned just barely out of reach, infants of 8–9 months often persist in trying to reach for it directly without pulling the box. Kohler made similar observations years ago in his "umwege problems": "[A female dog] was standing at B near a wire fence over which food is thrown to some distance; the bitch at once dashes out to it, describing a wide bend. It is worth noting that when, on repeating this experiment, the food is not thrown far out, but was dropped only just outside the fence, so that it lay directly in front of her, separated only by the wire, she stood seemingly helpless . . . ; she pushed again and again with her nose at the wire fence, and did not budge from the spot" (Kohler, 1925: 14).

At 9½–10½ months, infants retrieved the toy from the front of the box without ever having looked in the opening. When the left or right side of the box was open, they could now lean and look in the opening, then sit up, and reach in the side opening while looking through the top of the box. As they now reached from the upright position, the awkward reach was no longer seen. Finally, by 11–12 months, human infants could reach to even the left or right side of the box without having looked through that opening. Retrieval by 11–12-month-olds on all trials was typically accomplished in under 5 sec.

TABLE 4. Mean Trial Duration for Same Size Transparent and Opaque Boxes on Left-Open Trials with Toy Deep in Box[a]

Type of Box	7½ (10)	8 (15)	8½ (19)	9 (18)	9½ (17)	10 (17)	10½ (16)	11 (17)	11½ (14)	12 (14)
	Age in Months (*N*)									
Transparent	28.6	29.4	24.9	16.7	15.4	13.8	13.3	11.4	5.2	4.7
Opaque	15.7	16.5	14.0	11.3	10.4	10.3	9.8	11.2	6.8	3.3

[a] For a more detailed description see Diamond (submitted).

Infants always performed better when the opaque box was used than they did with the transparent box. For example, on comparable trials they retrieved the toy more quickly from the opaque box than from the transparent box (TABLE 4). Infants also passed through the sequence of phases in performance more quickly with the opaque box than they did with the transparent box, and never performed more poorly with the opaque box than they did with the transparent box. This is fully consistent with most other reports of infants' performance with opaque and transparent barriers (Bruner *et al.*, 1969; Church, 1971; Lockman, 1984; Schonen & Bresson, 1984), although McKenzie and Bigelow (1986) failed to find a difference.

It might seem counterintuitive that retrieval was easier with the opaque box. After all, more information was available and less demand was placed on memory when the box was transparent. However, when a transparent box was used, infants could see the toy directly through a closed side, and the pull to try to reach straight through that side to the toy was strong.[d] To succeed, infants had to inhibit this pull and instead reach around to the opening. Younger infants could not do this. In this sense, improvement on the object retrieval task traces the development of inhibitory control of reaching.

Infants succeeded earlier with the opaque box because it did not require that they resist reaching straight to where they saw the toy. They could not see the toy through a closed side. Thus, the counterintuitive finding that the task became easier when the goal was not initially visible supports the hypothesis that *seeing* the goal through a closed side makes the task harder. It makes the task harder because the tendency to reach straight to the goal must then be inhibited.

Developmental Progression in Infant Monkeys

Infant monkeys were tested with the same procedure as were human infants, with the following exceptions: (a) testing was conducted daily rather than biweekly, (b) food was used as the reward rather than a toy, (c) the box was locked into position, rather than held in place by the experimenter, (d) the dimensions of the box were 3 × 3 × 2.5 inches, and (e) subjects were tested with the front, left, and right of the box open, but not with the top open, as the box could not be positioned so that the monkeys would be unable to look in through the top. Five infant rhesus monkeys were tested on the task beginning at approximately 1½ months of age (range = 38–46 days). Each monkey was tested from the earliest age that particular monkey could retrieve a small piece of food (Diamond & Goldman-Rakic, 1986).

Infant monkeys never showed the behaviors characteristic of human infants below 7½ months. That is, even the youngest infant monkeys could retrieve the bait if it were near the open front of the box and the monkey could look into the front and see the bait (unlike human infants of 5–6 months who could not retrieve the bait from the front opening unless the bait was extending partially outside the box). Infant monkeys also moved around and tried to look in different sides of the box from the earliest age they could be tested—unlike human infants below 7½ months, who did not, on their own intitiative, try to change which side of the box they were looking through.

However, if the food was placed so that it extended partially out of the box opening and an infant monkey of 1½–2 months accidentally pushed the food back inside the box, the infant monkey was as stymied as were human infants of 7½–8 months. Even though the infant monkey had pushed the food inside the box him- or herself, the monkey deserted the opening and reached instead to the side through which the food could now be seen. The pull to try to reach straight through the transparent wall to the food was not resisted, and no other strategy was tried. In short, at the earliest age at which infant monkeys could be tested (about 1½ months), their performance closely resembled that of human infants of 7½–8 months. Infant monkeys never showed performance comparable to that of human infants younger than 7½ months.

Infant monkeys of 2–2½ months could retrieve the food reward if the left or right side of the box was open as long as the infant was looking in the opening. That is, the monkeys leaned and looked in the opening and reached with the hand contralateral to the opening—showing the same awkward reach seen in human infants of 8½–9 months.

By 3–4 months, infant monkeys were perfect at the object retrieval task, as are human infants of 11–12 months.

Three infant monkeys with unilateral left hemisphere prenatal lesions were also tested on object retrieval. Two of the infants received lesions of parietal cortex and one received a lesion of occipital cortex. The two who received lesions of parietal cortex performed normally on object retrieval, although the infant with the larger lesion showed errors in aiming the reach (misreaching errors) often seen in adult monkeys after lesions of parietal cortex. The infant with a lesion in occipital cortex, however, performed better on object retrieval than did any of the intact infants, performing perfectly on the very first day of testing (2 months of age). Moreover, this superior performance was limited to object retrieval, as this same infant was impaired in performance of A$\overline{\text{B}}$. A lesion in occipital cortex is likely to result in a visual impairment. It is possible that the degraded visual information available to this infant monkey helped him succeed at object retrieval in the same way that using an opaque box was helpful to human infants—the need for inhibition of the tendency to reach straight through a closed side of the box to the visible reward was obviated because the reward was much less visible.

Performance of Adult Monkeys with Selective Lesions of the Brain

We tested 3 groups of adult rhesus monkeys, (1) unoperated, (2) bilateral lesions of dorsolateral prefrontal cortex (Brodmann's Areas 8, 9, and 10), and (3) bilateral lesions of parietal cortex (Brodmann's Area 7) (Diamond & Goldman-Rakic, 1985), and 2 groups of adult cynomolgus monkeys, (1) unoperated and (2) bilateral lesions of the hippocampal formation (including much of the parahippocampal gyrus and entorhinal cortex, but sparing the amygdala and temporal stem) (Diamond, Zola-Morgan & Squire, 1989) on object retrieval. In addition, other investigators have tested African green monkeys (Taylor, Elsworth, Roth, Sladek & Redmond, 1990; Taylor, Roth, Sladek & Redmond, in preparation) and rhesus monkeys (Saint-Cyr, Wan, Doudet & Aigner, 1988) injected with MPTP, plus untreated controls, on the task.

All unoperated monkeys and all monkeys with lesions of parietal cortex or of the hippocampal formation detoured to reach in the box opening (although monkeys with parietal cortex lesions had some difficulty getting their hands inside the opening due to misreaching errors). Monkeys with lesions of dorsolateral prefrontal cortex, however, had great difficulty inhibiting the pull to reach through the side they were looking at.

When the food reward extended partially out of the box opening and a monkey with a lesion of dorsolateral prefrontal cortex accidentally pushed the food back inside the box in the course of trying to retrieve it, the monkey (like human infants

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[d] Schonen and Bresson (1984: 111) captured much the same sentiment when they wrote, "It is as if the visibility of the object through the transparent screen makes more difficult programming a detour for the hand than when an opaque screen actually masks the object. Programming a reach on the basis of a mental representation (opaque screen) seems to be easier, at the age of 9 months, than to program a hand path which makes a detour relative to the line of sight to the object (transparent screen)."

and infant monkeys) withdrew his hand and reached to the side of the box through which he was looking (FIG. 5). Monkeys with dorsolateral prefrontal cortex lesions also needed to look in the left or right side of the box as they were reaching if they were to reach through these openings. Thus, they leaned and looked in the opening, and reached into the box with the hand contralateral to the opening—showing the same awkward reach as seen in human infants of 8½–9 months and infant monkeys of 2–2½ months (see FIG. 6).

It should be noted that adult monkeys with dorsolateral prefrontal cortex lesions, like intact infant monkeys, never performed as poorly on object retrieval as do human infants below 7½ months of age. Frontal monkeys had no difficulty retrieving the reward from just inside the opening when they were looking in the opening, and they moved around, looking at the reward inside the box from different angles. Neither of these behaviors required inhibition of the tendency to reach straight to the goal, however. When such inhibition was required, frontal monkeys, like human infants and infant monkeys, showed a deficit in performance.[f]

The results on object retrieval are reminiscent of ones obtained by Moll and Kuypers (1977) when they placed monkeys in a cage with a transparent floor. A food reward could be seen under the center of the floor, but the only route to the food was through a hole in the side. Rhesus monkeys with a large unilateral lesion of frontal cortex that included dorsolateral prefrontal cortex, premotor cortex, and SMA (extending from the posterior two-thirds of the principal sulcus to the anterior portion of the precentral gyrus) *and* with a commissurotomy disconnecting the two hemispheres, tried to reach straight through the center of the floor to the food with the hand contralateral to the lesion, while the hand connected to the intact hemisphere of the same monkey detoured around to the opening on the side and retrieved the food. Unoperated monkeys and monkeys with lesions limited to the precentral gyrus retrieved the food straightaway and did not persist in trying to reach through the transparent barrier, as did the monkeys with the large frontal lesions.

Monkeys treated with MPTP showed deficits on object retrieval similar to those seen following dorsolateral prefrontal cortex lesions and similar to those seen in young infants. They try to reach straight through the transparent barrier, show the awkward reach with the hand contralateral to the opening, and perform significantly better when the box is opaque than when the box is transparent (Taylor *et al.*, 1990, in preparation; Saint-Cyr *et al.*, 1988). MPTP injection results in reduced levels of dopamine in the substantia nigra and in the frontal-striatal system (Elsworth,

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[f] It has also been shown that the deficit following large lesions of frontal cortex is lack of inhibition rather than perseveration, complementing the results for human infants discussed above: Jacobsen and colleagues (Jacobsen, Wolfe & Jackson, 1935; Crawford, Fulton, Jacobsen & Wolfe, 1948) presented chimpanzees with a row of 4 pegs. The chimpanzees were trained to push on the first 3 pegs and pull the fourth to obtain a reward. Then they received lesions of frontal cortex. Perseverative errors would have been to try to push peg 4, i.e., to repeat the response they had made at pegs 1, 2, and 3. The prepotent response, however, would be the one most closely associated with the reward. Because the reward was delivered after pulling the fourth peg, pulling would be prepotent here, and errors due to inadequate inhibitory control would be to try to pull on earlier pegs. The frontally lesioned chimpanzees did not try to push peg 4 (i.e., they did not perseverate in pushing), instead they tried to pull on the earlier pegs 2 and 3. These errors of "anticipation" were not overcome within the limits of testing.

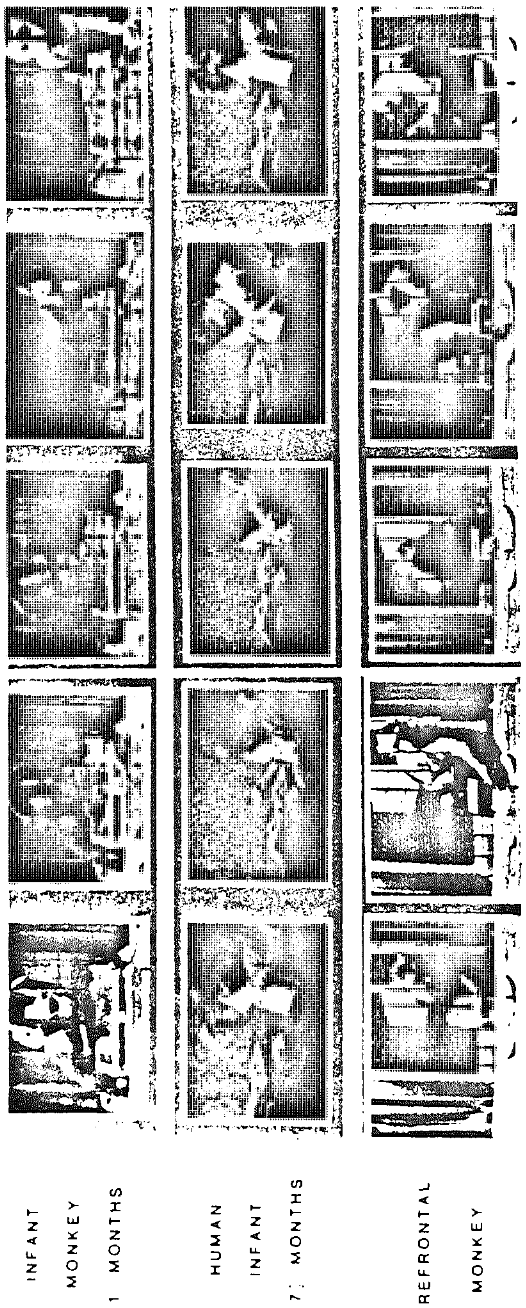


FIGURE 5. Failure after pushing the bait inside the box themselves: infant monkey of 1½ months, human infant of 7½ months, and adult monkey with bilateral lesions of dorsolateral prefrontal cortex (see Diamond, submitted).
Frame 1: Bait is partially out of box, subject reaches immediately for the part that is sticking out of the box.
Frame 2: Subject accidentally pushes bait into the box. Once bait is inside the box, subject is unable to retrieve it, even though subject was touching the bait, subject pushed the bait inside the box himself, and subject was at the opening.
Frame 3: Subject withdraws hand from opening and goes to the side of the box through which he sees the bait.
Frame 4: Subject looks at bait through front of box and reaches to the front.
Frame 5: Unable to retrieve the bait, subject gives up.

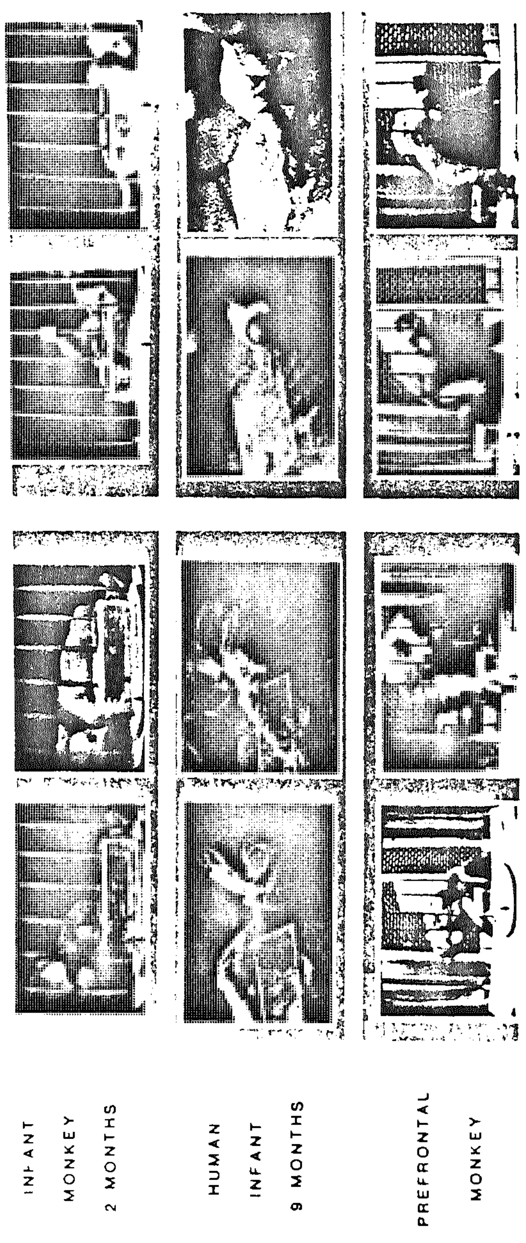


FIGURE 6. The "awkward reach" in an infant monkey of 2 months, a human infant of 9 months, and an adult monkey with bilateral lesions of dorsolateral prefrontal cortex (see Diamond, submitted).
Frame 1: Subject leans and looks at bait through opening of box.
Frame 2: Subject reaches in awkwardly with the far hand.
Frame 3: Opening is on the other side of the box. Performance is the same. Subject leans and looks into the opening.
Frame 4: Subject reaches in awkwardly with the far hand.

Deutsch, Redmond, Sladek & Roth, 1987; Mitchel, Cross, Sambrook & Crossman, 1986) and is thought to produce behavioral deficits similar to those seen in patients with Parkinson's disease (Burns, Chiueh, Markey, Ebert, Jacobowitz & Kopin, 1983; Stern & Langston, 1985). Thus, depletion of dopamine in the neural circuit appears to produce the same deficits on object retrieval as do lesions to the circuit.

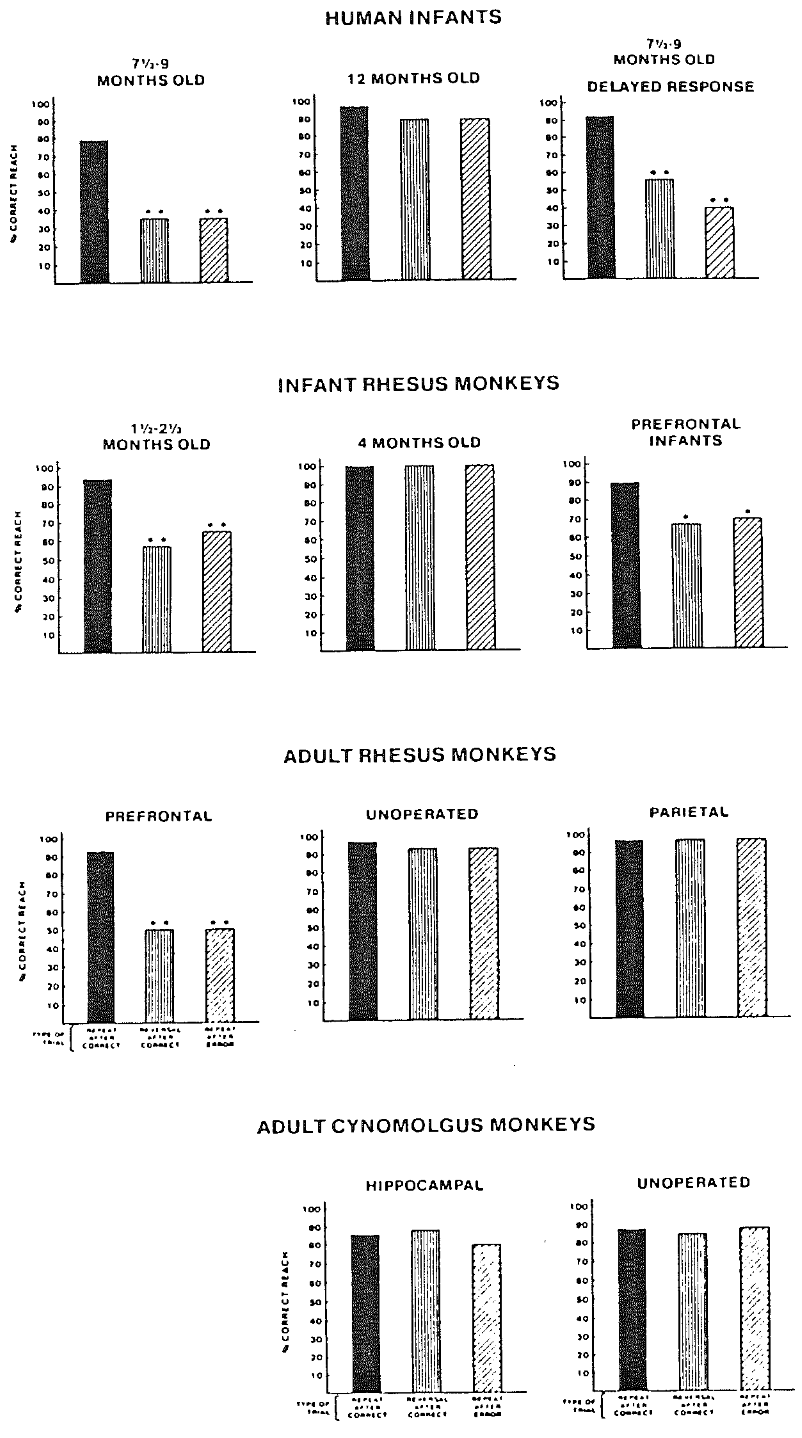
The A$\overline{B}$ and Delayed Response Tasks

In the A$\overline{B}$ and delayed response tasks, the subject watches as a reward is hidden in one of two identical wells, a brief delay is imposed during which visual fixation on the wells is broken, and then the subject is allowed to reach. The 2 tasks are identical except that where the reward is hidden is varied randomly in delayed response, while in A$\overline{B}$ the reward is always hidden in the same well until the subject is consistently correct, then the reward is hidden in the other well and the procedure repeated (see Diamond, this volume a, for a more complete discussion of the tasks).

Human infants of 7½–9 months, infant monkeys of 1½–2½ months, and infant and adult monkeys with lesions of dorsolateral prefrontal cortex err on both tasks with delays of only 2–5 sec. Their errors are not randomly distributed over trials, however, even though the delay and all testing procedures (except side of hiding) are identical on all trials. Their performance is excellent when the reward is hidden in the same well as on the previous trial and they were correct on the previous trial (repeat-following-correct trials). Their errors are confined to trials on which side of hiding is reversed and to the next few trials at that new location. Thus, human infants, infant monkeys, and prefrontally operated monkeys err when they were correct on the previous trial and side of hiding is reversed (reversal-following-correct trials) and when side of hiding is unchanged following an error (repeat-following-correct trials) (see FIG. 7). Forgetting cannot account for this pattern of differential performance across trials because delay, and therefore presumably the memory demands, is equal across trials, yet the error rate is not.

Positive reinforcement of a response (such as successful retrieval of the reward at one of the hiding wells) strengthens the tendency to repeat that response. The pattern of differential performance by type of trial reflects difficulty inhibiting this tendency. The very first trial does not require inhibition because no response tendency has been created by previous success experiences. All subjects perform well on trial 1. Similarly, when the bait is hidden where the subject was just rewarded there is no conflict between the memory of the hiding and the tendency to repeat a rewarded response, and again all subjects perform well. However, when the side of hiding changes and the subject has been rewarded for reaching to the first location, A$\overline{B}$ and delayed response set up a conflict between the subject's memory of where the bait is now hidden and the subject's tendency to repeat a rewarded response. To succeed on A$\overline{B}$, a subject must not only remember where the bait is hidden, but must also inhibit the response tendency to reach back to the previously correct location.

Further evidence that memory failure alone cannot account for the pattern of differential performance across trials comes from the performance of monkeys with lesions of the hippocampal formation on the A$\overline{B}$ task (Diamond, Zola-Morgan & Squire, 1989). These monkeys have a profound memory impairment, but they never show the differential pattern of performance on A$\overline{B}$. At the short delays at which



infants and prefrontal monkeys fail, hippocampal monkeys perform well. At delays of 15–30 sec, hippocampal monkeys have difficulty remembering where the reward has been hidden and their performance falls off, but it does not fall off selectively for reversal trials. Their performance when side of hiding is reversed, following their successful response at the old location, is not significantly worse than their performance when the reward continues to be hidden where they have been reaching successfully. When hippocampal monkeys reach incorrectly, they show some tendency to repeat that error on the next trial, but where these strings of errors begin is randomly distributed over a testing session.

Human infants show the pattern of differential performance by type of trial even when transparent covers are used (e.g., Butterworth, 1977). This, too, argues that a failure to remember cannot account for this pattern of error, for the reward is always visible when the covers are transparent. Infants perform better with transparent covers than they do with opaque covers, but when they do err with transparent covers those errors tend to be on reversal trials and on repeat-following-error trials.

Several investigators have tried to distinguish random reaching in human infants from reaching directed back toward the previously correct location by using multiple hiding wells.[f] This work has shown that infants do not reach randomly. When the new hiding location is not an endpoint, so that infants can err by reaching to either side of it, infants tend disproportionately to err in the direction of the previously correct location, although they do not reach all the way back to it (Diamond, Cruttenden & Neiderman, 1989). Their response reflects a compromise between their memory of the hiding they have just witnessed and their tendency to repeat their old response.

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[f] When only 2 hiding locations are used, an incorrect reach must necessarily be to the other hiding location.

FIGURE 7. Percent correct by type of trial at delays of 2–5 sec.

Human infants of 12 months perform perfectly. Human infants of 7½–9 months perform well on repeat-following-correct trials, but perform significantly worse on reversal trials and on repeat-following-error trials in both the A$\bar{B}$ task (Diamond, 1985) and the delayed response task (Diamond & Doar, 1989).

Infant rhesus monkeys of 4 months perform perfectly. Infant monkeys of 1½–2½ months, and infant monkeys who have received bilateral lesions of dorsolateral prefrontal cortex at 4 months and were re-tested at 5 months, show a similar pattern of differential performance over trials as do 7½–9-month-old human infants (Diamond & Goldman-Rakic, 1986).

Unoperated adult rhesus monkeys and those with bilateral lesions of parietal cortex perform perfectly. Adult rhesus monkeys with bilateral lesions of dorsolateral prefrontal cortex, however, show the same pattern of differential performance over trials as do 7½–9-month-old human infants (Diamond & Goldman-Rakic, 1989).

Unoperated adult cynomolgus monkeys and those with bilateral lesions of the hippocampal formation perform perfectly at delays of 2–5 sec (Diamond, Zola-Morgan & Squire, 1989). (At delays of 15–30 sec hippocampal monkeys no longer perform well on the task, but at these delays they still do not show the pattern of differential performance by type of trial seen in 7½–9-month-old human infants.)

Note that human infants of 7½–9 months, infant monkeys of 1½–2½ months, and infant and adult monkeys with lesions of dorsolateral prefrontal cortex show this pattern of differential performance by type of trial even though the same hiding procedure and delay are used on all trials.

If retrieving the reward at Location A builds up a conditioned tendency to reach to that location again, one would expect this tendency to be stronger the greater the number of reinforced trials at A. Within a narrow range, more reinforced trials at A do *not* lead to more errors when side of hiding is changed (1 vs. 3 reinforced trials at A [Diamond, 1983], 2 vs. 5 trials [Evans, 1973], and 3 vs. 5 trials [Butterworth, 1977]), but when 2 versus 8–10 consecutively correct reaches at A were compared, the expected result was found. Infants who reached correctly to A 8–10 times in a row made significantly longer strings of errors when the reward was hidden at Location B than did infants who reached correctly at A only twice in a row before side of hiding was reversed (Landers, 1971).

Infants sometimes indicate they know where the reward is even when they reach back incorrectly to where they last found it. Here, an inability to inhibit a response tendency appears to lead to errors despite evidence of correct recall. Infants of 8 months or older typically reach immediately to the correct well if their initial reach was incorrect. Often, they uncover the first well (A), but do *not* look in to see if the reward is there. Instead, they immediately desert that well and uncover the other well (B), this time looking into the well for the reward. It is as if they know the reward is at B, even though they reach first to A. Occasionally, an infant will look fixedly at B even as he or she reaches to A (see FIG. 8). Although this behavior is not common, it has been observed by many researchers in many laboratories, and it is very striking when it does occur because at this age infants almost always look where they are reaching. Here, infants appear to be telling us with their eyes that they know where the toy is hidden, even though they reach back to A anyway. Although infants of 8 months reach incorrectly on A$\bar{B}$ and delayed response at delays of 2–5 sec, Baillargeon has shown that, when you assess where subjects look instead of where they reach, 8-month-old infants appear to remember correctly in which location a toy has been hidden over delays of 20–50 sec (Baillargeon & Graber, 1988).

This is reminiscent of the behavior of human adults with damage to dorsolateral frontal cortex on the Wisconsin Card Sort Test. Here, the patient is presented with a deck of cards that can be sorted by color, shape, or number. Frontal patients are able to deduce the first criterion by which to sort the cards as well as anyone. However, after being rewarded for sorting by the first criterion, when the experimenter changes the sorting criterion, patients with frontal cortex damage are impaired in switching to the new rule. They continue to sort the cards by the first criterion—but they can sometimes tell you the new rule as they continue to sort the cards incorrectly. Indeed, frontal patients sometimes say, as they are sorting the cards by the old criterion, "This is wrong, and this is wrong. . ." (Luria & Homskaya, 1964; Milner, 1964). Infants can't tell you the correct answer verbally, but looking at A even as they reach to B may be the nonverbal equivalent. Frontal patients on the Wisconsin Card Sort, like infants looking at the correct hiding location while reaching back to the *previously* correct hiding location on A$\bar{B}$ or delayed response, appear to know the correct answer, but cannot restrain themselves from acting according to what used to be correct.

In short, a failure of inhibitory control can account for the pattern of errors that human and simian infants and prefrontal monkeys show on the A$\bar{B}$ and delayed response tasks. This pattern consists of (a) good performance when the reward is hidden where the subject just reached correctly, and repeated errors when the side of

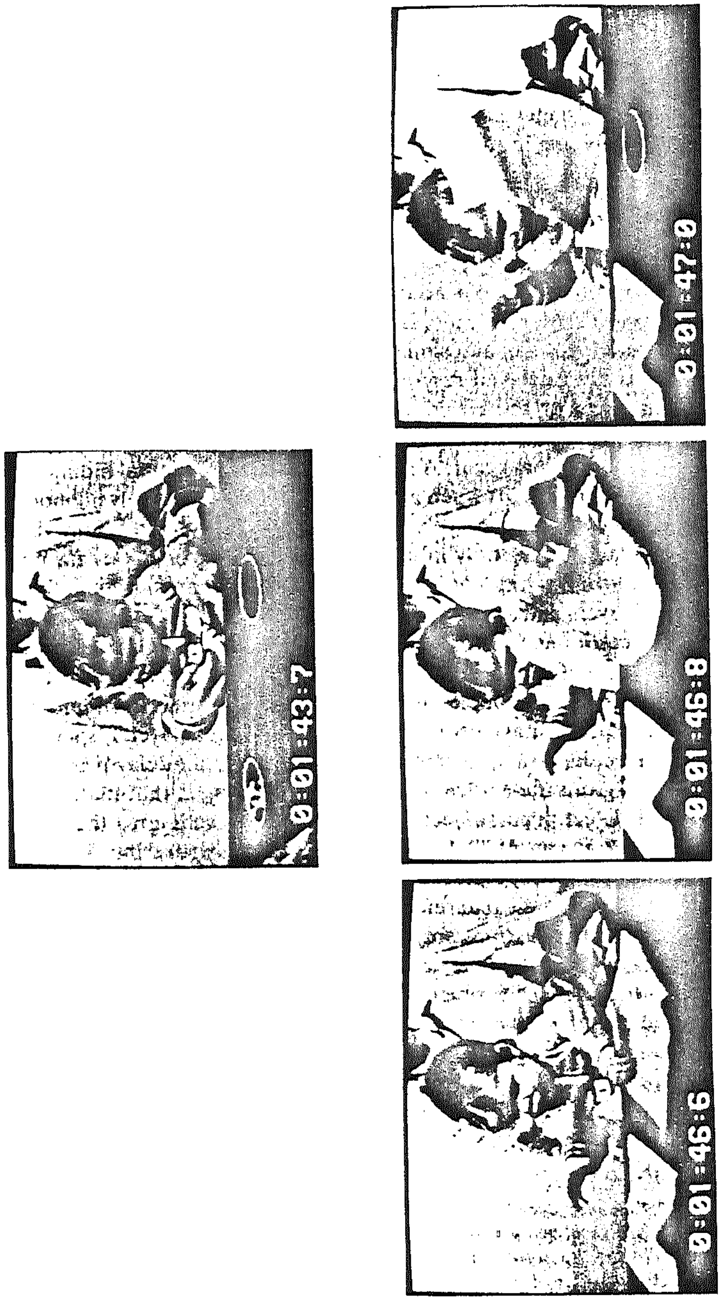

FIGURE 8. Instance of an infant looking at well B while reaching to well A. The infant had successfully retrieved the toy twice at well A. Side of hiding is now reversed to B.

Frame 1: Infant clearly sees the hiding at B.

After a brief delay, infant was allowed to reach.

Frames 2–4: Although infant is looking fixedly at well B, he is reaching to well A.

hiding is reversed (rather than errors being randomly distributed over trials), and (b) reaches skewed in the direction of the well where the subject last found the reward when multiple wells are used (rather than errors being randomly distributed over the wells on either side of the correct location). Hippocampal monkeys, who have poor memory but can inhibit their response tendency, do not show the pattern of differential performance over trials. At short delays they perform well and at long delays, where their performance is poor, they are no more likely to err on reversal trials than when side of hiding is unchanged. Moreover, failure of inhibitory control can also account for why some errors occur on A$\overline{B}$ and delayed response even when there are no memory demands (as when the covers are transparent) or when subjects appear to remember where the reward is (as when subjects look at the correct well while reaching to the wrong well).

Lack of inhibitory control cannot account for all of the findings on A$\overline{B}$ and delayed response, however. Memory, too, is required for success on these tasks (see Diamond, this volume, a). Human and simian infants and prefrontal monkeys make far fewer errors on A$\overline{B}$ and delayed response when their memory is not taxed, as when no delay is imposed or the covers are transparent, and older infants only continue to err if increasingly long delays are imposed. If only inhibitory control or only memory is taxed some errors occur: A few errors occur at the initial hiding place or on repeat-following-correct trials when a delay is imposed, taxing only memory. A few errors occur when side of hiding is reversed even when the reward is fully visible at the new "hiding" place, taxing only inhibitory control. Most errors by far occur when both memory and inhibitory control are taxed (e.g., when side of hiding is reversed with opaque covers and a delay).[g]

According to this reasoning, tasks most sensitive to dorsolateral prefrontal cortex function should be ones that require both memory and inhibitory control. If this is correct, the delayed matching to sample task (with trial-unique stimuli) should be as sensitive to dorsolateral prefrontal cortex function as is A$\overline{B}$ and delayed response. In delayed matching to sample, a sample object is presented, a brief delay is imposed, and then the subject is given the choice of reaching to the object that matches the sample or to a novel object. The subject is rewarded for reaching to the match. Infants (e.g., Fantz, 1964; Fagan, 1970; Diamond, this volume, b) and monkeys (e.g., Brush, Mishkin & Rosvold, 1961; Harlow, 1950) have a natural tendency to prefer novel stimuli over familiar ones. Therefore, to succeed at delayed matching to sample, an infant or monkey must not only remember what he or she has seen, but must inhibit the tendency to reach to the new object. (Hence, the importance of using new objects on each trial, for if the objects have been seen on previous trials then neither object will be novel and there will be no response bias to inhibit.). Delayed non-matching to sample, while formally similar to delayed matching to sample (sample presented, delay imposed, then the subject is given a choice of reaching to a novel or familiar object, but this time the subject is rewarded for reaching to the novel object) requires only memory, not inhibitory control, and is dependent on the hippocampus, not dorsolateral prefrontal cortex (see Zola-Morgan & Squire, this volume).

Indeed, one old study looked at the performance of monkeys with lesions of lateral frontal cortex on the delayed non-matching to sample and delayed matching to sample tasks, and found results exactly in accord with the reasoning in the preceding paragraph: "When required to select the old object [delayed matching to sample], the frontal group's final level of performance averaged only 57% correct. This was the poorest score obtained by any group. When trained to select the new object [delayed non-matching to sample], however, they achieved an average score of 84% correct. Indeed, 3 of the 4 frontal animals averaged 94% (range, 90–98), a level of 1-trial learning that approached the performance of the 4 normal animals (range, 95–100) and surpassed the performance of the 4 temporal animals (range, 77–91)" (Mishkin, Prockop & Rosvold, 1962: 180).

Improved performance on A$\overline{B}$ and delayed response seems to mark the emergence of the ability for a memory-based intention to override habit; the emergence of the ability to exercise choice. In A$\overline{B}$, delayed response, and the Wisconsin Card Sort, an initial response is strengthened by reinforcement. The ability to acquire a conditioned response, to be influenced by reinforcement, is a very important determiner of human behavior, but it is an ability present from earliest life (see Lipsitt, this volume) and an ability we share with most other organisms (including, for example, aplysia [see Marcus & Carew, this volume]). A later developing ability is the capacity to *resist* a dominant action tendency, whether it is innately strong or has been strengthened by reinforcement. It is this ability that is required when the correct well changes in A$\overline{B}$ or delayed response, the correct criterion changes in the Wisconsin Card Sort, or the subject sees the reward through one side of the object retrieval box but must reach through a different side. The ability to resist a strong response tendency is much more fragile than the ability to strengthen a response. It is not easy even for adults to resist making a habitual response when a change from the usual is required (see Reason [1979], Reason & Mycielska [1982], and Norman [1981] for a wealth of instances where the behavior of adults is captured by the habitual response when another response is more appropriate). However, with effort and concentration we are capable of exercising such inhibitory control. Organisms without frontal cortex may be incapable of this. Thus, although fragile, this ability may be one of the things that distinguishes us from lower organisms. The ability to resist the strongest response of the moment endows us with extraordinary flexibility and the freedom to choose and control our actions.

To some extent, infants appear to know more than they can demonstrate in their behavior. They know that an object continues to exist independently when it borders another object, and they often can remember where an object has been hidden. This is not always reflected in their ability to retrieve contiguous or hidden objects, however, because they have difficulty inhibiting the reflexes of the hand and inhibiting a prepotent response. It is as much of a developmental achievement for infants to inhibit these maladaptive reactions as it is to acquire new behaviors and knowledge. Advances in the inhibitory control of reaching appear to be mediated by maturation of frontal cortex. The earlier advance in inhibition of reflexive reactions to touch is probably mediated by SMA, while the subsequent advance in inhibition of response tendencies is probably mediated by dorsolateral prefrontal cortex.

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[g] It should be noted that because the delays dorsolateral prefrontal cortex is required to bridge on A$\overline{B}$ and delayed response are so brief (2–5 sec), this might be better described as "maintaining attention" than "memory." If one conceives of the ability to span a few second delay as an ability to resist distraction and maintain focussed attention, then one might conceive of A$\overline{B}$ and delayed response as requiring, not memory + inhibition, but 2 types of inhibition (the abilities to resist distraction and to resist repeating a rewarded response).

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DISCUSSION

C. Kopp (*University of California, Los Angeles, CA*): It seems to me that control of inhibition in the first 4 or 5 years of life is one of the primary tasks of infants and young children. Control of inhibition, it seems to me, brings together the cognitive, motor, linguistic, motivational, and emotional systems. It is really a convergence of all of those. Control of inhibition also relates both to the prehensile system and to the gross motor system. It is one of the few areas that we really have not studied very well. There are pockets of research on control of inhibition going back to the 1920s; then Luria and Bruner used barrier tasks and the like. If you look at what is required it is really very interesting. At 8–9 months we see the stopping of the motor response. For me, with my interest in the development during the second year in controlling the motor response in terms of a prohibition given by another, looking at Luria tasks with 2-year-olds and the like . . .[h] So there is this long progression where we expect it to occur, and we really have no idea of what is occurring. Also fascinating is what happens in the second year of life in terms of the gross motor system, because for a period of time with many children the gross motor system gets out of control. Children then have to inhibit the desire to run, walk, hop, climb, and the like, and begin to have the prehensile system become somewhat more important (that is, they can stop running and hopping, and begin to use their hands again). There are some interesting reports, and clearly we know from anecdotal evidence that this happens toward the end of the second year of life. So there are pockets of information, but it is certainly an area that we don't understand. Therefore, I think your research is a lovely program of research. It also leads to the question where do individual differences come in, in terms of what can children do and the long-range ramifications.

My second comment is shorter and relates to the fact that a number of years ago we looked at transparent versus opaque stimuli in a Piagetian problem-solving task with children who were 2, slightly older than 2 years, and there again the transparent stimulus was very confusing for children at that age and we got much better, significantly better, performance with the opaque stimulus.[i]

H. G. J. M. Kuypers (*University of Cambridge, Cambridge, England*): If I may refer to this point, we also were extremely struck by the magnetism that the animals

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[h] Luria, A. L. 1965. The directive function of speech in development and dissolution. *In* Readings in the Psychology of Cognition. R. C. Anderson & D. P. Ausubel, Eds.: 351–363. Holt, Rinehart & Winston. New York.

[i] Kopp, C. B., M. O'Connor & I. Finger. 1975. Task characteristics and a stage 6 sensory-motor problem. Child Development **46:** 569–573.

showed.[j] When you use a transparent floor, the animal's first reaction is to go to the food. Gradually after a couple of trials he sees the open hole, goes to the open hole, but then thinks that is not a good idea and goes back to the food again (which is the worst idea). Then he puts his hand *through* the hole but then pulls his hand back out and returns to his old ways. It's incredible; it looks as if the food which he sees forms a magnet for direct reaching. Now, we thought the only way that success on this task could be achieved was that normally the frontal lobe (it's not completely clear which area within the frontal lobe) would suppress a subcortical area which guides reaching. We thought that subcortical area was the superior colliculus.

In order to test this, I thought I should make a pedunculotomy involving the medial side of the cerebral peduncle, high up in the mesencephalon, so I would catch the bulk of the fibers which go from the cortex straight to the superior colliculus. In a series of 5 monkeys (*Macaca fascularis*) I made a transection of the medial half of the cerebral peduncle. All showed a motor defect, but none, *except one,* showed a defect in detour reaching. Either I didn't catch enough fibers *or* it is not the fibers in the peduncle that inhibit the superior colliculus, because I think inhibition of superior colliculus is what is required.

I tested detour reaching by presenting the animals with a round transparent plastic box. The piece of food (apple) was attached to the undersurface of the transparent top of the box, and the animals could reach the food only through large holes in the side of the box. The diameter of this box was approximately 30–40 cm, resembling your devices. It was a very effective test, because with unilateral frontal cortex lesions, animals with both hands free placed the affected hand on the top of the box, while the other hand reached through a hole in the side and retrieved the apple from the undersurface of the top of the box (without much training).

One of the 5 monkeys with the cerebral peduncle transection reached directly for the food at the top of the box with his affected arm (i.e., the arm contralateral to the lesion) and did not reach for the open hole. Now that animal had an exceptional lesion. In all the animals the lesion involved the medial part of the peduncle, but in this one animal, and *only* in this one animal, the transection damaged a blood vessel which enters the mesencephalon. I have always tried to avoid those blood vessels, but that one time I pulled one of the blood vessels, resulting in a medium-sized bleed, extending from the ventral tegmental area laterally into the substantia nigra (see FIG. 9). Thus, the lesion in the animal with a defect in detour reaching destroyed a part of the substantia nigra (in both pars reticulata and pars compacta). Now there are two things that are interesting in this respect. One, cells in the ventral tegmental area are the origin as far as I can find out (perhaps I'm wrong) of the dopaminergic innervation of the cortex. Adele has speculated that depletion of dopamine in the cortex might produce the deficit in detour reaching. If that is true, then the damage to the VTA in this monkey might have produced the behavioral deficit since it destroyed a portion of the dopaminergic cells. That is, damage to the dopaminergic system of the frontal lobe caused by damage to the ventral tegmental area in the mesencephalon might have been responsible for the defect in detour reaching.

On the other hand, there is another perspective. The pars reticulata of the substantia nigra was extensively damaged in this monkey. This region is known to have an inhibitory projection to the superior colliculus. In fact, it is a branching projection because collaterals of this projection go through the lateral part of the dorsomedial nucleus of the thalamus which goes to the frontal eye fields, so it looks as if everything is slightly in register. Anyway, perhaps what I did was interfere with this system. Perhaps the lesion in the medial part of the substantia nigra produced the defect in detour reaching by interfering with the nigro-collicular inhibitions. This is the interpretation that occurred to me at the time.

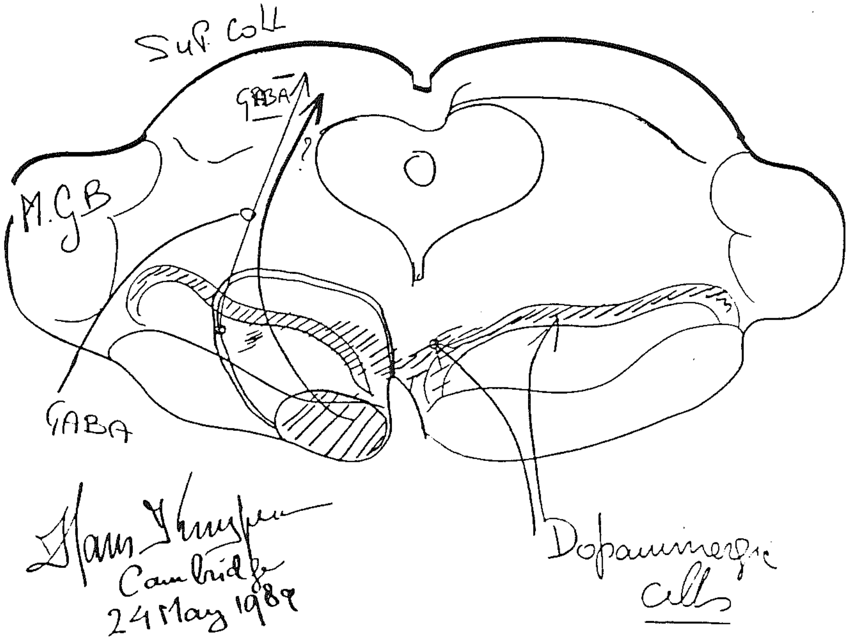

FIGURE 9. Freehand sketch by Hens Kuypers, illustrating the damage that occurred in the one animal who showed an impairment in detour reaching. This was drawn on an easel during the discussion of Diamond's paper.

The intended lesion site in the cerebral peduncle is the shaded circular area near the midline at the base of the diagram. This is the area that was damaged in all animals.

The larger circular area extending out from the intended lesion site indicates the extent of the additional area accidentally damaged in the one monkey who showed a deficit in detour reaching.

SUP. COLL = superior colliculus; MGB = medial geniculate body of the thalamus.

Dopaminergic cells are located in the ventral tegmental area and the substantia nigra pars compacta. GABA-containing cells in the substantia nigra pars reticulata exert an inhibitory influence on the superior colliculus.

A. DIAMOND (*University of Pennsylvania, PA*): Talking with Hens [Kuypers] last night gave me the courage to present a couple more slides to you which I thought would be too far-fetched, but given what he was saying I thought maybe it is not so far-fetched after all. FIGURE 10 is from David Ingle's work. A normal frog will detour around a transparent barrier (actually, it's a transparent barrier that has what looks like stalks of grass). A frog will detour around this to get a food reward. If you interrupt inhibition to the colliculus, Dave tells me, the frog tries to go straight

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[j] MOLL, L. & H. G. J. M. KUYPERS. 1977. Premotor cortical ablations in monkeys: Contralateral changes in visually guided reaching behavior. Science **198:** 317–319.

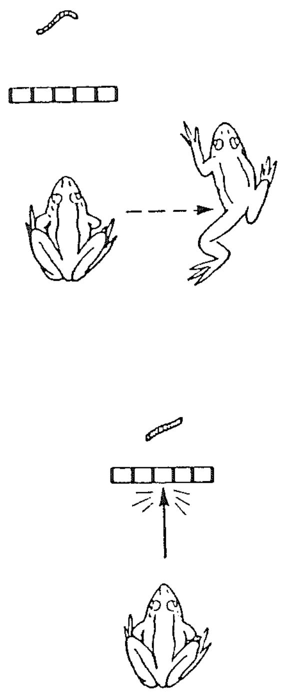

FIGURE 10. Illustration, from the work of David Ingle, of a normal frog detouring around a transparent barrier, while a frog in whom inhibition of the colliculus has been interrupted tries to go straight through the barrier, instead of detouring around it.

through the barrier. I didn't know about Hens's work suggesting the superior collicular involvement, so it was David's work that suggested to me that perhaps frontal cortex inhibition of the superior colliculus might be involved. We know that dorsolateral prefrontal cortex and premotor cortex project directly to the superior colliculus in the primate at least, and also they project indirectly to the superior colliculus via the substantia nigra.

Then the question became how would one test the hypothesis that what is maturing between 8 and 12 months is, at least in part, inhibition from frontal cortex to the superior colliculus? Well, Hikosaka and Wurtz at NIH have elegantly shown that if you interrupt inhibition of the superior colliculus (inhibition from the substantia nigra pars reticulata to the superior colliculus in the monkey) you get saccadic intrusions in smooth pursuit.[k] There is some suggestion that human adults with frontal lobe damage show saccadic intrusions in smooth pursuit.[l] (A saccadic intrusion is not a saccade to quickly catch up with the target, rather it's a saccade in which your eye darts away from the target and then darts back.) So I said, "Well, if I'm right about maturation of frontal inhibition of the superior colliculus in infants, then what we should see is that young infants below 7–8 months of age should show saccadic intrusions in smooth pursuit, and saccadic intrusions should disappear by 12 months of age." Note, there is nothing a priori about the object retrieval task that would lead one to make that prediction. It is only the hypothesis about the anatomy that led to the prediction. I called up Dick Aslin and asked what was known about saccadic intrusions in the smooth pursuit eye movements of infants. He said, "Well, we know that 2- to 3-month-olds show saccadic intrusions in smooth pursuit, and that's all we know so far." Naomi Wentworth, Marshall Haith, and I are gearing up now to see if 6-month-olds still show saccadic intrusions, while 12-month-olds do not.

One way I am trying to investigate the dopaminergic hypothesis (as opposed to inhibition of the superior colliculus hypothesis) is work I am starting with children with early-treated PKU. PKU (phenylketonuria) is a genetic disorder. If you do not regulate the diet of these children beginning very early, they become severely retarded. If you regulate their intake of the amino acid Phe (phenylalanine), however, they perform within the normal range on standardized tests of intelligence. It had been thought for many years that dietary regulation begun early and conscientiously maintained totally eliminated any deficit. But there have been some reports lately that even with dietary regulation there may be a residual deficit in cognitive functions dependent on frontal cortex. I am presently investigating this using tasks like A$\bar{B}$ and object retrieval, which we know are dependent specifically on frontal cortex, at least in the monkey. If infants who are treated early for PKU show a deficit on these tasks, it will most likely be because they have lower levels of dopamine in frontal cortex. (They have no structural damage to the brain that anybody has ever been able to detect with CAT or NMR.) However, they do have slightly elevated levels of Phe and slightly lower levels of dopamine than is normal. Their lower levels of dopamine could either be because the high levels of Phe disrupt production of tyrosine in the liver, or because high levels of Phe impair uptake of tyrosine across the blood–brain barrier, as both Phe and tyrosine share the same transport system and compete for the same transporter proteins. In any case, if infants with early-treated PKU are selectively impaired on these tasks it would seem to be because of their lower levels of dopamine, rather than because of structural damage to frontal cortex.

J. Fuster (*UCLA School of Medicine, Los Angeles, CA*): Thank you for this beautiful presentation, Adele. I have three comments, all brief. One is that, of course, this type of behavior in the immature individual reminds me very much of the magnetic reaction that Konorski described in dogs and cats with prefrontal lesions, and also in monkeys. Now, I would like to call your attention to the fact that indeed with your plastic cover you are introducing an obstacle in the perception–action cycle—a direct obstacle that requires a detour both in space and time in order to get to the goal. The third thing I would like to say is that the inhibitory component, which is undoubtedly there, too, and which also matures as a function of maturation in prefrontal cortex, is possibly contributed by the orbital part of the frontal cortex.

Diamond: I usually don't think about memory in connection with this test, but perhaps memory is indeed required even when the box is transparent. Certainly, when infants start to try other sides of the box, they need to remember which sides

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[k] Hikosaka, O. & R. H. Wurtz. 1983. Visual and oculomotor functions of monkey substantia nigra pars reticulata. IV. Relation of substantia nigra to superior colliculus. Journal of Neurophysiology **49:** 1285–1301.

Hikosaka, O. & R. H. Wurtz. 1985. Modification of saccadic eye movements by GABA-related substances. I. Effect of muscimol and bicuculline in the monkey superior colliculus. Journal of Neurophysiology **53:** 266–291.

Hikosaka, O. & R. H. Wurtz. 1985. Modification of saccadic eye movements by GABA-related substances. II. Effects of muscimol in monkey substantia nigra pars reticulata. Journal of Neurophysiology **53:** 292–308.

[l] Levin, S. 1984. Frontal lobe dysfunctions in schizophrenia—I. Eye movement impairments. Journal of Psychiatric Research **18:** 27–55.

they have already tried and found closed, otherwise they will keep trying those same sides over and over again. Infants of 6½–7 months don't try other sides of the box; they keep reaching at one side forever. But by 7½–9 months they do try other sides of the box, and then you get an explosion in the number of reaches all over the place. It is perhaps that they can't remember where they have already reached because if they remembered they had already tried the top of the box, then presumably they wouldn't try the top again. They keep going back to sides they have already tried and found closed.

You can think of it, perhaps, as a temporal order memory problem. For example, "Have I already tried the left side of the box on this trial, or was that on the last trial?"

R. Gelman (*University of California, Los Angeles, CA*) I have a question. You have taken the important step of showing this across tasks. Now, I am interested in what happens when the infant is in a different position. Has anybody done these experiments with the baby looking up, lying down?

Diamond: No, but Jeff Lockman did it with locomotion while they are on the floor.[m]

Gelman: Well, I am particularly interested in when they don't have to be supporting themselves as well as doing the task. Especially at the age you are talking about. They have just started to sit up. What would happen if it were overhead? Would they also show these errors?

Diamond: I don't know. But the infants are supported by their parents, most have been sitting up since 4 or 5 months of age, and we are talking about performance on the task between 6–12 months.

Gelman: It is important to know what would happen when they are lying down and not concerned about themselves if you want to talk about what might be the locus of the inhibition that is developing here.

As I listen to neuroscientists talk, there is also the possibility that what is going on here isn't so much inhibition as failure on the planning side. It is as if they know they need certain behavioral components. They keep trying again, they keep moving around because they haven't succeeded, but they can't succeed because the planner isn't yet ready for it. That is another way of thinking about it. You can't have a successful planner if it can't be controlled by both de-potentiated and potentiated acts, right? So it fits into a notion of inhibition, but it shifts the focus.

J. DeLoache (*University of Illinois, Urbana, IL*): I agree with Rochel's comment. In fact, I really like your phrase, "memory-based intention to override a habit," because it captures the memory component, the inhibition component, but it also says you have to inhibit something in order to carry out some plan.

I have some data with 2-year-olds that are very similar.[n] They have to find an object that is hidden in a room. There was one particular study in which some things about it made it quite challenging and unusual, and the children didn't perform very well. What we kept seeing across several different children was very bizarre search patterns. The most extreme, and in a way the most interesting, subject was one little girl who would come into the room, and each time she would go back and search in the same place. Then she would go off and her second search would be correct. It looked as if she knew *exactly* where the object was hidden. On the very last trial this little girl came in, and as she was beginning to search under the pillow, but before she had done so, said, "It's not there." Then she went to the correct hiding place. So, here was a conscious child, who could tell you it was not there, and yet for some reason she still searched there anyway.

Diamond: That's fascinating. Just like frontal patients on the Wisconsin Card Sort.

A. Shimamura (*University of California, Berkeley, CA*): I thought it was quite striking that Hans [Kuypers's] paradigm and the object retrieval task seemed very much like Stuart [Zola-Morgan's] lifesaver test in which the subjects have to maneuver a lifesaver along a circuitous wire path.[o]

Diamond: Yes, and monkeys with lesions of the hippocampal formation do fine on the lifesaver task and on object retrieval. No one has ever tested monkeys with frontal cortex lesions on the lifesaver task.

Shimamura: Although there is a skill-learning aspect to that task, one initial aspect is to inhibit dominant responses and to try to tune up the new responses. My question, I guess, would be that if you go through this task, and the monkey now learns the skill, when you lesion the system, will you find an impairment in the memory of that skill, or will they retain that skill, but be unable to learn other ones?

Diamond: That is an interesting question. This was a failure of nerve on the part of Pat [Goldman-Rakic] and me. I tested infant monkeys longitudinally on object retrieval, but after lesions of dorsolateral prefrontal cortex, we did not re-test them on the task, we only re-tested them on A$\bar{B}$. We were afraid that, since we had given them pre-operative training on object retrieval, when we did the lesion we wouldn't get the effect, so we never tested that, and we were very sorry we didn't test it.

When adult monkeys are trained on the task postoperatively, monkeys with dorsolateral prefrontal cortex lesions are significantly impaired. But although they take much longer to master the task, they do eventually master it.

J. Werker (*University of British Columbia, Vancouver, B.C.*): This development is possibly more general. My own work is in cross-language speech perception,[p] where we find, I think, somewhat important reorganization in the first year of life, where they go from what appear to be universal categories to language-specific categories. Basically, very young infants can discriminate any phonetic contrast that they have been tested on so far from any of the world's languages. What our work shows is that by about 10–12 months they, like older children and adults, start having difficulty with some non-native contrasts—not all, but some. In trying to make sense out of this, it seems to me they go from a universal, innately predisposed categorization to a more functional categorization of speech sounds. Now, we have been trying to relate this to developments in other domains, and if you look at the categorization

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[m] Lockman, J. J. 1984. The development of detour ability during infancy. Child Development 55: 482–491.

[n] DeLoache, J. S. 1989. The effect of physical similarity on young children's understanding of scale models. *In* "Perceptual Similarity and Relational Thought." J. DeLoache. Symposium presented at the meeting of Society for Research in Child Development, Kansas City.

[o] Zola-Morgan, S. & L. R. Squire. 1984. Preserved learning in monkeys with medial temporal lesions: Sparing of motor and cognitive skills. Journal of Neuroscience 4: 1072–1085.

[p] Werker, J. S. & R. C. Tees. 1984. Cross-language speech perception: Evidence for perceptual reorganization during the first year of life. Infant Behavior and Development 7: 49–63.

Werker, J. S. & C. E. Lalonde. 1988. The development of speech perception: Initial capability and the emergence of phonetic categories. Developmental Psychology 24: 672–682.

literature across infancy, what you find is young infants begin showing perceptual categorization of lots of stimuli in a way that seems functionally significant. They will categorize vertical lines as different from horizontal lines, and as you progress to more and more complex shapes they seem to show initial perceptual categorization. As they get to be about 10–12 months old they show this reorganization.[q]

There are certainly other domains of complex categorization where the infant has to take not just whatever perceptual propensities that they have when they are born, but they have to integrate that with information they have either learned in the course of experience, like in our language domain, or information that has been presented to them within a particular experimental task. But around 9–10 months, they seem to start showing the ability to be able to coordinate information that is presented to them, that is now functional, either out there in the world or in the experimental task, and reorganize these natural propensities so that they can begin to categorize along the lines of what is functionally significant. This is not coordinating a behavioral scheme with some information, but what it is, in fact, doing is coordinating functional information with an initial perceptual predisposition, and it might involve the same sorts of things. Now in terms of the different ages that Claire [Kopp] and other people were talking about, if I look at the literature selectively, I can find a lot of evidence for the ability to reorganize perceptual categories at around 8–10 months of age, but that is selective. If I look at easier sorts of perceptual categorization tasks, there is evidence that infants can start reorganizing biologically given categories, or whatever you want to call them, a little bit earlier. If I look at more complex perceptual categorization tasks, they are not doing it until a little bit later.

L. NADEL (*University of Arizona, Tucson, AZ*): Adele, you say that one of the functions of prefrontal cortex is to inhibit the dominant response. How does one know what the dominant response will be, other than by it being the response that small children and frontally lesioned monkeys show? Is it possible to predict what response will be prepotent in a given situation *before* one tests subjects with prefrontal cortex lesions?

DIAMOND: Obviously, independent criteria are needed. I think which response would be predominant for a given subject population in a given situation can be determined empirically. For example, what do most subjects from that population do in the situation? What does the same subject do on repeated testing in that situation? To illustrate, we say that monkeys and babies have a natural preference for novelty because when given a choice between familiar and novel stimuli, they overwhelmingly choose the novel ones. We say that a given subject has a right- or left-hand preference if on repeated testing that subject consistently uses that hand rather than the other. We don't know how monkeys with dorsolateral prefrontal cortex lesions will perform on delayed matching to sample (trial unique objects) because they have never been tested on that, but I am predicting they will fail because independent evidence indicates they have a novelty preference, and this task requires both memory and the inhibition of the novelty preference. Although I haven't turned my attention to establishing criteria for determining which response, if any, is predominant, I think it is possible to do so, and I agree with you that it is important to do so.

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[q] COHEN, L. B. 1988. An information processing view of infants cognitive development. *In* Thought without Language. L. Weiskrantz, Ed.: 211–228. Oxford University Press. Oxford, England.