

Shifting from the Perceptual Brain to the Logical Brain: The Neural Impact of Cognitive Inhibition Training

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Abstract

■ What happens in the human brain when the mind has to inhibit a perceptual process in order to activate a logical reasoning process? Here, we use functional imaging to show the networks of brain areas involved in a deductive logic task performed twice by the same subjects, first with a perceptual bias and then with a logical response following bias-inhibition training. The main finding is a striking shift in the cortical

anatomy of reasoning from the posterior part of the brain (the ventral and dorsal pathways) to a left-prefrontal network including the middle-frontal gyrus, Broca's area, the anterior insula, and the pre-SMA. This result indicates that such brain shifting is an essential element for human access to logical thinking. ■

INTRODUCTION

Since Aristotle, it has been known that the essence of the human mind is the “logos,” which encompasses both reason (logic) and language. Neuroimaging data on logical reasoning is scarce (Wharton & Grafman, 1998; Goel, Gold, Kapur, & Houle, 1997, 1998), and no research so far has looked at what happens in the brain when the mind has to inhibit a perceptual process in order to activate a logical reasoning process. In the study of human evolution to *Homo sapiens*, as well as in the study of cognitive development from infancy to adulthood (in the domains of object construction, numerical abilities, categorization, and logical reasoning), inhibitory control is regarded today as a crucial mechanism of adaptation (Houdé, in press; Dempster, 1995; Bjorklund & Harnishfeger, 1995; Pascual-Leone, 1988). It is an executive process involved in attention, self-regulation, and consciousness (Posner & Rothbart, 1998). Very often, intelligence is closely tied to the ability to inhibit a misleading behavior, judgment, or strategy. In adults, this is known to be true for the inhibition of perceptual biases in deductive reasoning (Houdé, 1997).

Research in the cognitive psychology of deduction has shown that most subjects do not apply the principles of logic; their reasoning is systematically biased (Evans, 1989). Therefore, to falsify the rule “If there is not a red square on the left, then there is a yellow circle on the right,” one correct response (true antecedent and false consequent: TF) consists of placing a blue square (not a red one) on the left of a green diamond (not a

yellow circle) (see Figure 1a). Yet, most subjects respond “red square, yellow circle” (FT)! This is a classic case of the perceptual matching bias, which consists of preferring the items (here, the colored geometric shapes) mentioned in the rule, and neglecting the logically correct ones (Evans, 1972, 1998). This reasoning bias is explained by the so-called “not-heuristic” (Evans, 1989), where the word “not” directs the subject's attention to the proposition it denies—in the above example, “a red square”. Another account (Oaksford & Stenning, 1992) is that the subject has trouble constructing the contrast class corresponding to the set of items that the negative assertion permits—in this case, the set of “not-a-red-square” figures.

Of interest to us here from the standpoint of the role of inhibition in deductive reasoning is the emphasis on selective attention processes (Evans, 1989). Clearly, if the linguistic function of not (not-heuristic) is to direct attention to the proposition that it negates—thus triggering the matching bias—then inhibition is precisely the cognitive mechanism that should allow one to redirect attention towards the logically relevant items (the contrast set).

Although the matching bias is very powerful, earlier data obtained in our laboratory (Houdé & Moutier, 1996, 1999) showed that executive training in inhibition of this bias (see Figure 1b and Methods) enabled subjects to respond logically on a posttraining task. The important point to note here is that neither repetition of the task (test–retest or practice effect) nor logical training enabled subjects to change their reasoning strategy.

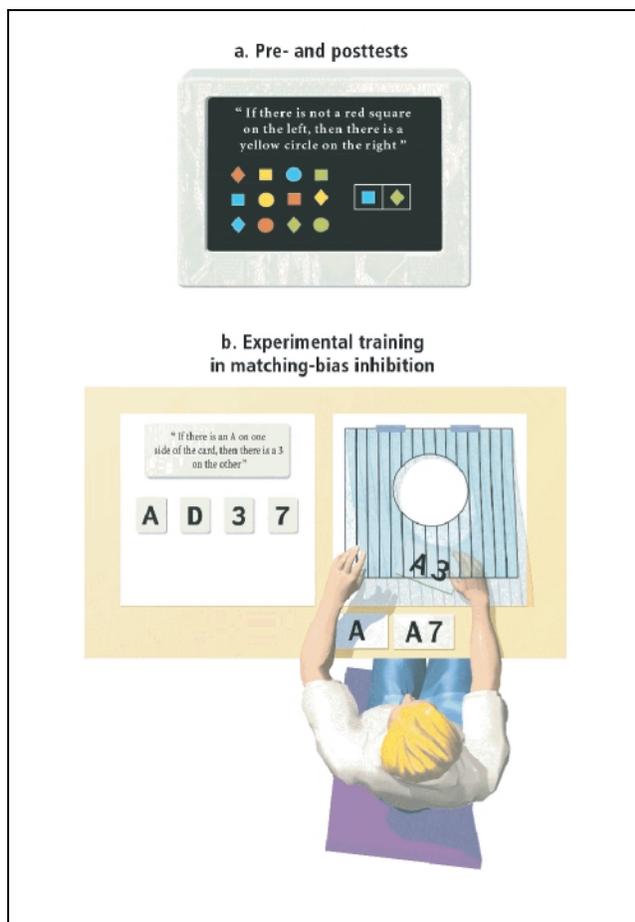


Figure 1. (a) Pretest (PET1) and posttest (PET2) materials on the conditional rule falsification task. (b) Materials used for experimental training in matching-bias inhibition (between PET1 and PET2). The first board was used for the card selection task. The second board depicts the executive process (inhibition, shown as hatching) required for correct task performance. (See Methods.)

Thus, the observed biased-to-logical shift stems specifically from the executive impact of matching-bias inhibition.

To map the network of brain areas involved in the conditional rule falsification task performed by the same subjects before (biased response expected) and after (logical response expected) executive training in matching-bias inhibition, we conducted a positron emission tomography (PET) study in which eight subjects were scanned twice (an hour apart), once on the pretest (PET1) and once on the posttest (PET2) (Figure 1a); experimental training in inhibition (Figure 1b) was held between the two tests.

RESULTS

Psychological Data

The eight subjects exhibited a perceptual matching bias on more than 90% of the pretest rules. The mean number of rules processed per task execution was 14 (11.5, 14.6, and 16 for the first, second, and

third repetitions of the rule falsification task, respectively; see Methods). On the posttest, the same subjects gave a logical response on more than 90% of the rules, and the mean number of rules processed was 16.5 (14.4, 17.1, and 18.2). Thus, we noted a striking biased-to-logical shift after matching-bias inhibition training. The difference in the mean number of rules processed on the pretest compared to the posttest was not significant.

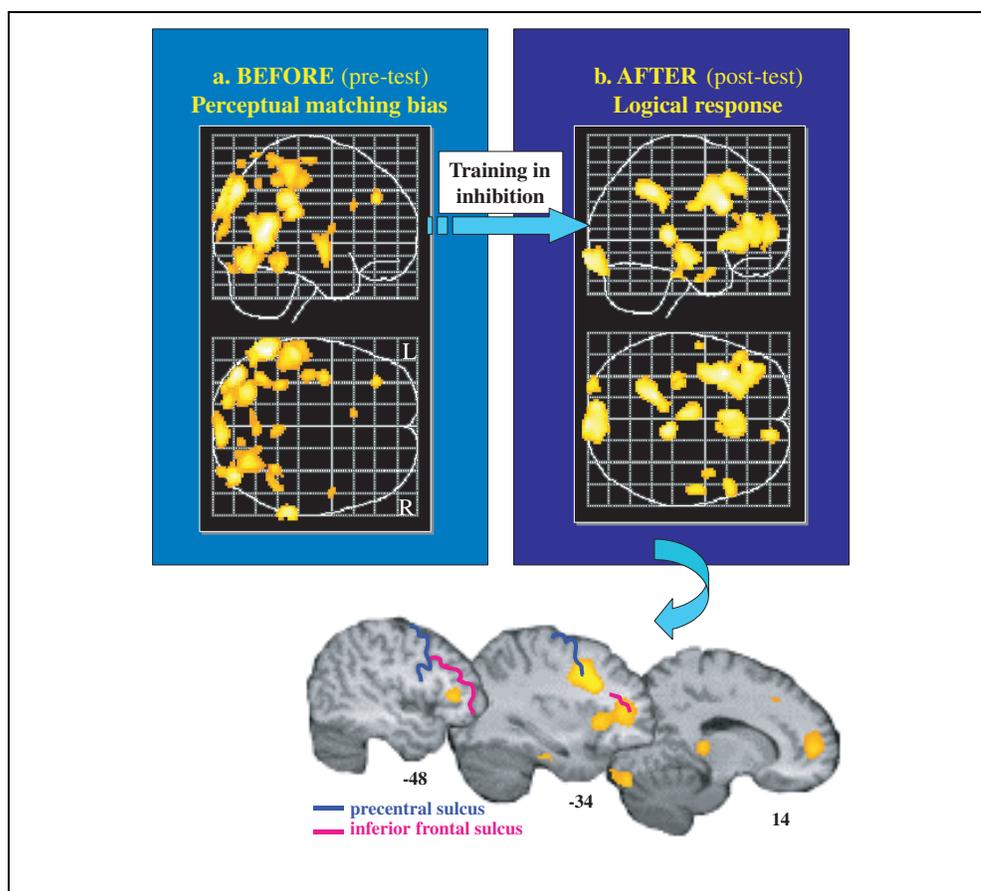
Neuroimaging Data

Prior to statistical analysis, the pre- and post-PET scans of each subject were aligned using AIR 3.0 software (Woods, Cherry, & Mazziotta, 1992). Data were further analyzed by statistical parametric mapping (SPM96) (Friston et al., 1995b), including spatial normalization using the PET template (Friston et al., 1995a), Gaussian spatial filtering (smoothness = 12 mm, full-width at half maximum), radioactivity count normalized by the whole brain mean radioactivity count (ratio correction), and contrast between task evaluations by t statistics (nine actual degrees of freedom). Averaged normalized blood flow maps obtained during the conditional rule falsification task were contrasted before (pretest) and after (posttest) inhibition training (PET1 and PET2). The pretest minus posttest and posttest minus pretest contrast t maps were converted in Z maps. The threshold for activation significance was set at $Z_{\min} = 3.09$ ($p < .001$, not corrected for multiple comparisons). A control condition (three rest states during PET1) was set up to make sure that we were dealing with pretest activations and not with posttest deactivations for the pretest minus posttest contrast. The corresponding verification was done for the posttest minus pretest contrast (three rest states during PET2).

The pretest minus posttest contrast (Figure 2a) pointed out a bilateral network involving posterior unimodal suppression and heteromodal areas (Mesulam, 1998). This network included the occipital regions located along the ventral pathway, namely, the left lingual gyrus and the bilateral fusiform gyrus (Haxby et al., 1991). Also included were some dorsal pathway regions. Activation in these occipital and parietal regions was noted for the bilateral middle-occipital gyrus, right cuneus, and bilateral supramarginalis gyrus. Finally, activation was found in the superior- and left-middle-temporal regions (Wernicke's area) and in the left-angular gyrus. (See Table 1 for a detailed anatomical and statistical description: extent in voxels, localization [MNI brain template], stereotactic coordinates [Talairach & Tournoux, 1988], and local maxima z scores.)

The opposite contrast (posttest minus pretest, Figure 2b) essentially pointed out activation in the heteromodal areas of a left-prefrontal network (Mesulam, 1998), including the middle-frontal gyrus (inferior-frontal sulcus/precentral gyrus, and either side of the antero-

Figure 2. Lateral and superior projections of statistical parametric z maps showing brain regions with increased cerebral blood flow (rCBF) during (a) the conditional rule falsification task when subjects were biased by perceptual matching (pretest) and (b) after the same subjects had been trained to inhibit the perceptual matching bias, i.e., to respond logically (posttest). Z maps were generated using SPM96 software by contrasting the pretest and posttest rCBF maps with a 3.09 z threshold ($p < 0.001$) (see Tables 1 and 2 for a detailed anatomical and statistical description). (b, bottom) Clusters of activation, whose anatomical localization, coordinates, and significance level are given in Table 2, were superimposed on selected sagittal slices of the MNI brain template. Each sagittal slice is labeled with its stereotactic x coordinate in millimeters: -48 , -34 , and 14 .



inferior part of the inferior-frontal sulcus), the inferior-frontal gyrus (Broca's area), the anterior insula, and the pre-SMA. This contrast also revealed right-hemisphere activation straddling the ventro-medial-prefrontal cortex and the anterior cingulate. In addition to these prefrontal areas, we found activation in the bilateral peristriate cortex, the right pulvinar, and the left-parahippocampal gyrus. (See Table 2 for a detailed anatomical and statistical description.)

DISCUSSION

The most striking result obtained here is the change in the cortical anatomy of reasoning, which shifted from the posterior part of the brain on the pretest to a left-prefrontal network on the posttest, thereby reflecting the change in the subjects' reasoning strategy. Remember that our previous studies (Houdé & Moutier, 1996, Houdé & Moutier, 1999) showed that neither the repetition of the task (test–retest control) nor logical training enabled subjects to shift from the biased to the logical response. This indicates that the present data cannot be explained as a practice effect, nor as an instruction (logic) effect, but as a specific consequence of the executive training in matching-bias inhibition.

The perceptual network pointed out by the pretest minus posttest contrast corresponds here to the match-

ing bias. This network included the superior- and left-middle-temporal regions (Wernicke's area) and the left-angular gyrus, known to be involved in the reading of shape and color words (Price, 1997; Vandenberghe, Price, Wise, Josephs, & Frakowiak, 1996). These activations are likely to reflect silent reading of the rule, with specific lexical–semantic focusing on the items mentioned in the antecedent and consequent (silent reading where, according to Evans (1989) and Evans (1998), the not-heuristic is setting in; see Introduction). Also included were the occipital regions located along the ventral pathway, namely, the left-lingual gyrus and the bilateral fusiform gyrus (associative visual area V4) (Haxby et al., 1991), known to be involved in the visual perception of colored shape (Gulyas, Heywood, Popplewell, Roland, & Cowey, 1994; Zeki et al., 1991). These structures were likely to be activated by the perceptual word-to-shape matching bias, which triggered visual focusing on the two colored shapes mentioned in the rule. The pretest minus posttest contrast also pointed out the activation of some dorsal pathway regions involved in visual-spatial information processing (Baker et al., 1996; Haxby et al., 1991).

The opposite contrast (posttest minus pretest), which corresponds to inhibition of the perceptual matching bias and activation of a deductive reasoning process, essentially revealed activation in the heteromodal areas

Table 1. Extent, Anatomical Localization (MNI Brain Template), Stereotactic Coordinates, and Local Maxima Z Scores of Areas of Activation Detected in the Pretest Minus Posttest Conditions. Threshold for Activation Significance Set at $Z_{\min} = 3.09$ ($p < 0.001$)

Extent (Voxels)	Anatomical Localization	Coordinates			z Score
		x	y	z	
835	L superior-temporal gyrus	-56	-52	14	6.10
	L superior-temporal gyrus	-58	-58	6	5.79
	L middle-temporal gyrus	-50	-66	16	4.00
535	L angular gyrus	-40	-80	40	5.64
	L cuneus	-18	-88	42	4.21
	L middle-occipital gyrus	-30	-90	28	3.86
311	R middle-occipital gyrus	38	-80	38	5.31
	R middle-occipital gyrus	34	-92	90	3.66
209	R supramarginalis gyrus	66	-36	34	5.03
232	L supramarginalis gyrus	-54	-32	26	4.90
307	R cuneus	8	-94	32	4.71
528	L lingual gyrus	-26	-72	-12	4.68
	L lingual gyrus	-36	-60	-2	4.16
417	R fusiform gyrus	28	-70	-16	4.41
393	L postcentral gyrus	-56	-34	54	4.37
214	L posterior insula	-36	-6	-6	4.26
59	L frontal-superior sulcus	-34	38	34	4.18
105	L fusiform gyrus	-30	-44	-16	3.97
72	R fusiform gyrus	32	-48	-14	3.77
39	L precentral gyrus	-38	-20	64	3.70
64	R cingulate sulcus	4	-46	46	3.66
66	R postcentral cortex	46	-46	64	3.61

L: left, R: right.

of a left-prefrontal network linked to the suppression paralimbic region (Mesulam, 1998). It included two spots in the left-middle-frontal gyrus, one at the junction of the inferior-frontal sulcus and the precentral gyrus, the other located on both sides of the antero-inferior part of the inferior-frontal sulcus. Several studies have found the middle-frontal gyrus to be involved in the executive component of object and spatial working memory (Owen, 1997). More specifically, it has been shown that the antero-inferior part of this region is recruited by cognitive set shifting on the Wisconsin Card Sorting Test (Konishi et al., 1998), where subjects have to inhibit a previously active sort criterion. In our study, it most likely reflects cognitive inhibition of the perceptual matching process used on the pretest (the perceptual network described above); as stated in the Introduction, inhibition allows here subjects to redirect attention to the logically correct shapes (a shifting on the contrast set; Oaksford & Stenning, 1992). Other activated areas in this left-prefrontal network were the

inferior-frontal gyrus (Broca's area) and the anterior insula, regions thought to be involved in inner speech, which fulfills a self-regulatory function, including inhibition (Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Martin, Wiggs, Ungerleider, & Haxby, 1996). This probably corresponds here to articulatory rehearsal in verbal working memory aimed at reactivating what was learned during the inhibition training in relation to the task instructions (Buckner, Kelley, & Petersen, 1999; Smith & Jonides, 1999) and the logical processing of the materials (Wharton & Grafman, 1998; Goel et al., 1997, 1998). Finally, activation was found in the pre-SMA, which reflects a state of preparedness for selecting the motor response (Petit, Courtney, Ungerleider, & Haxby et al., 1998). This is the executive component of motor programming, which, in the present case (in contrast to the pretest condition), involved inhibiting the matching response and selecting the two logically correct shapes.

Table 2. Extent, Anatomical Localization (MNI Brain Template), Stereotactic Coordinates, and Local Maxima z Scores of Areas of Activation Detected in the Posttest Minus Pretest Conditions. Threshold for Activation Significance Set at $Z_{\min} = 3.09$ ($p < 0.001$)

Extent (Voxels)	Anatomical Localization	Coordinates			z Score
		x	y	z	
780	L middle-frontal gyrus	-34	16	30	5.74
383	L posterior-cingulate	-18	-44	38	5.35
835	R peristriate cortex	6	-102	-14	5.19
	L peristriate cortex	-10	-92	-14	4.72
195	R pulvinar	10	-30	4	5.11
271	L midbrain/red nucleus	-4	-16	-12	4.72
1289	L middle-frontal gyrus	-40	38	16	4.64
	L anterior insula	-26	28	0	4.56
	L anterior insula	-30	16	12	4.36
	L middle-frontal gyrus	-34	38	6	4.31
	L inferior-frontal gyrus	-48	30	4	3.73
660	Pre-SMA	-2	22	44	4.63
	R anterior cingulate	6	12	28	3.64
256	R ventro-medial-prefrontal cortex/anterior cingulate	14	54	4	4.38
116	R inferior-frontal gyrus	52	20	-2	3.92
96	R postcentral cortex	56	-6	28	3.89
78	L peristriate cortex	-26	-98	18	3.89
108	L parahippocampal gyrus	-28	-20	-16	3.73
	L anterior fusiform gyrus	-30	-26	-28	3.62

L: left, R: right.

The posttest minus pretest contrast also revealed right-hemisphere activation straddling the ventro-medial-prefrontal cortex and the anterior cingulate, a region ensuring the emotional-motivational aspects of decision making linked to the consciousness of task difficulty (Nobre, Coull, Frith, & Mesulam, 1999; Bechara, Damasio, Tranel, & Anderson, 1998; Paus, Koski, Caramanos, & Westbury, 1998; Posner & Rothbart, 1998; Damasio, 1994). This probably corresponds here to the subject's postraining consciousness of the logical difficulty of the task, and, hence, of the necessity to inhibit the bias.

Recent neuroimaging studies have pointed out the importance of executive processes in the frontal lobes (Buckner et al., 1999; Smith & Jonides, 1999). Here, we demonstrate how a set of left-prefrontal regions recruited by the executive component of object, spatial, and verbal working memory, and a right-prefrontal region ensuring the emotional-motivational aspects of decision making, all work together in a dynamic way to inhibit a perceptual bias and activate a deductive reasoning process. This brain-imaging result in neurologically intact subjects is consistent

with classical data from neuropsychology on patients with prefrontal damage, whose executive functions, especially inhibition, are impaired (Nobre et al., 1999; Bechara et al., 1998; Damasio, 1994; Fuster, 1989; Lhermitte, Pillon, & Serdaru, 1986; Norman & Shallice, 1986). It is also consistent with previous PET studies on deductive reasoning showing activation of the left-inferior-prefrontal cortex (Wharton & Grafman, 1998; Goel et al., 1997, 1998), which is part of the network observed in the posttest minus pretest contrast.

In addition to these prefrontal areas, the posttest minus pretest contrast pointed out activations in the bilateral peristriate cortex and the right pulvinar. These regions are likely to reflect the attentional filtering of visual information irrelevant to the current task (Kastner, De Weerd, Desimone, & Ungerleider, 1998; LaBerge, 1990), i.e., the two shapes mentioned in the rule. This should correspond to a form of inhibitory linkage at the top (Fuster, 1998) supported by a left-prefrontal-and-peristriate perception-action cycle. Activation was also found in the left-parahippocampal gyrus, corresponding to the learning and remembering com-

ponents of the paradigm (Strange, Fletcher, & Henson, 1999).

What is original about the data presented here is that it shows how the activated brain networks can change radically, from posterior to anterior, in the same subjects, carrying out the same task, depending on their ability to inhibit a misleading strategy; a biased-to-logical shift takes place. This neurofunctional data thus argues for intraindividual variability in human reasoning, selection by training, and dynamic network cognition.

METHODS

Subjects

Eight right-handed male students (mean age 22, age range 19 to 26) were selected on the basis of their matching-bias response on the conditional rule falsification task. They had given a matching-bias response for at least 3/4 of the rules. They also had a score of 16 to 18 on the Embedded Figures Test (EFT; Oltman, Raskin, & Witkin, 1985; Witkin, Oltman, & Karp, 1971). A previous study showed that perceptual field-independent subjects (EFT score ≥ 16) are more receptive to inhibition training than field-dependent subjects (Houdé & Moutier, 1999). Subject selection took place about 2 weeks before the PET experiment. After the entire procedure had been fully explained, the selected subjects gave their written informed consent. The study was approved by the Basse Normandie (Caen, France) ethics committee.

Pre- and Posttests

The subjects were visually presented with 12 colored geometric shapes displayed randomly on a computer screen (Figure 1a). They had to falsify a conditional rule like “If there is not a red square on the left, then there is a yellow circle on the right.” (Houdé & Moutier, 1996; Evans, 1972, Evans, 1989). They responded with the mouse by putting two colored shapes in a two-part box drawn on the screen, one on the left for the antecedent and the other on the right for the consequent. At 1 sec after the subject’s response, the computer displayed a new stimulus. The task ended when the PET scanning was completed.

Experimental Training

The inhibition training lasted about 20 min and was both verbal and visual-spatial (for learning material manipulation, see Figure 1b) (Houdé & Moutier, 1996). It consisted of warning the subjects about the “trap” in the perceptual matching bias and teaching them how to avoid it. Given that a different task, the Wason’s classical card selection task (Wason, 1968), with different materi-

als and different answers were used, the inhibition training was executive or metacognitive in nature (i.e., not just training about the correct answer on the same task). Like the pre- and posttests, it involved a deductive logic task (conditional reasoning) that triggers a perceptual matching bias (Evans, 1989, 1998). In the Wason task, four cards (A, D, 3, and 7) with a letter on one side and a number on the other are laid out in front of the subject, who then has to state which one or ones have to be turned over to verify the rule “If there is an A on one side of a card, then there is a 3 on the other.” The correct answer is A and 7 (because one must test the TF cases since only they can falsify the rule). The matching-bias response is A and 3 (as on the pre- and posttests, negation processing here entails difficulty in constructing the contrast set, namely, considering 7 as a case of “not-3”). At the beginning of the matching-bias inhibition training, all eight subjects exhibited the bias. By the end, all subjects met the learning criterion (being able to explain how to avoid the matching bias) on the first unassisted attempt.

Below the illustration is an excerpt from the training (warning elements are shown in italics). The instructions were: “*In this problem, the source of the error lies in a habit we all have of concentrating on cards with the letter or number mentioned in the rule (the experimenter points to cards A and 3, and to the place where they are mentioned in the rule) and not paying attention to the other cards. [...]* Thus, the goal here is (1) *to not fall into the trap of the two cards A and 3 mentioned in the rule*, and (2) to consider all of the cards, A, D, 3, 7, one by one, by imagining the number or the letter it might have on the back to see whether these cards can make the rule false ... To help you understand, let’s consider the different answers and *eliminate the wrong ones—the ones that make you fall into the trap—to find the right answer.*” Then the subject was shown the second part of the experimental materials. These included another board placed right next to the first (see Figure 1b), on which the response repertoire was depicted as a box, *the inhibition process as a transparent hatched area on top of the box*, and the activation process as an unhatched circle cut out from the middle of the hatched area. The answers (A, A-3, and A-7) were represented on three cards, which could be slid onto the response repertoire. The answer cards were of different colors, depending on whether the answer was wrong (A, A-3) or right (A-7). The experimenter said to the subject: “In the box you see here, we’re going to put the different answers written on these cards, *while clearly separating the wrong answers, which make you fall into the trap—we’ll put them under the hatching—and the right answer.* Let’s start with answer A [...].” (complete instructions for A, A-3, and A-7 are available upon request).

Remember that our previous studies showed that logical training (the same procedure as above, but with-

out the warning elements shown in italics) did not enable subjects to shift from a matching bias to a logical strategy on the posttest (Houdé & Moutier, 1996, 1999). Thus, the specificity of the present training lies in the warning elements for inhibitory control.

PET Scanning

Three-dimensional PET volumes were obtained with a Siemens ECAT-HR+ (CTI, Knoxville, TN) and reconstructed as a series of 63 contiguous, 2.5-mm-thick cross-sectional images. PET volume spatial resolution was $6 \times 6 \times 6 \text{ mm}^3$ (full-width at half maximum). H_2^{15}O (6 mCi) was infused for 40 sec using a dedicated water infusion (Tochon-Tanguy, Clark, Janus, & Sachinidis, 1995). Subjects began the task at the end of the infusion period and scanning started ≈ 30 sec later when the brain radioactivity count reached 400% of the background radioactivity measured during the initial phase of the infusion. Scan duration was 90 sec. Each subject was scanned six times while performing the conditional rule falsification task, three times before (PET1: pretest) and three times after (PET2: posttest) training in matching-bias inhibition. The within-session between-scan time interval was 7 min, and the between-session time interval was 1 hr.

Acknowledgments

The authors are deeply indebted to V. Beaudouin, J.-C. Cabaret, P. Lochon, O. Tirel (GIP Cyceron), and G. Perchey (INSERM U320) for their invaluable help in data acquisition.

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