The What and How of Observational Learning

Sara Torriero[1], Massimiliano Oliveri[1,2], Giacomo Koch[1,3], Carlo Caltagirone[1,3], and Laura Petrosini[1,4]

Abstract

■ Neuroimaging evidence increasingly supports the hypothesis that the same neural structures subserve the execution, imagination, and observation of actions. We used repetitive transcranial magnetic stimulation (rTMS) to investigate the specific roles of cerebellum and dorsolateral prefrontal cortex (DLPFC) in observational learning of a visuomotor task. Subjects observed an actor detecting a hidden sequence in a matrix and then performed the task detecting either the previously observed sequence or a new one. rTMS applied over the cerebellum before the observational training interfered with performance of the new sequence, whereas rTMS applied over the DLPFC interfered with performance of the previously observed one. When rTMS applied over cerebellar or prefrontal site was delivered after the observational training, no influence was observed on the execution of the task. These results furnish new insights on the neural circuitry involved in the single component of observational learning and allow us to hypothesize that cerebellum and DLPFC interact in planning actions, the former by permitting the acquisition of procedural competencies and the latter by providing flexibility among already acquired solutions. ■

INTRODUCTION

Observational learning is the ability to learn to perform an action by seeing it done. It does not just involve copying an action but, rather, requires that the observer transform the observation into an action as similar as possible to the actor's in terms of the goal to be achieved and the motor strategies to be applied. Observational learning plays a pivotal role in the acquisition of social skills and in the transfer of cultural knowledge and tool use and, thus, becomes a fundamental process through which infants learn about adults (Meltzoff, 1999; Byrne & Russon, 1998). The mechanisms that couple observation and learning are very similar to those involved in learning "by doing." Experimental and neuroimaging studies support the position that these kinds of learning at least partially share common neural substrates related to the cognitive stages of motor control. Learning an action by observation and by mental practice involves rehearsal of the same neural pathways. In fact, common brain areas and computational processing are activated in preparing actions, in mentally representing one's own action, and in observing another's action (Grèzes & Decety, 2001). Using measures of human event-related brain potentials similar involvement of medial frontal and motor cortex was demonstrated in the monitoring of one's own actions and the actions of others (van Schie, Mars, Coles, & Bekkering,

2004). Studies in monkeys and in humans show the existence of a widespread "mirror system" in frontal, parietal, and temporal regions (Grèzes & Decety, 2002; Buccino et al., 2001; Rizzolatti, Fogassi, & Gallese, 2001; Iacoboni et al., 1999, 2001; Bonda, Petrides, Ostry, & Evans, 1996; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996). Thus, it is plausible to retain that during observation of action a diffuse neural network subserving motor representation is already tuned to imitate and learn the observed actions.

In this diffuse network, activation of the dorsolateral prefrontal cortex (DLPFC) was shown during observation of actions (Buccino et al., 2004). A recent functional magnetic resonance imaging study reported activation of the DLPFC related to the self-selection of intended action rather than the mere observation of action (Cunnington, Windischberger, Robinson, & Moser, 2006). It was proposed that the dorsolateral prefrontal areas could play an orchestrating role in the processes that occur in the mirror neuron system by selecting and recombining the motor elements to be imitated (Iacoboni, 2005).

Other research underlines the additional involvement of bilateral cerebellar areas in mental tasks that do not require overt movements. Examples are silent word generation and counting, tennis training movements, and the observation or imagination of grasping movements (Battaglia et al., 2006; Kuhtz-Buschbeck et al., 2003; Ross, Tkach, Ruggirei, Lieber, & Lapresto, 2003; Petersen, van Mier, Fiez, & Raichle, 1998; Thach, 1996, 1998; Decety & Ingvar, 1990). Positron emission tomography data report cerebellar activation during

[1]IRCCS Fondazione "Santa Lucia", [2]University of Palermo, [3]University of Rome Tor Vergata, [4]University of Rome "La Sapienza"

observation of meaningful and meaningless actions for the purpose of imitation and, conversely, no cerebellar activation during the mere observation of meaningless actions (Leslie, Johnson-Frey, & Grafton, 2004; Chaminade, Meltzoff, & Decety, 2002; Grèzes & Decety, 2001, 2002; Decety & Grèzes, 1999; Decety et al., 1997). Moreover, experimental findings demonstrate that in rats cerebellar lesions markedly impair the learning of new procedures not only by actual execution of a task (Leggio et al., 1999) but also by observation (Leggio et al., 2000). Thus, there are a number of indications that cerebellar circuits are involved in ''motor thought'' whether they are accompanied by actual motor acts.

The aim of the present work was to analyze the role of specific neural substrates in learning a sequential visuospatial task by observation. Learning complex actions by observation is not a unitary function because it requires the acquisition of very different competencies. In particular, when a subject learns a sequential visuomotor task by observation, they acquire both the specific sequence of items and the procedural rules about how to perform the task. In the present observational protocol, subjects observed an actor detecting a sequence. Then, they actually performed the task producing the sequence they had just viewed (old sequence) as well as a different sequence they had never seen (new sequence). Detection of the sequences required putting into action the procedural rules to solve the task (i.e., vertical or horizontal movement was allowed but never diagonal movement) as well as recalling from memory the series of correctly touched items. Nevertheless, reproducing the old sequence mainly required exploiting knowledge of the observed sequence, whereas detecting the new sequence mainly required exploiting procedural competencies linked to the rules of the task.

The proposal that the cerebellar network is fully engaged in the acquisition of the procedural components of a task is consistent with the functions attributed to it. As indicated by neuroimaging studies, cerebellar activation is closely linked to the first phases of acquisition and decreases to lower levels after practice (Petersen et al., 1998; Vaina, Belliveau, des Roziers, & Zeffiro, 1998), supporting the cerebellar role as a procedural machine. Moreover, during the implicit acquisition of a sequential visuomotor task, cerebellar lesions induce a procedural impairment that can be bypassed by exploiting previously acquired declarative knowledge (Molinari et al., 1997).

Conversely, the prefrontal circuits are primarily engaged in the declarative components of a task. This is in accordance with the well-known role of the frontal cortex in encoding and retrieval of memory span (Rossi et al., 2001, 2004) and in visuospatial working memory (Koch et al., 2005; Hoshi et al., 2000).

By taking into account these different competencies in learning by observation, we analyzed the interfering effects evoked by low-frequency repetitive transcranial magnetic stimulation (rTMS) on the cerebellum or on the DLPFC in an observational visuomotor task. Furthermore, given the crucial role of the cerebellar and prefrontal networks in motor performance, it seemed crucial to verify the effects of rTMS on actual execution of the same task. Because the rTMS technique induces inhibition of the stimulated brain areas for several minutes after the stimulation period (Oliveri, Koch, Torriero, & Caltagirone, 2005), it was possible to distinguish the effects on the observation or actual execution of the task.

METHODS

Subjects

Seventy-five right-handed healthy subjects (35 men and 40 women; mean age = 24.1 years) participated in the experiments after providing written informed consent. The Fondazione ''Santa Lucia'' ethical committee approved the study.

Experimental Setting

A 10 × 10 black matrix appeared on a computer touch screen. The subjects were asked to find a hidden sequence of ''correct'' squares arranged in advance by the experimenter. The sequence was composed of 20 adjacent spatial positions in the matrix, forming a complex ''snakelike'' pattern without any semantically or geometrically describable arrangement. The subjects had to start by touching a gray square, representing the first element of the sequence, which always remained lit up. In the search for the second correct position, they had to touch the black squares bordering the gray square by moving vertically or horizontally, but never diagonally, in the matrix. When the correct position was discovered, the touched square turned gray; conversely, when an incorrect position was touched, the square turned red. An alert sound signaled the touching of an incorrect position. Each (correct or incorrect) touched square was lit up for 500 msec and then became black again; thus, no trace of the performed sequence remained on the screen. Subjects had to start the performed sequence again each time they found a new correct position in the matrix. They were helped by a sound produced by the program that signaled them to return to the first square of the sequence. In the search for the following positions, they had to obey the same rules. The task ended when the subjects found the 20th correct position.

Experimental Protocol

Four different 20-item sequences, which did not differ for degree of difficulty,[1] were arranged. Subjects were

submitted to an observational training that consisted of observing a subject (actor) while discovering one out of four correct sequences by trial and error. Then, the observers were required to actually execute the task. They executed both the previously observed "old" sequence and a "new" sequence they had never observed. The presentation order between old and new sequences was randomized and counterbalanced among subjects.

Repetitive Transcranial Magnetic Stimulation

rTMS was delivered by means of a MagStim rapid magnetic stimulator, using a figure-eight coil (70 mm in diameter) over the left lateral cerebellum and the right DLPFC. For cerebellar stimulation, the coil was positioned tangentially to the scalp, with the handle pointing upward, 1 cm under and 3 cm to the left of the inion (Torriero, Oliveri, Koch, Caltagirone, & Petrosini, 2004; Theoret, Haque, & Pascual-Leone, 2001). For the DLPFC stimulation, the anterior end of the coil wings junction was placed over the F4 site of the International 10/20 EEG system. The coil was applied tangentially to the scalp surface with the handle directed backward and angled at about 45° to the midline.

To verify the specificity of the effects of cerebellar and prefrontal rTMS, a control region, presumably not involved in the task, was stimulated. The coil was placed over a mesial fronto-parietal site, corresponding to the Cz scalp position of the 10/20 EEG system, with the handle pointing backward.

Anatomical information about the brain areas stimulated was obtained by performing magnetic resonance imaging on a single experimental subject after marking the cerebellar and frontal scalp sites with capsules containing soy oil. Off-line rTMS was applied at 1-Hz frequency for 10 min (600 stimuli) at 90% intensity of the motor threshold. The latter was defined as the lowest TMS intensity (as assessed with single-pulse TMS) able to induce a visible muscle twitch of the contralateral hand in at least 50% of a sequence of 10 consecutive trials.

Experimental Groups

Seventy-five subjects were divided into seven groups. The first group (actors, $n = 20$) was composed of actors who served as models for the remaining groups of observers. The second group (controls, $n = 10$) was composed of subjects submitted to observational training before their own performance. These two groups were not submitted to any rTMS. The subjects in the following three groups were submitted to observational training at the end of the rTMS train over the Cz (Cz + Obs, $n = 10$), the left cerebellar hemisphere (Cb + Obs, $n = 11$), or the right DLPFC (DLPFC + Obs, $n = 10$). Immediately after the observation, they actually performed the task. The subjects in the last two groups

were first submitted to observational training and immediately afterward to an rTMS train over the left cerebellar hemisphere (Obs + Cb, $n = 7$) or the right DLPFC (Obs + DLPFC, $n = 7$). Subsequently, they performed the task.

Data Analysis

The total number of incorrect positions (total errors) touched on the screen in detecting the correct sequence was analyzed. To further evaluate the qualitative aspects of errors, the incorrect span, calculated as the maximum number of consecutive touching of incorrect squares, and the perseverative errors, calculated as the sum of consecutive touching of the same square or of a fixed sequence of squares, were analyzed.

Logarithmic transformations significantly improved the distribution of total errors and incorrect span. Even if the resulting distribution was not Gaussian (Kolmogorov-Smirnov test, $p < .001$), the number of outliers was strongly reduced, and good variance homogeneity was obtained (before transformation, Levene's test, $p < .009$; after transformation, Levene's test, $p > .05$).

Two-way analyses of variance (ANOVAs) with repeated measures were used followed by multiple comparisons with post hoc Duncan's test.

RESULTS

To verify whether observational training influenced the learning of the visuo-spatial task, we compared the performances of the actors with the performances of observer controls who executed the previously observed (old) sequence and a never observed (new) sequence. When the observers reproduced the previously observed sequence, they made significantly fewer errors than the actors [one-way ANOVA: $F(1,28) = 12.40$, $p = .001$]. Interestingly, a beneficial effect of observational
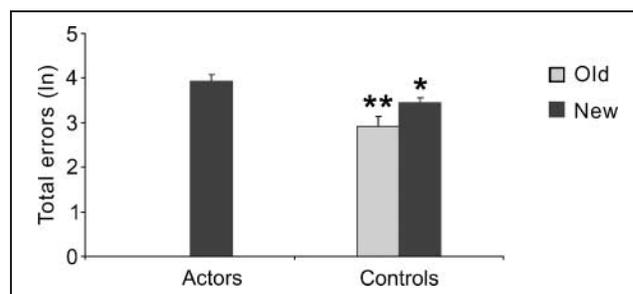

Figure 1. Behavioral results. Total errors are shown as natural logarithms. Vertical bars indicate *SEM*. Gray columns = old sequence; black columns = new sequence. Controls made significantly fewer errors than actors in performing both new and old sequence. *$p < .05$; **$p < .001$.

training was found when the observers performed a never observed sequence [one-way ANOVA: $F_{(1,28)}$ = 4.19, p = .05] (Figure 1). In any case, by comparing the performances of the observers in the old and new sequences, a significant difference was found [one-way ANOVA: $F_{(1,9)}$ = 6.21, p = .03]. These findings indicate that observing an actor performing a sequential visuo-motor task is advantageous in learning both the rules and the specific sequence of items, even if the beneficial effect is sequence specific.

A two-way ANOVA (3 groups × 2 sequences) comparing the performances of the Cb + Obs and DLPFC + Obs groups against the (no-TMS) controls revealed highly significant sequence [$F_{(1,28)}$ = 28.41, p = .00001] and interaction effects [$F_{(2,28)}$ = 6.56, p = .004]. Post hoc comparisons indicated that the Cb + Obs group made significantly more errors than the controls in detecting the new sequence (p = .01), but performed comparably to the controls in reproducing the old sequence (p = .50). On the contrary, the DLPFC + Obs group made significantly more errors than the controls in reproducing the old sequence (p = .006) and performed comparably to the controls in detecting the new sequence (p = .11) (Table 1).

To account for generic effects of rTMS, the performances of the Cb + Obs and DLPFC + Obs groups were compared with the performances of the Cz + Obs group. A two-way ANOVA (3 groups × 2 sequences) revealed significant sequence [$F_{(1,28)}$ = 30.78, p = .00001] and interaction effects [$F_{(2,28)}$ = 6.02, p = .007]. Once more, post hoc comparisons indicated that the Cb + Obs group made significantly more errors than the Cz + Obs group in detecting the new sequence (p = .05) but performed comparably to the Cz + Obs group in reproducing the old sequence (p = .41). Again, the DLPFC + Obs group made significantly more errors than the Cz + Obs group in reproducing the old sequence (p = .01) but performed comparably to the Cz + Obs group in detecting the new sequence (p = .34) (Figure 2, Table 1).

Given the peculiar role played by prefrontal as well as cerebellar regions in sequential behaviors (Hauser, 1999; Schmahmann & Sherman, 1997), additional analyses were performed on incorrect span and perseverations.

A two-way ANOVA (2 groups × 2 sequences) comparing the incorrect span of the Cz + Obs and Cb + Obs groups showed significant sequence [$F_{(1,19)}$ = 7.07, p = .01] and interaction [$F_{(1,19)}$ = 6.41, p = .02] effects. Post hoc analyses revealed a significant difference between groups in detecting the new sequence (p = .01).
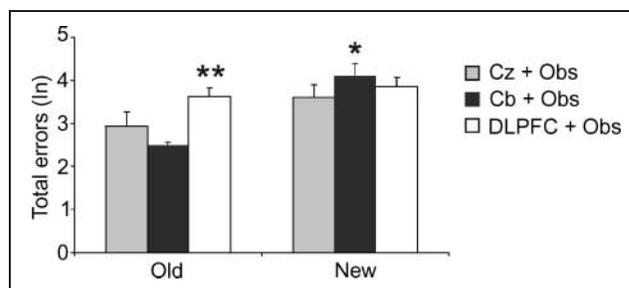
Figure 2. Total errors in rTMS groups. Total errors are shown as natural logarithms. Vertical bars indicate *SEM*. Gray columns = Cz + Obs group; black columns = Cb + Obs; white columns = DLPFC + Obs group. In comparison with rTMS of control site (Cz + Obs), cerebellar rTMS (Cb + Obs) produced a selective increase in total errors in performing the new sequence, whereas DLPFC rTMS (DLPFC + Obs) produced an increase in total errors in reproducing the old sequence. *p < .05; **p < .01.

A two-way ANOVA (2 groups × 2 sequences) comparing the Cz + Obs and DLPFC + Obs groups showed a significant group effect [$F_{(1,18)}$ = 5.44, p = .03] (Figure 3A).

A two-way ANOVA (2 groups × 2 sequences) comparing the perseverative errors of the Cz + Obs and Cb + Obs groups showed a significant interaction effect [$F_{(1,19)}$ = 7.91, p = .01]. Post hoc analyses revealed a significant difference between groups in detecting the new sequence (p = .002). A two-way ANOVA (2 groups × 2 sequences) comparing the Cz + Obs and DLPFC + Obs groups showed a significant group effect [$F_{(1,18)}$ = 6.60, p = .02] (Figure 3B).

Finally, the effects of rTMS applied before the actual execution of the task were analyzed to verify whether the previously obtained results were because of influences on task execution rather than on observational training. Thus, the Obs + Cb, Obs + DLPFC, and control groups' performances in the two sequences were compared. A two-way ANOVA (3 groups × 2 sequences) showed a significant main effect of sequence [$F_{(1,21)}$ = 9.40, p = .005]. Once more, this result confirms that the improving effect of observational training is sequence specific. The ANOVA failed to reveal any significant group or interaction effects (Table 1).

DISCUSSION

The present research demonstrates that rTMS is able to influence learning by observation of a visuospatial task by exerting different effects on the various components of

Table 1. Number of Total Errors (Mean ± *SEM*)

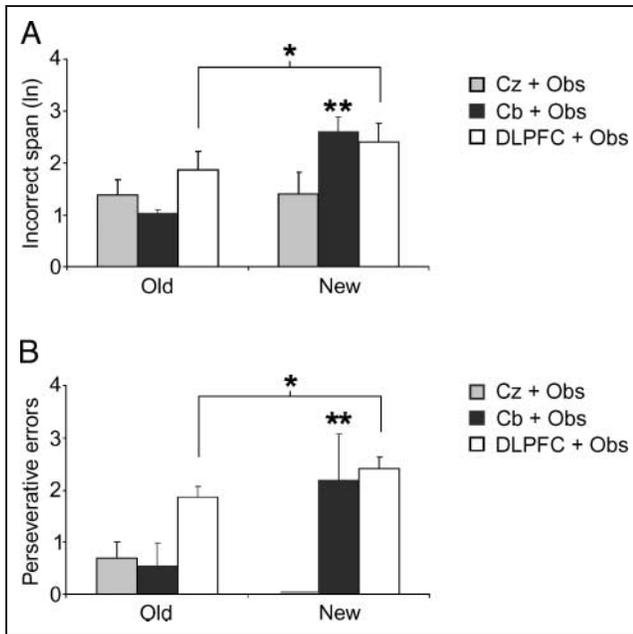| Actors		Controls	Cz + Obs	Cb + Obs	DLPFC + Obs	Obs + Cb	Obs + DLPFC
63.5 ± 10.5	Old	30.0 ± 7.6	22.0 ± 4.8	18.2 ± 4.6	45.9 ± 10.3	30.8 ± 10.0	27.7 ± 7.3
	New	35.21 ± 4.4	38.3 ± 4.3	89.8 ± 24.1	59.0 ± 13.1	34.2 ± 7.1	38.0 ± 16.1

Figure 3. Incorrect span and perseverative errors. Incorrect span is shown as a natural logarithm. Vertical bars indicate *SEM*. Gray columns = Cz + Obs group; black columns = Cb + Obs; white columns = DLPFC + Obs group. (A) Incorrect span was significantly longer in detecting the new sequence after cerebellar rTMS (Cb + Obs) in comparison with the span after control site rTMS (Cz + Obs); DLPFC rTMS (DLPFC + Obs) provoked a lengthening of the incorrect span, regardless of the kind of sequences performed. (B) Cb + Obs showed more perseverative errors than Cz + Obs only in detecting the new sequence, whereas DLPFC + Obs showed more perseverative errors regardless of the kind of sequences performed. Note that Cz + Obs group showed no perseverative errors at all in detecting the new sequence. *$p < .05$; **$p < .01$.

the task depending on which neuronal structures are inhibited. In fact, when the observational training followed rTMS of the left lateral cerebellum, we found clear interference with detection of a new sequence, different from the previously observed one. Conversely, when observational training followed rTMS of the right DLPFC, we found interference with the reproduction of the old previously observed sequence. The effect of rTMS resulted in an increase in total errors and lengthening of incorrect span and an enhancement of perseverative errors. The remarkable result regarding perseverative errors was found after cerebellar rTMS when the new sequence had to be detected and after DLPFC rTMS when both sequences were performed. Perseverations are distinctive symptoms linked to prefrontal dysfunction (Hauser, 1999), and interestingly, they are also elicited by cerebellar damage (Mandolesi, Leggio, Graziano, Neri, & Petrosini, 2001; Schmahmann & Sherman, 1997; Botez-Marquard & Botez, 1993). This finding is in line with the view that cerebellar lesions might provoke ''frontal-like'' cognitive deficits, supported by clinical reports of severe problems in initiation/perseveration and cognitive planning in cerebellar patients (Hauser, 1999;

Schmahmann & Sherman, 1997; Appollonio, Grafman, Schwartz, Massaquoi, & Hallett, 1993; Grafman et al., 1992; el-Awar et al., 1991). The rTMS influence was specifically linked to the observation phase and was completely lacking in the execution phase. In fact, cerebellar and prefrontal rTMS applied when the observational training was over did not evoke any effect in reproducing the old sequence or in detecting a new sequence.

The interfering effects of cerebellar rTMS on observational learning could be because of impairment in planning intentional strategies (i.e., in the ability to access and effectively use a procedural rule already acquired or in difficulty in acquiring a new one). Indeed, clinical reports on cerebellar patients describe severe problems in cognitive planning and procedural learning (Gomez-Beldarrain, Garcia-Monco, Rubio, & Pascual-Leone, 1998; Molinari et al., 1997; Appollonio et al., 1993; Pascual-Leone et al., 1993; Grafman et al., 1992). The present findings allow extending to humans the experimentally demonstrated notion that the cerebellum is involved in learning a visuospatial task not only when acquisition is achieved by actually executing a sequence of procedural acts but also when procedure acquisition is achieved by observation (Petrosini et al., 2003; Graziano et al., 2002).

The disruption of observational learning after cerebellar rTMS demonstrates the need for functionally intact cerebellar structures in the critical phase of the observation/execution matching process, supporting their crucial role in the acquisition phases of observational learning. In fact, the procedural competencies were fully maintained (and then put into action) when cerebellar rTMS was performed after observational training. This finding is in agreement with neuroimaging evidence demonstrating high cerebellar activation during the acquisition phase of learning and decreased cerebellar activation after prolonged practice (Petersen et al., 1998; Vaina et al., 1998).

The present results also support the role of the DLPFC in learning by observation. In fact, DLPFC rTMS provoked the worsening of performances mainly in reproducing the old sequence and an increase in perseverative errors and incorrect span in performing both sequences. The interfering effect of DLPFC rTMS on both sequences emphasizes the sequence-specific effect found when rTMS was delivered over the cerebellar region. Many studies report activation of the DLPFC when free selection between different response alternatives is required and when there is a high attentional demand (Hadland, Rushworth, Passingham, Jahanshahi, & Rothwell, 2001; Jueptner et al., 1997). Moreover, it was recently demonstrated that the DLPFC is specifically activated in conjunction with the selection of an item from memory to guide a response (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). In the present visuomotor task, reproducing the old sequence required selection from competing actions, retrieval from long-term memories of the sequence of positions previously learned, and on-line maintenance and updating in working memory

of the progressively touched items. All of these competencies have been attributed to the prefrontal circuits (Mottaghy, 2006; Faw, 2003; Manes et al., 2002).

In conclusion, the present study provides new insights on the neural circuitry involved in observational learning. It was recently suggested (Iacoboni, 2005; Buccino et al., 2004) that imitative learning of novel actions is supported by a core circuit for imitation comprising the fronto-parietal mirror neuron system that interacts with DLPFC and motor preparation areas. Other research underlined the additional activation of bilateral cerebellar areas when the observation of action has the goal of imitation. Such cerebellar activation was not documented when observation was not aimed toward imitation (Chaminade et al., 2002; Decety & Grèzes, 1999). The interplay between cerebellar and prefrontal areas, supported also by their important anatomofunctional connections (Middleton & Strick, 2001), allows for speculation that the cerebellum and prefrontal cortex interact in planning actions—that is, the former permits acquisition of efficient procedural competencies and the latter provides flexibility among already acquired and stored solutions (Pochon et al., 2001; Spence, Hirsch, Brooks, & Grasby, 1998; Hyder et al., 1997; Frith, Friston, Liddle, & Frackowiak, 1991).

Acknowledgments

Note

1. The number of errors made by four groups of five subjects in detecting one of the four sequences was calculated. A one-way ANOVA with sequence as main effect failed to reveal any significant difference in number of errors among groups [$F(3,16) = 0.29$, $p = .83$], demonstrating the same degree of difficulty in the four sequences.

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