RESEARCH ARTICLE

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Conditions for interference versus facilitation during sequential sensorimotor adaptation

Abstract We investigated how sensorimotor adaptation acquired during *one* experimental session influenced the adaptation in a *subsequent* session. The subjects' task was to track a visual target using a joystick-controlled cursor, while the relationship between joystick and cursor position was manipulated to introduce a sensorimotor discordance. Each subject participated in two sessions, separated by a pause of 2 min to 1 month duration. We found that adaptation was achieved within minutes, and persisted in the memory for at least a month, with only a small decay (experiment A). When the discordances administered in the two sessions were in mutual conflict, we found evidence for task interference (experiment B). However, when the discordances were independent, we found facilitation rather than interference (experiment C); the latter finding could not be explained by the use of an "easier" discordance in the second session (experiment D). We conclude that interference is due to an incompatibility between task requirements, and not to a competition of tasks for short-term memory. We further conclude that the *ability to adapt* to a sensorimotor discordance can be improved by practicing with an unrelated discordance.

Keywords Humans · Sensorimotor integration · Motor learning · Sensorimotor adaptation · Tracking

Introduction

Numerous studies have shown that human subjects can adapt to sensorimotor discordance, produced, e.g., by visual (Bock 1992; Pine et al. 1996; Stratton 1897) or mechanical perturbations (Lackner and DiZio 1994;

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Shadmehr and Mussa-Ivaldi 1994). When the exposure to discordance is terminated, the adapted state can be stored in the sensorimotor memory, and reactivated at a later time if required. This has been documented by experiments where subjects were adapted to a discordance, and were re-tested in a second session using the *same* or a *stronger* discordance: It was found that subjects' performance at the onset of the second session was better than at the onset of the first (Brashers-Krug et al. 1995; Klapp et al. 1974; Krakauer et al. 1999; Lazar and van Laer 1968; Welch et al. 1993), indicating that the adapted state was partially or fully retained across the interval between sessions.

In other experiments, subjects were exposed in the second session to the *opposite* discordance than in the first (Shadmehr and Brashers-Krug 1997; Shadmehr and Holcomb 1999). When the two sessions were scheduled less than 5 h apart, initial performance in the second session was *substantially worse* than in the first. Furthermore a third session, administered one or several days later, yielded no evidence for a retention of the originally adapted state. Taken together, these findings were attributed to a mutual interference between two concurrent adapted states. No such interference was found, however, when the first two sessions were more than 5 h apart: In this case, performance in the second session was similar to that of naive subjects, and the third session yielded full retention of the originally adapted state. The cited findings were obtained during adaptation to an external force field, but mutual interference was also documented during adaptation to a rotated visual display (Krakauer et al. 1999).

To explain the above findings, it has been argued that adaptation needs several hours after exposure to consolidate from a fragile representation in the short-term memory to a stable one in the long-term memory. When the second task is presented too early, it will compete with the first for the limited capacity of short-term memory, will therefore disturb the fragile original memory traces and, in turn, will be disturbed by them. However, when the second task is presented after the original consolida-

tion is completed, it can be acquired without mutual interference. Both adapted states can thereafter coexist in the long-term memory, as shown by studies where subjects were repeatedly exposed to multiple discordances: After some training, subjects could switch between several adaptive states in a context-dependent fashion (Shelhamer et al. 1992; Welch et al. 1993), or combine them to quickly adapt to a composite discordance (Flanagan et al. 1999).

The present study was designed to further explore the interaction of successive discordances in sensorimotor adaptation. In the cited experiments, the second discordance was always incompatible with the first: What was learned in the first session was counterproductive to success in the second, and had to be suppressed in order to achieve satisfactory performance. We wondered whether a second discordance which does not require such suppression would produce interference as well. If so, we would have support for the above view, that interference is related to the fragility of memory traces, before consolidation to long-term memory. If not, interference would better be described as competition between conflicting task requirements.

Materials and methods

The experimental setup is illustrated schematically in Fig. 1a. Subjects stood in front of a vertical projection screen S, viewing it through a tilted mirror M, such that it appeared in a horizontal plane H at waist level. A visual target (luminous dot of 2 cm diameter) moved smoothly across the screen; the horizontal and vertical components of motion were each the sum of 5 sinewaves (0.04, 0.08, 0.1, 0.16, and 0.2 Hz), with a relative phase of 90 deg between components. Thus, the target trajectory was repetitive with a cycle length of 50 s, but subjects were not aware of this periodicity; for them, the trajectory was essentially unpredictable.

In their preferred hand, subjects held a springless, low-friction joystick which controlled the movement of a cursor on the screen. Thus the perceived motion of target, cursor, and joystick all occurred in the same – horizontal – plane. The subjects' task was to track the target with the cursor as accurately as possible. To prevent fatigue, each experimental session was subdivided into tracking episodes of 50 s duration, separated by rest breaks. Subjects were free to terminate the breaks whenever they felt ready, typically within a few seconds.

The joystick position was sampled every 52 ms with a resolution of 0.1 deg in the lateral, and 0.14 deg in the sagittal, dimension. The recorded signal was mapped onto displayed cursor position either non-inverted (e.g., leftward or forward joystick movement yielded a leftward or forward cursor movement, respectively), inverted along one of the two axes, or inverted along both axes, depending on the experimental condition (see below). The data were stored to hard disk, and the root mean square tracking error of each tracking episode was calculated using:

$$RMSE = \sqrt{\frac{\sum_{i=2}^{n}(\Delta x_{\mathrm{I}})^2 + \sum_{i=2}^{n}(\Delta y_{\mathrm{I}})^2}{n}} \quad (1)$$

where Δx_{i} and Δy_{i} are the lateral and forward distance between target and cursor in the i'th data sample, and n is the number of samples analyzed. The first 500 ms of each tracking episode was discarded from analysis, to prevent an initial misplacement of the cursor from having a substantial effect on RMSE.

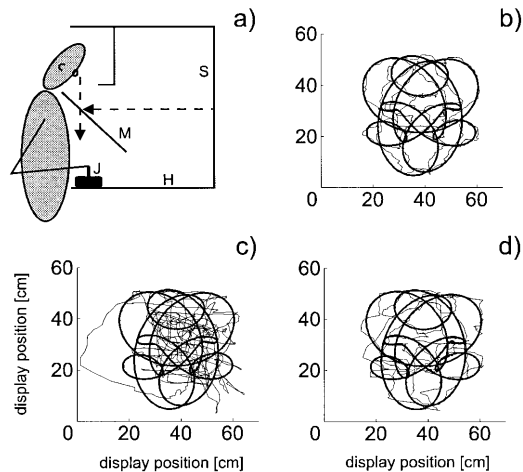Eighty-four volunteers participated in our study. None of them had previous experience in our task, or was familiar with playing joystick games. Each subject participated in only one of our four experiments. The subjects were 19–43 years of age, had corrected-for-normal vision and exhibited no overt sensorimotor or other neurological problems. As an incentive, we announced that the participant who achieved the lowest RMS score would receive a small monetary reward. All subjects signed an informed consent form for this study, which was approved by the Ethics Committee of the German Sport University.

Fig. 1 a A schematic view of the experimental apparatus with back-projection screen (*S*), mirror (*M*), horizontal surface (*H*), and joystick (*J*); due to the mirror, the virtual screen position coincided with *H*. **b–d** Tracking performance of a subject before (**a**), immediately after (**b**) and 30 min after (**c**) introducing a left-right visuomotor reversal; *the bold line* represents the target, *the thin line cursor* the movement

Experiment A

The purpose of experiment A was to confirm the validity of our experimental procedure as an adaptation paradigm, and to quantify the period of time over which the adapted state can be retained. Twenty subjects participated in two experimental sessions. The first session started with ten episodes under normal cursor control, i.e., the cursor always moved in the same direction as the joystick. This "warm-up" period was followed by 30 episodes where cursor control was manipulated: For ten subjects, cursor movement was left-right reversed with respect to joystick movement, and for the other ten subjects it was up-down reversed.

All subjects were tested again in a second session for another ten tracking episodes, using the *same* discordance as in the first (i.e., left-right or up-down reversal). The pause between sessions was 8 min, 25 min, 1 h, 2 h or 1 month, and two subjects were assigned to each of the ten discordance × pause length combinations.

Results and discussion

Figure 1 shows raw tracking data of a subject during a warm-up episode (1b), the first episode under left-right
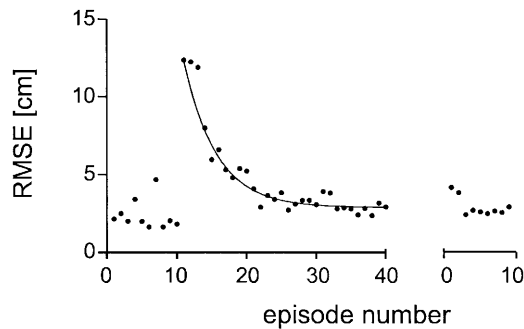
Fig. 2 Tracking performance of one subject in experiment A. *Each dot* represents the RMSE value for one 50-s tracking episode, and the curve indicates an exponential fit. *The horizontal axis is interrupted where a pause occurred between sessions 1 and 2*

Fig. 3 Tracking performance of one subject in experiment B. For explanations see Fig. 2

reversal (1c), and a late episode under left-right reversal (1d). Clearly, tracking performance was severely degraded when the reversal was introduced, but recovered after prolonged exposure. This observation is confirmed by the RMSE data in Fig. 2: The tracking error increased dramatically after discordance onset, and then gradually settled at about the warm-up level. It can be further noted in Fig. 2 that RMSE at the onset of the second session was not much higher than at the end of the first.

As a measure of between-subject variability, we calculated the mean RMSE of each subject across all warm-up episodes, yielding values between 1.93 and 2.94 cm. Overall variability was calculated as standard deviation across warm-up episodes and subjects, yielding 0.92 cm.

For a statistical analysis, we compared the first RMSE value after reversal in session 1 with the mean of the last three values in that session. An analysis of variance (ANOVA) was applied, using the within-factor Episode (levels: first, last three) and the between-factor Discordance (levels: left-right, up-down). There was a significant main effect of Episode ($F_{(1,18)}$=233.1, $P<0.001$), which confirms that subjects were able to adapt, but no significant effects of Discordance and its interaction, which suggests that the initial and final errors with both discordance types were similar.

In another ANOVA, we compared the last three RMSE values of session 1 with the first three of session 2, using the within-factor Episode (last three, first three) and the between-factor Pause (8 min, 25 min, 1 h, 2 h, 1 month). Only the Episode × Pause interaction was significant (F=4.15, $P<0.05$), due to a slight increase in RMSE after the *longest* pause: At the end of session 1, the RMSE (mean±SD) was 3.32±0.65 cm; it remained virtually unchanged at 3.29±0.69 cm at the beginning of session 2 after pauses of up to 2 h, but increased somewhat to 4.00±0.38 cm after a 1-month pause. Although this increase was statistically significant, the RMSE was still substantially lower than at discordance onset in session 1 (10.78±2.55 cm), which indicates that retention of the adapted state remained nearly complete even after an extended pause.
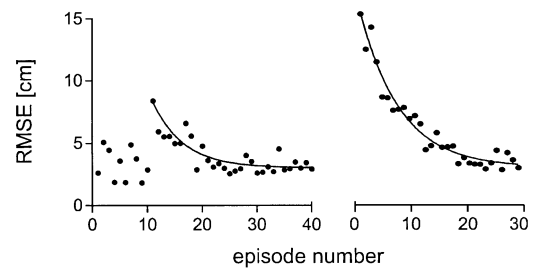
In conclusion, experiment A documents that our paradigm is suitable for the study of sensorimotor adaptation, and that it yields long-lasting retention. This finding is in accordance with previous work, reporting partial or full retention of adapted behavior even across substantial intervals (Brashers-Krug et al. 1995; Klapp et al. 1974; Krakauer et al. 1999; Lackner and Lobovitz 1977; Lazar and van Laer 1968).

Experiment B

Our second experiment was designed to replicate the previously observed negative interference between successive adaptations, and to explore over which time intervals this interference occurs. As in experiment A, the first session consisted of 10 warm-up episodes, followed by 30 episodes under left-right or up-down reversal. The second session was administered after a pause of 2 min, 8 min, 25 min, 60 min, 2 h, 18 h, 1 week or 1 month, and consisted of another 30 episodes under a *different* discordance: Subjects which have been exposed to left-right reversal in their first session were now tested under up-down reversal, and vice versa. A total of 32 subjects participated, two in each discordance × pause combination.

Results and discussion

The RMSE values of one subject are plotted in Fig. 3. As in experiment A, the error increased abruptly when the discordance was introduced in session 1, and then gradually decayed. At the onset of the second session, when the subject was confronted for the first time with a new type of discordance, the RMSE increased again, *even to a distinctly higher level* than in session 1, and then decayed back to the baseline.

While the data in Fig. 3 are well fitted by an exponential function, data from a few subjects yielded no satisfactory fits with single and double exponentials, or other customary parametric functions. We therefore adopted the following alternative procedure to quantify the time-course of all data sets. The *initial error* was determined as the first RMSE value under a discordance, the *final error* as the mean of the last three RMSE values in a session. We then calculated the *half-time* of decay by fitting

Table 1 Means across subjects, and standard deviations, of the three response parameters determined in experiments B–D

Experiment		Session 1	Session 2
B	Initial error	11.59±3.32	17.74±4.29
	Final error	3.78±0.93	4.67±1.54
	Half-time	4.21±1.56	5.93±2.38
C	Initial error	11.29±2.58	8.23±3.80
	Final error	3.20±1.10	2.58±0.69
	Half-time	3.80±2.02	2.29±1.52
D	Initial error	N/A	11.91±3.74
	Final error	N/A	2.72±0.56
	Half-time	N/A	2.01±1.29

Table 2 Summary of ANOVA results. *Each line* represents one analysis, with the dependent variable specified by *the two leftmost columns*. Data are F values, and *NS*, *, **, and *** indicate $P>0.05$, $P<0.05$, $P<0.01$, and $P<0.001$, respectively

Experiment		Session	Pause length	S*P
B	Initial error	95.65***	0.54NS	1.96NS
	Final error	21.85***	1.66NS	1.45NS
	Half-time	17.84***	0.79NS	1.35NS
C	Initial error	9.33*	1.46NS	0.79NS
	Final error	11.62**	0.68NS	2.51NS
	Half-time	7.11*	0.38NS	1.22NS

a single exponential to all the remaining data points (i.e., to 30–4=26 values), while at the same time forcing it to pass through the initial error, and to asymptotically approach the final error. We confirmed that the final error indeed represents the asymptote of decay by comparing the mean of episodes 38–40 with that of episodes 35–37 in a paired-samples t-test: The means were not significantly different ($t_{(61)}=1,36$; $P>0.05$), which indicates that the decay was complete before session end. The values yielded by this procedure are summarized in Table 1.

Each of the above three variables was subjected to an ANOVA, using the within-factor Session and the between-factor Pause, as shown by the first three rows of Table 2. The significant effect of Session is due to an increase in all three variable values from session 1 to 2 (see Table 1). The lack of a significant Session by Pause interaction indicates that we found no evidence for a dependence of any variable on pause length. This conclusion is supported by the outcome of a paired-samples t-test, yielding a significant difference between sessions even for the longest pause duration ($t=3.18$, $P<0.05$).

Our findings document that tracking performance in the second session is inferior to that in the first, which confirms previous data on interference between successive adaptations to non-compatible force fields (Shadmehr and Brashers-Krug 1997; Shadmehr and Holcomb 1999) and visual rotations (Krakauer et al. 1999). However, the available data disagree on the time scale of this effect: One group reported that interference is limited to pauses of up to 5 h duration (Shadmehr and Brashers-Krug 1997; Shadmehr and Holcomb 1999),

while the other group found interference even after 24 h (Krakauer et al. 1999). Our own data are in accordance with the latter study, providing no evidence for a dependence on pause length for up to a full month. Thus, the slight decay of retention after 1 month pause observed in experiment A was not reflected by a similar decay of interference in experiment B.

The conflicting data on the time scale of interference in force-field studies and in the present work could be interpreted in at least two ways. Firstly, our subjects were exposed to their first discordance for 30 min, while the cumulated exposure time in the force field studies can be estimated as about 8 min. It is possible that longer exposure produces more pronounced memory traces, which offer more resistance to conflicting task requirements. Secondly, dynamic tasks such as force field adaptation require the integrity of the lateral cerebellum, while mapping tasks such as a mirror-reversal do not (Fukuzawa et al. 1999), suggesting that adaptation to these discordances is based on different neuronal mechanisms. It would not be surprising if different mechanisms had different interference characteristics.[1]

Experiment C

The purpose of this main experiment of our study was to introduce in the second session a discordance which is *independent* of the first. Thus, the two discordances should be *neither conflicting* as in experiment B and in previous interference studies (Krakauer et al. 1999; Shadmehr and Brashers-Krug 1997), *nor synergic* as in studies using incremental discordances of a single type (Lazar and van Laer 1968; Welch et al. 1993). In our experiment C, the first session was similar to that of experiments A and B, except that the warm-up period was reduced to five episodes in consideration of our subjects' patience. After a pause of 8 min, 2 h, 1 week or 1 month, the second session exposed all subjects to a 180-deg rotation between joystick and cursor movement for 30 episodes. Note that this transformation represents a combination of left-right *and* up-down reversal, i.e., subjects which adapted to a left-right reversal in their first session now had to "add" an up-down reversal, and vice versa. Sixteen subjects participated in experiment C, two for each discordance × pause combination.

Results and discussion

As expected, session 1 performance was similar to that in experiments A and B, as illustrated by the data in Fig. 4 and Table 1. In contrast, the initial performance in session 2 was *not* worse than in session 1, as expected in the case of negative interference, nor was it similar to

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[1] However, experimental evidence suggests that at least some dynamic tasks produce interference even after a 24-h pause (Krakauer et al. 1999).

Fig. 4 Tracking performance of one subject in experiment C. For explanations see Fig. 2
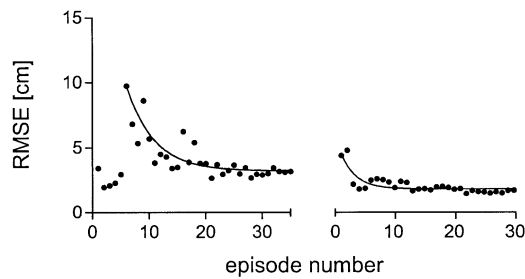

Fig. 5 Tracking performance of one subject in experiment D. For explanations see Fig. 2

session 1, as it would have been if both session were independent. Instead, initial performance in session 2 was *substantially better* than in session 1. The ANOVA results in Table 2 confirm that these changes were significant. The table further shows that the Session by Pause interaction was not significant, which suggests that the difference between sessions 1 and 2 persisted even after a 1-month pause.

In conclusion, the results of experiment C seem to indicate that adaptation to one discordance can be beneficial for a subsequent adaptation to another discordance. This finding can *not* be explained by the argument that subjects have "partially" learned the second discordance by participating in the first session, as the two discordances were independent: Subjects adapting first to a left-right reversal have acquired no knowledge that would make a subsequent additional up-down reversal an easier transformation. Rather, it appears that by participating in the first session, subjects have improved their *ability to adapt*, and benefitted from this improvement in the second session. Such a phenomenon is called "learning to learn" in the literature, but little experimental evidence supporting its existence has been presented in the past (see "General discussion").

However, an alternative interpretation of experiment C is also conceivable. A 180-deg rotation might just be an "easy" type of discordance to adapt, irrespective of whether it is preceded by another session. Indeed, it has been shown that rotations of 180 deg are easier to learn than other rotational transformations (Cunningham 1989). The following experiment was designed to scrutinize this possibility.

Experiment D

In this control experiment, the first session consisted of 35 episodes of warm-up (i.e., no reversal), and the second session of 30 episodes under 180-deg rotation; pauses were as in experiment C. Thus, subjects in this experiment had the same amount of experience with our apparatus as subjects in experiment C, but were exposed to 180-deg rotation without prior exposure to another discordance. Sixteen subjects participated, four for each pause duration.
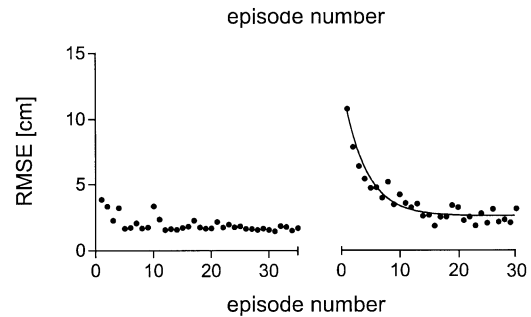
Results and discussion

The RMSE data of one subject are shown in Fig. 5, and are summarized across subjects in Table 1. It is quite obvious that the initial error in the second session of experiment D was similar to that in the first session of experiment C, but larger than in the second session of experiment C. This observation was confirmed by ANOVAs (session 2 of experiment D vs session 1 of experiment C: $F=0.25$, $P>0.05$; session 2 of experiment D vs session 2 of experiment C: $F=6.44$, $P<0.05$). This outcome indicates that a 180 deg rotation is not an easier adaptation task than a left-right or an up-down reversal, and thus rejects the alternative interpretation of experiment C.

General discussion

The present study dealt with adaptation to sensorimotor discordance administered in two successive sessions. We confirmed that the adapted state can remain in the memory for at least a month (experiment A), and that two non-compatible adapted states will interfere in the memory even if they are acquired up to a month apart (experiment B). However, when the two adapted states were compatible, we found facilitation rather than interference (experiment C). The latter finding could not be explained by assuming that the second discordance was easier to learn (experiment D).

It has been suggested in the past that interference during successive adaptations is due to the competition for short-term memory (STM) resources, and will subside once the originally adapted state is consolidated into the long-term memory (see "Introduction"). Subsequent work has shown a lack of interference between two tasks, one involving a kinematic, and the other a dynamic, perturbation; this finding was not interpreted as a challenge to the above consolidation hypothesis, but rather as evidence for the existence of separate STM systems related to kinematic versus dynamic learning (Krakauer et al. 1999). However, the present findings are not as readily compatible with the consolidation interpretation, for two main reasons. Firstly, interference persist-

ed in our study across exposure-free intervals of at least a *full month*, while consolidation should be completed within just a few hours (McGaugh 1966). Secondly, we found interference only when the two tasks had conflicting, but not when they had independent, requirements, while interference through consolidation should apply to *any* two tasks, as long as they concurrently require STM resources. Therefore, while consolidation might be a valuable concept for our understanding of motor learning, it cannot explain interference in our study. In contrast, the other available interpretation, that interference is due to the conflict between two incompatible tasks (see "Introduction"), is in full agreement with the outcome of our experiments B and C.

Of course, the present findings do *not* imply that motor learning occurs without *any* involvement of the STM; we can only argue that limitations of STM storage space appear not to be the main reason for interference. However, other work provides experimental evidence that STM is indeed not a major factor in motor learning: It was found that electroconvulsive therapy may produce retrograde amnesia for sensorimotor activities *while sparing the skills acquired through those very activities* (Squire et al. 1984).

Probably the most interesting outcome of the present study is the facilitation when adapting to discordances which are independent, i.e., which have neither conflicting nor synergic task requirements (experiment C). The very nature of independence precludes the interpretation that subjects in their second session simply continued to learn what they have partially acquired in the first. It rather appears that subjects have implemented some general strategies for coping with visuomotor transformations in the first session, and apply them to their benefit in the second session. If so, this phenomenon would reflect an improvement in the *ability to adapt*, called "learning to learn" in the previous literature. However, previous evidence claiming support for this phenomenon has been equivocal at best: Subjects were exposed first to a small and then to a larger discordance *of the same type*, and it was found that adaptation in the second session was better than for control subjects who skipped the first (Lazar and van Laer 1968; Welch et al. 1993). This finding probably does not reflect "learning to learn," but rather indicates that in the second session subjects were able to build upon the knowledge they already have acquired by the end of the first. True "learning to learn" can only be confirmed in experiments where successive discordances are independent, as was the case in our experiment C.

From our data, it appears that "learning to learn" is long-lasting, with beneficial effects even after an exposure-free interval of one full month. It would be interesting to determine the decay time of this phenomenon (if any), to find out whether it becomes even more expressed when more than two discordances are administered, and whether it generalizes to all adaptation tasks or rather is limited to similar discordance categories, as were the mirror reversals used in the present study. In particular, it has been shown that different categories of motor learning are based on different neural circuits (Fukuzawa et al. 1999; Ghilardi et al. 2000; Martin et al. 1996), and it is therefore quite conceivable that "learning to learn" is limited to tasks based in the *same* brain areas. Finally, it would be interesting to determine whether "learning to learn" and "interference" are two mutually exclusive phenomena, or whether they can occur concomitantly in the same task, with the one or the other phenomenon predominating, depending on specific task characteristics.

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