

Katsumi Watanabe · Hanako Ikeda · Okihide Hikosaka

## Effects of explicit knowledge of workspace rotation in visuomotor sequence learning

Received: 2 October 2005 / Accepted: 13 April 2006 / Published online: 25 May 2006  
© Springer-Verlag 2006

**Abstract** Previous experimental and theoretical studies have suggested that two separate neural networks contribute to visuomotor learning of spatial sequences, one to the accuracy of performance and the other to the speed of performance (Nakahara et al. in *J Cogn Neurosci* 13:626–647, 2001). This study examined the influence of explicit knowledge of stimulus configuration (workspace) in visuomotor sequence learning. Twenty-eight right-handed subjects learned the sequences of button presses by trial and error (Hikosaka et al. in *J Neurophysiol* 76:617–621, 1996) in the course of two sessions. In the first session, both the number of completion failures (accuracy measure) and the performance time to complete a sequence (speed measure) decreased. In the second session, the workspace was rotated without notifying the subjects. About half the subjects remained unaware of the workspace rotation, and no transfer of learning occurred (i.e., neither accuracy nor speed of performance was preserved in the second session). The remaining subjects spontaneously noticed the rotation and they were able to use this knowledge to perform the task with less completion failures in the second session.

However, the knowledge of workspace rotation did not decrease the performance time in the second session. The lack of influence of explicit knowledge on the speed of performance is consistent with the two-loop model of visuomotor sequence learning (Nakahara et al. in *J Cogn Neurosci* 13:626–647, 2001).

**Keywords** Sequential learning · Accuracy · Speed · Explicit knowledge · Human

### Introduction

Does knowing where to go always help in learning to produce an action sequence quickly? Recent studies on procedural learning (i.e., learning governed by rules or procedures) have implied that this may not always be the case; behavioral studies showed that the accuracy (knowing where to go) and speed (deciding how quickly to go) in completing action sequences may be based on different mechanisms (Hikosaka et al. 2002). For example, Hikosaka et al. (1995) demonstrated that, in visuomotor sequence learning, the accuracy of performance (measured by the number of completion failures) is acquired earlier than the speed of performance (measured by the performance time to complete a learned sequence). In addition, the improvement in the accuracy measure is relatively unspecific to the effector (e.g., showing intermanual transfer at an early learning stage) whereas the improvement in the speed measure is effector-specific (Rand et al. 1998; Bapi et al. 2000). Neuroimaging studies on humans have also supported the idea of separate processes for accuracy and speed in visuomotor sequence learning and parallel neural networks that are distributed among many brain areas (Toni et al. 1998; Petersen et al. 1998; Grafton et al. 1998; Honda et al. 1998; Sakai et al. 1998; for a review, see Hikosaka et al. 2002).

Having the above evidence, a model was proposed, where two sets of cortico-basal ganglia and cortico-cerebellum loop circuits act independently to promote visuomotor sequence learning in spatial and motor coordi-

---

K. Watanabe (✉)  
Research Center for Advanced Science and Technology,  
University of Tokyo, 4-6-1, Komaba, Meguro-ku, Tokyo,  
153-8904, Japan  
E-mail: kw@fennel.rcast.u-tokyo.ac.jp

K. Watanabe · H. Ikeda  
National Institute of Advanced Industrial Science  
and Technology, Tsukuba, Ibaraki, Japan

K. Watanabe  
Shimojo Implicit Brain Function Project, ERATO, JST,  
Kawaguchi, Saitama, Japan

H. Ikeda  
Graduate School of Comprehensive Human Sciences,  
University of Tsukuba, Tsukuba, Ibaraki, Japan

O. Hikosaka  
Laboratory of Sensorimotor Research, National Eye Institute,  
National Institutes of Health, Bethesda, MD, USA

nates (Hikosaka et al. 1999, 2002; Nakahara et al. 2001). The model successfully accounts for various empirical observations, including coordinate transformation, inter-manual transfer, attention cost, and awareness. Among these, the role of awareness (e.g., Willingham 1998; Honda et al. 1998), or explicit knowledge, in visuomotor sequence learning is relatively unexplored in the context of parallel network model.

To examine the effect of explicit knowledge on visuomotor sequence learning, we employed a sequential button press task that was originally devised for monkeys as subjects (Hikosaka et al. 1995; Rand et al. 1998) and subsequently used for humans (Hikosaka et al. 1995, 1996, 2002; Sakai et al. 1998, 2003). In this study, we examined specifically the effect of a change in the orientation of the workspace on visuomotor sequence learning. After a session in which the human subject learned a fixed spatio-temporal sequence, he/she was asked to perform the same sequence (in terms of relative spatiotemporal sequence) without being notified that the entire stimulus configuration had been rotated by a fixed angle. Any improvement in performance in the second session would indicate that the learning had been transferred to a different orientation. It is noteworthy that only about half of the subjects participating in the study were aware of the workspace rotation. The patterns of improvement (i.e., transfer) were different for the two measures of learning: the number of failures in completing a sequence (indicating “accuracy”) and the time to complete a learned sequence (indicating “speed”). More specifically, we found that the awareness of workspace rotation (hence knowing where to go in the new configuration) does not lead to a speed advantage; producing a learned action sequence was equally slow, whether or not the subjects noticed the workspace rotation.

---

## Materials and methods

### Subjects

Thirty-two right-handed subjects (14 females, 18 males) participated in the experiment. They were naive as to the purpose of the experiment. All subjects gave written informed consent prior to participation. All procedures were conducted in accordance with the 1964 Declaration of Helsinki.

### Procedure

The subjects were trained to perform a sequential button press task, which we call “2×10 task” and which was basically the same as the one used in our previous experiments (e.g., Sakai et al. 2003).

To describe the experiment briefly, a panel on which 16 LED buttons were mounted in a 4×4 matrix was placed before a subject seated on an armchair. The LED buttons were square in shape (10 mm×10 mm) and were

separated from each other by 8 mm space. At the bottom of the panel was another LED button, which was used as the “home” key. The subjects used their right index fingers to press the buttons.

The home key was turned on at the beginning of each trial. When the subjects pressed the home key for 500 ms, 2 of the 16 target LEDs, which we call “set,” turned on simultaneously. The subjects were required to press the illuminated buttons in the correct order, which they were required to uncover by trial and error. If they were successful, the LEDs turned off one by one and another pair of LEDs, a second set, was illuminated, which the subjects were required to press again in the correct order. A total of 10 sets, which we call “hyperset,” were presented in a fixed order for the completion of a trial. When the subjects pressed a wrong button, all the LED buttons were briefly illuminated and the trial was aborted. The subjects then had to restart the trial from the home key. A trial was considered to be successful when the subject completed an entire hyperset (10 sets). The same hyperset was repeated until the subject completed it successfully for a total of 20 trials (called a “block”). The subjects were asked to perform the task as quickly and as accurately as possible.

### Rotation of workspace

First, four hypersets, called H1, H2, H3, and H4, were randomly generated. For each hyperset, new hypersets were generated by rotating the entire stimulus configuration by 0°, 90°, 180°, and 270° (clockwise). Note that the rotated hypersets were identical to the original hypersets with 0° rotation. The subjects were asked to learn 8 hypersets each until the criteria (20 successful trials) was reached. The hypersets consisted of four original hypersets and their rotated versions (one of four types of rotations for each hyperset), unknown to the subject. The rotated hyperset always followed the corresponding original hyperset. For example, one subject performed the experiment in the following order (angle of rotation in parentheses): H3, H3(270), H4, H4(0), H1, H1(90), H2, H2(180). The order of the four types of rotation and that of the hypersets were counterbalanced across the subjects. Each of the eight sessions (for each hyperset) was separated by a break of approximately 1 min. After the experiment, the subjects were first asked whether they had noticed anything peculiar. If the answer was yes, then they were questioned further and asked if they had noticed the workspace rotation (and if so, then in which block).

### Data analysis

We used two measures to assess the accuracy and speed of performance in each block. As a measure of “accuracy,” we counted the number of trials before completing one block (i.e., 20 successful trials). To evaluate “speed,” we measured the time that had elapsed from the moment the home key was pressed to the moment the second

button of the final (10th) set was pressed for each successful trial and averaged the time recorded across 20 successful trials. These parameters were employed in our previous studies and had proved to be useful (Hikosaka et al. 1999, 2002). Note that the “speed” and “accuracy” defined in the 2×10 task are different from those in the Fitts’ law (speed–accuracy trade-off; Fitts 1954). This is because the 2×10 task concerns a sequential combination of discrete movements, whereas the Fitts’ law concerns speed and accuracy in a single motor action. In addition, the speed measure is based on successfully completed trials and the accuracy measure is based on uncompleted trials.

To clarify the improvement of the task performance, we defined transfer indices by normalizing the parameters for each subject. The accuracy and speed measures of the original hyperset [ $H^{\text{org}}$ ; e.g., H1 in the first session] were subtracted from those of the rotated hyperset [ $H^{\text{rot}}$ ; e.g., H1(90) in the second session]. Subsequently, this value was divided by the accuracy and speed measures with the original hyperset ( $H^{\text{org}}$ ; H1) and multiplied by 100. This transfer index [ $100 \times (H^{\text{rot}} - H^{\text{org}}) / H^{\text{org}}$ ] represents the percentage magnitude of the transfer of learning between different workspace orientations.

---

## Results

Data from two female and two male subjects were excluded due to a procedural failure that occurred during the experiment. Among the remaining 28 subjects, 14 reported that no rotation occurred during the experiment; they were therefore classified as the “unaware” group. The other 14 subjects noticed at least one workspace rotation during the experiment and were classified as the “aware” group. Most of the subjects in the aware group (12 subjects) detected the workspace rotation in the block in which the rotation was introduced for the first time. One subject in the aware group noticed the rotation when it was introduced for the second time; the remaining subject noticed it when it was introduced for the third time.<sup>1</sup> Interestingly, the male subjects noticed the workspace rotation (10 out of 16) more frequently than the female subjects (4 out of 12;  $\chi^2 = 6.13$ ,  $P < 0.05$ ).

A significant decrease was found in both the accuracy (the number of completion failures) and speed measures (averaged completion time for successful trials), irrespective of subject group (Fig. 1), indicating that learning did occur [ANOVA;  $F(19,243) > 22.35$ ;  $P < 0.01$  for both measures]. The accuracy measure decreased rapidly in the first few completed trials while the speed measure decreased more gradually. This result is in accordance with our previous studies (Hikosaka et al. 1995, 1996, 2002; Sakai et al. 1998, 2003). Figure 2 shows the accu-

racy and speed transfer indices, averaged across subjects. When the subjects performed hypersets for two sessions without rotation (i.e., 0° rotation), there was approximately a 50% transfer of the accuracy of performance and about a 10% transfer of the speed of performance. When the hypersets were rotated, the accuracy showed clear transfers in the aware group but not in the unaware group. In other words, the explicit knowledge of workspace rotation was useful in performing the task accurately in the rotated workspace, as compared to the case of the unaware group. In contrast, the speed of performance showed no transfer to the rotated hypersets—this was true for both the aware and the unaware groups. Statistical analyses supported these observations: for the accuracy transfer index, there were significant main effects of the rotation angle [ANOVA,  $F(3,78) = 6.01$ ,  $P < 0.01$ ] and the awareness of rotation [ $F(1,26) = 16.08$ ,  $P < 0.01$ ]. The interaction between these factors was also significant [ $F(3,78) = 4.21$ ,  $P < 0.01$ ]. For the speed transfer index, the main effect of the rotation angle was significant [ $F(3,78) = 11.81$ ,  $P < 0.01$ ] whereas the awareness of rotation had no effect [ $F(1,26) = 1.27$ ,  $P = 0.28$ ]. The interaction was not significant [ $F(3,78) = 1.30$ ,  $P = 0.28$ ]. Briefly, the awareness of workspace rotation helped the subjects perform the task with the rotated hypersets with less completion failures. Nonetheless, such explicit knowledge (knowing where to go) did not foster quick performance.

---

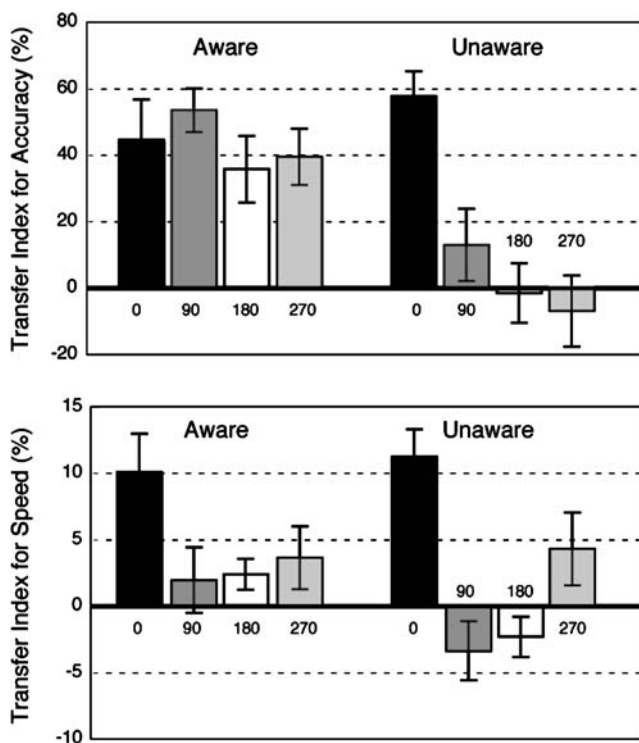
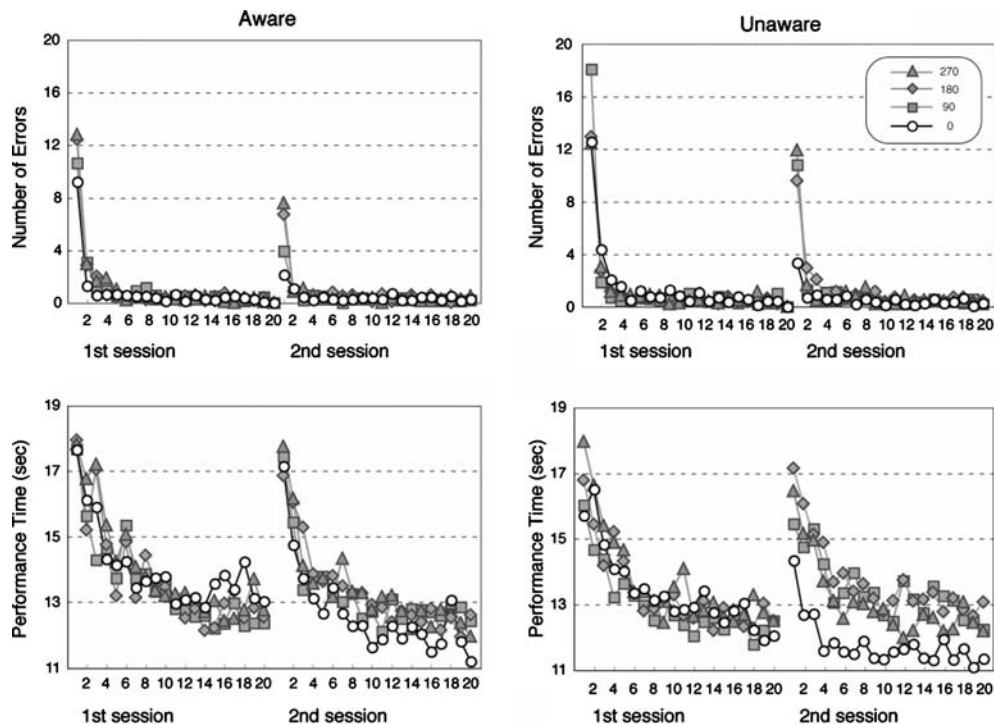
## Discussion

By using the 2×10 task, this study demonstrates the differential effects of the explicit knowledge of workspace rotation on the accuracy and speed measures in visuomotor sequence learning. When the subjects noticed a workspace rotation, they were able to use the explicit knowledge to perform the task with less completion failures even in the rotated workspace. This is not surprising because the 2×10 task is set up so that knowing where to go can only be known explicitly. Importantly, however, the awareness of the rotation did not lead to faster performance. In other words, knowing where to go does not necessarily speed up the sequential action. Giving a more familiar (though not completely accurate) example: assume that you are about to dial a phone number that you know well. You can dial it fast. Someone rotates the phone pad and you know it. You can still dial it correctly. Most likely, you would think you can dial (or learn to dial) the well-learned phone number faster than a new phone number. Actually, however, your speed of dialing for the well-learned but rotated phone number will be as slow as for your speed of dialing for a new phone number.

The evidence collected has suggested that the accuracy and speed performance in trial-and-error learning of visuomotor sequences are achieved by separate processes (Hikosaka et al. 2002). Therefore, the results of this study may be considered additional evidence for the parallel

<sup>1</sup> Reclassifying these two subjects as the unaware group did not change the results of our statistical analyses (with  $\alpha = 0.05$ ).

**Fig. 1** Averaged learning curves for the number of errors before the successful completion of 20 trials (accuracy measure: *top*) and the mean performance time for the successful trials (speed measure: *bottom*). The *left panels* represent the results of the aware group and the *right panels* show those of the unaware group



**Fig. 2** Averaged transfer indices for the accuracy (*top*) and speed measures (*bottom*), shown separately for the aware and unaware groups. *Vertical bars* = standard errors of mean. The awareness of workspace rotation (confirmed by accuracy transfer in the aware group; *left*) did not lead to a speed advantage in the rotated hyperset; the subjects who noticed the workspace rotation went as slow as the subjects who did not notice

neural network model of procedural learning (Nakahara et al. 2001). In the light of this model, one possible inter-

pretation is that the differential effects of explicit knowledge may be related to the differential time courses of the learning processes. With practice, the accuracy measure reaches a plateau of performance earlier than the speed measure (Hikosaka et al. 1995; Bapi et al. 2000). The parallel neural network model predicts that a sequence representation in visual coordinates (broadly reflected in the accuracy measure) may develop faster than one in motor coordinates (broadly reflected in the speed measure) while representations in both coordinates are learned concurrently (Nakahara et al. 2001), and several other studies have also supported this prediction (Clegg et al. 1998; Grafton et al. 1998; Bapi et al. 2000; Korman et al. 2003; Lehericy et al. 2005). However, this schema obviously oversimplifies the processes involved in the visuomotor sequence learning because the link between accuracy and visual representations and that between speed and motor representations are not straightforward. Complex visuomotor learning processes would contain some crosstalk between learning processes for accurate performance and that for speedy performance. Therefore, in different experimental conditions, it is possible that these measures and representations interact to produce the learning pattern in the  $2 \times 10$  task. Yet, the present experiment sets a good starting point for further investigations by demonstrating the case that explicit knowledge of where to go does not lead to a speed advantage.

#### Roles and effects of explicit knowledge in procedural learning

The role of explicit knowledge may differ for different paradigms of sequential learning. For example, the serial reaction time (SRT) task (Nissen and Bullemer 1987)



and the  $2 \times 10$  task are similar in that both include implicit learning process that leads to faster performance. However, spatial sequence is learned explicitly in the  $2 \times 10$  task (by trial and error; thus it is a form of instrumental learning), whereas the learning process of spatial sequence in the SRT task is implicit (although it is explicitly shown for each single movement). Hence, in the  $2 \times 10$  task, explicit knowledge of the sequence is critical for performing and proceeding the task (as in other learning paradigms that involve explicit instructions of sequences; Jueptner et al. 1997a, 1997b; Karni et al. 1995).

For certain types of procedural learning, including rotary movement pursuit and mirror tracing, explicit knowledge has little effect on the accuracy and/or speed performance (e.g., Heindel et al. 1989). In contrast, in the SRT task, it has been reported that explicit knowledge of the sequence leads to faster performance (Curran and Keele 1993; Willingham et al. 1989). The present experiment examined whether explicit knowledge of the sequence produces any speed advantage in the  $2 \times 10$  task (a form of instrumental sequential learning) and it proved false; the subjects who spontaneously noticed the rotation of workspace can successfully use the knowledge in the rotated workspace, nonetheless it does not lead to faster performance.

Having these influences of explicit knowledge of spatial sequences, it would be interesting to examine whether our findings might generalize to other types of sequence learning. For example, there is evidence for separate learning systems for spatial and non-spatial stimuli sequences; a sequence of locations can be learned independently of a sequence of stimuli defined by non-spatial feature (e.g., shape) (Mayr 1996; Helmuth et al. 2000). Interestingly, a sequence of non-spatial stimuli is more likely to be associated with explicit knowledge than a sequence of locations (Willingham et al. 1989; Mayr 1996; Koch and Hoffmann 2000). This may be because non-spatial learning depends more on response control processes, whereas spatial learning is more linked to the direct connection from input to output (Posner and Rothbart 1992), resulting in the spatial stimulus–response compatibility effect (Lu and Proctor 1995). A workspace rotation of spatial sequences could be regarded analogous to a change in surface (or stimulus) structure while keeping abstract (or rule) structure of non-spatial sequences (Dominey and Lelekov 1998). With further investigations, it might be possible to compare spatial and non-spatial sequence learning from a more general perspective of explicit knowledge and surface–abstract structure (Gomez 1997).

Possible sex difference in tolerance against workspace rotation

Interestingly, we found that our male subjects noticed the workspace rotation more often than female subjects. Mental rotation tests traditionally show a male performance advantage (Voyer et al. 1995). Therefore, the sub-

jects in the aware group noticed the workspace rotation because they might be better at performing mental rotation. Studies have suggested that visual mental rotation and visuomotor mental rotation may share the same, or at least overlapping, processes (e.g., Pellizzer and Georgopoulos 1993). Further research is required to examine whether mental rotation ability is related to individual differences of performance in detecting a rotation of visuomotor workspace.

---

### Concluding remark

The present study showed that, in the instrumental learning of visuomotor learning ( $2 \times 10$  task), there is the case that knowing where to go (in the rotated configuration) does not lead to a speed advantage, as compared to not knowing it. It would be fruitful to investigate whether this pattern of results is observed for other paradigms of sequential learning (e.g., the SRT task; Curran and Keele 1993; Willingham et al. 1989) and other changes in stimulus configuration (e.g., mirror reversal of workspace).

Functional brain imaging studies on human subjects have also revealed the differential involvement of brain areas in the early and late phases of procedural learning (e.g., presupplementary vs. supplementary motor areas, Hikosaka et al. 1996; dorsolateral prefrontal cortex and presupplementary vs. precuneus and intraparietal sulcus, Sakai et al. 1998; also see Toni et al. 1998; Petersen et al. 1998; Lehericy et al. 2005)<sup>2</sup> and in awareness-dependent and awareness-independent learning processes (e.g., prefrontal and premotor cortex vs. primary–secondary motor cortex, and sensorimotor cortex; Honda et al. 1998; Rauch et al. 1995; Grafton et al. 1995; 1998; Hazeltine et al. 1997; Willingham et al. 2001; Sakai et al. 1998). The present experimental paradigm can be used in human neuroimaging studies to explore possible interactions between differential involvements of awareness and differential time courses in the accuracy and speed of performance during visuomotor sequence learning.

---

### References

- Bapi RS, Doya K, Harner AM (2000) Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. *Exp Brain Res* 132:149–162
- Clegg BA, DiGirolamo GJ, Keele SW (1998) Sequence learning. *Trends Cogn Sci* 2:275–281

<sup>2</sup> It is important to note that the present study focused on the later stage of the  $2 \times 10$  task; the speed measure is based on successfully completed trials. The dependency on the initial stage of learning is an important issue because it is likely that the effect of explicit knowledge on accuracy measure would be most pronounced in the initial stage of learning. However, in the present set of the data, the variances among subjects and sessions were very large, and we did not find a consistent pattern.

- Curran T, Keele SW (1993) Attentional and nonattentional forms of sequence learning. *J Exp Psychol Learn Mem Cogn* 19:189–202
- Dominey PF, Lelekov TS (1998) Dissociable processes for learning the surface structure and abstract structure of sensorimotor sequences. *J Cogn Neurosci* 10:734–775
- Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 47:381–391
- Gomez RL (1997) Transfer and complexity in artificial grammar learning. *Cogn Psychol* 33:154–207
- Grafton ST, Hazeltine E, Ivry R (1995) Functional anatomy of sequence learning in normal humans. *J Cogn Neurosci* 7:497–510
- Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and effector-specific representations of motor sequences identified with PET. *J Neurosci* 18:9420–9428
- Hazeltine E, Grafton ST, Ivry R (1997) Attention and stimulus characteristics determine the locus of motor-sequence encoding: a PET study. *Brain* 120:123–140
- Heindel WC, Salmon DP, Shults CW, Walicke PA, Butters N (1989) Neuropsychological evidence for multiple implicit memory systems: a comparison of Alzheimer's, Huntington's, and Parkinson's disease patients. *J Neurosci* 9:582–587
- Helmuth LL, Mayr U, Daum I (2000) Sequence learning in Parkinson's disease: a comparison of spatial attention and number-response sequence. *Neuropsychologia* 38:1143–1451
- Hikosaka O, Rand MK, Miyachi S, Miyashita K (1995) Learning of sequential movements in the monkey: process of learning and retention of memory. *J Neurophysiol* 74:1652–1661
- Hikosaka O, Sakai K, Miyauchi S, Takino R, Sasaki Y, Pütz B (1996) Activation of human presupplementary motor area in learning of sequential procedures: a functional MRI study. *J Neurophysiol* 76:617–621
- Hikosaka O, Nakahara H, Rand MK, Sakai K, Lu X, Nakamura K, Miyachi S, Doya K (1999) Parallel neural networks for learning sequential procedures. *Trends Neurosci* 22:464–471
- Hikosaka O, Nakamura K, Sakai K, Nakahara H (2002) Central mechanisms of motor skill learning. *Curr Opin Neurobiol* 12:217–222
- Honda M, Deiber M-P, Ibanez V, Pascual-Leone A, Zhuang P, Hallett M (1998) Dynamic cortical involvement in implicit and explicit motor sequence learning: a PET study. *Brain* 121:2159–2173
- Jueptner M, Stephan K, Frith C, Brooks D, Frackowiak R, Passingham R (1997a) The anatomy of motor learning. I. Frontal cortex and attention to action. *J Neurophysiol* 77:1313–1324
- Jueptner M, Stephan K, Frith C, Brooks D, Frackowiak R, Passingham R (1997b) The anatomy of motor learning. II. Subcortical structures and learning by trial and error. *J Neurophysiol* 3:1325–1337
- Karni A, Meyer G, Jezzard P, Adams MM, Turner R, Ungerleider LG (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377:155–158
- Koch I, Hoffmann J (2000) The role of stimulus-based and response-based spatial information in sequence learning. *J Exp Psychol Learn Mem Cogn* 26:863–882
- Korman M, Raz N, Flash T, Karni A (2003) Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proc Natl Acad Sci USA* 100:12492–12497
- Lehericy S, Benali H, Van de Moortele PF, Pelegrini-Issac M, Waechter T, Ugurbil K, Doyon J (2005) Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. *Proc Natl Acad Sci USA* 102:12566–12571
- Lu CH, Proctor RW (1995) The influence of irrelevant location information on performance: a review of the Simon and spatial Stroop effects. *Psychon Bull Rev* 2:174–207
- Mayr U (1996) Spatial attention and implicit learning: evidence for independent learning of spatial and non-spatial sequences. *J Exp Psychol Learn Mem Cogn* 22:350–364
- Nakahara H, Doya K, Hikosaka O (2001) Parallel cortico-basal ganglia mechanisms for acquisition and execution of visuomotor sequences: a computational approach. *J Cogn Neurosci* 13:626–647
- Nissen MJ, Bullemer P (1987) Attentional requirements of learning: evidence from performance measures. *Cogn Psychol* 19:1–32
- Pellizzer G, Georgopoulos AP (1993) Common processing constraints for visuomotor and visual mental rotations. *Exp Brain Res* 93:165–172
- Petersen SE, Van Mier H, Fiez JA, Raichle ME (1998) The effect of practice on the functional anatomy of task performance. *Proc Natl Acad Sci USA* 95:853–860
- Posner MI, Rothbart M (1992) Attentional mechanisms and consciousness experience. In: Milner AD, Rugg MD (eds) *The neuropsychology of consciousness*. Academic, San Diego, pp 91–111
- Rand MK, Hikosaka O, Miyachi S, Lu X, Miyashita K (1998) Characteristics of a long-term procedural skill in the monkey. *Exp Brain Res* 118:293–297
- Rauch SL, Savage CR, Brown HD, Curran T, Alpert NM, Kendrick A, Fischman AJ, Kosslyn SM (1995) A PET investigation of implicit and explicit sequence learning. *Hum Brain Mapp* 3:271–286
- Sakai K, Hikosaka O, Miyachi S, Takino R, Sasaki Y, Pütz B (1998) Transition of brain activation from frontal to parietal areas in visuomotor sequence learning. *J Neurosci* 18:1877–1840
- Sakai K, Kitaguchi K, Hikosaka O (2003) Chunking during human visuomotor learning. *Exp Brain Res* 152:229–242
- Toni I, Krams M, Turner R, Passingham RE (1998) The time course of changes during motor sequence learning: a whole-brain fMRI study. *Neuroimage* 8:50–61
- Voyer D, Voyer S, Bryden MP (1995) Magnitude of sex-differences in spatial abilities: a metaanalysis and consideration of critical variables. *Psychol Bull* 117:250–270
- Willingham DB (1998) A neuropsychological theory of motor skill learning. *Psychol Rev* 105:558–584
- Willingham DB, Nissen MJ, Bullemer P (1989) On the development of procedural knowledge. *J Exp Psychol Learn Mem Cogn* 15:1047–1060
- Willingham D, Slidis J, Gabrieli J (2001) Direct comparison of neural systems mediating conscious and unconscious skill learning. *J Neurophysiol* 10:1451–1460