WORKING MEMORY AND ACQUISITION OF IMPLICIT KNOWLEDGE BY IMAGERY TRAINING, WITHOUT ACTUAL TASK PERFORMANCE

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Abstract—This study investigated acquisition of a mirrorreading skill via imagery training, without the actual performance of a mirror-reading task. In experiment I, healthy volunteers simulated writing on an imaginary, transparent screen placed at eye level, which could be read by an experimenter facing the subject. Performance of this irrelevant motor task required the subject to imagine the letters inverted, as if seen in a mirror from their own point of view (imagery training). A second group performed the same imagery training interspersed with a complex, secondary spelling and counting task. A third, control, group simply wrote the words as they would normally appear from their own point of view. After training with 300 words, all subjects were tested in a mirror-reading task using 60 non-words, constructed according to acceptable letter combinations of the Portuguese language. Compared with control subjects, those exposed to imagery training, including those who switched between imagery and the complex task, exhibited shorter reading times in the mirror-reading task. Experiment II employed a 2×3 design, including two training conditions (imagery and actual mirror-reading) and three competing task conditions (a spelling and counting switching task, a visual working memory concurrent task, and no concurrent task). Training sessions were interspersed with mirror-reading testing sessions for non-words, allowing evaluation of the mirror-reading acquisition process during training. The subjects exposed to imagery training acquired the mirror-reading skill as quickly as those exposed to the actual mirror-reading task. Further, performance of concurrent tasks together with actual mirror-reading training severely disrupted mirror-reading skill acquisition; this interference effect was not seen in subjects exposed to imagery training and performance of the switching and the concurrent tasks. These results unequivocally show that acquisition of implicit skills by top-down imagery training is at least as efficient as bottom-up acquisition. © 2005 Published by Elsevier Ltd on behalf of IBRO.

Key words: mental practice, attention, supervisory attentional system, skills, procedural memory, central executive.

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Abbreviations: A, actual mirror-reading training; ANOVA, analysis of variance; A-SC, actual mirror-reading and spelling and counting complex task; A-VS, actual mirror-reading and visuo-spatial attention deviation; C, control; I, imagery; I-SC, imagery and spelling and counting complex task; I-VS, imagery and visuo-spatial working memory task; SAS, supervisory attentional system; SC, complex spelling and counting; VS, visuo-spatial.

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Baddeley and Hitch (1974) proposed a working memory model to describe the temporary maintenance and manipulation of information in memory. This model and its dissociable sub-components were supported by a large body of experimental evidence obtained from normal, healthy volunteers performing dual-tasks. The subjects performed a main task, concurrently with a secondary task; the greater the similarities between the two tasks, and presumably of the underlying processing resources, the greater the interference on performance. This approach allowed the fractioning of working memory into three major components (see Baddeley, 1986, 1992). The phonological loop, specialized in verbal material, comprises a storage buffer capable of holding phonological information for one or two seconds, coupled with an articulatory control process responsible for refreshing the stored information by sub-vocal, "internal" speech. The visuo-spatial (VS) sketchpad, specialized in maintaining visual-spatial material, seems to entail a component involved with color and shape, and another dealing with location. The central executive component, specified as relying on the supervisory attentional system (SAS) component, as described in Norman and Shallice's (1980) model for attentional control of action (see Shallice, 1988), is required for performance of less routine tasks dealing with novelty, decision making, resisting temptation, or dealing with danger; it is also involved in producing willed actions. The dorsal-lateral portions of the frontal cortex are considered to underlie SAS functions (Baddeley, 1986; Berman, 1995; Cowey and Green, 1996; D'Esposito et al., 1995; Fuster, 1984; Petrides et al., 1993; Roland, 1984).

Working memory is considered critical for performing a variety of cognitive functions, including reasoning, problem solving, language understanding and imagery (Baddeley, 1986, 1992; Just and Carpenter, 1992; Malouin et al., 2004).

Long-term memory may be divided into explicit (or declarative) knowledge of facts and events, expressed by the deliberate recollection of information, and implicit (or procedural) knowledge, which is expressed as improved performance in previously trained tasks, including perceptual and motor skills, habits and priming, without the need for conscious recollection of prior exposure to such tasks (Squire and Zola-Morgan, 1991).

Imagery

Imagery corresponds to a dynamic state in which representations of perceptions or actions, including those stored in long-term memory, are reactivated, maintained and manipulated within working memory, without the actual occurrence of sensory stimulation or of observable motor performance.

Neuro-imaging (Goldenberg et al., 1989; Le Bihan et al., 1993; Roland and Gulyas, 1995; Ishai and Sagi, 1995; Kosslyn et al., 1999a,b; Klein et al., 2000; Lambert et al., 2002) and electrophysiological studies (Farah et al., 1988) have shown that visual imagery and visual perception share functional similarities. For instance, the enactment of visual imagery, like visual perception, is associated with activation of the occipitoparietal and occipitotemporal visual association regions (Roland and Gulyas, 1995; Mellet et al., 1995; D'Esposito et al., 1997) and the primary visual cortex (Le Bihan et al., 1993; Kosslyn et al., 1999a; Klein et al., 2000; Lambert et al., 2002), suggesting that generation of visual images involves representations associated with these brain regions. Further, part of the network underlying imagery includes the prefrontal and the anterior cingulate cortex (Decety et al., 1992), brain regions that are also involved in working memory and attention (Roland, 1984; Smith and Jonides, 1995).

Most studies of imagery involve mental practice aiming at motor learning (Yaguez et al., 1998). Decety (1996) showed that imagined and executed actions share neural mechanisms in part. Vogt (1996) analyzed mediation of perception-action, showing that the representational basis for motor control is already formed during model observation. Mental practice involves repeated motor imagery, i.e. covert rehearsal of motor performance in the absence of observable movement, and improves motor performance (e.g. Vandell et al., 1943; Twining, 1949; Clark, 1960; Feltz and Landers, 1983; Denis, 1985; Decety, 1996; Yaguez et al., 1998). These abilities, usually classified as implicit knowledge, are apparently linked to specific processing structures and procedures engaged by learning the tasks, and requiring gradual, cumulative modifications of these elements, expressed as the facilitated performance of the skill rather than a detailed verbal report of the procedures involved (Cohen, 1984). The acquisition of motor skills may thus include learned connections between stimuli and responses (e.g. Tulving, 1985).

On discussing skill acquisition by mental practice, Denis (1985) noted that ". . . we are confronted with what may legitimately be considered 'paradoxical' effects, in that a mental activity which apparently does not involve motor effectors in a direct way nevertheless has a significant, measurable impact on later motor performance" (p. 7). This statement underscores a critical issue related to acquisition of implicit knowledge by imagery training: can it be accounted for purely in terms of top-down-induced changes in the central structures involved in skill acquisition by way of their active manipulation in working memory, or does it require some form of bottom-up peripheral feedback? Electrophysiological recordings demonstrate subliminal activation of neuromuscular units during imagined movement (Jacobson, 1932; Shaw, 1940) with vivid imagery leading to higher levels of subliminal muscular activation (Shaw, 1940); such activation is sufficient to generate kinesthetic stimulation capable of providing feedback corresponding to the actual movement (Feltz and Landers,

1983; Johnson, 1982; Kohl and Roenker, 1983). These findings favor the notion that bottom-up processes contribute to acquisition via motor imagery. However, Kohl and Roenker (1980; 1983) showed that, to a certain extent, the performance improvement that follows from motor imagery involving one limb may be transferable to the contralateral limb. Further, interference of motor imaging on actual, future performance may be inhibited by the introduction of a visually distracting task during imagery enactment (Johnson, 1982). Interpretation of these findings in terms of proprioceptive feedback is difficult; they favor the notion that cognitive operations generated during imagery enactment, in a top-down fashion, contribute to the actual performance of the task. The nature of this contribution is not clear: imagery may help develop motor programs used in future task performance.

The present investigation aimed to evaluate the hvpothesis that imagery training leads to acquisition of implicit knowledge via top-down processes. We examined to what extent an automatic perceptual skill can be acquired, i.e. mirror-reading, considered a typical example of implicit perceptual knowledge (see Cohen, 1984), by means of imagery enactment alone, without visual feedback that might contribute to such acquisition. The effect of visual imagery training with inverted letters embedded in an irrelevant motor task on the later performance of a mirrorreading task was assessed in a group of healthy volunteers. Further, considering the critical involvement of working memory in imagery, and given that it relies on limited capacity resources (Baddeley, 1986), we also examined the impact of switching and of concurrent tasks on acquisition of this perceptual skill via imagery. The choice of a perceptual skill task, as opposed to a motor skill task, derives from its potential for controlling peripheral visual feedback associated with the imagery, thus revealing skill acquisition via top-down processes.

Experiment I. Acquisition of implicit knowledge by extensive imagery training and impact of a concurrent task

This experiment included two separate phases: (1) an imagery training phase in which subjects imagined each letter of individually presented, correctly written, sevenletter words; and (2) an actual mirror-reading test, involving non-words. To assure that during imagery training the subjects did imagine the letters as being inverted (i.e. as if seen in a mirror), they performed an irrelevant motor task, the outcome of which depended on that imagery. Thus, the subjects simulated the actual motion of writing the imagined letters on an imaginary, transparent screen held at the eye level, such that the experimenter facing the subject would be able to read; this task was performed with the eyes closed, and visual feedback from the hand movements was thus avoided (this procedure will be termed "simulation"). The outcome of the imagery training was evaluated in a separate, actual mirror-reading (perceptual skill) task.

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EXPERIMENTAL PROCEDURES

Subjects

The study group consisted of 30, healthy, right-handed, undergraduate biology students (15 men and 15 women), enrolled at the University of São Paulo. Subjects were aged between 19 and 27 years (23.1 ± 2.2), had normal or corrected vision, and had no prior experience in mirror-reading. All students voluntarily provided informed consent forms to participate in the study. The procedures were approved by the Ethics Committee of the Biomedical Institute of the University of São Paulo.

The volunteers were assigned to three groups of 10 subjects each, matched by age, gender and education level.

Training

Subjects were seated individually in front of a computer screen positioned 57-cm distant at eye level. Seven-letter, Portuguese words, formatted as 3×4-cm Courier font small capitals, were individually presented on the computer screen. Subjects were previously instructed to close their eyes after cache reading and to perform the simulation. Thus, they imagined the letters as being inverted, as if seen through a mirror from their own point of view (imagery training). Keeping their eyes closed assured that the volunteers did not receive visual feedback during performance of the inverted-letter imagery task (Group I). Accompanying their performance, the experimenter confirmed that each letter was imaged correctly, and assured that the subjects were committed to the imagery training. The subjects in the "imagery and switching attention" group proceeded like Group I; however, they also had to alternate imagery with a spelling and counting task (SC), involving stating aloud, after writing each single letter, the number of vowels and consonants already written for the specific word (Group I-SC). The control subjects were instructed to close their eyes after cache reading and simulate the motion of writing the word simply as it would normally appear to them from their own point of view (Group C).

Subjects simulated writing 100 words per day for three consecutive days, totaling 300 words) (see Table 1).

The time taken between the presentation of each word on the computer screen and the end of the simulation was recorded (writing time).

Testing

Shortly after the third day of training, testing began. During the actual mirror-reading test, the subjects individually read mirrored non-words constructed according to acceptable letter combinations in Portuguese language. Since the Portuguese language has a transparent orthography, non-words that follow the orthographic rules may be read directly. Sixty, seven-letter, non-words were used (see Table 1). Non-words were chosen for this phase to render the task more difficult. Subjects read each non-word as quickly and correctly as possible. The time from the presentation of an inverted non-word to the end of reading was recorded (reading time).

 Table 1. Number and type of stimuli used during three training sessions, one per day, and in a subsequent testing session, run immediately after training on the third day

Day	Training			Testing
	First	Second	Third	Third
Number of stimuli Stimulus type	100 Words	100 Words	100 Words	60 Non-words

Statistics

Data are expressed as writing time values (mean±S.E.M.) in five blocks of 20 words for each day of training, over three days, and of reading time values in blocks of 10 non-words tested. The results were analyzed using a repeated measures analysis of variance (ANOVA) with "Group" as the "between subjects" factor, and "days" and "blocks" as the "within subjects" factors. Post hoc analysis included the Tukey honest significant differences test.

RESULTS

Training

Fig. 1 shows the latency for the simulation over 3 days of training. ANOVA revealed significant Group (F2,27=14.74, P<0.0001), Days (F2,54=137.68, P<0.0001) and Blocks (F4,108=78.16, P<0.0001) effects, and Group vs Days (F4,54=10.27, P<0.0001), Groups vs Blocks (F8,108= 6.51, P<0.0001), Days vs Blocks (F8,216=36.17, P< 0.0001) and Groups vs Days vs Blocks (F16,216=6.5, P<0.0001) interaction effects. Post hoc comparisons revealed that the scores for Groups I (imagery) and I-SC differed (Group effect, F1,18=9.24, P<0.01) but paralleled each other throughout training [Group vs Day (F2,26= 0.81, P>0.40), Group vs Block (F4,72=0.60, P>0.65) and Group vs Day vs Block (F8,144=0.70, P>0.68) interaction effects], showing that although the Group I-SC subjects performed a concurrent task, which led to a substantial increase in writing times, their acquisition rate for the ability to simulate writing inverted words was not disrupted. Further, the scores of both Groups I and I-SC were significantly longer than those for Group C, particularly in the early stages of task acquisition. This suggests that (1) previous writing experience promptly transfers to the task of simulating writing on a imaginary, transparent screen and benefits its performance (see Fig. 1, Group C scores); and (2) the use of inverted-letter imagery to simulate writing demands more time, particularly in the early stages of task acquisition, reflecting these subjects lack of experience with this task; however, as training proceeded, the Groups I and I-SC subjects improved substantially, indicating task acquisition. Interestingly, post hoc analysis also revealed that the performance of the Group I did not differ significantly from that of Group C over all five blocks for day 3 (F1,18=2.41, P>0.10); these findings suggest that although Group I subjects had to invert letters through imagery to perform the inverted writing task, while Group C subjects simply simulated ordinary writing, both groups achieved the same level of performance. Group I-SC exhibited the longest training latencies. In addition to simulating writing through visualization of inverted letters, subjects in this group performed the additional task of stating aloud, after writing each letter, the number of vowels and consonants already written.

Note that Group I reached a level of performance equivalent to Group C by the end of the training phase (Fig. 1); this shows that the Group I subjects reached a proficient and asymptotic level of performance, having mastered inverted-letter imagery for simulating writing. Further, although Group I-SC subjects switched between the per-

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Fig. 1. Mean (\pm S.E.M.) writing times per word (in seconds) for imagery and simulation of writing inverted words (Groups I and I-SC) or as used normally (Group C), over a 3-day training period, each day comprising five blocks of 20 words, for all groups in experiment I.

formance of a spelling and counting task and imagery of inverted letters and writing simulation, and thus exhibited longer writing times (Fig. 1), their acquisition rate was similar to that of Group I. This shows that the attention deviation imposed by this task did not interfere with acquisition of the ability to imagine inverted letters so as to simulate their writing.

Testing

Subjects were individually tested in an actual mirror-reading task. Fig. 2 shows the mean reading times per non-word exhibited by Groups C, I and I-SC over six blocks of 10 non-words each. ANOVA revealed significant Group (F2,27=5.61, P<0.01) and Blocks (F2,135=10.39, P< 0.0001) effects, and a significant Group vs Block interaction effect (F10,135=2.57, P<0.01). Post hoc comparisons revealed that while Groups I and I-SC did not differ significantly (F1,18=0.02, P=0.95), both differed significantly from Group C (F1,18=9.13, P<0.01). Fig. 2 reveals that the reading times for Group C in the early stages of testing were substantially longer than those of Groups I and I-SC. Further, as testing proceeded, reading time decreased markedly in Group C, but not in Groups I and I-SC. These findings indicate that while Group C was acquiring the mirror-reading task during the testing phase, Groups I and I-SC had already acquired it previously to a markedly higher level of performance, during imagery training. This was the first mirror-reading experience for all subjects; their only experience with inverted letters was not real but had occurred during imagery training. Also, the asymptotic

level of performance achieved by Group C at the end of mirror-reading testing corresponded to the level of performance achieved by Groups I and I-SC during the first block of this test (Fig. 2). Together, these results show that imagery training with inverted letters leads to acquisition of the ability to mirror-read, and that attention deviation, as imposed by the switching task used here did not interfere with this acquisition.

DISCUSSION

The present finding show that inverted-letter imagery training leads subjects to a high proficiency level in a mirrorreading task not previously experienced. Thus, repetitive manipulation of information in working memory to imagine inverted letters, without visual sensory feedback, leads to top-down-induced modifications in brain mechanisms usually modified by bottom-up repetitive training such as occurs in implicit memory tasks; these changes underlie a proficient performance in the mirror-reading task.

This study used an irrelevant motor task to stimulate the subjects to perform the inverted-letter imagery; this task was performed with closed eyes to prevent subjects from receiving visual feedback from their own simulated "drawing" of the letters. Thus, the possibility that any improvement achieved by the subjects is related to bottom-up visual processes can be discarded.

The actual simulation of the motion of writing letters in an inverted fashion could have contributed to the perceptual skill acquisition because of the somatosensory feed-

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Fig. 2. Mean (±S.E.M.) mirror-reading times per non-word (in seconds) over six blocks of 10 non-words each for groups exposed to imagery and simulation of inverted writing in the training phase of experiment I.

back provided. This would corroborate observations by Amedi et al., (2002) showing that a region within the lateral occipital complex is preferentially activated by both visual and haptic presentations of objects, revealing that vision and touch share shape representations. However, it is questionable whether the sensorimotor feedback from to the movements of drawing inverted letters might have provided any relevant, specific information to the visual system to aid in the acquisition of the mirror-reading task, such as occurs when haptic and (object) visual stimulation are involved. When simulating writing inverted letters, hand movement was linear and continuous, including the space where no imaginary line was drawn in both (1) the transition between one line and the next within a given letter, and (2) in the transition between letters. Sensorimotor feedback included both movements related to the imaginary drawing of the lines that composed a given letter, interspersed with movements associated with the transition between "empty" spaces where no imaginary lines were drawn. Thus, it seems unlikely that this somatosensory feedback could have provided information sufficiently specific to the visual system to assist in the mirror-reading task. Further, many volunteers reported that the only way they could perform the required motor task was to visually imagine the inverted letters, lending support to the interpretation that, to perform the required irrelevant motor task, the subjects depended on visually imagined inverted letters.

During imaging and simulation of the motion of writing inverted letters, the subjects may also have exhibited a corresponding pattern of eye movements; this could help later with the mirror-reading task. In some subjects, we observed movements of the eyes beneath the eyelids, which apparently followed the hand movements. Specific measurements would be required to evaluate to what extent such eye movements followed the hand movements either (1) over their linear and continuous trajectory, or (2) only during the movements related to the imaginary lines corresponding to the letter-drawing but not during the movements corresponding to the empty space where no imaginary line was drawn (see above). However, letter identification by subjects having frequent reading habits, including the university students participating in this study, is most likely holistic processing (see Pelli et al., 2003). Thus, continuous patterns of eye movement possibly learned during imagery training may be of no help for mirror-reading. However, as emphasized by Pelli et al. (2003), holistic processing seems to occur only with extensively exposed materials. Further experiments are necessary to evaluate this hypothesis.

The results of the current experiment support the hypothesis that the acquisition of the mirror-reading skill occurred via top-down processes. That is, manipulation of information in working memory was effective in promoting brain changes which apparently correspond to those resulting in the acquisition of implicit knowledge via repetitive actual practice.

Imagery training requires that subjects maintain and manipulate visual information in their working memory. Thus, impairment or interference in working memory may disrupt the ability to engage successfully in imaging, and interfere with skill acquisition (Malouin et al., 2004). Subjects in the I-SC condition switched between the performances of two tasks. The parallel learning curves for Group I show that these subjects exhibited similar improvements during imagery training, independently of ex-

posure to the double-task condition (Fig. 1). This shows that exposure to a switching task condition interfered with performance but not with acquisition of the ability to imagine inverted letters and to simulate their writing.

Test scores for I-SC subjects were similar to those for the I condition subjects. This suggests that the type of attention deviation imposed by the switching task was not effective in interfering with the acquisition of implicit knowledge by imagery training (see below).

Such interference may have occurred, but was masked by the extensive imagery training. That is, imagery training involved 300, seven-letter words, and thus a total of 2100 letters. The subjects in the control group achieved an asymptotic level of mirror-reading performance after about 40, seven-letter, non-words (Fig. 2), i.e. after reading about 280 inverted letters. Even though the acquisition rates by imagery and actual performance may differ, limiting this comparison, these findings suggest that if the degree of imagery training had been less, an interference effect may have been revealed during testing. The shorter mirrorreading times in the groups subjected to imagery training compared with Group C support this hypothesis. A further explanation for the lack of interference by the spelling and counting task concerns its nature. Previous studies on working memory sub-components reveal that, the greater the similarities between the main and the concurrent tasks (and presumably of their underlying processing resources) the greater the interference on performance. In contrast, when the concurrent tasks involve distinct processing resources, interference is absent (see Baddeley, 1986, 1992). While the main task in the present experiment involved inverted-letter imagery and writing simulation, the spelling and counting task involved stating aloud the number of vowels and consonants already written after writing each single letter. The underlying processing resources involved in these functions may be different, with the VS sketchpad processing the main task, and the phonological loop processing the concurrent task; this may explain the lack of interference by the concurrent task. However, the present data do not allow evaluation of this hypothesis.

Experiment II was designed to evaluate these possibilities.

Experiment II. Testing acquisition of implicit knowledge through imagery training, and the impact of concurrent task performance involving spelling and counting or visual working memory

Experiment I shows the performance of a mirror-reading task not previously experienced. Surprisingly, performance of a distracting task did not seem to interfere with acquisition of implicit knowledge via imagery. Several tentative hypotheses can be raised to explain this unexpected result. First, the interference effect may have been masked by the substantial degree of imagery training. Second, the concurrent task demanded processing resources not engaged in performance of the visual imagery task, avoiding competition for limited capacity resources. Third, the spelling and counting task was not an actual concurrent task since subjects could switch between imagery and this task.

The present experiment addresses these possibilities. The testing sessions were interspersed with training sessions to continuously monitor the acquisition process, thus eliminating the risk that a possible interference effect might go undetected by the amount of training. Further, the dualtask approach was employed to evaluate the effect of attention deviation on the acquisition of implicit knowledge either by imagery or by actual training. The concurrent tasks included (1) performance in a modified version of the Brooks matrix (adapted from Phillips and Christie, 1977) aimed at producing VS attention deviation, and (2) the spelling and counting task used in experiment I. An additional control group not exposed to any concurrent task was included. The effectiveness of these procedures in promoting attention deviation was additionally investigated by asking the subjects to perform a free recall test and a recognition test for the words used during either the imagery or the actual mirror-reading training (depending on the group). Since attention plays a critical role in the acquisition of declarative memory (Moray, 1959; Norman, 1969; Glucksberg and Cowan, 1970), it was expected that subjects performing concurrent tasks would exhibit an inferior performance compared with their corresponding controls not subjected to a concurrent task.

EXPERIMENTAL PROCEDURES

Subjects

Forty-eight, normal, right-handed, undergraduate biology students (21 men and 27 women) enrolled at the University of São Paulo participated in this study. Subjects were aged between 21 and 35 years old (24.3 ± 3.1 years), had normal or corrected vision, and no previous experience in mirror-reading. All students provided voluntary, informed consent to participate in the study. The procedures were approved by the Ethics Committee of the Biomedical Institute of the University of São Paulo.

The volunteers were assigned to six groups of eight subjects each, matched for age, gender and educational level, and submitted to a one-day experiment.

Training and testing

The equipment, and training and testing conditions were similar to those described in experiment I.

A 2×3 design, involving two training conditions (imagery×actual training) and three concurrent-task conditions (VS×spelling and counting×no concurrent task; see below) was used, resulting in six independent groups, with eight volunteers each.

The imagery training was similar to that used in experiment I. The actual performance of the mirror-reading task involved the individual presentation of inverted seven-letter words, as if seen through a mirror, on a computer screen; the subject's task was to read them as quickly and correctly as possible. The time spent by the subjects to perform these tasks for each word was recorded (training time per word).

Two groups, one subjected to imagery training (Group I) and the other subjected to the actual mirror-reading task (Group A), included subjects not exposed to a concurrent task. The remaining four groups were trained using the dual-task technique. The VS concurrent task involved performance in a modified version of the Brooks matrix (see Phillips and Christie, 1977). In short, a 3×3 array with five of its cells containing a black circle was presented for 3 s before the presentation of each single training word (information matrix). After training with a specific word, the subjects

were asked to indicate, on a new 3×3 array, which of two black circles had changed to a new array location (comparison matrix). The accuracy of this response provided an index for this VS working memory task; thus, it was also possible to evaluate whether concurrent performance of the visual imagery task performed in this study caused greater interference compared with the concurrent performance of actual mirror-reading, as predicted by the working memory model. Different pairs of information and comparison matrixes were used for each training word. The subjects were previously informed that they should execute the visual working memory task as accurately as possible. The task was performed by two groups, one concurrently with imagery training (Group I-VS) and the other concurrently with actual training (Group A-VS). The number of correct matrix identifications was also recorded to evaluate whether imagery of the actual training interfered with performance of this visual, working memory task. The concurrent spelling and counting task required the subjects to state aloud, the number of vowels and consonants already written for that specific word, after (1) simulation of writing each syllable for the group subjected to imagery training (Group I-SC), or (2) reading each syllable aloud for the group subjected to actual training (Group A-SC). Thus, this task was performed by two groups, one concurrently with imagery training (Group I-SC) and the other concurrently with actual training (Group A-SC).

Testing sessions were interspersed with training sessions allowing the acquisition process to be accompanied. Eight testing sessions, each involving the mirror-reading of three, 12-letter, non-words, were interspersed with seven training sessions of either imagery or actual training (according to the group), each involving 12, seven-letter, words. Thus, performance in testing sessions revealed the acquisition of the mirror-reading skill throughout the training process, allowing detection of possible interference effects that might otherwise pass undetected (see experiment I).

The time taken from the presentation of each word until it was completely written (by the imagery groups), or read (by the actual mirror-reading training groups) in the training sessions corresponded to the training time. The time spent from the presentation of the mirrored non-word until it was read in the testing sessions corresponded to the reading times.

Free recall

Immediately after the last testing session, without prior notice, the subjects were asked to freely recall and write down as many words as possible seen during training, for 5 min. The number of recalled words was used to express performance in this task.

Recognition test

Soon after the free recall test, the subjects received a printed list of 60, seven-letter words; 30 of these words had been presented during training; the remaining 30 words were new and had not been used during training. The previously presented words and the new words were randomly combined. Subjects were asked to indicate which words had or had not been presented during training. The number of correctly indicated words was used to express performance in this task.

Statistics

Data are expressed as the mean (\pm S.E.M.) values of (1) training time in seven blocks of words; (2) reading time in eight blocks of non-words; (3) number of words correctly recalled; and (4) number of words correctly recognized. The results were compared using a two-way repeated measures ANOVA having "training condition" as one factor (actual vs imagery training) and "concurrent task" as the other factor (phonological vs VS vs no concurrent task), and "blocks" as the "within subjects" factor.

RESULTS

Training

Fig. 3 shows the time spent by independent groups of subjects to perform either imagery or actual training (1) without a concurrent task (left panel), (2) with a spelling and counting task (middle panel) or (3) with a VS concurrent task (right panel), for seven blocks of 12 seven-letter words. ANOVA revealed significant training condition (imagery vs actual training) (F1,42=59.64, P<0.0001), concur-



Fig. 3. Mean (\pm S.E.M.) training time per word (in seconds) for six groups trained according to a 2×3 design, consisting of two training conditions (I and A) combined with three, concurrent task conditions (SC, VS working memory or no concurrent task), over seven blocks of 12 words each, in experiment II.

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Fig. 4. Mean (\pm S.E.M.) mirror-reading time per non-word (in seconds) for six groups trained according to a 2×3 design, consisting of two training conditions (I and A) combined with three, concurrent task conditions SC), VS working memory or no concurrent task), over eight blocks of three non-words each in experiment II.

rent-task condition (SC vs VS vs NO) (F2,42=39.112, P<0.0001) and block (F6,252=81.14, P<0.0001) effects, and training condition vs block (F6,252=15.44, P<0.0001), concurrent-task condition vs block (F12,252=4.28, P<0.0001) and training condition vs concurrent-task condition vs block (F12,252=3,78, P<0.0001) interaction effects.

Fig. 3 shows that the time spent by the subjects submitted to imagery training was longer than the corresponding scores of the subjects submitted to actual training, suggesting that the imagery task was more difficult to perform than the actual mirror-reading task. The data also show that the concurrent performance of a distracting task (either spelling and counting or VS) leads to an additional increase in both imagery and actual training time (Fig. 3, middle and right panels). This effect was particularly pronounced for the subjects performing the spelling and counting task (Fig. 3, middle panel), possibly because switching is time consuming. Conversely, the VS concurrent task involved the presentation of a matrix before the word to be used in training, with later identification of the change, after the end of training with that specific word; thus, even though it did not add extra time, procedurally speaking, to the training time, it led to an increase in training time for subjects exposed to both imagery and actual training, particularly in the early stages of training, an effect that was stronger for subjects exposed to imagery training (Fig. 3, middle panel). Thus, the mere holding of information concerning the first matrix in working memory, to compare it later with the second matrix, interfered with imagery.

As expected, subject's performance improved with repetitive training, indicating task acquisition; this effect was usually stronger in those volunteers subjected to imagery training, possibly because their initial performance level was poor compared with that of the groups subjected to the actual mirror-reading training (Fig. 3).

Testing

Fig. 4 shows the mean mirror-reading times per non-word exhibited by Groups I and A (left panel), I-SC and A-SC (middle panel), and I-VS and A-VS (right panel) for eight blocks of three non-words each. ANOVA revealed significant training condition (F1,42=8.83, P<0.01), concurrent-task condition (F2,42=3.37, P<0.04) and block (F7,294=36.28, P < 0.0001) effects, and a training condition vs block (F14,294=4.65, P<0.0001) interaction effect. The interaction between training condition vs concurrent-task condition nearly reached statistical significance (F2,42=2.59, P=0.08). These findings suggest that even though both imagery and actual training lead to acquisition of the mirror-reading skill, subjects submitted to imagery training attained proficiency quicker (Fig. 4). Further, the results show that performance of concurrent tasks interferes with the acquisition of the mirror-reading skill via actual training (Fig. 4); this effect was stronger when the concurrent task involved VS compared with the spelling and counting information (Fig. 4, compare middle and right panels). The VS concurrent task also interfered with acquisition of mirror-reading by imagery training; however, this interference was lesser compared with that seen when acquisition involved actual training. Thus, mirror-reading acquisition via imagery training seems more resistant to interference.

Free recall and recognition test

Fig. 5A shows the number of words recalled, and Fig. 5B the number of words recognized by the subjects for each training condition and concurrent task condition. With regard to the number of words recalled (Fig. 5A), ANOVA revealed a virtually significant training condition effect (F1,42=3.93, P=0.053), but lack of significant concurrent task effect (F2,42=0.69, P=0.50) and training condition vs

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Fig. 5. Mean (\pm S.E.M.) number of words (A) recalled and (B) recognized per subject in the free recall and recognition memory tests, respectively, for six groups previously trained according to a 2×3 design, consisting of two training conditions (I and A) combined with three, concurrent task conditions (SC, VS working memory or no concurrent task) in experiment II.

concurrent task interaction effect (F2,42=2.29, P=0.11). With respect to the number of words recognized (Fig. 5B), ANOVA revealed a significant training condition effect (F1,42=8.40, P<0.01). Fig. 5A and 5B show that as expected, subjects exposed to imagery training recalled fewer words compared with the subjects submitted to the actual mirror-reading training. This suggests that requisite working memory resources involved in performing the imagery task are greater than that required by actual mirror-reading; consequently, resources available for (declarative) holding of information about the subject matter (words) used in training decrease, leading to greater interference. Fig. 5A

reveals that this interference effect was particularly pronounced in subjects submitted to acquisition via visual imagery training and exposed to the concurrent VS task suggesting that they compete for limited resources.

Brooks matrix visual working memory test

Fig. 6 shows the number of correct matrix identifications over seven blocks of testing by subjects performing the inverted-letter imagery (and simulation of their drawing) or the actual mirror-reading test between the presentation of the first (information) and second matrixes. Statistical analvsis revealed significant training condition effects (F1,14= 12.51, P<0.004) and Block (F6,84=135.81, P<0.0001), and training condition vs block interaction effects (F18.43, P<0.0001). Fig. 6 reveals that performance of both groups in the initial testing sessions was poor, improving similarly as training proceeded to the third block; subsequently, while performance of the subjects submitted to imagery training reached a plateau of about 65% correct responses, performance by the subjects submitted to actual mirror-reading training improved steadily to block seven, reaching \approx 90% correct responses.

DISCUSSION

The session schedule used in this experiment allowed monitoring the rate of mirror-reading acquisition via different training procedures. The results show that in the absence of a concurrent task, the rate of mirror-reading skill acquisition via inverted letter imagery was similar to that achieved with the actual performance of a mirror-reading task (Fig. 4, left panel), indicating that implicit perceptual knowledge is acquired by top-down processes as efficiently as by bottom-up processes. Conversely, when a spelling and counting task or a VS task, is performed concurrently with actual mirror-reading training, acquisition of the mirror-reading skill decreased compared with the corresponding group exposed to imagery training (Fig. 4), particularly with respect to the concurrent VS task (Fig. 4). Thus, while performance of distracting tasks together with training strongly interfered with acquisition of the mirror-reading skill via actual mirror-reading, distraction interfered only slightly with efficient acquisition via inverted-letter imagery.

This robustness of mirror-reading, perceptual skill acquisition via inverted letter imagery may be related to quantitative and qualitative differences regarding actual mirror-reading acquisition. The time invested by the subjects in performing the inverted-letter imagery was greater compared with the time spent by the corresponding groups performing the actual mirror-reading (Fig. 3). That is, the imagery task required detailed manipulation of each individual letter to simulate its inverted writing; together with this performance, the visual image of the letter was actively maintained in working memory. Thus, the amount of rehearsal involving this subject matter was certainly longer and more in-depth compared with that concerning actual mirror-reading for the same words. This extensive, imagery-related rehearsal either (1) concurrently with the maintenance in working memory of VS information concerning

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Fig. 6. Percent correct responses per subject in a Brooks matrix, VS working memory task (VS) performed concurrently with either I or A training, over eight blocks of 12 working memory trials each.

the Brooks matrix (Group I-VS) or (2) interspersed with the spelling and counting task in a task switching situation (Group I-SC), substantially increased training time (Fig. 3). The extensive processing of inverted letters via imagery for inverted writing prevented interference by the concurrent tasks (Fig. 4), possibly because priority was given to processing information related to this task; consequently, processing resources available for performance of the Brooks matrix, VS working memory task were restricted, thus leading to an inferior performance (Fig. 6, Group I-VS).

Conversely, acquisition of the mirror-reading skill via the actual performance of the mirror-reading task was disturbed by the concurrent performance of both distracting tasks (Fig. 4); interestingly, this disturbing effect was greater when the concurrent task was the Brooks matrix, VS working memory test (Fig. 4, middle and right panels). Thus, this interference effect may occur because performance of the mirror-reading training task involved limited resources also required for performance of the concurrent Brooks matrix, VS working memory task; in this case, the available resources seem to have been primarily engaged in performance of this latter task, leading to substantial improvement in performance (Fig. 6, Group A-VS) and, consequently, to poorer acquisition of the actual mirrorreading skill (Fig. 4, right panel).

Landau et al. (2004) used event-related, functional magnetic resonance imaging to investigate the effects of practice on working memory for faces. By comparing early and late session changes in brain activity, these authors

showed that the major influence of practice concerns encoding, indicating that this function is "an active process requiring attention, whereas retrieval processes . . . are more automatic" (p. 217). In the present experiment, performance of the Brooks matrix, VS concurrent task substantially increased training time, particularly in subjects exposed to imagery training, demonstrating that deviation of processing resources from the main imagery task interferes with performance during training. On the other hand, a slight interference effect was seen for the mirror-reading skill acquisition. Thus, apparently, the subjects compensated the deviation of working memory resources by increasing the time spent in imagery during training.

The free recall and the recognition memory tests for words presented together with either imagery training (Groups I, I-SC and I-VS) or actual mirror reading training (Groups A, A-SC and A-VS) revealed poorer performance by subjects exposed to imagery training (Fig. 5), suggesting that the concentration of attention in the inverted letter imagery task partially disrupted memory for this subject matter. Interestingly, subjects exposed to the actual mirror reading training concurrently with the spelling and counting task also exhibited partial disruption of performance in the free recall test compared with the remaining groups also exposed to the actual mirror-reading training, including those subjected to the concurrent VS task (Fig. 5A). Considering the nature of the imagery and the actual mirrorreading training used in this study, the imagery task appears to direct attention to individual letters to a greater

extent than the actual mirror-reading training, which may direct attention to the whole words. This may explain why performance was better in subjects performing actual mirrorreading training. In addition, the inferior performance of subjects exposed to actual mirror-reading together with the spelling and counting task (Fig. 5A), suggests that performance of this latter task requires resources also used for word holding in working memory, and thus interfered with its performance.

General discussion

Acquisition of implicit knowledge by imagery training. The two experiments in the present study were designed to evaluate acquisition of mirror-reading implicit perceptual skills via imagery training, avoiding visual feedback during performance of the imagery task, thus eliminating this possible pathway for acquisition. While experiment I involved extensive, inverted-letter imagery training before testing, and evaluation of the impact of a distracting spelling and counting task on acquisition of the mirror-reading skill, experiment II tested acquisition together with imagery training and evaluation of the impact of an additional concurrent task, involving a VS working memory task. The findings showed that imagery training led to proficient levels of skill performance (Figs. 2 and 4), demonstrating that maintenance and manipulation of relevant letter information in working memory during imagery enactment of this subject matter produce substantial implicit knowledge acquisition.

Long-term memory may be divided into explicit (or declarative) knowledge of facts and events, expressed by the deliberate recollection of information, and implicit (or procedural) knowledge, which is expressed as improved performance in previously trained tasks, including perceptual and motor skills, habits and priming, without the need for conscious recollection of having been previously exposed to the tasks (Squire and Zola-Morgan, 1991). Attention or controlled processing allocation to the incoming information plays a critical role in the acquisition of declarative memory. Conversely, acquisition of implicit knowledge may be tied to the particular processing structures and procedures engaged in learning the tasks; plasticity inherent to these systems may lead to cumulative, longterm modifications of the elements, gradually, through repetitive practice (Cohen, 1984).

Kolers (1976) reported that healthy subjects improved their ability to read inverted text via actual mirror-reading training, and that this acquisition was independent of remembering the contents of the text read, suggesting that skilled reading involves the application of procedures that process information at the level of visual patterns.

In the present experiments, implicit knowledge represented by mirror-reading skills (Kolers, 1976; Cohen, 1984) was acquired via imagery training. Our experimental design prevented visual feedback; thus, processing structures and procedures usually engaged in the actual performance of a mirror-reading task must have been engaged by maintenance of imagery information in working memory, leading to changes in the system and, thus, to acquisition of knowledge, expressed as the skilled performance of a mirror-reading task. However, experiment II shows that acquisition rates via imagery and actual training for subjects not exposed to concurrent tasks are similar (Fig. 4, left panel), and seem to follow the same rules (e.g. the need for repetition for acquisition to occur, and acquisition involving gradual, cumulative changes). This suggests that processing structures and procedures involved in acquisition via imagery and actual training are at least partially related, despite the fact that in imagery training their activation occurs by top-down processes.

Attention and acquisition of implicit knowledge by imagery training. The role played by attention in the acquisition of implicit knowledge may not be as critical as in the acquisition of explicit knowledge. For instance, Eysenck and Thompson (1966) trained independent groups of subjects in a rotary pursuit task, either alone or concurrently with distracting tasks of variable levels of difficulty; subject's performance was later tested without a concurrent task. Although time on target in the rotary pursuit task decreased as the level of difficulty of the distracting task increased during training, no differences in performance were observed during the post-acquisition test, run without a distracting task. These authors concluded that distraction interfered with performance but not with acquisition of the task.

However, Nissen and Bullemer (1987) showed that the acquisition of a serial reaction time task is strongly dependent on attentional processing. These authors trained volunteers in a serial reaction time task to react to the presentation of a light at one of four locations on a video monitor by pressing a corresponding key located directly below each light; a repeated sequence of 10 light locations was used for one of the groups, and a random sequence was used for another group. In an additional experiment, some of the subjects in each group performed either the repeated or the random sequence under dual-task conditions; i.e. subjects performed this task simultaneously with a tone-counting task in which performance required attention. Under single-task conditions, the reaction time for subjects trained with the repeated sequence decreased substantially with training compared with the corresponding scores of subjects trained with the random sequence, reflecting learning of the sequence. Under dual-task conditions, the concurrent performance of a tone-counting task strongly interfered with learning of the repeated sequence, indicating that attention is required for this acquisition.

Data from our experiment I show that imagery-induced acquisition of implicit knowledge is not altered by concurrent performance of a spelling and counting task (Fig. 2).

The design of experiment II allowed us to accompany mirror-reading skill acquisition during the imagery and the actual mirror-reading training; the results show that the acquisition rates for these training conditions are similar (Fig. 4, left panel), indicating that implicit perceptual knowledge is acquired by top-down processes as efficiently as by bottom-up processes. Further, in addition to the spelling and counting task, a concurrent VS working memory task was also performed together with either imagery or actual training. For subjects exposed to actual mirror-reading training, concurrent performance of these tasks increased training 12

time (Fig. 3), and also disrupted acquisition of the mirror reading skill. Thus, distraction by a concurrent task interferes with training performance (Fig. 3) and with acquisition of the task as revealed by testing (Fig. 4). The concurrent spelling and counting task caused greater interference with training performance, in terms of training time, when compared with the concurrent, visual working memory task; this effect may be related to the fact that performance of the spelling and counting task is time consuming and often involves switching of attention between tasks, thus differing from the visual working memory task. Conversely, the visual, working memory concurrent task induced greater interference with mirror-reading acquisition, possibly because its performance requires resources also demanded by the actual mirror-reading task. Thus, similar to Nissen and Bullemer's (1987) observations, these findings suggest that attention is required for acquisition. Conversely, for subjects exposed to the inverted-letter imagery training, concurrent performance of either the spelling and counting task or the VS, working memory task substantially increased training time (Fig. 3), but only slightly interfered with acquisition of the mirror reading skill (Fig. 4). Together, these findings indicate that, depending on the priority given by the subjects to the content of the tasks concurrently performed, interference may or may not occur. The working memory model (Baddeley, 1986, 1992) helps explain these results in terms of the availability of processing resources regarding the extent of their engagement in other processing tasks.

Inverted letter imagery thus appears to depend on a system of limited informational capacity, including the central executive of the Baddeley (1986) working memory model and the VS sketchpad. The imagery task demanded constant intervention of the central executive SAS to invert the letters; this repeated intervention rendered the processing of inverted letters throughout training automatic, via top-down mechanisms. Since the central executive was engaged in this process, its availability for other types of processing was diminished. This helps explain why the performance of subjects exposed to imagery training in the Brooks matrix, VS working memory task was inferior compared with that of subjects exposed to actual mirror-reading training (Fig. 6). It also helps explain why subjects exposed to imagery training exhibited poorer performance in the free recall and recognition tasks (Fig. 5). In other words, recruitment of resources for performance of inverted-letter visual imagery interfered with performance in the VS, working memory task possibly because priority was given by the subjects, and because these tasks demanded similar resources.

Imagery may be useful in rehabilitating patients with either perceptual or motor skill disturbances produced by brain dysfunctions, neurodegeneration and cerebral damage (see Malouin et al., 2004).

Neuro-imaging and electrophysiological studies have shown that visual imagery and visual perception share functional similarities (Farah et al., 1988; Goldenberg et al., 1989; Le Bihan et al., 1993; Roland and Gulyas, 1995; Ishai and Sagi, 1995; Kosslyn et al., 1999a; Klein et al., 2000; Lambert et al., 2002), that is, common neural structures and mechanisms seem to be activated by both (Farah, 1988; Kosslyn et al., 1993). Similarly, a number of studies have shown that most of the cortical and subcortical structures involved in overt performance are also activated during motor imagery (e.g. Decety, 1996; Decety and Ingvar, 1990; Jeannerod, 1994), and that perceptual and motor skills are related to representations of procedural knowledge. Decety (1996) showed that the pattern of cortical activation, which includes the pre-motor areas and the supplementary motor area, is strikingly similar to that observed during the actual execution of the same movement sequence. However, in imagery training, a marked difference concerns the primary motor cortex which is activated only if the movements are actually executed (Ingvar and Philipson, 1977; Annett, 1996; Roland et al., 1980). Decety et al. (1990) showed that sub-cortical areas, including the cerebellum and the basal ganglia, are also activated during motor imagery. Apparently, part of the network underlying imagery includes the prefrontal and the anterior cingulate cortex (Decety et al., 1992), brain regions also involved in working memory and attention (Roland, 1984; Smith and Jonides, 1995).

It would be interesting to identify those brain regions activated by performance of this imagery task. It would not be surprising if the prefrontal and the anterior cingulate cortex were involved, in addition to visual association regions. This is a question wide open to experimental scrutiny.

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REFERENCES

- Amedi A, Jacobson G, Hendler T, Malach R, Zohary E (2002) Convergence of visual and tactile shape processing in the human lateral occipital complex. Cereb Cortex 12(11):1202–1212.
- Annett J (1996) On knowing how to do things: a theory of motor imagery. Brain Res Cogn Brain Res 3:65–69.
- Baddeley AD (1986) Working memory. Oxford: Clarendon Press. Baddeley AD (1992) Is working memory working? Q J Exp Psychol A 44·1–31
- Baddeley AD, Hitch G (1974) Working memory. In: The psychology of learning and motivation, Vol. 8 (Bower GA, ed), pp 47–89. New York: Academic Press
- Berman J (1995) Imaging pain in humans. Br J Anaesth 75:209-216.
- Clark LV (1960) Effect of mental practice on the development of a certain motor skill. Res Q 31:560–569.
- Cohen NJ (1984) Preserved learning capacity in amnesia: evidence for multiple memory systems. In: The neuropsychology of memory (Squire LR, Butters N, eds), pp 83–103. New York: Guilford Press.
- Cowey CM, Green S (1996) The hippocampus: a "working memory" structure? The effect of hippocampal sclerosis on working memory. Memory 4:19–30.
- Decety J (1996) Do imagined and executed actions share the same neural substrate? Brain Res Cogn Brain Res 3:87–93.
- Decety J, Ingvar DH (1990) Brain structures participating in mental simulation of motor behavior: a neuropsychological interpretation. Acta Psychol (Amst) 73:13–34.
- Decety J, Kawashima R, Gulyas B, Roland PE (1992) Preparation for reaching: a PET study of the participating structures in the human brain. Neuroreport 3:761–764.

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- Denis M (1985) Visual imagery and the use of mental practice in the development of motor skills. Can J Appl Sport Sci 10:4S–16S.
- D'Esposito M, Detre JA, Aguirre GK, Stallcup M, Alsop DC, Tippet LJ, Farah MJ (1997) A functional MRI study of mental image generation. Neuropsychologia 35:725–730.
- D'Esposito M, Detre JA, Alsop DC, Shin RK, Atlas S, Grossman M (1995) The neural basis of the central executive system of working memory. Nature 378:279–281.
- Eysenck HJ, Thompson W (1966) The effects of distraction on pursuit rotor learning, performance and reminiscence. Br J Psychol 57: 99–106.
- Farah MJ (1988) Is mental imagery really visual? Overlooked evidence from neuropsychology. Psychol Rev 95:307–317.
- Farah MJ, Peronnet F, Gonon MA, Giard MH (1988) Electrophysiological evidence for a shared representational medium for visual images and visual percepts. J Exp Psychol Gen 117:248–257.
- Feltz DL, Landers DM (1983) The effects of mental practice on motor skill learning and performance: a meta-analysis. J Sport Psychol 5:25–27.
- Fuster JM (1984) Behavioral electrophysiology of the prefrontal cortex. Trends Neurosci 7:408–414.
- Glucksberg S, Cowan GN (1970) Memory for nonattended auditory material. Cognit Psychol 1:149–156.
- Goldenberg G, Podreka I, Steiner M, Willmes K, Suess E, Deecke L (1989) Regional cerebral blood flow patterns in visual imagery. Neuropsychologia 27:641–664.
- Ingvar DH, Philipson L (1977) Distribution of cerebral blood flow in the dominant hemisphere during motor ideation and motor performance. Ann Neurol 2:230–237.
- Ishai A, Sagi D (1995) Common mechanisms of visual imagery and perception. Science 268:1772–1774.
- Jacobson E (1932) Electrophysiology of mental activities. Am J Psychol 44:677–694.
- Jeannerod M (1994) Contribution of J. M. Charcot to the study of motor localizations in man. Rev Neurol (Paris) 150:536–542.
- Johnson P (1982) The functional equivalence of imagery and movement. Am Q J Exp Psychol A 34:677–694.
- Just MA, Carpenter PA (1992) A capacity theory of comprehension: individual differences in working memory. Psychol Rev 99:122–149.
- Klein I, Paradis AL, Poline JB, Kosslyn SM, Le Bihan D (2000) Transient activity in the human calcarine cortex during visual-mental imagery: an event-related fMRI study. J Cogn Neurosci 12 (Suppl 2):15–23.
- Kohl RM, Roenker DL (1980) Bilateral transfer as a function of mental imagery. J Mot Behav 12(3):197–206.
- Kohl RM, Roenker DL (1983) Mechanism involvement during skill imagery. J Mot Behav 15:179–190.
- Kolers PA (1976) Pattern-analyzing memory. Science 191:1280–1281.
- Kosslyn SM, LeSueur LL, Dror IE, Gazzaniga MS (1993) The role of the corpus callosum in the representation of lateral orientation. Neuropsychologia 31:675–686.
- Kosslyn SM, Pascual-Leone A, Felician O, Camposano S, Keenan JP, Thompson WL, Ganis G, Sukel KE, Alpert NM (1999a) The role of area 17 in visual imagery: convergent evidence from PET and rTMS. Science 284:167–170.
- Kosslyn SM, Sukel KE, Bly BM (1999b) Squinting with the mind's eye: effects of stimulus resolution on imaginal and perceptual comparisons. Mem Cognit 27:276–287.
- Lambert S, Sampaio E, Scheiber C, Mauss Y (2002) Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement-an fMRI study. Brain Res 924:176–183.

- Landau SM, Schumacher EH, Garavan H, Druzgal TJ, D'Esposito M (2004) A functional MRI study of the influence of practice on component processes of working memory. Neuroimage 22(1): 211–221.
- Le Bihan D, Turner R, Zeffiro TA, Cuenod CA, Jezzard P, Bonnerot V (1993) Activation of human primary visual cortex during visual recall: a magnetic resonance imaging study. Proc Natl Acad Sci U S A 90:11802–11805.
- Malouin F, Belleville S, Richards CL, Desrosiers J, Doyon J (2004) Working memory and mental practice outcomes after stroke. Arch Phys Med Rehabil 85:177–183.
- Mellet E, Tzourio N, Denis M, Mazoyer B (1995) A positron emission tomography study of visual and mental spatial exploration. J Cogn Neurosci 7:6504–6512.
- Moray N (1959) Attention in dichotic listening: affective cues and the influence of instructions. Q J Exp Psychol 9:56–60.
- Nissen MJ, Bullemer P (1987) Attentional requirements of learning: evidence from performance measures. Cognit Psychol 19:1–32.
- Norman D (1969) Memory and attention: an introduction to human information processing. New York: Wiley.
- Norman DA, Shallice T (1980) Attention to action: willed and automatic control of behavior. San Diego: University of California.
- Pelli DG, Farrell B, Moore DC (2003) The remarkable inefficiency of word recognition. Nature 423(6941):752–756.
- Petrides M, Alivisatos B, Evans AC, Meyer E (1993) Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. Proc Natl Acad Sci U S A 90:873–877.
- Phillips WA, Christie DF (1977) Interference with visualization. Q J Exp Psychol 29:637–650.
- Roland PE (1984) Metabolic measurements of the working frontal cortex in man. Trends Neurosci 7:430–435.
- Roland PE, Gulyas B (1995) Visual memory, visual imagery, and visual recognition of large field patterns by the human brain: functional anatomy by positron emission tomography. Cereb Cortex 5:79–93.
- Roland PE, Skinhoj E, Lassen NA, Larsen B (1980) Different cortical areas in man in organization of voluntary movements in extrapersonal space. J Neurophysiol 43:137–150.
- Shallice T (1988) From neuropsychology to mental structure. Cambridge: Cambridge University Press.
- Shaw WA (1940) The retention of muscular actions potentials to imaginal weight lifting. Arch Psychol 35:(Whole No. 247).
- Smith EE, Jonides J (1995) Working memory in humans: Neuropsychological evidence. In: The cognitive neuroscience (Gazzaniga MS, ed), pp 1009–1020. London: MIT Press.
- Squire LR, Zola-Morgan S (1991) The medial temporal lobe memory system. Science 253(5026):1380–1386.
- Tulving E (1985) How many memory systems are there? Am Psychol 40:385–398.
- Twining WE (1949) Mental practice and physical practice in learning a motor skill. Res Q 20:432–435.
- Vandell RA, Davis RA, Clugston HA (1943) The function of mental practice in learning in the acquisition of motor skills. J Gen Psychol 29:243–250.
- Vogt S (1996) Imagery and perception-action mediation in imitative actions. Brain Res Cogn Brain Res 3:79-86.
- Yaguez L, Nagel D, Hoffman H, Canavan AG, Wist E, Homberg V (1998) A mental route to motor learning: improving trajectorial kinematics through imagery training. Behav Brain Res 90:95–106.

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