Direct Current Stimulation over V5 Enhances Visuomotor Coordination by Improving Motion Perception in Humans

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Abstract

■ The primary aim of this study was to determine the extent to which human MT+/V5, an extrastriate visual area known to mediate motion processing, is involved in visuomotor coordination. To pursue this we increased or decreased the excitability of MT+/V5, primary motor, and primary visual cortex by the application of 7 min of anodal and cathodal transcranial direct current stimulation (tDCS) in healthy human subjects while they were performing a visuomotor tracking task involving hand movements. The percentage of correct tracking movements increased specifically during and immediately after cathodal stimulation, which decreases cortical excitability, only when V5 was stimulated. None of the other stimulation conditions affected visuomotor performance. We propose that the improvement in performance caused by cathodal tDCS of V5 is due to a focusing effect on to the complex motion perception conditions involved in this task. This hypothesis was proven by additional experiments: Testing simple and complex motion perception in dot kinetograms, we found that a diminution in excitability induced by cathodal stimulation improved the subject's perception of the direction of the coherent motion only if this was presented among random dots (complex motion perception), and worsened it if only one motion direction was presented (simple movement perception). Our data suggest that area V5 is critically involved in complex motion perception and identification processes important for visuomotor coordination. The results also raise the possibility of the usefulness of tDCS in rehabilitation strategies for neurological patients with visuomotor disorders. ■

INTRODUCTION

Visually guided reaching and tracking movements are essential to control our environment. A challenging problem in neuroscience is to understand at what stages the visual input is connected to motor performance and how visual guidance can be used to modify and execute motor responses. In the human, specific feed-forward and feedback connections involved in visually guided reaching and tracking movements have been characterized by transcranial magnetic stimulation (TMS) or the combination of TMS and functional neuroimaging (Buneo, Jarvis, Batista, & Anderson, 2002; Sabes, 2000; Desmurget et al., 1999; Iacoboni, 1999; Rizzolatti, Fogassi, & Gallese, 1997). Most of the studies underline the role of the posterior and superior parietal cortex in planning, updating, and modifying reaching movements. However, evidence is growing that the middle temporal (MT) and the medial superior temporal (MST) areas of monkeys and the homologous region of the human cortex, MT+ or V5—an extrastriate area in which neurons are broadly tuned to identify the direction and velocity of visual motion—are also highly activated during reaching (Savaki & Dalezios, 1999), during passive tracking of motion (Culham at al., 1998), and during active tracking hand movements (Kleiser, Oreja-Guevara, Hoffman, & Seitz, 2002; Kruse, Dannenberg, Kleiser, & Hoffmann, 2002). Because functional imaging techniques deliver information only about the global involvement of a given cortical area in a specific task but are not well suited to clarify its specific role, we applied transcranial direct current stimulation (tDCS), a noninvasive electrical stimulation technique, to gain insight into the functional importance of V5 for visuomotor coordination.

tDCS has already been shown to modulate the excitability of motor (Baudewig, Nitsche, Paulus, & Frahm, 2001; Nitsche & Paulus, 2000, 2001; Nitsche, Nitsche, et al. 2003; Nitsche, Schauenburg, et al., 2003; Rosenkranz, Nitsche, Tergau, & Paulus, 2000) and visual cortices (Antal, Nitsche, & Paulus, 2001; Antal, Kincses, Nitsche, & Paulus, 2003) in human subjects. Previous animal studies suggest that cathodal tDCS reduces spontaneous firing rates of cortical cells, most likely by hyperpolarizing the cell body, whereas anodal stimulation results in a reversed effect during and after the end of the stimulation (Ward & Weiskrantz, 1969; Bindman, Lippold, & Redfearn, 1964; Creutzfeldt, Fromm, & Kapp,

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1962). In human subjects the aftereffects can be prolonged up to 1 hr after the end of the stimulation (Nitsche & Paulus, 2000, 2001; Nitsche, Nitsche, et al., 2003). The underlying cellular/molecular changes induced by tDCS are largely unknown so far, however, the elicited effects are most probably localized intracortically, at least in the motor cortex (Nitsche & Paulus, 2001; Nitsche, Nitsche, et al., 2003). The aftereffects are NMDA receptor dependent (Liebetanz, Nitsche, Tergau, & Paulus, 2002), and thus share a certain similarity with other well-known neuroplastic mechanisms (Bennett, 2000). tDCS most likely acts through a modulation of spontaneous cortical activity, not through a disruption, as do most of the other stimulation techniques applicable in the human. Thus, depending on task characteristics and accompanying activation states of a given cortical area, tDCS can result in different effects: It has already been shown that specifically anodal stimulation of the motor cortex in the acquisition phase of an implicit motor learning task enhances performance, most likely due to a strengthening of the neuronal representation of the to-be-learned pattern (Nitsche, Schauenburg, et al., 2003). However, the same kind of stimulation can reverse a transient, training-induced shift in a specific motor cortical excitability pattern, which does not include learning processes, back to the old pattern of excitability, most probably by reestablishing the former dominant excitability pattern of this area (Rosenkranz et al., 2000).

The aim of our study was to find further evidence for the function of the human V5 in visually guided, manual tracking processes. Therefore, to learn about the specific involvement of V5 in a visuomotor coordination task, we performed a first set of experiments in which we modulated the excitability of V5 by tDCS on the one hand, and V1 and the primary motor cortex on the other, during performance of this task. To gain more detailed insight into the probable function of V5, we examined in a second set of experiments the involvement of this area in complex and elementary movement perception processes by modulating its excitability with tDCS.

For the first set of experiments, we used a visuomotor coordination task in which a moving target dot has to be followed by a feedback cursor on a computer screen. Motion direction and velocity of the latter is manually controlled by the subject by moving a 2-D manipulandum. In this task, the subjects have to first position the feedback cursor in a small window in the middle of the screen. Then the target dot travels from one of four possible peripheral positions toward the central window with constant velocity and direction. Once it has arrived in the center, the subjects must follow the target dot with the feedback cursor until it stops (Figure 1) without leaving a small (1.5°) tracking window. When this window is left by the feedback cursor, this is counted as an error. Previous primate studies have suggested that this task shows the dynamic interaction between visual input and movement, that its experimental parameters can be well controlled, and that it allows the modulation of performance in two directions: improvement and impairment (Kruse et al., 2002). For a correct execution of this task, a combination of intact motion perception, integration, and motor execution is needed. In the first part of the task only a correct perception of the target motion is necessary. In the second phase, when the target stimulus must be followed by the feedback cursor, a continuous, high-resolution evaluation of both the correct direction and speed of the motion, according to the target–feedback cursor combination, is necessary to choose the optimum motor reaction. From an information processing perspective, this phase of the task must be regarded as complex. It may involve simultaneous activations of different motion direction- and velocity-encoding neuronal patterns in V5, as well as their degree of activation depending on the correctness of motion perception. Subjects had about 100–200 practice trials first, until performance had reached a stable level. The resulting performance level was taken as a baseline. Performance was then tested repeatedly during and after tDCS of V5, V1, or the primary motor cortex.

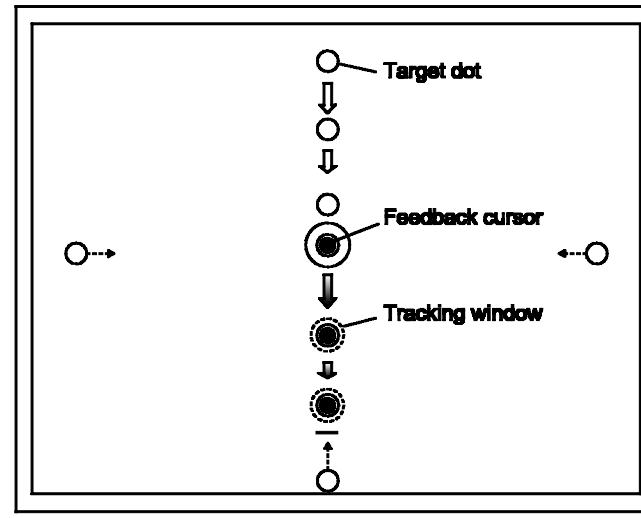

Figure 1. The figure shows a sketch of the visuomotor task we used. After the feedback cursor was positioned in the middle of the screen by the subject, the target dot appeared in one of the four possible positions and moved toward the feedback cursor. When it reached the feedback cursor, the subject had to follow it with the feedback cursor until it stopped. It counted as an error if the feedback cursor left the tracking window before a trial was completed or did not stop when the target stopped. The tracking window could not be seen by the subject.

The second set of experiments was conducted to learn more about the specific role of V5 in complex, compared to elementary, motion perception. Here we introduced dot kinetograms, which are frequently used to assess the function of V5 (Braddick et al., 2001; Scase, Braddick, & Raymond, 1996; Watamaniuk, 1993; Newsome & Pare, 1988). In these tasks, subjects have to indicate the direction of a coherent motion by pushing the suitable mouse button. We compared motion per-

ception with and without distractors: In the first task the coherent motion was presented in an incoherent environment (complex motion identification) whereas in the second task, only an up or down motion was presented, without incoherently moving dots (elementary motion identification, Figure 2). At the beginning of the first task, 40% of the dots were moving coherently. After two consecutive correct or incorrect responses the percentage of coherently moving dots decreased or increased by at first 4%, respectively. The final step size was 1%. In this way, the motion perception threshold representing the lowest percentage of coherently moving dots needed to identify a direction was determined before, during, and after tDCS of V5. In the second task, the motion direction of only coherently moving dots had to be identified. First, to establish a baseline, the presentation time of stimuli was adjusted to achieve about 80% correct identification of motion direction. Then the task was repeated during and after tDCS using the determined presentation time. Compared to the second task, in which only one direction of motion is presented, the first task is complex and thus similar to the perceptual component of the tracking task: In addition to the correct motion direction, which had to be identified, several other motion directions, which could also stimulate the suitable motion-sensitive neurons in V5, were displayed.

RESULTS

Visuomotor Coordination Task (Experiment I)

All of the subjects were able to learn the task. The mean baseline number of correct tracking movements was 33 of 45 trials (range: 20–40, *SD* 6).

Using the V5–Cz electrode montage, cathodal stimulation enhanced the relative number of correct tracking movements, whereas anodal stimulation had no such effect. The main effect of stimulation, $F(1,11) = 5.10$, $p < .05$, but not of the time course, $F(3,33) = 0.56$, $p > .6$, was significant. The interaction between stimulation type and time course was significant, $F(3,33) = 2.90$, $p < .05$. According to Tukey's HSD test, performance increased significantly ($p < .05$) during and immediately after cathodal stimulation (Figure 3).

In contrast, using the Oz–Cz montage or the LM–RPF montage, there was no significant main effect of stimulation, $F(1,11) = 0.98$, $p > .1$, or time course, $F(3,33) = 0.75$, $p > .4$. The interactions between stimulation type and time course were also not significant ($p > .5$).

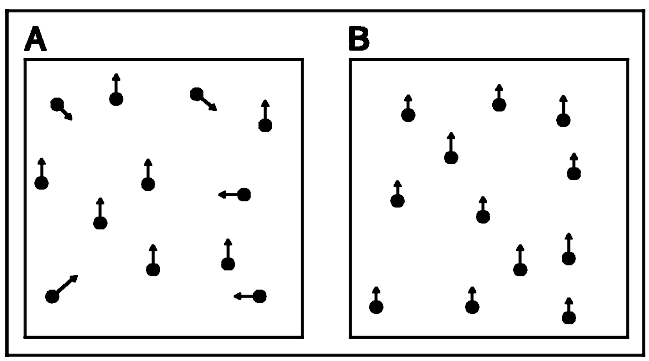

Figure 2. Illustration of the random dot tasks. The subject's task was to indicate the direction of the coherent movement by pushing the suitable mouse button. The direction of the coherent motion was varied randomly between up and down. (A) Originally, 40% of the dots were moving coherently; after two consecutive correct or incorrect responses the percentage of coherently moving dots decreased or increased by 4%, respectively. The final step size was 1%. (B) In this task, only coherent motion could be seen. Note that the presentation time of the stimuli was decreased to make the task difficult.

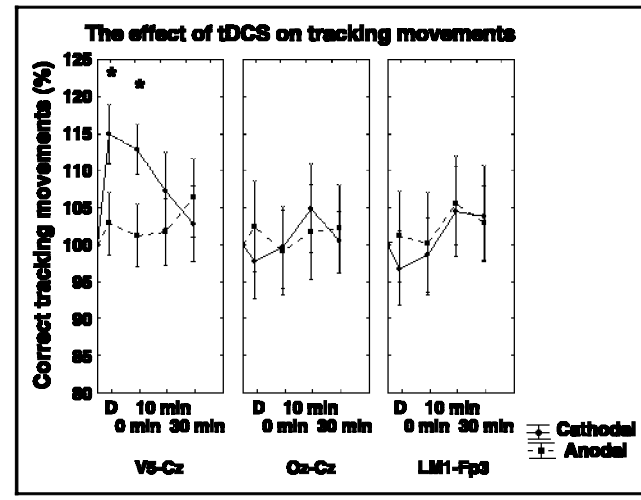

Figure 3. Effect of tDCS on the relative number of correct tracking movements. The results are normalized; 100% performance corresponds to the performance of the subjects before stimulation. Changes in percentage can be seen before, during, immediately after, and 10 and 30 min after cathodal (continuous line) and anodal stimulation (dotted line) compared to the relative number of correct tracking movements before the stimulation. Error bars show *SEM*s. Only cathodal tDCS affects performance. Asterisk shows significant effects.

Coherently Moving Dots among Incoherently Moving Dots (Experiment IIA)

The mean motion perception threshold was 44.29% (range: 32.4–60.0, *SD* 8.63). Similar to the visuomotor coordination task, cathodal stimulation of V5 resulted in improved performance: The percentage of coherently moving dots needed for correct identification of a motion direction was decreased during and after cathodal stimulation compared to the baseline (Figure 4). Anodal stimulation did not change performance. Two-way ANOVA revealed that the main effect of stimulation was significant, $F(1,9) = 8.24$, $p < .02$, whereas the main effect of the time course was not, $F(3,27) = 0.58$, $p > .6$. The interaction between type of stimulation and time course was significant, $F(3,27) = 4.13$, $p < .02$. According to Tukey's HSD test, the percentage of the coherently moving dots was significantly reduced dur-

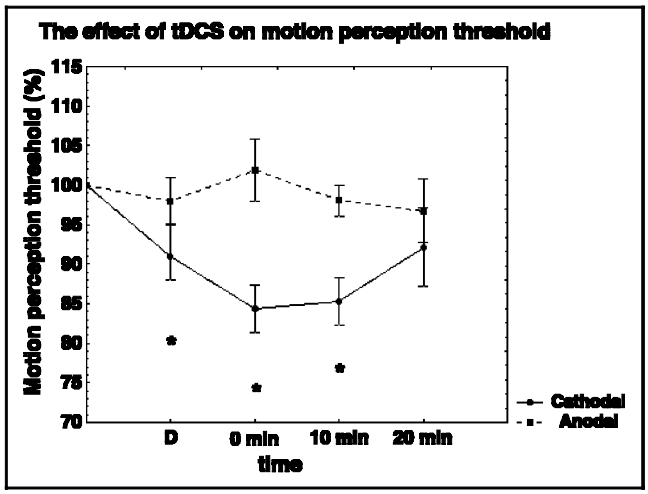

Figure 4. Effect of tDCS on movement perception when subjects were asked to detect the direction of coherent movement among randomly moving dots. Changes in percentage are depicted during, immediately after, and 10 and 20 min after cathodal (continuous line) and anodal stimulation (dotted line) compared to the data before stimulation. Error bars represent *SEM*s. Only cathodal tDCS affects performance. Asterisk shows significant effects.

ing, immediately after, and 10 min after cathodal stimulation ($p < .05$).

Only Coherently Moving Dots (Experiment IIB)

The mean percentage of performance was 75.61% (range 56–90, *SD* 14.7). The main effect of stimulation was significant, $F(1,9) = 11.39$, $p < .05$ (Figure 5), whereas the main effect of time course was not, $F(1,9) = 0.35$, $p > .7$. The interaction between type of stimulation and time course was also not significant, $F(1,9) = 2.02$, $p > .1$. According to Tukey's HSD test, the number of correctly identified directions was significantly reduced during and immediately after cathodal stimulation ($p < .05$), whereas it increased during and immediately after anodal stimulation ($p < .05$).

DISCUSSION

The main finding of our study is that cathodal tDCS applied to the left V5 improved performance in a visuomotor coordination task that encompassed both dynamic, high-resolution perception and selection of motion predetermined by a moving target. Stimulation of the primary visual cortex and the left motor cortex did not result in significant changes in performance, nor were the reaction times in the random dot kinetogram task significantly affected. These results suggest that tDCS indeed modified visual motion perception and motor performance.

Because of the size of our stimulating electrode, it cannot be completely ruled out that in our study other motion-sensitive areas, such as V3A, were also activated. Previous studies suggest that areas in region V3A/V3 are well activated by coherent motion and may therefore also determine psychophysical performance (Tootell et al., 1997). However, the non-effect of V1 stimulation on performance when the tDCS electrode was positioned near but not over V5, as well as other studies, indicate that areas beyond the stimulating electrode should not be affected to a relevant extent by tDCS (Nitsche, Schauenburg, et al., 2003; Rush & Driscoll, 1968).

From earlier human motor and visual studies it is obvious that tDCS can modulate cortical excitability, both during and after stimulation (Nitsche, Nitsche, et al., 2003; Nitsche, Schauenburg, et al., 2003; Antal et al., 2001; Baudewig et al., 2001; Nitsche & Paulus, 2000, 2001; Rosenkranz et al., 2000). Weak cathodal stimulation decreases cortical excitability by membrane hyperpolarization, whereas anodal stimulation enhances it by subthreshold membrane depolarization. The highly specific effect of reducing excitability in V5 that results in enhanced performance of this visually guided tracking task is most probably explained by the complexity of perceptual information processing needed for this task, namely, high-resolution temporal-spatial analysis and comparison of motion velocity and direction of the target and the feedback cursor. This probably results in a kind of ''fuzzy'' activation state of the encoding neuronal pattern in response to different velocity and movement directions where not only the optimum, but also some suboptimum patterns are simultaneously activated to a certain degree. We speculate that in this case cathodal stimulation may focus the correct perception of these parameters by decreasing global excitation level and thus diminishing the amount of activation of concurrent patterns below threshold (Figure 6A).

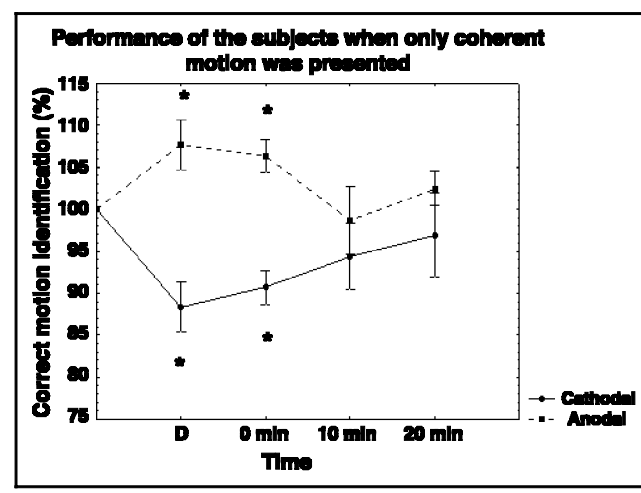

Figure 5. Effect of tDCS on identifying movement direction when only coherent movement was presented. Changes in percentage can be seen before (100%), during, immediately after, and 10 and 20 min after cathodal (continuous line) and anodal stimulation (dotted line) compared to the baseline values. Error bars represent *SEM*s. Cathodal stimulation impaired whereas anodal stimulation improved performance. Asterisk shows significant effects.

To prove this focusing hypothesis, we conducted two additional experiments in which subjects had to identify the correct motion directions in dot kinetograms. In the first task, coherent and noncoherent motion were simultaneously presented, and therefore represented the fuzzy or complex perceptional condition, where different motion-encoding neuronal patterns should be simultaneously activated to different degrees. In the second task only one motion direction was presented, thus representing the elementary perceptual condition, where only one motion-encoding pattern should be activated during one trial. Thus, if cathodal stimulation really focuses the activity of motion-encoding network components in the complex condition, it would enhance perception in a random dot task where coherent movement is presented among randomly moving dots. In contrast, performance should be impaired by cathodal stimulation when the motion on the screen is uniform and no focusing is necessary, because here the lowered excitation level would reduce activity, in this case, in the only active, correct movement-encoding neuronal pattern. Conversely, an anodal tDCS-generated excitability enhancement should improve performance (Figure 6B). Our data confirmed these hypotheses: The perception of moving dots was improved by cathodal tDCS when the coherent motion was presented among randomly moving dots. If the direction of uniformly moving dots needed to be determined, performance decreased during and after cathodal stimulation, but was improved by anodal tDCS, similar to our previous data on the primary visual cortex (Antal et al., 2001).

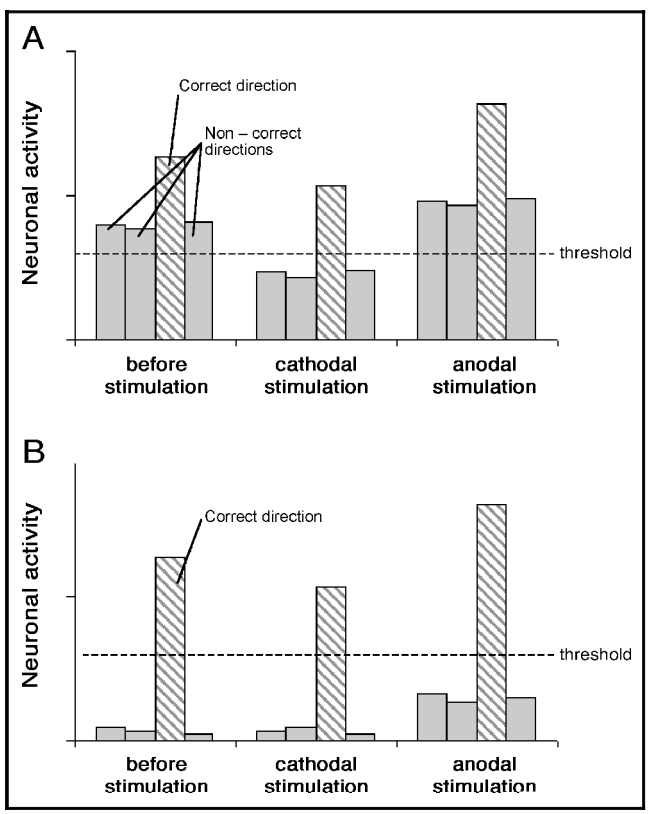

Figure 6. This figure illustrates the possible different mechanisms of tDCS, depending on the complexity of a given task. In a complex perceptual task, where not only the correct encoding, but also concurrent neuronal patterns are activated, cathodal stimulation would suppress the concurrent patterns below threshold (dotted line), while the correct pattern is still suprathreshold, and thus focuses neuronal activity. In this case, a global excitability increase by anodal tDCS will not focus activity, and the relation between the concurrent patterns remains identical (A). (B) depicts the situation in an elementary perceptional task, where essentially only one correct encoding pattern is activated. Here an excitability diminution (cathodal tDCS) will reduce the activity of this pattern and thus worsen perception, while an excitability enhancement (anodal tDCS) will increase it and thus improve performance.

There is growing evidence that the middle temporal complex (MT/MST, MT+/(V5) is involved in the transformation of visual motion perception toward a motor, executive function. Previous investigations have heavily relied on fMRI or PET data, which can provide associations between brain regions and behavior but cannot establish how these areas are specifically involved in the examined functions (see, e.g., Braddick et al., 2001). To our knowledge, this is the first human study using tDCS and showing that V5 is specifically involved in the perceptual aspect of identification of complex tracking movements. Another important finding is that performance in a visuomotor coordination task could be improved by cathodal tDCS by modifying *only* visual information processing. The most parsimonious explanation for this result is that cathodal tDCS probably focuses cortical activity onto the optimum motion encoding neuronal pattern in the cortex. Our results raise the possibility of using tDCS in the rehabilitation of brain injuries where visuomotor coordination is impaired because of deficient visual processing.

METHODS

The visuomotor coordination task involved 12 subjects; the random dot kinetogram studies involved 10 subjects (mean age: 26.8 years, range: 20–56 years, *SD* 10.9, 9 men). They all had a visual acuity score better than 0.9 (VA). All of the subjects gave their written informed consent. The study was approved by the Ethics Committee of the University of Göttingen.

In the visuomotor coordination task (Experiment I), the subjects were seated 75 cm in front of a SONY Trinitron high-resolution color monitor at approximately eye level. Under the monitor, a horizontal, planar work surface was placed, on which a two-dimensional, self-built, articulated manipulandum could be moved manually. The movement of the manipulandum on the surface was measured continuously and displayed in real time as a feedback red dot (feedback cursor) on the screen (Figure 1). After the feedback cursor was placed in the middle of the screen into a 1.5°-diameter center hold window, a white target dot appeared on the upper, lower, right, or left middle part of the screen

and traveled toward the red feedback dot (Figure 1). Subjects were instructed to follow the white target dot after it reached the position of the feedback cursor and to stop when the target stopped on the opposite side of the screen (correct tracking movement). The direction of the tracking movement was always straight. An error occurred if the feedback cursor left the tracking window before a trial was completed or it did not stop when the target stopped. The size of the target and feedback dot was 0.8° and 1.0°, and the diameter of the tracking window was 1.5°. The tracking window could not be seen by the subjects. The premovement and tracking times were both 1250 msec; the velocity of the target dot was 2.0°/sec. Tracking movements were recorded on-line. Forty-five trials were presented before, during, immediately after, and 10 and 30 min after 7 min of cathodal and anodal tDCS. The changes in percentage of correct tracking movements were entered into a 2 (stimulation—anodal or cathodal) × 5 (time) analysis of variance (ANOVA). Tukey's HSD tests were used for post hoc comparisons. Before the test sessions, subjects were trained until they reached and were able to maintain 70–80% of correct tracking movements.

Random dot kinetograms (Experiment II) were generated using a standard VisionWorks system (VisionWorks, USA). The visual stimulus was presented on a high-resolution color monitor. The stimulus display subtended from a viewing distance of 75 cm. The steady-state luminance of a stationary dot was 10 cd/m^2, and the background luminance was 2 cd/m^2. In the first experiment, a single-interval, forced-choice, motion-direction discrimination task was used (Figure 2). Subjects had to report the direction (up or down) of coherent motion in a 10° × 10° random dot stimulus by pushing the suitable button on a computer mouse. The middle of the stimulus was placed 10° apart from the fixation point on the left side of the screen to stimulate the left occipital cortex. In the first experiment, the presentation time was six frames and the stimuli contained 300 white square dots; the dot speed was 5°/sec. The direction of the coherent motion was randomly varied between up and down. At the beginning of the first experiment, 40% of the dots were moving coherently; after two consecutive correct or incorrect responses the percentage of coherently moving dots decreased or increased by 4%, respectively. The final step size was 1%. In this way, the motion perception threshold, the lowest percentage of coherently moving dots needed to identify a direction, was determined.

Before the test session, subjects were trained until they achieved and maintained 70–80% of correct discrimination. Performances were measured before, during, immediately after, and 10 and 20 min after the end of stimulation. The percentage of coherently moving dots at threshold was entered into a 2 (stimulation—anodal or cathodal) × 4 (time) ANOVA. Tukey's HSD tests were used for post hoc comparisons.

In the second experiment, the method of constant stimuli was used. The presentation time was four frames; it was adjusted to result in about 80% correct responses. The stimuli contained 200 dots, all moving coherently. In each block, 70 stimuli were presented and the dot speed was 5°/sec. The subject's task was to identify the direction (up or down) by pushing the suitable mouse button. In this task, the number of correctly identified directions was counted.

Performances were measured before, during, immediately after, and 10 and 20 min after the end of stimulation. The number of correctly identified directions was entered into a 2 (stimulation—anodal or cathodal) × 5 (time) ANOVA. Tukey's HSD tests were used for post hoc comparisons.

tDCS was delivered by a battery-driven, constant-current stimulator (Schneider Electronic, Gleichen, Germany) through a pair of electrodes in a 5 × 7-cm water-soaked synthetic sponge. Three different electrode montages were used in the visuomotor coordination task: (1) For cathodal stimulation, the cathode was placed approximately 3–4 cm above the mastoid–inion line and 6–7 cm left of the midline in the sagittal plane (left V5). The coordinates were selected on the basis of previous imaging and TMS studies of V5 (Hotson & Anand, 1999; Hotson, Braun, Herzberg, & Boman, 1994; Stewart, Battelli, Walsh, & Cowey, 1999; Walsh, Ellison, Battelli, & Cowey, 1998; Watson et al., 1993). These studies suggest that TMS over the left V5 produces a greater disturbance to a visual motion task than TMS over the right V5. PET studies also support a greater prominence of motion processing in the left hemisphere (Zeki et al., 1991). The reference electrode was placed over Cz (V5–Cz montage). For anodal stimulation, the direction of electric flux was reversed. (2) For stimulation of the V1 one electrode was placed at Oz, the reference over Cz (Oz–Cz montage). (3) For stimulation of the left primary motor cortex one electrode was placed over C3 (the task was performed with the right hand) and the reference above the right eye (right prefrontal cortex) (LM–RPF montage). Polarity of stimulation refers to the V1 and motor cortical electrodes, respectively. When the random dot kinetograms were used, only the V5–Cz electrode position was applied. For each subject cathodal and anodal stimulation was applied in separate experiments at least 1 day apart. The current was applied for 7 min with an intensity of 1.0 mA. Constant current flow was measured by an amperemeter and controlled by the experimenter.

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