RESEARCH ARTICLE

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Dorsal and ventral visual stream contributions to perception-action interactions during pointing

Abstract The Ebbinghaus illusion, in which a central circle surrounded by large circles appears to be smaller than a central circle surrounded by small circles, affects the speed of pointing movements. When the central circle appears to be big, pointing movements directed towards it are faster than when the central circle appears to be small. This effect could be due to an interaction between ventral stream processing associated with determining relative object size and dorsal stream processing associated with sensorimotor output. Alternatively, the dorsal stream alone could mediate the effect via the transformation of object shape representations into motor output within the parietal lobe. Finally, ventral stream processing could be integrated into motor output through projections to the prefrontal cortex and subsequently to the motor areas of the cortex, thus bypassing the dorsal stream. These three alternatives were tested by disrupting either the ventral or dorsal stream processing using transcranial magnetic stimulation (TMS) while subjects made pointing movements as quickly and accurately as possible to the central target circles within the Ebbinghaus illusion display. The relative changes in reaction time, movement speed, and movement accuracy for small versus large appearing target circles were compared when TMS was delivered over each site as well as at a control site (SMA). The results showed that TMS over either the dorsal or ventral stream but not the SMA reduced the influence of the illusion on the pointing movement speed but did not affect reaction time or movement accuracy. A second control experiment was completed in which TMS was delivered during pointing movements to target circles of physically different sizes that were not surrounded by either large or small circles. This allowed us to determined whether the effect we observed in the main experiment was due specifically to the relative size information contained within the illusory display and the effect this has on the preparation of pointing responses or to an influence on basic perceptual and sensorimotor processes occurring within the ventral and dorsal streams, respectively. The results showed that the affect on pointing movement speed was still present with dorsal but not ventral stream stimulation. Taken together, this evidence suggests that the ventral stream contributes to pointing movements based on relative object size information via its projections to the prefrontal areas and not necessarily through interactions with the dorsal stream.

Keywords Ebbinghaus illusion · Ventral stream · Dorsal stream · Transcranial magnetic stimulation · Pointing movements

Introduction

The theory that the visual perception of objects and the visual control of action directed at those objects rely on relatively distinct circuits in the human brain has been widely recognized. In general, visual information is divided into two streams once it passes the primary visual cortex (Goodale and Milner 1992; Ungerleider and Mishkin 1982). Information about object attributes – e.g., size, shape, orientation, and color – proceeds through the ventral pathway projecting from the visual cortex to the inferotemporal cortex, whereas information concerning the egocentric location of objects used for visually guided action proceeds through the dorsal pathway projecting from the visual cortex to the posterior parietal cortex.

Although this division is theoretical, and there are extensive interconnections between the two streams, it nevertheless is largely consistent with a body of evidence in both humans and non-human primates. For example, patients with ventral damage have difficulty perceiving basic object features, yet can reach out and grasp those objects accurately – a task that requires the integra-

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tion of information related to object size, shape, and orientation into the grasping motor output (Goodale and Milner 1992). By contrast, patients with dorsal damage have the converse deficit – they can accurately perceive objects but cannot reach out and grasp them in a coordinated fashion (Jeannerod 1988).

This functional dissociation has also been examined in healthy subjects by assessing the influence of visual illusions on motor output directed at those illusions. Goodale and colleagues have demonstrated that the Ebbinghaus illusion, in which a central circle surrounded by an annulus of small circles is perceived to be larger than a physically identical central circle surrounded by an annulus of large circles, does not influence grip aperture (Aglioti et al. 1995; Haffenden and Goodale 1998, 2000). In contrast to grasping movements, pointing responses do appear to be influenced by the illusion (van Donkelaar 1999): pointing movements to the perceptually large target circle are completed more quickly than those to the perceptually small target circle. Although Fischer (2001) has subsequently shown that this effect could be partially due to making delayed responses, there were a number of other methodological differences between the two studies that could account for the different results. Given this caveat, we contend that the effect is real and is likely due to interactions between the ventral and dorsal streams. Fitts' law (Fitts 1954) states that the distance to and width of the target determine pointing movement time. The fact that movement times are influenced by the Ebbinghaus illusion suggests that Fitts' law can be modulated by contextual information concerning relative object size. This result also suggests that pointing movements have more direct access to the perceptual attributes of a target object than do grasping movements.

The present experiments were completed to gain a better understanding of how the influence of relative size information on pointing responses is carried out within the brain. There are at least three possible alternatives. In the first, it is proposed that ventral stream processing of relative object size information interacts with dorsal stream processing associated with the preparation and control of pointing responses. Such an interaction is neuroanatomically possible because of the extensive interconnections that have been shown to exist in the monkey between the ventral and dorsal streams (Merigan and Maunsell 1993). The second alternative proposes that the dorsal stream alone is responsible for the effect since object shape information is represented in the parietal lobe (Sereno and Maunsell 1998; Sakata et al. 1999). The third alternative suggests that the processing of relative size information occurring within the ventral stream influences motor output indirectly through projections to the prefrontal cortex (Ungerleider et al. 1998) and subsequently to the motor areas of the brain (Lu et al. 1994), thus bypassing the dorsal stream altogether. In effect, these three alternatives can be reduced to the question of whether interactions between the dorsal and ventral stream are responsible for the influence of relative size information on pointing responses or whether one stream or the other accounts for the effect alone.

To test these three alternatives transcranial magnetic stimulation (TMS) was delivered over either the ventral or dorsal stream while subjects made pointing movements to physically identical target circles embedded within the Ebbinghaus illusion. The first alternative would predict that TMS should disrupt the influence of the illusion on the pointing response regardless of whether the ventral or dorsal stream is stimulated. The second alternative would predict that only dorsal stream stimulation would have this effect and the third that only ventral stream stimulation would do so. Portions of this work have been published previously in abstract form (Lee and van Donkelaar 2000).

Materials and methods

Subjects

Five young adults (three male, two female), whose mean age was 24 years, served as subjects after giving informed consent. Each subject had normal vision and possessed no neurological impairments affecting manual or oculomotor control. The University of Oregon Human Subjects Committee approved the experimental procedures.

Experimental setup

The subject was seated in a dimly illuminated room and was instructed to look down at a horizontally oriented mirror onto which target images were projected. Pointing movements were performed in an open-loop fashion with the right hand on a table underneath the mirror. A Watsmart system was used to collect kinematic data at 200 Hz from an infrared marker placed on the tip of the right index finger. A chin-rest was used to stabilize the head.

Transcranial magnetic stimulation

The subject wore a nylon swimming cap on which marks were made at the TMS sites. Earplugs were used to minimize the possibility of potential hearing damage. Stimulation was accomplished with a Magstim 200 device that delivered a single magnetic pulse through a figure-eight coil. The coil was held by hand tangential to the skull at a 45° angle from the midline. Initially, the motor hot point for eliciting muscle twitches in the contralateral hand was identified in the left motor cortex. The motor threshold at this spot was defined as the magnitude of stimulator output below which hand muscle twitches were never observed. For the experimental sessions, TMS was applied at 110% of the motor threshold. The stimulation site for the left ventral stream was identified by placing the coil halfway between a line from the inion to a point 7 cm lateral to the hot point. This latter site was used as a control stimulation site within the temporal cortex in a recent study by Desmurget et al. (1999). Thus, we feel safe to assume that we are within the ventral visual stream by stimulating at a point halfway between the occipital and temporal cortices. In addition, the fact that we observed different effects following ventral stream stimulation across conditions (see "Results") implies that it is possible to successfully disrupt processing occurring in this region of cortex using TMS. Stimulation of the left dorsal stream was accomplished by moving the coil to a position 7 cm posterior from the hot point (Terao et al. 1998). These two sites were confirmed in one of the subjects by placing high contrast markers at the locations prior to
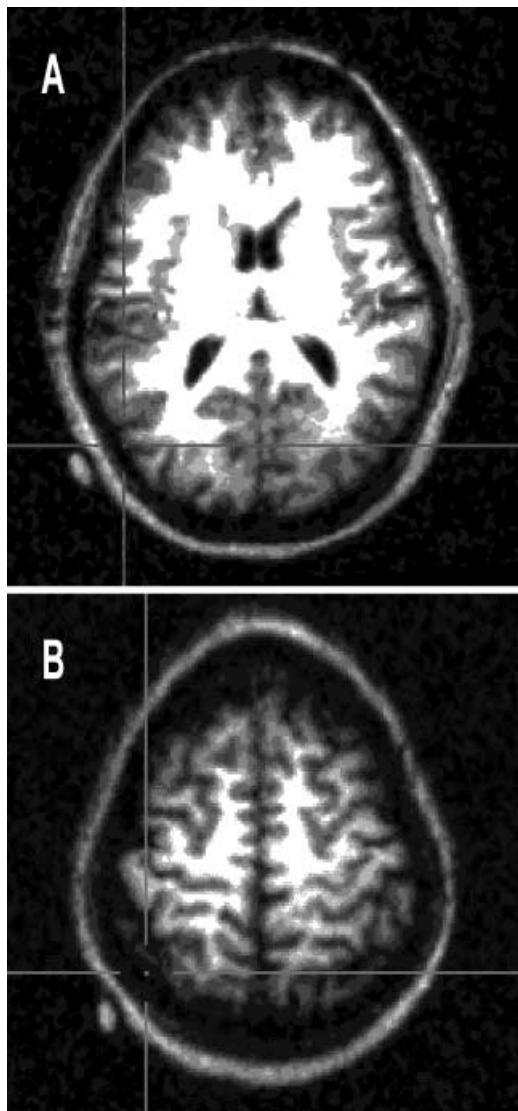
Fig. 1 TMS location sites over the ventral **(A)** and dorsal **(B)** visual streams determined by a three-dimensional MRI for a single subject using high-intensity signal markers. The crosshairs represent the estimated location of stimulation on the cortex

Fig. 2A, B Target displays used in the main and control experiments. **A** "Look-Small" condition used in the main experiment in which the target circle for the pointing response is embedded within an array of five larger circles. In the "Look-Big" condition the target display was reversed. **B** "Big" condition used in the control experiment in which the target circle for the pointing response was larger than the starting target circle. In the "Little" condition the target display was reversed

a structural magnetic resonance imaging (MRI) scan. The marker locations were reconstructed and the affected cortical sites were approximated in the Talairach and Tournoux (1988) coordinate system. The ventral site was found to be at the border between area 37 and extrastriate cortex (Fig. 1A), whereas the dorsal site was at the border between area 7 and 40 (Fig. 1B). In addition, a control TMS site [the supplementary motor area (SMA) 3 cm anterior to the vertex along the midline (Cunnington et al. 1996)] was also tested to confirm that the effects we observed were not due to any non-specific influences of the stimulation. In all cases, subjects reported no ill effects following stimulation.

Procedure

During each trial two target images were presented in a pseudo-random order. In the "Look-Little" condition, two center circles of identical size (30 mm diameter) were presented 60 mm to the left and right of center. Around the center circle on the right were five larger (54 mm diameter) circles, and around the center circle on the left were 11 smaller (10 mm diameter) circles. With this dis-
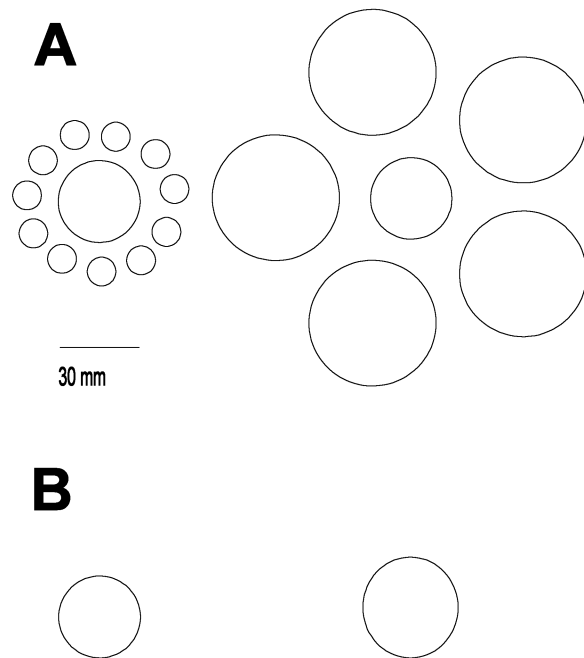
play, the center circle surrounded by the larger circles appeared to be smaller than the center circle surrounded by little circles (Fig. 2A). In the "Look-Big" condition, this display was reversed. In a control experiment, the center circles appeared without the surrounding annuli of smaller or larger circles. In the "Big" condition the circle on the right was 32 mm in diameter and the circle on the left was 30 mm in diameter (Fig. 2B). In the "Little" condition the display was reversed.

At the start of each trial, the subject pointed the right index finger at the starting position where the center of the left circle would be displayed. A small disk attached to the table allowed the subject to find this position easily. A variable period of time (500–1500 ms) afterwards the target image appeared and remained on for the rest of the trial. Five hundred milliseconds later a brief tone was presented as a "go" signal. The TMS pulse was delivered at the same time as this tone so that the effect of TMS could occur during the subject's reaction time. An initial 500-ms target viewing period was chosen because a pilot study showed that subjects exhibited the greatest effect of the illusion on their pointing movements after watching the display for this duration. The synchronization of the tone and the TMS pulse was chosen based on the fact that another pilot study demonstrated the greatest disruption of the effect with this timing. After the "go" signal, the subject was asked to move as quickly and accurately as possible to the center of the target circle on the right. After a series of warm-up trials, each subject performed 10 repetitions of each condition with stimulation over either the ventral or dorsal stream or SMA, along with control trials without stimulation resulting in a total of 140 trials for both the main and control experiments.

Statistical analysis

The mean velocity of the pointing response was the main dependent variable examined. In our previous paper we measured move-
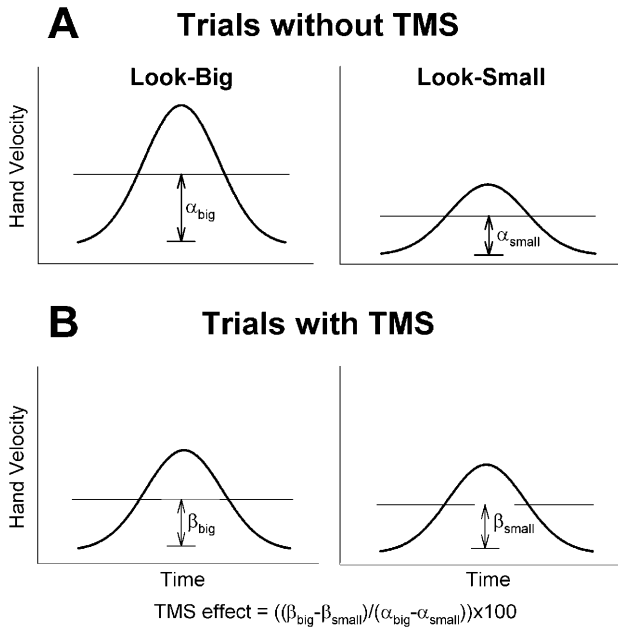
A Trials without TMS

B Trials with TMS

$$\text{TMS effect} = ((\beta_{big} - \beta_{small})/(\alpha_{big} - \alpha_{small})) \times 100$$

Fig. 3A, B Method for determining change in average velocity difference between the "Look-Big" and "Look-Small" conditions when TMS was delivered. **A** The difference in average hand velocity in each condition was first determined for trials without TMS ($\alpha_{big} - \alpha_{small}$). **B** This difference was also obtained for each of the stimulation sites ($\beta_{big} - \beta_{small}$). An index of the effect of TMS was determined by obtaining the relative percentage of the difference with TMS compared to without TMS

ment duration (van Donkelaar 1999). In these experiments, mean velocity was used because it is more intuitive and takes into account both movement time and distance. To a certain extent, therefore, this also answers one of the criticisms made by Fischer (2001) of our previous paper. To determine the effect of TMS on the influence of the illusion on the pointing responses, we first obtained the difference in velocity between the "Look-Little" and "Look-Big" conditions when TMS was not given. This value was then used to normalize the velocity differences in the conditions with TMS (Fig. 3). This same comparison was also made for the difference between the "Little" and "Big" conditions in the control experiment. In addition to the velocity measure, the movement amplitude and reaction time were also obtained. Analyses of variance were used to test whether significant differences existed among stimulation sites for each measured variable.

Results

Figure 4A displays the mean reaction times for the "Look-Big" and "Look-Small" targets from the trials with TMS delivered to different sites as well as from trials in which TMS was not given. Figure 4B shows the mean amplitudes of the pointing movements across the same conditions. A 2 (target) × 4 (stimulation condition) ANOVA revealed no significant main effects or interactions for either variable. In other words, the pointing movements took similar durations to prepare and were of equal amplitude regardless of the perceived size of the target circle or whether TMS was delivered or not.

Figure 5 shows the TMS effect on the mean movement-velocity differences between the "Look-Big" and
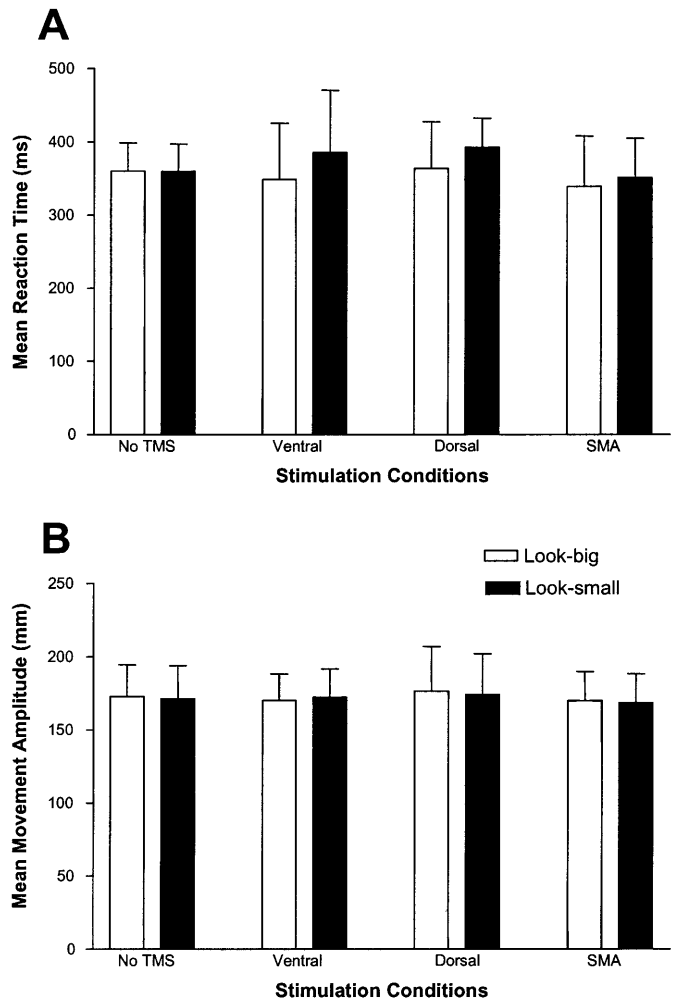

Fig. 4 Group mean reaction times for the "Look-Big" (*open bars*) and "Look-Small" (*solid bars*) targets from the trials without TMS and from trials with TMS delivered to the ventral stream, dorsal stream, and SMA (**A**) (*error bars* 1 SE). Group mean amplitudes for the "Look-Big" (*open bars*) and "Look-Small" (*solid bars*) targets from the trials without TMS and from trials with TMS delivered to the ventral stream, dorsal stream, and SMA (**B**) (*error bars* 1 SE)
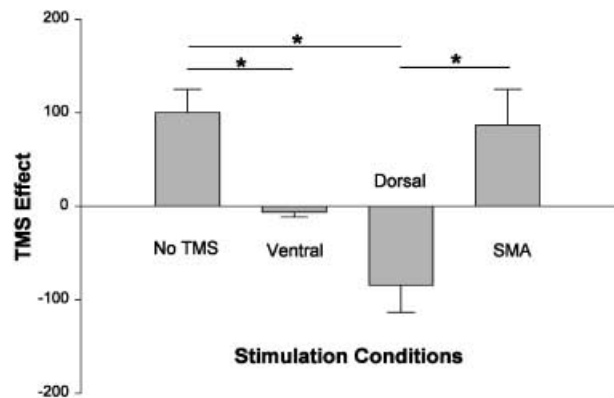

Fig. 5 Group mean differences (Look-Big–Look-Small) for pointing movement velocity during ventral and dorsal stream and SMA stimulation conditions normalized to trials without TMS. *Asterisks* represent a significant difference between the conditions (*error bars* 1 SE)

"Look-Small" conditions. With this analysis the value of the mean movement-velocity difference in the trials without TMS is 100. Thus, any value significantly below 100 would mean that the illusion had a smaller influence on the pointing velocity difference than normal. A one-way ANOVA test showed significant differences among the stimulation conditions for this measure ($F_{(3,12)}$=9.68, P=0.001). Post hoc Tukey's tests revealed that the values for the ventral and dorsal stream stimulation conditions were significantly smaller than those from the condition without TMS (P<0.05). This was also true for the comparison of the values from the SMA and dorsal stream conditions (P<0.05). Finally, the difference in the values from the SMA and ventral stream conditions just failed to reach significance (P=0.065). Thus, the illusory effect on movement velocity observed in the condition without TMS disappeared or even reversed when the ventral and dorsal streams were stimulated. Further, when the SMA was stimulated, the effect of the illusion remained. This implies that the changes that occurred with TMS over the ventral and dorsal streams were not due to some non-specific effect of the stimulation.

The results from this experiment provide support for the first alternative explanation of how relative size information influences pointing movements. In particular, they suggest that this effect occurs through direct interactions between the ventral and dorsal streams. However, it is possible that the TMS could simply be influencing basic perceptual and sensorimotor processes occurring within the ventral and dorsal streams, respectively. If this is the case, then it should also affect pointing responses made towards target displays that do not contain relative size information. This was tested in the control condition in which two circles of unequal size appeared without the surrounding annuli. Figure 6 displays the mean movement-velocity differences between the "Big" and "Little" conditions when TMS was delivered to each of the stimulation sites normalized to the mean movement-velocity difference in the condition without TMS. As in Fig. 5, a value significantly less than 100 indicates that the movement-velocity difference observed between the different-sized targets was smaller than normal. The figure shows that stimulation at the different sites caused systematic changes in the value of the movement-velocity difference as reflected in a significant effect of condition ($F_{(3,12)}$=12.8, P=0.002) in a one-way ANOVA. Post hoc Tukey's tests showed that this significant effect was due to the movement-velocity difference values in the ventral SMA, and no TMS conditions being larger than that in the dorsal condition (P<0.05). Although there was a reduction in the movement-velocity difference values in the ventral, and SMA conditions compared to the control condition, these differences did not reach significance. Thus, when pointing at targets that are physically different in size, stimulation of the dorsal stream appears to disrupt the preparation of the response; whereas stimulation of the ventral stream has a much smaller, non-significant effect. This implies that the results observed for dorsal stream stimulation in
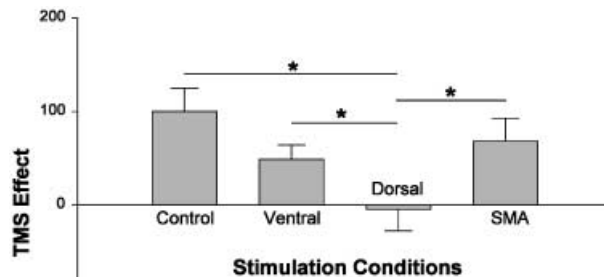

Fig. 6 Group mean differences (Big–Small) for pointing movement velocity during ventral and dorsal stream and SMA stimulation conditions normalized to trials without TMS. *Asterisks* represent a significant difference between the conditions (*error bars* 1 SE)

the main experiment were likely due to the same influence on basic sensorimotor processing and were not specific to the influence of relative size information. Taken together, the two experiments indicate that the third alternative explanation described above is more tenable. In particular, the influence of relative size information on pointing movements is mediated mainly by ventral processing that bypasses the dorsal stream – most likely via projections to the prefrontal cortex and subsequently the motor areas of the brain.

Discussion

When a person observes an object in space, the visual information about that object is divided into two major categories: perceptual and action-related information. Subsequently, these two categories of information are thought to follow two different functional pathways: the ventral and dorsal streams. Even though the existence of these two visual streams has been traditionally recognized and neuroanatomical studies in non-human primates have demonstrated extensive interconnections between them (Merigan and Maunsell 1993), the extent to which functional interactions may occur within this system of cortical sites is poorly understood. Several recent studies, however, have provided evidence that such interactions do indeed take place. At a neurophysiological level, for example, there is evidence that color information modulates the activity in motion processing cells within area MT (Seidemann et al. 1999). In addition, cells in V4 that carry object orientation information are systematically modulated by eye position (Bremmer 2000) and the preparation of saccadic eye movements (Moore 1999; Moore et al. 1998).

Behaviorally, there is evidence that visual illusions mediated perceptually by the ventral stream have, under certain circumstances, effects on motor actions that are consistent with the illusion. For example, we have shown

previously that subjects move faster toward the perceptually larger target circle of the Ebbinghaus illusion, and vice versa (van Donkelaar 1999). In the present study we used TMS to disrupt processing in selected cortical sites in an attempt to gain a better understanding of how this behavioral interaction may map onto potential neural interactions at the level of the ventral and dorsal streams. These streams are composed of a group of cortical areas which each make a unique contribution to the overall function associated with the stream. Thus, it is very likely that we would have obtained different results had we stimulated in different portions of each pathway. For example, Rushworth and colleagues (2001) have recently demonstrated that within the parietal lobe, changing the stimulation site from the angular gyrus to the supramarginal gyrus can differentially disrupt orienting versus motor attention, respectively. The dorsal site we stimulated was in the posterior portion of the parietal cortex. In the one subject in whom the stimulation site was approximated using structural MRI scans, the site was located adjacent to the intraparietal sulcus – an area known to integrate visual information into eye and arm movements (e.g., Andersen et al. 1997). The ventral stimulation site was within the posterior aspect of the inferotemporal cortex – an area known to process object shape information (e.g., Buckner et al. 1998).

The results from the main experiment showed that TMS delivered over either stream disrupted the influence of the illusion on the pointing response. At first glance, this appears to demonstrate that the influence of relative size information on pointing responses is mediated by direct interactions between the ventral and dorsal streams. In particular, if during our task the ventral stream processing associated with relative size information modulates the preparation and control of the pointing response occurring in the dorsal stream (Desmurget et al. 1999), then TMS delivered over either of these sites should disrupt the normally observed effect. In fact, this is exactly what was found (see Fig. 5).

However, these results could also have been due to the TMS affecting basic perceptual processing in the ventral stream and basic sensorimotor processing in the dorsal stream without having anything to do specifically with the influence of relative size information on pointing responses. To test this possibility we completed a control experiment in which two physically different sized target circles were used without any surrounding annuli. If the result in the main experiment was due to the TMS affecting basic processing, then the influence of TMS in the control condition should have been the same, in particular, a reduction in the effect of target size on the pointing responses following ventral stream stimulation due presumably to a disruption of the perception of object attributes; and a similar reduction following dorsal stream stimulation due most likely to a disruption in the ability to prepare and control the pointing response in a manner consistent with the different target sizes. The results showed that there was indeed a similar reduction in the effect following dorsal but not ventral stream stim-

ulation. This has two implications. First, it demonstrates that the effect of dorsal stream stimulation in the main experiment was due to a disruption in the preparation and control of pointing movements in general and had nothing to do specifically with the relative size information contained within the Ebbinghaus display. This suggests that the dorsal stream contributes to sensorimotor transformations required for pointing responses based on *both* real and illusory size information.

The second implication of this result is that the ventral stream most certainly contributes to the influence of the illusion on the pointing response and that this contribution must be at least partially mediated through projections other than those to the dorsal stream. This is neuranatomically feasible because the ventral stream projects to parts of the prefrontal cortex (Ungerleider et al. 1998) that subsequently interact with motor areas (Lu et al. 1994). This conclusion is also supported by the fact that parietal lobe lesions influence motor output driven by visuospatial but not color information (Pisella et al. 2000); that prefrontal activity is correlated with learning the association between a specific visual context and the responses that are appropriate in that context (Passingham and Toni 2001); and that different subgroups of prefrontal cells reflect the perception induced by a visual illusion versus the planning of the motor response based on the illusion (Lebedev et al. 2001). Obviously, our interpretation of the results from the present experiment could be directly tested by delivering TMS over the prefrontal cortex during this task. If the prefrontal cortex is truly contributing to the illusory effects on the pointing responses, then TMS here should also be disruptive. Such an experiment is planned in the near future. Finally, the fact that ventral stream stimulation had an effect when illusory, but not real, size differences were present does not suggest that the temporal lobe only mediates the perception of the former but not the latter. Rather, it implies that the ventral stream makes a significant contribution to *pointing* movements based on illusory size information but not to those based on real size information.

It is possible that the effects we observed were due to a disruption in attentional mechanisms that are vital for task performance. However, we think that this is unlikely based on the fact that the reaction times and movement amplitude measures were not influenced by the stimulation. If attention were affected in a general way by the stimulation, then one might have expected to observe at least an increase in variability in the time taken to respond or the distance moved on each trial. However, this was not the case. This conclusion is supported by the fact that stimulation at a control site (SMA) did not lead to any changes in performance when compared to trials without stimulation.

One could also argue that our version of the task did not require a substantial contribution from the dorsal stream because "non-standard" sensorimotor mappings apply under these conditions (Carey 2001). In other words, because the subject was not required to react to

the appearance of the target when it first appeared and made the pointing response without full visual feedback, the task may be mediated more by processing occurring in the ventral stream. This certainly could account for the fact that the ventral stream stimulation was effective in the illusory, but not the real, size difference conditions. However, we feel that the dorsal stream is making a significant contribution to this effect, albeit more in terms of the motor response that is generated. As for the conditions stressing ventral more than dorsal processing, we have shown previously that eye-hand interactions generated under similar conditions are disrupted by posterior parietal stimulation (van Donkelaar et al. 2000). Thus, we feel confident that the effects observed in the present experiment are not due simply to the nature of the experimental conditions, but rather to real contributions from each stream.

Conclusion

The present results suggest that the ventral stream contributes to pointing movements based on relative object size information via its projections to the prefrontal areas and not necessarily through interactions with the dorsal stream. By contrast, the dorsal stream contributes to pointing movements in general and the influence it has during pointing movements made towards target circles embedded within the Ebbinghaus illusion does not appear to be related to the fact that relative size information is present in the display.

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