TMS can reveal contrasting functions of the dorsal and ventral visual processing streams.

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Abstract:

In order to investigate the functional specificity of the dorsal and ventral visual processing steams we used transcranial magnetic stimulation (TMS) to briefly disrupt one or the other while subjects performed three tasks, involving discrimination of colour or shape or relative position. TMS was delivered over right posterior parietal cortex (PPC) or right lateral occipital (LO) cortex, regions known to have visuo-spatial and object processing properties respectively. LO but not PPC stimulation had a significant effect on reaction time when subjects were asked to make a discrimination of relative shape. PPC stimulation had a significant effect when subjects were asked to discriminate relative position of the same shapes. Stimulation of LO also lengthened reaction times on the position task. There were no effects of stimulation at either site on colour discrimination. Results are discussed within the framework of how the dorsal stream and ventral stream are dissociated following their damage in neurological patients and possible ways in which they may interact in the normal brain.

Introduction

Neurological patients with dorsolateral parietal damage and classical left hemineglect also have deficits in processing line bisection or landmark tasks (Harvey *et al.*, 1995). However, if they are asked to point to the middle of the screen or a shape, they can do this accurately, presumably by making a discrimination based on shape rather than spatial extent and thereby recruiting their undamaged ventral stream (Bartelomeo *et al.*, 2003), even though there is a visuomotor component to the task which may recruit dorsal function (Goodale & Milner 1992). The following study seeks to investigate the difference, if any, between the dorsal and ventral streams in how they process space, items in space, and colour.

Much of the recent research investigating the differential function of the dorsal and ventral streams has focussed on the influential Goodale and Milner "what and how" model (1992). This theory was formulated in part by observations made in two neuropsychological conditions, optic ataxia and visual form agnosia. It was revealed that patients with damage to the ventral and ventro-lateral occipito-temporal regions could no longer recognise objects or estimate their size or shape but could physically manipulate them correctly (Milner *et al.*, 1991; Carey *et al.*, 1996). On the other hand, patients with dorsal damage centred on the angular and supramarginal gyri of the posterior parietal cortex demonstrate severe visuomotor deficits, dissociated from their preserved ability to recognise objects and perceive their shape and size etc. (Milner *et al.*, 2001, Jeannerod *et al.*, 1994; Perenin and Vighetto, 1988).

The model of Goodale and Milner is a modification of the original two streams hypothesis of Ungerleider and Mishkin (1982), which established a distinction between "what and where" pathways for the ventral and dorsal streams respectively. There has been intensive subsequent investigation into interactions between "what and where" and "what and how" and the anatomical overlap of these systems as shown by neuroimaging techniques, which have been very successful in confirming the underlying basis of functional dissociations seen in neuropsychology. (Faillenot *et al.*, 1997; James *et al.*, 2003). These investigations indicate that object-oriented action and object recognition activate a common posterior parietal area. Hence, regardless of the task required, some aspects of object perception appear to be involved in the analysis of object properties. As Creem & Proffitt (2001) point out, this type of object

analysis appears to be distinct from an analysis performed in the ventral temporal and lateral-occipital cortex and is more consistent with theories that there is some object-based analysis in the dorsal stream (Jeannerod, 1997; Milner & Goodale, 1995; Creem-Regehr & Lee, 2005).

The present study attempts to delineate the perceptual dissociation of these two streams using transcranial magnetic stimulation (TMS) and three simple visual tasks involving a spatial, colour and form discrimination. TMS provides a means of briefly disrupting neural functioning, allowing us to probe the necessity of the region of interest in the processing of the task. As previously discussed, neuropsychology and neuroimaging have identified many areas of specialisation interacting in broad streams of processing in these domains. However, our aim is to investigate the differential involvement of two areas in these three tasks: right lateral-occipital area (LO) known to be an important region in object recognition in the ventral stream (Ferber et al, 2005, Avidan *et al.*, 2003, Lerner *et al.*, 2002; Kourtzi & Kanwisher, 2001) and an area of right posterior parietal cortex (PPC) known from many studies to have visuospatial specialisation (Avidan at al., 2003, Ellison *et al.*, 2003; Bjoertomt *et al.*, 2002). As these areas are part of the established processing streams, if either is involved in the processing of a task, a deficit in performance should be demonstrated following disruption by TMS.

It could be predicted that as spatial considerations are important in the perception of shape, right dorsal PPC will be just as involved as ventral LO in the shape task. Equally, as the task is presented in distributed space, right PPC may have a role on these grounds. Another factor that may influence involvement of PPC in this task is the nature of the performance indicator. Subjects are asked to press a button related to which item matches a foveally fixated comparison item, which is an action based on perception. If these two acts (one perceptual, one motor) are in any way linked, one would expect PPC involvement in all tasks. However, due to the regional spatial specificity of TMS, if LO is the only critical area involved in the processing of this task, then a dissociation between involvement of LO and PPC would be expected.

The other two tasks involve a visuospatial allocentric discrimination (relative position or distance) and a colour matching task. One would predict little involvement of the

LO site in the distance discrimination and little involvement of PPC in the colour task (unless the action to be taken upon this discrimination drives PPC involvement in accordance with the Goodale and Milner (1995) model). Colour recognition and naming in visual-form agnosia patients is usually spared (Aglioti *et al.*, 1999; Milner & Heywood,1989) allowing patients the ability to use this information for implicit perception of shape (Kentridge, Heywood & Milner 2004). However, we are particularly interested in the possible role of LO in the use of colour information for discrimination in normal neural processes.

Methods

Subjects

Eight healthy subjects, aged 19-23, with normal or corrected to normal vision (all right handed; 4 female, 4 male), participated in all three tasks. Subjects gave their signed informed consent in accordance with the Declaration of Helsinki and with the approval of Durham University Ethics Advisory Committee, and could leave the experiment at any point. Subject selection complied with current guidelines for rTMS research (Wassermann, 1998).

Stimuli

All stimuli were presented on a 32cm x 24cm VDU driven by a Pentium-4 PC programmed in E-Prime (Psychology Software Tools, Inc). Subjects were seated 57.5 cm away from the screen with the centre of the screen at eye level. The subjects' head and trunk sagittal midline was aligned with the centre of the screen, and head position was controlled by a chinrest. Eye movements and eye blinks were not continuously monitored, given our earlier experiments in which TMS in these regions did not affect either of them. Also, direct observations by the experimenters, which readily reveals blinks and saccades during the half second period of stimulus presentation and TMS, showed no such effects.

Visual Tasks

Three visual tasks were used (see Figure 1). The threshold for 80 per cent correct performance in each task had first to be determined. In all tasks one item was presented in the centre of the screen with two items presented at a lateral, left, eccentricity, one either side of the horizontal midline as detailed below (see Figure 1).

In each task, every trial began with 500ms central fixation cross (0.5º x 0.5º) after which the three stimuli were presented for 500ms, one of them replacing the fixation cross. The background colour was a uniform grey with a luminance of 30cd/m^2. There was a 4 second interval between trials. The difficulty of the task was titrated by making it progressively more or less difficult according to the following rule. Difficulty was modulated after each set of five trials. After five consecutive correct responses difficulty was increased by one step (steps are described in detail below in the description of each task). If two or more incorrect responses out of five were made, the difficulty was decreased by one step. Performance was deemed stable when performance reached 80% correct (4 out of five) in two subsequent sets.

Distance Task:

Stimuli were presented as green (11 cd/m^2) squares of 1º x 1º with one square presented in the centre of the screen. The other two items were presented 5º to the left of the vertical midline. One square (either the top or the bottom) was always 3º above or below the horizontal midline. The other square was initially presented at a vertical eccentricity of 4 degrees from the horizontal meridian and progressively it approached it in 0.2º steps until the threshold for 80% correct was reached. The experimental value of the distance of the furthest object from the centre was then set at 0.2º more than the threshold value found. The subject was asked to respond by indicating which item was closest to the item in the centre by pressing the bottom button on a keypad if the bottom item was closest and the top button if it was the top item. The top square was the closer item in 50% of trials, at random. See Figure 1.

FIGURE 1 ABOUT HERE

Shape task:

Two shape sets comprised this task. The first set used an outlined central square (1º x 1º) and in the other set the central shape was an outlined oblong of equal area, subtending 1.47º x 0.69º. Stimuli were presented in the same format as the distance task but position was fixed 5 degrees to the left of the vertical midline and 4º either side of the horizontal midline (see Figure 1). The non-identical shape differed from the central shape by 0.5º in the x and y axis (in order to maintain equal area) initially. It approached the shape of the central item in 0.1 degree steps until threshold was

reached at 80% correct. On half of the trials, at random, the central shape was the square and on the other half it was the oblong. The experimental value of the shape different from that in the centre was then set at 0.1° larger than the threshold value found. The subject was asked to respond by indicating which item was the same shape as the item in the centre by pressing the bottom button on a keypad if the bottom item was identical and the top button if it was the top item. The top item was the same shape in 50% of trials (see Figure 1).

Colour task:

All three items used in this task were a coloured square subtending 1° x 1°. Stimuli were presented in the same manner as the shape task with position of squares fixed 5° to the left of the vertical midline and 4 degrees either side of the horizontal midline (see Figure 1). Two colour sets were used, in the first the central colour was bluish (x = .208, y = .265) and in the second set was purple (x = .173, y = .084). Non-identical colours differed from the central colour in increasingly small steps, as shown in Figure 2, until threshold was reached at 80% correct.

FIGURE 2 about here

Half the trials, at random, used the first colour set with the other half comprising the second colour set. The experimental value of the colour that differed from that in the centre was then set at one step higher than the threshold value found. The colours in each set were not photometrically isoluminant (which is difficult to achieve with E-prime) but at threshold performance the luminance difference between the sample and the odd-one-out was just below 10 per cent for the blues and just above for the purples. Given the notorious difficulty of judging the relative brightness of different colours and the subsequent statements of all subjects, when asked, that their judgments were based on colour, we can be confident that the task was not being solved on the basis of small luminance differences. The subject was asked to respond by indicating which item was the same colour as the item in the centre by pressing the bottom button on a keypad if the bottom item was identical and the top button if it was the top item. The top item was the same colour in 50% of trials. See Figure 1.

TMS

A Magstim™ SuperRapid machine was used to apply pulses at 10Hz for 500ms at 65% of the stimulator's maximum power (*i.e.* 1.3 Tesla) using a 70mm figure-of-eight coil held in place by the experimenter and placed tangential to the skull, with the handle pointing backward, parallel to the horizontal and the mid-sagittal plane. This magnetic intensity is greater than the threshold intensity required to induce movement (over motor cortex) or the perception of phosphenes (over primary visual cortex, V1) in all of the subjects but did not produce phosphenes when delivered over LO or PPC. The TMS train of 5 pulses began at stimulus onset in each case. If the experimenter detected any head movement the coil was always repositioned, even if both head and coil probably moved in unison.

Two sites of stimulation were used, a right ventral stream site (LO) and a right dorsal stream site (PPC). The dorsal site was chosen as an area of posterior parietal cortex (PPC) known to be involved in difficult conjunction visual search tasks that engage dorsal functions. To this effect it was identified by using a hunting procedure with the hard conjunction task, as described in Ashbridge *et al.* (1997) in which 10 trials of single-pulse TMS are given to each site in a 3 x 3 grid (each point 1 cm apart) around a central point 9 cm dorsal to the mastoid-inion and 6cm lateral to the right. The "hotspot" for activation is denoted by a roughly 100ms increase in reaction time compared to the trials in which no TMS was administered. The position of this area as co-registered with cortical position using BrainSight software (Rogue Research™) is shown in Figure 1. The ventral site was chosen in relation to area right V5 (generally corresponding to 3cm above the mastoid-inion and 5cm lateral to the right) which was precisely identified by localising the area where a train of TMS pulses (10Hz, 500ms) elicited the strongest and most salient moving phosphenes (see Schenk *et al.*, 2005) at the lowest TMS intensity. The ventral site LO was then calculated to be 1-1.5cm caudal on the skull in a direct line towards the inion in accordance with various anatomical and functional maps (e.g. van Essen et al., 2001) and co-registration with structural MRI using frameless stereotaxy (BrainSight™). This area can be seen to correspond well with lateral occipital cortex (LO) (see Figure 1).

Trials were administered in six blocks of 20 trials (per task) each randomised across subjects to minimise either order or practice effects; two blocks with TMS over PPC on each trial, two blocks with TMS over LO on each trial and two blocks of sham TMS. In sham TMS, a non-discharging coil was placed over either the PPC or LO site whilst the discharging coil was placed a few cm above it so that the subjective experience of the noise associated with a TMS pulse was the same as was the tactile experience of a coil placed on the head. However, no effective pulse was administered to the brain. The testing session usually lasted no more than 1.5 hours.

Results

Thresholds:

The mean threshold achieved across subjects in the distance task was a difference of 0.43 ± 0.10 degrees for 80% correct. This led to a fixed distance of 0.63 ± 0.10 for the furthest square in the experimental task. In the shape task, performance reached threshold at a 0.12º ± 0.02º difference in shape, leading to a fixed 0.21º ± 0.02º difference in the experimental session. A threshold difference of 35 ± 5 units was achieved in the colour task meaning the difference in colour was fixed at 52.5 ± 3.66 units in the experimental task. Although the colours were not initially isoluminant, the final colours determined by prior titration differed only slightly in luminance. Also, all subjects confirmed that their judgement was based on the colour of the targets. Across all three tasks the chosen stimulus values corresponded to about 90% correct in each subject to maximise the possible effect of TMS on reaction time in each task without encountering the problem of ceiling effects.

Effect of TMS:

A two factor (Task [distance, shape, colour] x TMS [LO, PPC, sham]) ANOVA revealed a main effect of task ($F_{(2, 14)} = 5.183$, $p = 0.021$) and TMS ($F_{(2, 14)} = 20.203$, $p < 0.001$) and a significant interaction between task and TMS ($F_{(4, 28)} = 5.510$, $p = 0.002$). A corrected α of 0.0025 was used in the post-hoc Bonferroni tests, reflecting the two comparisons done within each task (sham v PPC and sham v LO). These revealed significant differences between sham and LO TMS for the shape task ($t = -4.009$, $df = 7$, $p = 0.005$) and between sham and PPC TMS for the distance task ($t = -4.241$, $df = 7$, $p = 0.004$) . TMS over LO also induced a significant increase in reaction time in the distance task ($t = -3.371$, $df = 7$, $p = 0.012$). No significant differences were seen in the colour task at either site (see Figure 3).

FIGURE 3 about here

Discussion:

The results show that posterior parietal cortex has an influential, possibly vital role in the processing of a task requiring a spatial discrimination (distance task) but not one that requires a discrimination based on either shape or colour features. Conversely, the ventral stream is clearly involved in the processing of a shape discrimination but, apparently paradoxically, not colour discrimination.

Whilst it was not unexpected to demonstrate involvement of right PPC in the processing of a visuospatial task, the involvement of the ventral stream cannot be ignored. If LO has a specialisation for perceptual shape as neuropsychological (Goodale *et al.*, 1994) and functional neuroimaging (Kourtzi & Kanwisher, 2001, Malach *et al.*, 1995) results indicate, then it is reasonable to assume that some shape based processing must contribute to how the brain computes the distance discrimination. This reinforces the dissociation reported by Barolomeo and colleagues (2003) that when patients with neglect are asked to point to the middle of a screen or shape they are unimpaired, presumably as a result of the functional processing of shape in their intact ventral stream. Taken together, these findings evince the contribution of shape processing to the processing of space.

Our tasks did not require visuomotor manipulation of the visual target, unlike many of the neuropsychological dissociation studies of dorsal and ventral streams (Milner et al, 1991; Goodale et al, 1994). However they did require a motor action based on a cognitive perceptual decision. Nonetheless, this motor component was not sufficient to involve PPC in the shape task, and so it is reasonable to assume that the involvement of this region in the distance task was visuospatial in nature. Indeed, as Grafton *et al.* (1992) suggested, there may be functionally distinct portions of the superior posterior parietal lobe that are necessary for integrating visual cues with movement selection and that it is damage to these regions that causes the visuomotor problems seen in parietal patients with neglect. In contrast, the inferior parietal lobule may be more responsible for directed visual attention and may be more involved in "where" functions. Due to the focal nature of TMS disruption, these functions can be teased apart for each stimulated site.

Our results show that there are regionally separable processes in the brain for shape based discrimination and a less clear dissociation for a spatial discrimination. Following a neuroimaging study, Fink *et al.*, (1997) suggested that "object-based and space-based attention share common neural mechanisms in the parietal lobe". If this were the case, we should have seen involvement of right PPC in both the object and spatial discriminations, which we did not. Instead, the current disruption study suggests that spatial discrimination recruits a mechanism used in object processing but not vice-versa. Furthermore, these mechanisms occur in disparate regions of cortex, namely right PPC and LO. Future experiments should investigate how and what these areas contribute to spatial processing perhaps by looking at the timing of their involvement. Any differences uncovered here might shed some light on this surprising result and go some way to investigating how PPC and LO work together in the processing of this task.

Stimulation of neither PPC nor LO had an effect on the processing of the colour task. Although it could be argued that subjects were solving the colour task on the basis of small unavoidable luminance differences between the colours, as mentioned under methods, this cannot be correct because PPC stimulation should have disrupted such luminance judgements. The simplest explanation is that it is another area, such as ventro-medial human V4, which is the most indispensable area for the processing of colour, although lesions to area V4 alone in monkeys have only slight effects on colour discrimination and are certainly not sufficient to produce achromatopsia (Cowey & Heywood, 1995). It would seem that co-operation between areas is required to process colour fully, both cortically and sub-cortically (Cowey & Heywood, 1995; Heywood *et al.*, 1992; Zeki & Marini, 1998; Bartels & Zeki, 2000) However, although patients with visual shape agnosia caused by damage to the ventral stream are usually unimpaired in colour naming and recognition (Aglioti *et al.*, 1999; Milner & Heywood 1989), we were interested in the role of LO in the use of colour information for discrimination in normal neural processes. However, such an involvement may only be uncovered if the shape discrimination is made to be contingent upon colour discrimination.

All the effects reported here involved the lengthening of reaction times; percentage correct performance was not altered. We are now exploring a variety of other displays

together with briefer stimulus presentations in order to determine whether performance as well as reaction time can be selectively impaired.

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Figure legends

Figure 1: Tasks used (distance, shape and colour) and anatomical localisation of magnetic stimulation sites (right LO and right PPC).

Figure 2: CIE diagram showing the position in colour space of the eight bluish stimuli (top cluster) and the eight purplish stimuli (bottom cluster). For each cluster the dot at the left is the foveally fixated stimulus and the dot at the right is the colour most different from it. Intervening dots show the colours of smaller hue difference. It should be noted that the bluish stimuli are less saturated (closer to the centre of CIE space) than the purples.

Figure 3: Reaction times compared for each task at each site of stimulation.

Distance task

Shape task
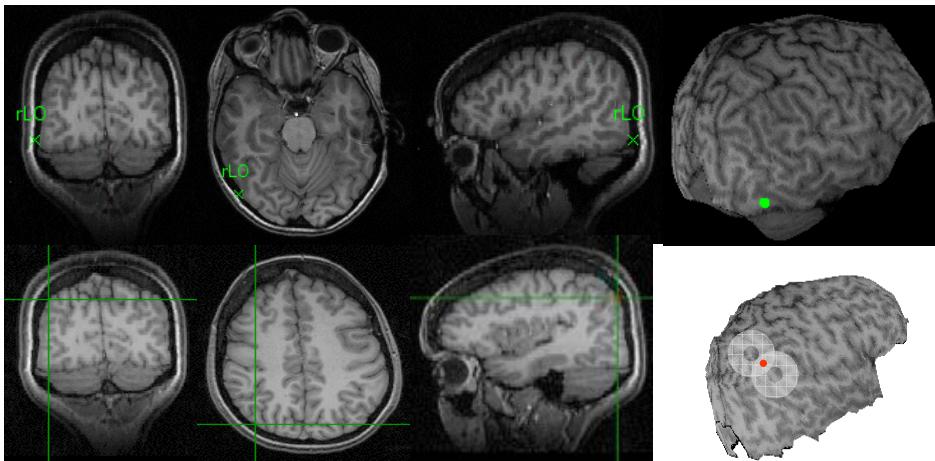
Colour task

Which is closer to the central item?

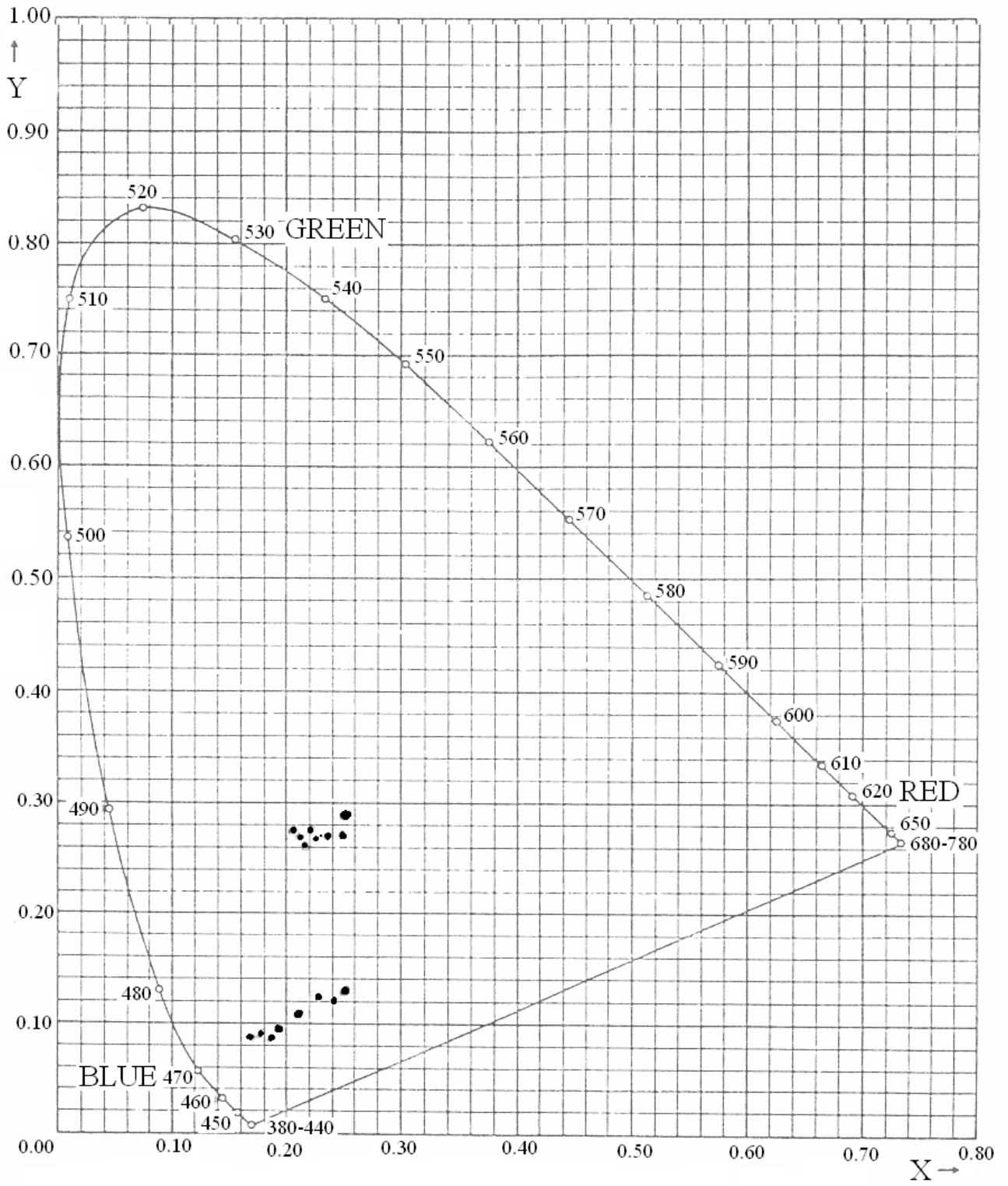*Which is the same shape as the central item?*

Which is the same colour as the central item?

LO

PPC

Reaction time data in all tasks for each site