Neuropsychologia 48 (2010) 1376–1384

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Degraded transfer of memories between the visual hemifields in normal macaques revealed by a novel infrared eyetracking method without head fixation

Charles R.E. Wilson*, Mark J. Buckley, David Gaffan

Department of Experimental Psychology, Oxford University, South Parks Road, Oxford OX1 3UD, UK

ARTICLE INFO

Article history:
Received 5 August 2008
Received in revised form 5 January 2010
Accepted 6 January 2010
Available online 14 January 2010

Keywords:
Monkey
Macaque
Visual field
Memory
Eyetracking

ABSTRACT

Electrophysiological evidence in macaque monkeys indicates that when the monkey views a visual scene with objects present in both visual hemifields, the cells of the temporal lobe respond to objects in the contralateral field, but are hardly affected by objects in the ipsilateral field. If visual memories are stored in the temporal lobes, as is generally believed, then this implies that the transfer of visual object memories from one hemifield to the other should either fail or at least suffer decrement. Building on a previous study in human subjects, we tested this prediction in rhesus monkeys (*Macaca mulatta*). We developed a method for tracking the eye movements of the awake, behaving monkey, which does not require the monkey to be restrained or surgically prepared. We optimised the system to provide reliable feedback of eye position in real time, and so provide hemifield-specific presentation of visual objects. In each acquisition phase the monkeys learned several object discriminations concurrently, each object only ever being presented to one hemifield, and with an object present in each hemifield on every trial. In subsequent transfer tests with the same objects, the monkeys performed significantly worse when the objects were shifted to the opposite hemifield than if shifted the same distance within one hemifield. Thus, in monkeys as well as in humans, and in association learning as well as in recognition memory, visual memories can be to a large extent hemifield-specific. This result shows that, like perceptual systems, mnemonic systems of the temporal lobe are largely hemifield-specific, and this has clear implications for studies of the temporal lobes. Further, the validation of our method will allow us to use it, in future experiments, to investigate in monkeys the effects of specific unilateral lesions on visual perception and memory for objects that are presented in known positions in the visual field.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

When a primate views a complex visual scene, the mnemonic processing of the scene and the objects within it is in part dependent on the temporal lobe, and it has been proposed that inter-hemispheric exchange of information via the corpus callosum and anterior commissure allows the scene to be remembered as a unified whole (Black & Myers, 1964; Eacott & Gaffan, 1989). Early evidence indicated that there is bilateral representation of visual memories (Myers & Sperry, 1958) distributed across both temporal lobes via these forebrain commissures (Ringo, 1993).

Investigations of the effects of unilateral lesions in the human brain on memory, however, often show lateralised effects in the visual hemifield opposite the lesion (e.g. Hornak, Oxbury, Oxbury, Iversen, & Gaffan, 1997; Vuilleumier et al., 2007). Further, electrophysiological evidence has questioned the simple account of the integration of information across the meridian. When a monkey views a single visual object on a blank background, neurons in inferotemporal cortex of both hemispheres respond to the object in a manner reflecting its identity regardless of its location with respect to the vertical meridian (Chelazzi, Duncan, Miller, & Desimone, 1998), in line with the stated idea of bilateral representation of the visual memories (Myers & Sperry, 1958; Ringo, 1993). Chelazzi et al., however, also included a condition with one object presented in each hemisphere. In this condition, neurons in the temporal lobe only responded to objects in the contralateral visual field, and were barely affected by objects in the ipsilateral field. This latter condition, with objects present in both hemifields, is a much more naturalistic example of a visual scene. Ringo (1993), in common with a range of early studies of inter-hemispheric transfer (Black & Myers, 1964; Gazzaniga, 1966; Myers & Sperry, 1958), employed the technique of sagittal section of the optic chiasm and monocular occlusion. Whilst this preparation ensures that visual information is only present in one hemifield, it also leaves the other hemi-

* Corresponding author. Tel.: +44 1865 271417; fax: +44 1865 310447.
E-mail address: charles.wilson@psy.ox.ac.uk (C.R.E. Wilson).

0028-3932/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2010.01.003

field completely blank. The electrophysiological evidence above suggests that it may be *only* in this special case that objects are represented in both temporal lobes (Chelazzi et al., 1998).

The data therefore suggest that under conditions of viewing a naturalistic scene containing several objects, with at least one per hemifield, the visual object information in the temporal lobes is confined to the objects presented to the hemifield contralateral to presentation. The modification of neuronal responses in the same area of temporal cortex is thought to be involved in the laying down of associative memories (Miyashita, 1988; Miyashita & Chang, 1988). Combined, then, these data derive the somewhat counterintuitive prediction that in the case in which a visual object memory is acquired solely in one hemifield, and then presented for retention solely in the other hemifield, the retention should fail or suffer significant decrement, even in a completely intact subject, so long as there are objects present in both hemifields. The current experiment tested this hypothesis in the macaque. The monkeys learned several concurrent object discriminations in which the objects only ever appeared in a single hemifield, and in which there was always one object in each hemifield. We then tested their performance on these discriminations following one of two possible shifts of the objects' retinal position, either vertically within a hemifield or horizontally from one hemifield to the other. We predicted that the latter case would induce a retention decrement relative to the other condition.

Previous work in humans hints that this indeed may be the case. In two cases, recognition of objects presented in one hemifield and tested in the opposite hemifield was impaired when compared to recognition of objects learned and tested in different locations within the same hemifield (Gratton, Corballis, & Jain, 1997; Hornak, Duncan, & Gaffan, 2002). The current study built on these results in several important ways.

First, the experiment used rhesus monkeys, in an attempt to confirm the prediction derived from the electrophysiological result of Chelazzi et al. (1998) in the same species. If the reported neuronal mechanism has the behavioural effect predicted, there are wide ranging implications for the way in which visual object information is transferred between the hemifields. Second, the current study employs an associative learning task, rather than the recognition memory employed in the human studies, allowing us to show that the effect applies to visual object memory in general. Third, related to the previous point, because the task is associative, the memory test is applied over a number of trials, rather than the single recognition trial employed in the human studies, again demonstrating that the effect is robust and generalised in visual memory. Fourth, the current study employs an eyetracking technique, which allows the monkeys to view the objects in the periphery for an extended amount of time, and not the limited 200 ms or 100 ms tachistoscopic presentation used by Gratton et al. (1997) and Hornak et al. (2002). This means that the viewing of the presented objects is more naturalistic in the current experiment.

Existing methods for measuring the direction of gaze in the monkey require the surgical implantation of a head-post for head restraint, and often the implantation of scleral search coils (Fuchs & Robinson, 1966; Judge, Richmond, & Chu, 1980). The current study represents the start of a project to investigate inter-hemispheric transfer of visual information using lesions in the monkey. It is difficult to use the head-post technique in experiments to investigate lesion effects, because the presence of a head-post impedes surgical access to the brain, and ideally, in a lesion experiment with monkeys, one should measure the pre-operative ability of each animal in the task of interest before making any lesion. As such we have developed a method for measuring gaze direction that allows us to present visual stimuli at known positions in the visual field in normal monkeys with no head-post or other surgical preparation.

Our eyetracking method was designed with two important constraints. First, it had to be able to use information about eye position to control the presentation of visual stimuli online, so that stimuli could be presented at a known retinal location and blanked immediately whenever the monkey broke central fixation. Second, it had to be able to provide these data in a freely moving monkey, i.e. one without an implanted head-post. This latter constraint provides two advantages. First, it allows subsequent investigation of lesion effects as described. Second, it represents a significant refinement of the technique for monkey eyetracking, which may substantially improve the welfare of monkeys used in experiments on visual perception and memory.

The monitoring of gaze direction in monkeys without head restraint has been accomplished before. Bagshaw, Mackworth, and Pribram (1970b) produced a method that has been modified and adapted for a number of uses (Bagshaw, Mackworth, & Pribram, 1970a, 1972; Oscar-Berman, Heywood, & Gross, 1971; Pascalis & Bachevalier, 1999). In general these methods require the monkey to observe stimuli through a window, as our method does, though they control eye placement with a facemask into which the monkey places its face at the start of each trial, something that our method does not require. Gaze direction is then analysed post hoc using a frame-by-frame analysis, usually employing the reflection of stimuli on the cornea as a reference. This provides information about which of two lateralised stimuli the monkey is observing, or whether or not the monkey is observing the stimulus at all. The method presented here has a much greater degree of accuracy, can provide precise information about fixation of any point on the display, and crucially provides gaze direction information in real time such that it can be used to control stimulus presentation, allowing hemisphere specific stimulus presentation. We therefore regard it as a significant advance.

2. Methods

2.1. Part 1: eyetracking procedure

2.1.1. Subjects

Eight male rhesus monkeys (*Macaca mulatta*) acted as subjects in the development of the eyetracking technique. The monkeys' mean weight was 6.8 kg (range 4.3–7.6 kg) and their mean age was 5 years 9 months (range 3 years 11 months to 6 years 3 months) at the start of testing. The monkeys are labelled M1–M8. Monkeys M1 and M2 subsequently acted as subjects in the inter-hemispheric transfer experiment (see Part 3). These two monkeys were the first to master the use of the eyetracker via the shaping procedure described below. All of the monkeys were experimentally naïve prior to the commencement of the current study. All monkeys were housed socially in accordance with UK Home Office guidelines, and water was continually available in the home cage.

2.1.2. Apparatus

Monkeys were wheeled to the testing cubicle in a metal transport cage with a sitting area of 600 mm × 500 mm × 450 mm. One side of the cage allowed the monkey access to the experimental area. The bottom 125 mm of this side was open so the monkeys were able to reach to obtain food rewards (see below). The top section was solid metal with three holes cut into it. The first was the viewing window, and was placed 390 mm above the base of the transport cage, centrally in left-right terms, and was 65 mm × 35 mm. This window was designed for the monkeys to view the stimuli through, and was sized and positioned such that the monkeys could comfortably look out through the window with both eyes. The remaining two were the hand holes, and allowed the monkeys to grasp external bars to make the viewing position more comfortable.

The experiment was conducted in an automated testing apparatus contained within an experimental cubicle that was dark except for the display background illumination, and the infrared camera (see below). The transport cage was secured such that the viewing side was opposite and 870 mm from a large display screen 860 mm × 520 mm with a display resolution of 800 × 600 pixels. In the current experiments the area used for stimulus presentation was a square of length 520 mm, subtending an angle of 34.7° at the focus point (see below), and utilizing the full height but not width of the screen. The screen was positioned such that the centre of the viewing window was vertically and horizontally in line with the centre of this stimulus presentation area.

Positioned 445 mm from the transport cage in front of the screen was the eyetracking camera with infrared probe lights (Sony AF CCD EVI-D31, Sony, Tokyo,

Japan), which formed part of the ASL 5000 Eyetracking System (Applied Science Laboratories, Bedford, MA). The lens of the camera was situated 174 mm below the centre of the viewing window, and thus barely obscured the screen behind it, but had a complete view of the viewing window itself. The camera was zoomed and directed on one half of the viewing window, with its lens focussed 20 mm inside the transport cage. These parameters were derived from measures of the positions monkeys M1–M5 initially adopted in the apparatus when looking through the viewing window. The effect of the camera settings was that when the monkey viewed the screen with both eyes positioned centrally in the viewing window, the camera was focussed on the monkey's right eye. Throughout the development of the technique the monitoring of eye position used the right eye, and the direction of the camera, its state of zoom, and the location of focus relative to the viewing window remained constant. The location 20 mm inside the cage will be referred to as the focus point. The monkey was able to learn an optimal position within the transport cage from which to provide the eyetracking camera with data sufficient to control the behavioural tasks. The monkey therefore adopted the same position for each trial, with his right eye at the focus point, because otherwise the apparatus would not register the presence of his eye, and he would be unable to obtain food rewards. Hence we can be confident of the measures of visual angle described here, despite the lack of physical head fixation. All measures of visual angle are described from the focus point.

Through the bottom of the transport cage, monkeys were able to access the inside of an otherwise closed wooden box. An automated pellet-dispensing device made an audible beep when delivering banana flavoured reward pellets (190 mg; P.J. Noyes, Lancaster, NH) into a hopper on the right of the box. Left of this was an automated spring loaded lunchbox (200 mm × 100 mm × 100 mm), which opened immediately following the end of each daily session to deliver the animals' daily diet of wet primate chow, pieces of fruit, dates, and peanuts. On the top of the wooden box were two smaller metal boxes containing bars that could be reached by the monkeys through the hand holes.

The apparatus as described above, including the cage, and both metal and wooden boxes, was designed such that when in place in the cubicle, monkeys were able to see the screen only by looking through the viewing window.

Four closed-circuit TV cameras positioned around the testing cubicle were used for observation from outside the room of the monkey and apparatus throughout testing. The stimulus display, eyetracking, food delivery, and experimental contingencies were all computer-controlled from outside the cubicle. The eyetracking was controlled by an ASL Model 5000 Eyetracking Control Unit (Applied Science Laboratories, Bedford, MA) that interfaced with a standard PC running Windows 98 and proprietary ASL software, E5 for Windows. Stimulus presentation was controlled by a DOS based computer running in-house programmes in Pascal.

We created a Pascal interface between the eyetracking system and our own stimulus presentation software, which extracted raw data from the eyetracking computer giving eye position on a cycle-by-cycle basis at 60 Hz. These data were used to control the presentation of the stimuli on the screen. The eyetracking system provided the DOS PC, via the Pascal interface, with a range the following data each cycle: presence of a pupil; presence of a corneal reflection; *X* gaze-coordinate; *Y* gaze-coordinate. Each of these was used in real time to guide the behavioural tasks at different stages of the training procedure.

The ASL system (Applied Science Laboratories, Bedford, MA) generates *X* and *Y* coordinates which are provided in point of gaze units (POGS). Henceforth stated measurements of *X* and *Y* eye position refer to measurements of these POGs. The commercial nature of the ASL software and hardware mean that we do not have direct access to the method of POG calculation. This does not impact our ability to work with the system and calibrate monkeys to use it. The method of POG calculation is constant, and therefore we calibrate the monkeys on the basis of gaining a stable POG reading when the monkey is looking at the same position. This method will become clear below.

2.1.3. Theory of operation

A brief consideration of the theory of operation of the eyetracking system will be informative when considering the training procedure that we employed and that is described below.

The system is based on the comparison of corneal reflection and pupil location. If a subject's single eye fixates a point of light, a proportion of that light will reflect back from the cornea. An observer (or camera) located in the same place as the point of light will see the corneal reflection (CR) as located in the centre of the subject's pupil. If the subject shifts fixation away from the point of light, the CR will shift relative to the centre of the pupil, in a manner that is consistent with the size of the shift in gaze. Hence the point of gaze can be reliably calculated from the pupil-CR separation (PCR). The PCR varies with eye rotation, and therefore change in point of gaze, but does not vary significantly with eye translation, for example as a result of head movement. As such PCR provides a reliable manner of calculating point of gaze independent of irrelevant head movements.

In the current system, the camera lens is closely surrounded by a ring of infrared LEDs, which provide the light from which the CR can be measured. They also provide light that reflects from the retina and passes back out through the pupil (though of course not the iris) thereby illuminating (in a sense back-lighting) the pupil to allow the camera to locate it more easily, and therefore facilitate calculation of the PCR. As such, in order to track the gaze direction of a subject, the camera must be set up such that a clear reflection from the cornea, and a clear pupil, can both be recorded.

2.1.4. Optimisation of camera

Prior to training on behavioural tasks, the camera needed to be optimised for the monkey eye. This was carried out using adjustments in the E5 for Windows programme described above (Applied Science Laboratories, Bedford, MA). We first optimised the system for a human observer with dark eyes. We then introduced pilot monkeys to the apparatus, and encouraged them to look through the viewing window. We adjusted the strength of the camera's response to the pupil and CR using the software, in order to obtain optimal co-detection of monkey pupil and CR. A lower sensitivity was required in general for detection of these features in monkeys compared to humans, suggesting a higher level of reflectivity in the monkey eye. We also found no significant differences in the settings required for optimal detection between monkeys, and therefore maintained the same settings for all of these and subsequent monkeys throughout training.

2.1.5. Stimuli

Throughout shaping and object discrimination learning, a consistent form of stimulus was used. They were all square bitmap stimuli with a side of 128 pixels, subtending 5.5° visual angle at the focus point, and with 20 colours. All of the presented images had black backgrounds, and all of the tasks were presented on a black screen.

In the shaping procedure, the bitmap images were derived from photographs of the faces of rhesus monkeys. The face used for a given trial was selected at random from a pool of 24 photographs of other macaque monkeys unfamiliar to the experimental monkeys. The stimulus monkeys had their eyes open and were looking at the camera.

In the object discrimination task, clipart images were used from a pre-selected pool of 2600 images with black backgrounds so that when presented on the black screen, the images would not all have a square 128 × 128 pixel silhouette. The images were screened to ensure they were distinct against a black background, and that there were no repeats. For each monkey, the 2600 stimuli were separately randomised to a unique order, to be used session by session. At no point in the current study were any stimuli re-used.

2.1.6. Shaping

Prior to introduction to the eyetracking apparatus, the monkeys had been trained to come into a transport cage, and familiarised with the processes of spending time in a darkened testing cubicle, receiving reward pellets, and receiving the large food reward.

Upon introduction to the eyetracker, monkeys performed a shaping task that, over a series of training levels, taught them to operate behavioural tasks using their gaze and its direction. Schematic diagrams of the screen during these levels can be seen in the top section of Fig. 1. For level 1, a small, grey, circular fixation spot (diameter 5 mm, 0.3° visual angle from the eye point of the monkey) was presented on the screen, and any record of the presence of the monkey's pupil by the camera in its field of view was counted as a response. Upon production of a response, the fixation spot was immediately replaced by a clipart image of the face of another monkey. The use of monkey faces as stimuli in this early stage of training was deliberate, the aim being to provide an engaging stimulus and encourage the monkeys to look more carefully at the screen, as monkeys value the social information derived from such faces (Deaner, Khera, & Platt, 2005). Monkeys had to present their pupil for a total of 1000 ms (not necessarily consecutive) in order to obtain a food reward. If the pupil response was lost prior to the 1000 ms then the monkey face image was immediately replaced by the fixation spot. After the completion of a trial the reward was immediately dispensed to the hopper, the screen was blanked, and a 10 s inter trial interval began. In the first session, monkeys had to obtain 10 food rewards. Completion of the 10th correct trial, and therefore completion of the session, led to automatic opening of the lunchbox, and consequent dispensing of the large food reward. Over subsequent sessions the number of trials required in order to complete the session was gradually increased, determined by the speed of work and level of motivation of individual monkeys, up to a level of 50 rewards per session. Monkeys quickly learned to complete this task efficiently within the first session in almost all cases. Subsequently the required looking duration was increased to 2000 ms. Once monkeys were performing this level comfortably, they began level 2.

In level 2 of shaping, the procedure was identical to level 1, but here the response that was required for the production of the monkey face stimulus was for the eyetracking software to record not only a pupil being present, but also valid *X* and *Y* coordinates for eye position. *X* and *Y* coordinates are the output format of the eyetracking system, and are provided when the system is able to calculate the PCR. This therefore requires that the monkey present his eye such that the location of both the pupil and CR can be measured. In order to achieve this, the monkey must not only have his eye present in the correct area of the viewing window, but also be facing towards the camera, and not moving at high speed. Because the focus point is always in the same place relative to the viewing window and hand bars, optimal performance at this level was obtained when the monkey learned to sit in a position with his pupil at the focus point. As in level 1, a response caused the fixation spot to be replaced by a monkey face stimulus, and the monkey had to accumulate 2000 ms

of not necessarily continuous looking in order to obtain a food reward. Monkeys generally showed competent performance at this level within two sessions.

Level 3 of the shaping programme was identical to level 2, but with two exceptions. First, the fixation spot and subsequent monkey face appeared in any one of five cardinal points on the screen, selected at random before each trial (see Fig. 2). Second, the monkeys were required to provide the requisite eye response for a continuous duration, rather than a cumulative one. This was initially 300 ms, and then gradually increased in subsequent sessions to a maximum of 1000 ms. The requirement for continuous looking was harder for the monkeys to acquire, but in general they were able to meet the 1000 ms criterion within 700 trials. Progress throughout this phase of the training for all eight monkeys can be seen in Fig. 3.

It is critical to point out that in the process of shaping, and in order to meet the criterion of level 3 of the shaping task, the monkeys had to learn exactly how best to place their heads and look out of the viewing window such that their pupil lay at the focus point, and to remain relatively still for the duration of the trial. Our apparatus therefore provides a behavioural solution to the problem of a lack of head fixation.

2.1.7. Calibration

The final stage of the pre-training was to calibrate individual monkeys' point of gaze relative to objects on the screen. The relationship between the raw data provided by the PCR and the actual direction of gaze varies slightly for each subject, and therefore an individual calibration is necessary.

The standard procedure for this is to require a subject to look at five or nine cardinal points on the presentation screen, and record their PCR values, such that the ASL calibration software can account for the individual differences of that subject. Obviously, this is not a trivial matter with monkeys, or indeed infants, with whom similar systems have been used (Aslin & McMurray, 2004). In order to facilitate accurate eyetracking for hemifield-specific object presentation, we sought a calibration accurate to within approximately 2° of visual angle, which is more accurate than that generally obtained by two-point calibration methods often employed with infants (Aslin & McMurray, 2004). We carried out a number of pilot experiments in which there was a behavioural requirement for the monkey to fixate the required locations, but found that fixation was rarely stable enough to use for a daily calibration, and therefore this approach was not practical. These pilots did, however, provide two important pieces of information. First, that the POGs for a monkey assumed to be looking at the same position because the monkey face was in that position were consistent, and that the POGs for a monkey looking at different positions were different from each other in a predictable manner. This means that, regardless of the method of POG calculation, when the monkey looks in the same place the eyetracking system gives consistent readings. Second, that the offset of individual monkeys between PCR and actual point of gaze is very stable over time, and this assertion was supported by the data presented below.

Hence, to calibrate individual monkeys, we first implemented a standard human calibration in the system, using the five cardinal points (Fig. 2a) and the E5 for Windows software. Monkeys then performed stage 3 of the calibration task, and we collected *X* and *Y* coordinates in real time during each trial, obtaining one reading per cycle. We analysed these data with respect to the location in which the stimuli were presented in the task, and noted strong clustering of coordinates. This showed that, despite no overt behavioural requirement, monkeys were strongly fixating the monkey face stimuli (see Fig. 4), and that the eyetracker with a human calibration was providing very stable output when tracking a monkey eye. For each monkey, we obtained a mean *X* and *Y* coordinate for each of the five cardinal points. Occasionally

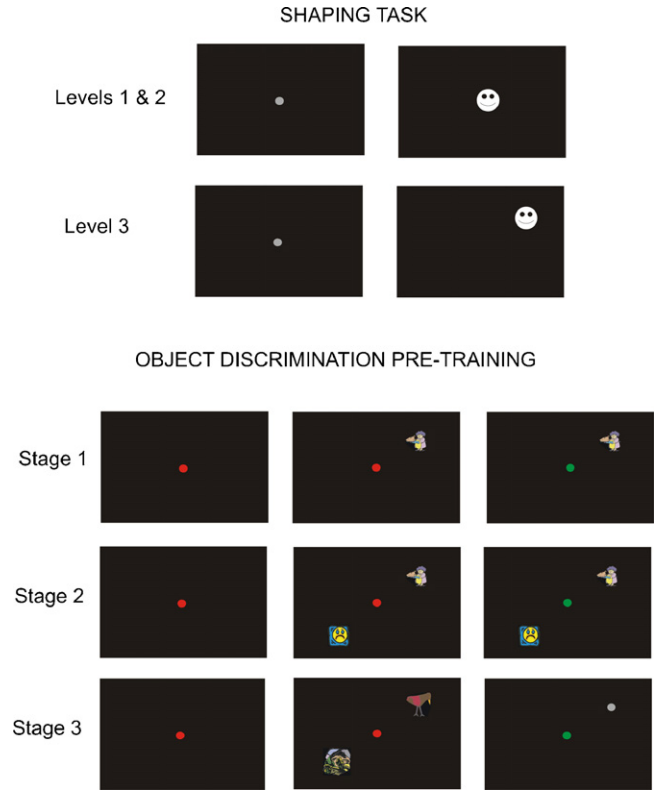


Fig. 1. Illustrations of the levels and stages in the shaping and object discrimination pre-training phases of monkey training in the eyetracking apparatus. Each panel represents all of the items on the screen (not to scale) during a single period of each task, with the task progressing from left to right for each level or stage of training. For full details of the procedure see materials and methods. *Shaping task*: Monkeys learned that the presence of a grey fixation spot allowed them to initiate a trial, and that showing their eye to the eyetracker at this time caused the presentation of a monkey face stimulus. Actual photographs of monkeys within the colony were used, but are only represented diagrammatically here. *Object discrimination pre-training*: Monkeys learned to fixate a red fixation spot whilst stimuli were presented peripherally. When the fixation spot became green, the monkey was permitted to break fixation from the central spot. The right-most panel displays the items presented to the monkey as soon as fixation was broken. Therefore, in stage 3, the monkey is never able to fixate the clipart stimuli.

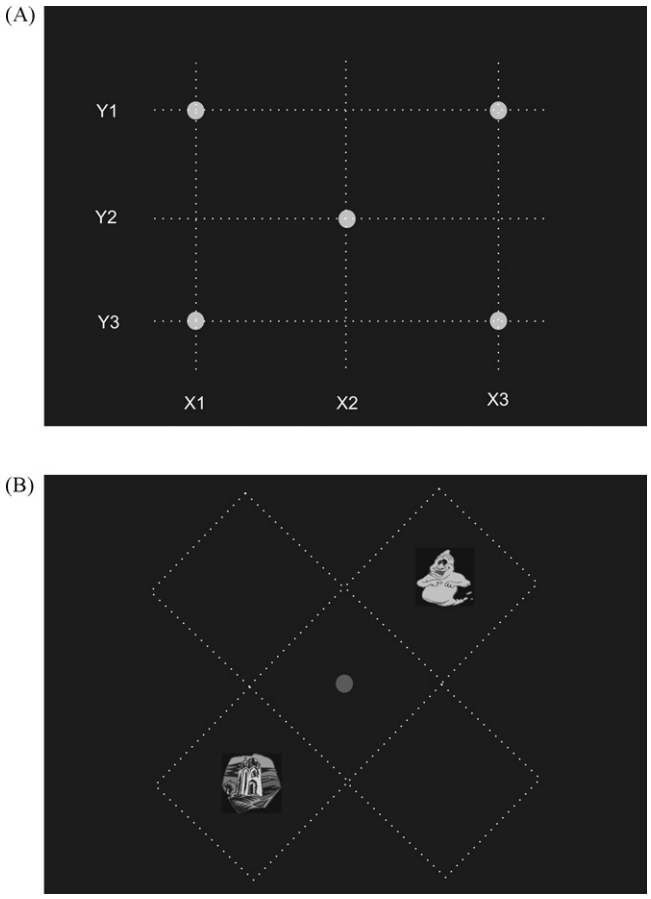


Fig. 2. Illustrations of the layout of the screen for eyetracking. (A) Representation of the positions in which stimuli were presented (not to scale). The grey fixation spots represent the five possible stimulus locations. Monkey faces were presented in all five locations for the shaping task. In the object discrimination task, only fixation spots appeared at the central location, whilst the objects were presented in the four corner locations. These four locations are referred to as the S+ locations. The five points can be determined by the six coordinates noted and named by the dotted lines. These six coordinates for each individual monkey were used in the calibration process. (B) Representation of a sample screen shot from the object discrimination task. Problems always contained one object in each hemifield. Dotted lines represent the edges of the fixation areas, and would not be seen on the screen. These areas are abutting, such that a point of gaze crossing from one to the other can be in one or the other area, but not in both or neither, at any point in time. A point of gaze within the central area, for example, was considered to be fixation of the central fixation spot.

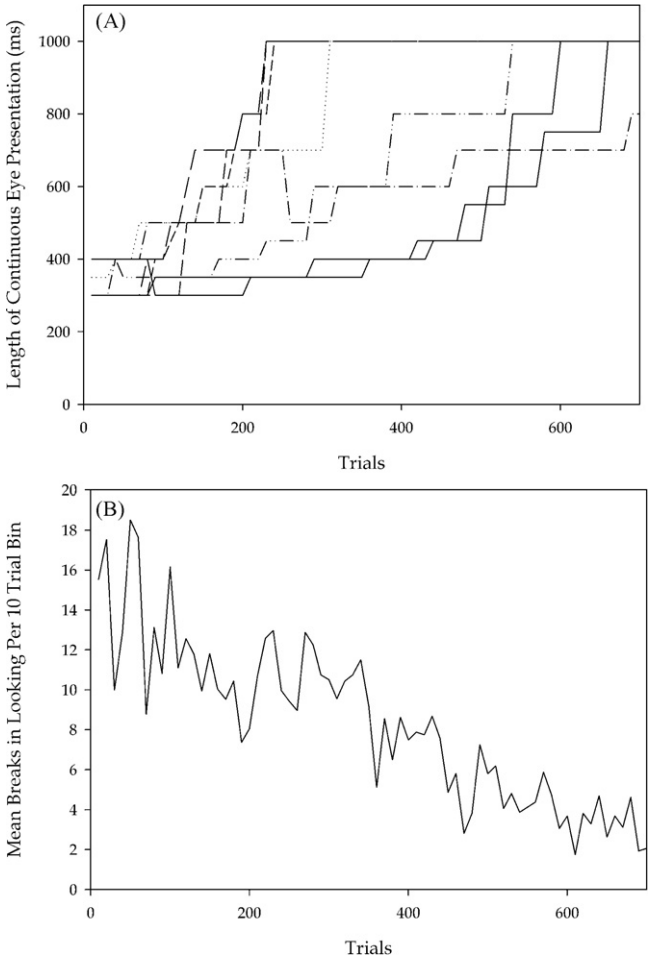


Fig. 3. Progress of the eight monkeys during level 3 of the initial shaping procedure. (A) Increase in length of continuous eye presentation. In level 3 monkeys learned to present their eye at the viewing window in a manner stable enough to generate *X* and *Y* coordinates for a continuous period, initially of 300 ms, up to a maximum of 1000 ms. As the monkeys became proficient at this, the required period of fixation was increased as a parameter of the task, and this progress is shown graphically here. Monkeys received a minimum of 700 trials of shaping at this level. (B) Decrease in number of breaks in looking. During level 3 of the shaping task, we recorded the number of occasions the monkey removed his eye from the viewing window, or otherwise caused the recording of *X* and *Y* coordinates to be lost before a trial was completed. Here we display the mean number of such breaks in looking in 10 trial bins for the period of shaping also shown in (A), across all eight monkeys. The number of breaks in looking decreases during the shaping, such that on average the monkeys are making far fewer than one break per trial by the end of shaping.

the monkey made a saccade away from the stimulus during the calibration sessions, so we calculated the mean of the *X* and *Y* coordinates generated within two standard deviations of the modal coordinate. From these data we generated a mean for the six coordinates required to specify the five possible fixation locations employed in the task (Fig. 2a). We then compared these coordinates for each monkey with those generated by the human subject to whom the system was correctly calibrated, which had been collected in the same manner. This simple procedure provided an offset vector for each monkey, relative to the human calibration implemented by the software.

Finally we used our interface between eyetracker and stimulus presentation system to correct for the offset in real time, so that the coordinates generated by the eyetracking software were individually corrected for a given monkey before being converted into coordinates reflecting gaze location on the screen. These corrected and therefore calibrated coordinates of gaze position on the screen were used to control the subsequent tasks.

2.2. Part 2: validation of method

In order to calculate the spatial resolution of the eyetracking system thus calibrated, we recorded the error produced by the system when the five pilot monkeys performed stage 1 of the object discrimination pre-training task described below. Specifically, we recorded fixation coordinates in the period during which the monkey was required to fixate the 0.3° visual angle fixation spot in the absence of any other visual stimuli, and then calculated the error in these coordinates from the fixation spot assuming constant fixation of the spot. The maximum root mean square error calculated from this procedure was 2.4°, representing a suitable spatial resolution of the system for our purposes.

Standard procedure in human eyetracking studies would be to calibrate subjects before each session. The calibration procedure described above, however, is not practical for daily use, but data from the five pilot monkeys suggested that because our system operated on the same settings day after day, with the apparatus unchanged, and because the monkeys had behaviourally learned to adopt a stable position for each trial during the shaping procedure because the focus point remained the same throughout, our calibration system was stable once implemented.

In order to ensure that the calibration did indeed remain stable over time, we retested the offset between the human subject and each of the eight monkeys, both 7 days and 2 months (mean 61.5 days) after initial calibration. The procedure in each case was identical to that described above for initial calibration. At each of these three tests, we therefore derived a set of 3 *X* coordinates and 3 *Y* coordinates for each monkey. The first set of these coordinates were the set originally used to drive the calibration offset procedure described above.

The data for the calibration stability test are presented in Table 1. Inspection of Table 1 reveals consistent readings within each monkey, and no overlap between coordinates over the course of the three tests for a given monkey. To confirm this, we applied simple trigonometry to calculate the distance between the derived coordinates of a single point for a given monkey over the three tests. This therefore provided a measure of whether the derived coordinates were varying, and therefore whether or not the calibration was stable. The mean of this distance was 3.83 POGs, and the maximum distance was 9.85 POGs for any point. We contrasted this with the distance between adjacent points over the three tests, which had a mean of 28.73 POGs and a minimum of 20 POGs. Hence the change in derived coordinates in our calibration stability test over time was small when compared to the distance between the points the monkeys were required to fixate. This reveals the stability of our calibration procedure, and suggests that the data from eyetracking and hemifield-specific presentation are reliable. We were therefore able to maintain the calibration for each monkey over a period of time, rather than replacing it for each session.

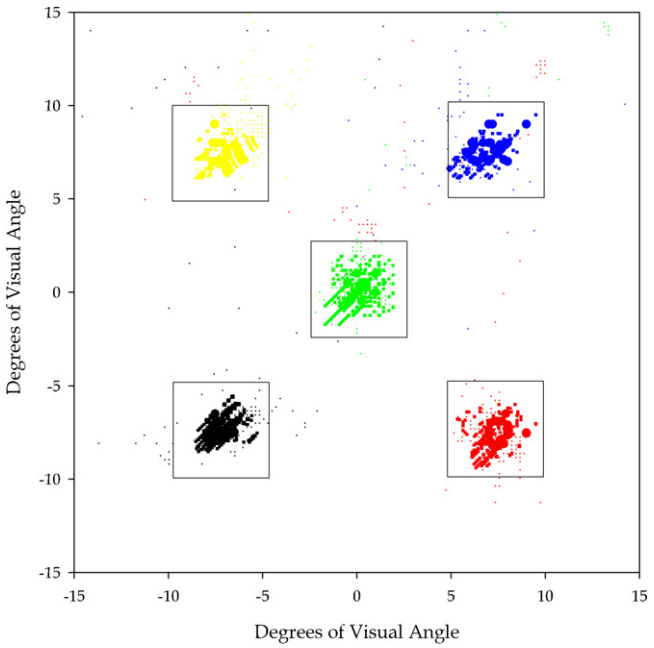


Fig. 4. Example of data from one monkey used for calibration. *X* and *Y* coordinates are plotted for every recorded eyetracker response during a trial, measured in POGs, and for display here converted to degrees of visual angle from the central point of the screen, which is also the centre of the fixation spot. Small circles represent a single fixation at that coordinate; medium sized squares represent 2 or more fixations; and large circles represent 20 or more fixations. Different colours refer to trials in which the monkey face stimulus was presented in different locations on the screen. The black squares represent the maximum size of the clipart images on the screen in the five locations in which they were presented. It should be noted that the outline of the stimuli fell well within these areas, as the stimuli had black backgrounds, and the screen background was the same shade of black. The strong clustering of the points shows that, despite the lack of overt behavioural requirement to do so, monkeys were carefully fixating the stimuli. Mean *X*–*Y* coordinates for each point for each monkey were derived from these data, and use to drive the calibration procedure.

Table 1
Mean coordinates, measured in point of gaze units (POGs) for all eight monkeys derived from fixation of stimuli in the shaping task.

Monkey	Testing point	*X1*	*X2*	*X3*	*Y1*	*Y2*	*Y3*
M1	1st calibration	91	118	144	128	163	195
	+7 days	93	121	144	125	161	198
	+2 months	93	120	144	129	162	197
M2	1st calibration	95	121	144	123	153	186
	+7 days	95	118	139	130	155	187
	+2 months	102	123	145	129	159	187
M3	1st calibration	101	124	149	132	164	193
	+7 days	99	125	148	133	164	191
	+2 months	103	129	149	139	164	190
M4	1st calibration	96	119	142	123	153	184
	+7 days	96	117	141	121	152	189
	+2 months	94	116	141	126	149	190
M5	1st calibration	94	119	141	141	172	199
	+7 days	91	119	139	138	167	203
	+2 months	93	120	142	137	168	198
M6	1st calibration	94	122	145	120	157	185
	+7 days	94	121	146	122	159	186
	+2 months	94	119	149	129	156	190
M7	1st calibration	91	122	145	109	146	183
	+7 days	92	122	146	110	146	184
	+2 months	92	130	150	111	144	187
M8	1st calibration	99	123	153	104	141	177
	+7 days	98	121	151	106	143	176
	+2 months	96	120	149	106	139	174

The six readings correspond to the six key coordinates described in Fig. 2. The readings given at the three time periods are consistent within a given monkey, and show no overlap with the other coordinates, suggesting a stable calibration procedure.

We have maintained regular checks of the calibration since it was initiated, and noted no significant deviations in any monkey, despite performance of up to 500 sessions per monkey.

2.3. Part 3: behavioural experiment

2.3.1. Control of behavioural tasks with eye movement – object discrimination pre-training

Monkeys were now able to control aspects of behavioural tasks with their eye movements. They were taught a simple object discrimination task in the periphery across three stages. Schematic diagrams of the screen during these stages can be seen in Fig. 1.

For this and subsequent tasks, the screen was divided into five diamond shaped fixation areas, shown in Fig. 2. At the centre of each was a location in which a fixation spot or stimulus might appear. The eyetracker provided information in real time about which region of the screen the monkey was fixating. Fig. 2 shows these fixation areas.

In stage 1 of object discrimination training, monkeys were presented with an initial red fixation spot, in the centre of the screen. This spot was of the same size and luminance as the grey spot employed in the shaping procedure. Any fixation within the central fixation area was deemed a fixation of this spot, and at its widest point this fixation area occupied 5.8° of visual angle. When fixation of the central spot was confirmed, a single clipart stimulus was presented in one of four possible locations, each with its own fixation area, surrounding the fixation spot (see Fig. 2). In stage 1, the same four stimuli were used throughout, one for each of the four fixation areas.

The task for the monkey was to maintain fixation on the central red spot until that spot changed to green, and then make a saccade to the stimulus. Over a number of trials monkeys were gradually trained to fixate the red spot for 2000 ms including 1000 ms of continuous fixation. Any fixation outside the central fixation area prior to the fixation spot change caused immediate blanking of the stimuli (but not the fixation spot) until central fixation was rejoined. Once the green spot appeared, fixation of the area containing the stimulus was deemed a 'correct' trial. The stimulus remained on the screen for 2000 ms to allow fixation of it, and an immediate food reward was dispensed. If the gaze passed any of the three other fixation areas, or anywhere else, the trial was deemed 'missed', the screen blanked, and no reward delivered. Monkeys were trained on this task until they were responding comfortably with few missed responses.

Stage 2 of the task was identical to stage 1, but with new unseen stimuli and a second stimulus presented in the diagonally opposite fixation area. From now on, stimuli were only ever presented with one in each hemifield, diagonally opposite to each other. Examples of the screen during such trials can be seen in Fig. 5. Of these two stimuli in a trial, one was deemed the S+ and one the S− consistently, and from here onwards, a presentation of an S+ with an S− will be referred to as a single problem. The monkey's task was to fixate the S+ when the fixation spot became green, learning which stimulus was the S+ by trial and error. Fixation of the S+ was a 'correct' response and elicited the same reward and events as in stage 1 above, with the addition of the removal of the S−. Fixation of the S− was designated an 'incorrect' response, whilst fixation of anywhere else on the screen was designated as 'missed', both eliciting the blanking of the screen, and no reward. Monkeys were trained on this task until they were performing at a stable level above chance, and therefore showing learning of the discrimination between the two stimuli. At this point they were moved onto stage 3.

Initial training in stage 3 employed the same four discriminations learned in stage 2, and therefore the stimuli were familiar, but from stage 3 onwards, at no point was the monkey able to fixate the clipart stimuli. If the monkey made a correct response, the S+ was immediately replaced by a grey fixation spot to provide positive feedback. If the monkey made any other response, the screen was immediately blanked. The eye position was updated at sufficient frequency (60 Hz), that blanking or replacement of the stimuli occurred before the monkey had a chance to complete a saccade and fixate the peripheral stimulus. The behavioural difference between transfer within hemifields and between hemifields reported below confirms that this was the case. As a result, stage 3 ensured that monkeys continued to learn about stimuli that were now presented solely to a single hemifield. Monkeys were trained on this set of problems, carried over from stage 2, to a criterion of 90%

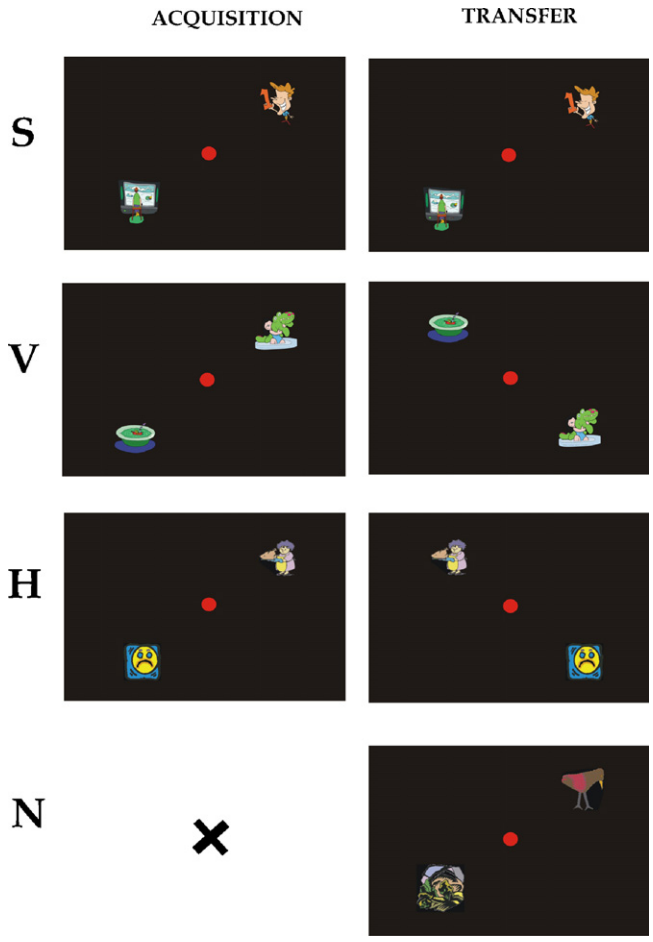


Fig. 5. Example screenshots from the object discrimination task. Each panel represents all of the items on the screen (not to scale) during a fixation period of the task. Monkeys had to fixate the central red spot in order to initiate presentation of stimuli as shown. They then had to maintain fixation until the spot became green, at which point they were able to make a saccade to their chosen object. As soon as fixation was broken from the central spot the objects were removed, and so could never be fixated. In the initial acquisition phase (left half of figure) there were 12 problems. Here three are shown with an S+ in the top right hand corner. The remaining nine problems were 3 each for the remaining 3 S+ locations. In the transfer phase (right half of figure) there were 16 problems, with one of each transfer type (see Section 2) per original S+ location, in addition to the one novel problem per S+ location. The four transfer types are referred to in the left hand column. S: same problem; V: vertical shift; H: horizontal shift; N: novel problem.

correct in a session of 80 rewards. To complete stage 3 of training, monkeys were trained on another set of four new discrimination problems to a criterion of 90%. In this set, unlike the previous one carried over from stage 2, the monkeys were never able to fixate the stimuli. As such the discrimination learning was carried out entirely in peripheral vision.

Performance on the task was measured as a percent correct of responses to objects. This meant that a "miss" response, when central fixation was broken but not directed to either stimulus, was not counted as an error, and merely re-set the trial. This method of measurement was employed because monkeys made multiple miss errors (mean 31.4 per session in stage 1) whilst accustoming themselves to the procedure. We required the monkeys to reach a criterion of fewer than 10 miss errors in 3 consecutive sessions, as well as completing the sets of problems described above, before progressing to the full task below. In practice both monkeys M1 and M2 reached the miss error criterion before they completed the sets of problems, and were making minimal miss errors (mean 4.2 per session) at the end of pre-training.

The learning rate for all monkeys on this task was slightly slower than anticipated, with M1 taking 38 sessions and M2 taking 42 sessions to complete the pre-training. Although we are unable to provide directly comparable data between the two, it seems likely that monkeys learning about similar objects in free vision, for example in a touch-screen apparatus, show faster learning, or are able to learn about more concurrent pairs than monkeys learning about peripherally presented objects. This is a topic of ongoing research. Once monkeys M1 and M2 had completed this stage, they began the full task.

2.3.2. Object discrimination task

Example screen shots of the main object discrimination task, and demonstrations of the two stages of the task, can be seen in Fig. 5. In the initial acquisition phase monkeys learned 12 problems concurrently, but the task was otherwise identical to that in stage 3 above. There were three problems per S+ location. The criterion for this task was again 90% correct in a session, with the additional criterion that each individual problem should be performed at 75% or above in the criterial session. Throughout the task a session is defined as the acquisition of 80 rewards.

Monkey M1 showed proficient learning at this task, achieving criterion in seven sessions, but monkey M2 showed a significantly slower initial learning rate, showing no significant improvement above chance performance of 50% in his first three sessions. In the third session of the task, for example, M1 performed at 74% correct, whereas M2 only performed at 58% correct. Monkey M2 therefore received a phase of training in which the same 12 problems were presented as the main task, but only 2 of those problems were presented concurrently within a session. The monkey learned each pair of problems to the same criterion until he had learned about all 12 problems. In each case, the two problems were chosen such that their S+s were located in diagonally opposite S+ locations. Monkey M2 took 22 sessions to complete this extra stage, and upon completion he reverted to the main task with 12 concurrent problems, which he learned for a further 24 sessions until he reached the same criterion of 90% overall and 75% for each problem.

After learning the 12 problems to criterion, the monkeys received a transfer test, seen on the right of Fig. 5. This consisted of 16 problems presented concurrently. There were four 'transfer types', each with one exemplar for every S+ location. Four of the problems were identical to acquisition, the "Same" (S) problems. For four of the problems the stimuli were shifted vertically to the opposite stimulus location. So a stimulus in the top left in acquisition moved to the bottom left in the transfer test, etc. These were the "Vertical" (V) problems. Four more problems had a horizontal shift in stimulus location, and were the "Horizontal" (H) problems, and represented the critical test of inter-hemispheric transfer. The stimuli were shifted the same distance relative to acquisition in H and V problems. Finally, four of the problems were completely novel and were the "Novel" (N) problems. The monkeys did not complete the transfer test to criterion, but rather completed a number of sessions (3 for M1 and 5 for M2) commensurate with their general level of performance.

Both monkeys now learned a new acquisition set of 12 problems concurrently. Monkey M1 took 13 sessions to learn the new set of problems, and M2 took 40 sessions but in this case required no extra training. They then completed a second transfer test, as above.

The monkeys now learned a set of eight concurrent problems, two per S+ location, to the same criterion as above. Monkey M1 took 6 sessions and monkey M2 took 11 sessions to learn this set of problems. They then performed a third transfer test. In this case, four of the problems were H problems, with a horizontal shift relative to acquisition, and the other four were V problems. This final stage served to provide further data on the critical contrast.

Upon completion of this final transfer test, the experiment was complete.

2.3.3. Statistical analysis

The justification for the current experiment derives from the electrophysiological data of Chelazzi et al. (1998), and the study was designed to search for a behavioural effect of the data they have reported, on the basis of an equivalent result in human subjects (Hornak et al., 2002). As such, we analysed the data here in a similar fashion to that employed in electrophysiological experiments, that is to say we analysed data from individual monkeys to look for significant effects within a single monkey. The measure was the number of errors committed across the three transfer tests in the task, analysed on an individual problem basis over the 40 problems the monkeys learned, with the transfer type as a factor with four levels corresponding to the same (S), horizontal (H), vertical (V), and new (N) problems. In testing individual contrasts, we were testing the specific hypothesis that transfer is degraded in the monkey in the same manner as in the human subjects of Hornak et al. (2002). As such, we employed one-tailed designed comparison tests. We applied a log transform to the error scores, as the raw error scores were not normally distributed. This is a standard procedure in our laboratory (e.g. Buckley, Charles, Browning, & Gaffan, 2004).

3. Results

The combined data of the three transfer tests are shown for each monkey in Fig. 6. The graph clearly shows that, as expected, S and V problems have similar scores, whilst there is an increase in errors for H problems, to a level approaching that of the novel N problems. As the monkey encounters N problems a number of times in each transfer test, the performance on these problems overall is above

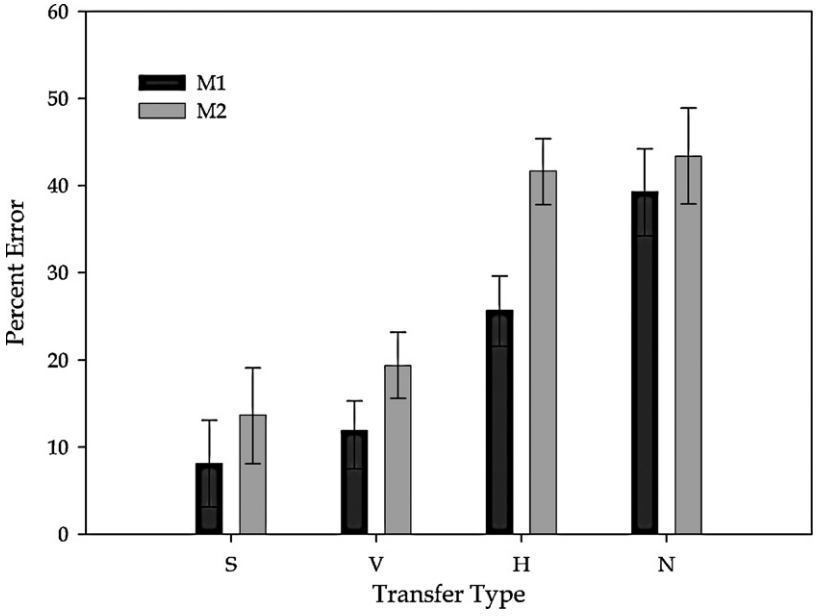


Fig. 6. Performance of monkeys M1 and M2 on the four types of problem in the transfer test of the object discrimination task. The data are presented as percent error committed within the combined transfer tests, and the error bars represent the standard error of the mean.

the chance level of 50%. When considering the critical contrast required to test the effects of inter-hemifield transfer, the percent error of each monkey more than doubles from V to H problems, demonstrating a large effect.

For monkey M1, a one-way ANOVA revealed a significant effect of transfer type: $F_{(3,36)} = 4.579$, $p = 0.008$. A designed comparison between the critical H and V shifts employing the pooled error term revealed that, as predicted, H shifts elicited significantly more errors than V shifts $t_{(36)} = 1.874$, $p = 0.035$ one tailed. Designed comparisons between the other adjacent error scores (see Fig. 6) revealed no other significant effects, with the largest t in the H vs. N comparison, where $t_{(36)} = 1.355$, $p = 0.092$ one tailed.

For monkey M2, the one-way ANOVA also revealed a significant effect of transfer type: $F_{(3,36)} = 3.917$, $p = 0.016$. The designed comparison between H and V problems confirmed the predicted result and that seen in M1, i.e. a significant difference in error levels between the two: $t_{(36)} = 1.840$, $p = 0.037$ one tailed. Again, the further designed comparisons revealed no other significant effects, the largest t in this case being the V vs. S comparison: $t_{(36)} = 1.063$, $p = 0.147$ one tailed.

As such it is clear that there is an effect of the transfer type, and that, as predicted, there is a significant difference between V and H problems, showing that shifting a discrimination previously learned in one hemifield to another hemifield causes a decrement in performance relative to shifting it the same distance but within the same hemifield. There was no significant difference between the un-moved S problems and the V problems shifted within the same hemifield. There was also no significant difference between the H problems shifted between hemifields and the completely novel N problems, although Fig. 6 and the analysis above seem to suggest that there is a trend for fewer errors on the H problems, at least in monkey M1.

Hornak et al. (2002) found that subjects performing horizontal shifts in their task performed at a level above chance, and they used this result to argue that there is an extra-temporal object memory store in which information is integrated across the hemifields, proposing the prefrontal cortex as a candidate. The equivalent result in the current study would be if H trials were performed significantly better than the N trials, thus demonstrating a degree of benefit from prior training in the opposite hemifield. We found no such significant difference, merely a trend in one monkey. The presence or not of this effect in monkeys, and its neural basis, is the topic of ongoing research. This question is critical to further elucidation of the methods of transfer of visual and mnemonic information between the hemifields in monkeys, and critically the development of the eyetracking technique now enables direct testing of the extent of the hemifield-specific nature of the memory stores, for example using unilateral lesions to the temporal lobes.

4. General discussion

We have shown here that, in normal monkeys, object discrimination problems learned solely in one hemifield are largely forgotten when they are transferred to the other hemifield. Performance of the transferred problems was in fact not significantly better than performance of novel problems learned at the same time, although there was a trend towards significance in at least one monkey.

In gathering these data, we have also shown that it is feasible to use an infrared eyetracker apparatus to present visual stimuli to specific retinal locations in awake, behaving, freely moving macaque monkeys. The monkeys are capable of learning visual discrimination problems between stimuli presented in this fashion. This method for eyetracking in the freely moving monkey opens up a range of new experimental avenues, and provides a significant refinement in experimental technique for behavioural research with macaques.

As discussed above, our behavioural result supports and builds upon data from normal human subjects (Gratton et al., 1997; Hornak et al., 2002). Specifically, our result confirms that this effect is generalized to a variety of forms of visual memory, even well rehearsed and repeatedly used memories; that the effect is consistent between humans and monkeys; and that the electrophysiological data in monkeys is supported by a behavioural outcome in the same species. Furthermore, the memories studied in the current task were acquired over a number of daily sessions and repeatedly tested, and are therefore clearly long term in nature, unlike those in the study by Hornak et al. (2002) which were within-session memories.

Although the current data, along with that from normal human subjects cited above, do not allow us to draw conclusions about specific systems within each hemisphere, when considered in conjunction with the electrophysiological data from cells in the temporal lobe (Chelazzi et al., 1998), these studies contribute to the idea that when the visual field contains items in both hemifields, i.e. in most normal conditions of viewing a scene, those scenes and the objects within them are processed mnemonically as well as perceptually in a hemifield-specific manner in the temporal lobe to a much greater extent than previously thought. Previous studies arguing that inferotemporal neurons have receptive fields extending into the ipsilateral hemifield (Gross, Rocha-Miranda, & Bender, 1972), and that there is bilateral representation of visual memories (Ringo, 1993), consistently presented objects only to a single hemifield, with the opposite hemifield completely blank, and therefore do not contradict our conclusion. The conclusion that not all visual object memory is automatically integrated across the vertical meridian could be seen as adding to the evidence for the increasingly supported idea that perceptual and mnemonic systems of the brain should not be regarded as separate entities with independent neural bases (Buckley & Gaffan, 1998; Buckley, Booth, Rolls, & Gaffan, 2001; Murray, Bussey, & Saksida, 2007).

If the processing of perceptual and mnemonic information in the temporal lobes is hemifield-specific, there remains the question of why, in the special case where one hemifield is devoid of input, either because the contralateral visual field contains no stimuli (Chelazzi et al., 1998), or because the optic chiasm has been sectioned and one eye occluded (Ringo, 1993), is there good transfer between the hemifields. Eacott and Gaffan (1989) argue that this commissural input from the ipsilateral field is necessary in order for the identification of objects that straddle the vertical meridian to be successful and based on both halves. They showed that monkeys can perform a discrimination task in which a single object has independent elements in the two hemifields, even when those elements are switched between fields. This ability was impaired by section of the splenium and anterior commissure. It therefore appears that this is an important function of commissural input to the temporal lobes. Any object particularly important to a given task is likely to be fixated such that it falls across the vertical meridian, as the objects in Eacott and Gaffan's study did. It seems, therefore, that the brain is only adapted to bilaterally represent information about such objects, and not all objects in general. This makes a great deal of sense in terms of the economical use of representational space.

The data presented here suggest that, in viewing conditions with objects in both hemifields, unilateral damage to the temporal lobe will cause impairments in memory for the part of a scene that is presented contralateral to the lesion, and this is indeed the case (Hornak et al., 1997). The further study of such hemifield-specific impairments following unilateral lesions will reveal important information about the nature of the storage of visual information and the way in which such information is integrated across hemifields. The eyetracking apparatus presented here provides an

excellent opportunity for further study in this area with controlled lesions in monkeys.

Acknowledgements

This work was supported by the Medical Research Council UK. CREW was supported by the Christopher Welch Trust. We thank Dr Mark Baxter for helpful comments on the manuscript, and Steven Young for assistance in computer programming.

References

Aslin, R. N., & McMurray, B. (2004). Automated corneal-reflection eye tracking in infancy: Methodological developments and applications to cognition. *Infancy*, *6*, 155–163.

Bagshaw, M. H., Mackworth, N. H., & Pribram, K. H. (1970a). The effect of inferotemporal cortex ablations on eye movements of monkeys during discrimination training. *International Journal of Neuroscience*, *1*, 153–158.

Bagshaw, M. H., Mackworth, N. H., & Pribram, K. H. (1970b). Method for recording and analyzing visual fixations in the unrestrained monkey. *Perceptual and Motor Skills*, *31*, 219–222.

Bagshaw, M. H., Mackworth, N. H., & Pribram, K. H. (1972). The effect of resections of the inferotemporal cortex or the amygdala on visual orienting and habituation. *Neuropsychologia*, *10*, 153–162.

Black, P., & Myers, R. E. (1964). Visual function of the forebrain commissures in the chimpanzee. *Science*, *146*, 799–800.

Buckley, M. J., & Gaffan, D. (1998). Perirhinal cortex ablation impairs visual object identification. *Journal of Neuroscience*, *18*, 2268–2275.

Buckley, M. J., Booth, M. C., Rolls, E. T., & Gaffan, D. (2001). Selective perceptual impairments after perirhinal cortex ablation. *Journal of Neuroscience*, *21*, 9824–9836.

Buckley, M. J., Charles, D. P., Browning, P. G., & Gaffan, D. (2004). Learning and retrieval of concurrently presented spatial discrimination tasks, role of the fornix. *Behavioral Neuroscience*, *118*, 138–149.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*, 2918–2940.

Deaner, R. O., Khera, A. V., & Platt, M. L. (2005). Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Current Biology*, *15*, 543–548.

Eacott, M. J., & Gaffan, D. (1989). Interhemispheric transfer of visual learning in monkeys with intact optic chiasm. *Experimental Brain Research*, *74*, 348–352.

Fuchs, A. F., & Robinson, D. A. (1966). A method for measuring horizontal and vertical eye movement chronically in the monkey. *Journal of Applied Physiology*, *21*, 1068–1070.

Gazzaniga, M. S. (1966). Interhemispheric communication of visual learning. *Neuropsychologia*, *4*, 183–189.

Gratton, G., Corballis, P. M., & Jain, S. (1997). Hemispheric organization of visual memories. *Journal of Cognitive Neuroscience*, *9*, 92–104.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, *35*, 96–111.

Hornak, J., Duncan, J., & Gaffan, D. (2002). The role of the vertical meridian in visual memory for objects. *Neuropsychologia*, *40*, 1873–1880.

Hornak, J., Oxbury, S., Oxbury, J., Iversen, S. D., & Gaffan, D. (1997). Hemifield-specific visual recognition memory impairments in patients with unilateral temporal lobe removals. *Neuropsychologia*, *35*, 1311–1315.

Judge, S. J., Richmond, B. J., & Chu, F. C. (1980). Implantation of magnetic search coils for measurement of eye position: An improved method. *Vision Research*, *20*, 535–538.

Miyashita, Y. (1988). Neuronal correlate of visual associative long-term memory in the primate temporal cortex. *Nature*, *335*, 817–820.

Miyashita, Y., & Chang, H. S. (1988). Neuronal correlate of pictorial short-term memory in the primate temporal cortex. *Nature*, *331*, 68–70.

Murray, E. A., Bussey, T. J., & Saksida, L. M. (2007). Visual perception and memory: A new view of medial temporal lobe function in primates and rodents. *Annual Review of Neuroscience*, *30*, 99–122.

Myers, R. E., & Sperry, R. W. (1958). Interhemispheric communication through the corpus callosum: Mnemonic carry-over between the hemispheres. *AMA Archieves of Neurology Psychiatry*, *80*, 298–303.

Oscar-Berman, M., Heywood, S. P., & Gross, C. G. (1971). Eye orientation during visual discrimination learning by monkeys. *Neuropsychologia*, *9*, 351–358.

Pascalis, O., & Bachevalier, J. (1999). Neonatal aspiration lesions of the hippocampal formation impair visual recognition memory when assessed by paired-comparison task but not by delayed nonmatching-to-sample task. *Hippocampus*, *9*, 609–616.

Ringo, J. L. (1993). The medial temporal lobe in encoding, retention, retrieval and interhemispheric transfer of visual memory in primates. *Experimental Brain Research*, *96*, 387–403.

Vuilleumier, P., Sergent, C., Schwartz, S., Valenza, N., Girardi, M., Husain, M., et al. (2007). Impaired perceptual memory of locations across gaze-shifts in patients with unilateral spatial neglect. *Journal of Cognitive Neuroscience*, *19*, 1388–1406.