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A Role for the Ventral Visual Stream in Reporting Movements

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In this experiment we contrast the neural activity associated with reporting a stimulus attribute with the activity that occurs when the same stimulus attribute is used to guide behavior. Reporting the characteristics of a stimulus differs from simply tracking that stimulus since reporting requires that a stimulus is explicitly recognized and associated with an arbitrary response. In one condition the subject used his right finger to follow a square that moved randomly on a screen. In a second condition he had to indicate changes in the direction of the square's movements by touching one of two report buttons with his right finger. Two other conditions were added to control for the differences in the form of movement between the two primary conditions. When the reporting condition was contrasted with the tracking condition (controlling for the differences in the form of movement), areas in the ventral visual system (the left ventral prefrontal cortex and the left inferior temporal cortex) were activated. This study shows that contrasting a manual task which involves a report with a manual task which does not activates the ventral visual system. However, the observation of additional activity in other areas suggests that, while activity in the ventral stream is necessary for reporting, it is not sufficient.

INTRODUCTION

We behave differently toward the same object depending upon the goal we wish to attain and/or the context. For example, we can act on an object or recognize what the object is. Several studies have shown that visual information is processed in a different manner during the performances of these two kinds of tasks (Bridgeman *et al.*, 1981; Castiello *et al.*, 1991; Goodale *et al.*, 1991; Goodale and Milner, 1992). Acting on an object relies on a pragmatic process that uses a representation of the stimulus in a suitable form for use by the motor system. On the other hand, recognition of an object relies on semantic processing of the stimulus leading to a perceptual representation of it, which may be necessary for subjective awareness of that stimulus (Jeannerod, 1994). Another version of this distinction contrasts behaving toward a stimulus with reporting the presence of the stimulus. Reporting the presence of the stimulus is strongly associated with the ability to consciously recognize that stimulus. Some blindisght patients with lesions to their primary visual cortex fail to report the presence of a stimulus and demonstrate an absence of perceptual awareness or conscious recognition, even though they show residual visual capacity and can produce behaviors appropriate to the stimulus (Weiskrantz, 1986). Cowey and Stoerig (1995) have shown similar phenomena in monkeys with their left striate cortex removed. In this experiment the report was, of necessity, nonverbal. The monkey reported the presence of a stimulus by pressing a button. When a stimulus was presented in its "blind" field the monkey reported that no stimulus was present. However, when forced to guess the whereabouts of this unseen stimulus the monkey touched the screen in the correct place.

Studies in patients with lesions and also electrophysiological and neuroimaging studies have shown that these two visual processes rely on different neural networks (Ungerleider and Mishkin, 1982; Boussaoud *et al.*, 1990; Morel and Bullier, 1990; Goodale and Milner, 1992; Jeannerod *et al.*, 1994; Faillenot *et al.*, 1997). The dorsal stream, which projects from the primary visual cortex into the dorsolateral prefrontal cortex via the posterior parietal lobe, has been shown to be involved in the visual guidance of actions. The ventral visual stream from the primary visual cortex to the ventrolateral prefrontal cortex via the inferotemporal cortex is involved in object recognition and conscious visual perception (Goodale and Milner, 1992). Another attempt at distinguishing the contributions between these two visual streams has been put forward by Passingham and Toni (2001). According to these au-

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thors, these different brain systems are concerned with different types of actions. The ventral visual stream is activated in association tasks in which subjects have to explicitly recognize a visual cue and associate it with an arbitrary response (Toni *et al.*, 1998, 1999). Reporting the presence of a stimulus also requires that an arbitrary response (e.g., naming the stimulus or pressing a button) (Passingham and Toni, 2001) is associated with the appearance of the stimulus. The dorsal stream is involved in the processing of visuospatial cues for control of reaching movements (Sakata *et al.*, 1996; Jeannerod, 1994). Such goal-directed movements do not need an explicit representation of the object since both the object information and the movement can be described in a spatial coordinate system and there can be a direct interaction between the dorsal visual system and the premotor cortex.

The aim of this experiment was to directly compare brain areas involved in reporting the presence of a stimulus with behaving toward that stimulus by touching it. We hypothesized that, in contrast to simply touching the stimulus, reporting the presence of the stimulus would be associated with activity in the ventral stream. The two experimental conditions were chosen so that they differed principally in their requirement to report or to track. The paradigm we used was similar to the one used by Cowey and Stoerig (1995). In the first condition (report condition) subjects had to explicitly and nonverbally report the movements of a self-propelled square. To do this they had to associate a visual cue (direction of displacement of the square) with a precise response (pressing the designated button). In a second condition (follow condition) subjects had to follow directly the movements of the square without explicitly reporting them. We predicted that the ventral stream (the primary visual cortex, the ventrolateral prefrontal cortex, and the inferotemporal cortex) would be engaged by the report condition and that the dorsal stream (the primary visual cortex, the dorsolateral prefrontal cortex, and the posterior parietal lobe) would be engaged by the track condition. In order to control for the differences in hand movements and eye movements between these two conditions, we introduced two additional conditions (drag and move conditions), which involved the same differences in movement, but did not differ in the requirement to report. Subjects had to perform self-generated actions, defined as a free selection by the subjects of the movement of the square. They had to execute these actions with their right hand for all the conditions. The hand movements and eye movements required in the drag condition correspond to those required in the follow condition and the hand movements and eye movements required in the move condition correspond to those required in the report condition.

MATERIALS AND METHODS

We studied 11 healthy right-handed male subjects (mean age 30.54 ± 10.04 years). None had a history of neurological or psychiatric disease. All the subjects gave written informed consent. The study was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee and permission to administer radioactivity was obtained from the Administration of Radioactive Substances Advisory Committee of the Department of Health, United Kingdom.

The subjects underwent 12 perfusion scans with positron emission tomography in a single session. The subject lay in the scanner with head movements minimized by a helmet. Radioactivity was administered as an intravenous injection of water (which was labeled with radioactive oxygen tracer) by a plastic canula placed in the left cubital vein. A touch screen computer (detecting tactile pressure) was placed above the subject's head; the distance was adjusted so that the subject could drag his finger on it without moving other parts of his body.

The main aim of this experiment was to compare "tracking" and "reporting." In both cases the subject observed a target square that moved randomly from side to side across the screen. These random movements of the target were identical in the two conditions. In the "follow" condition the subject followed the square with his finger. In the "report" condition the subject indicated changes in the direction of the square's movement by touching one of two "report buttons" located on the left and right of the screen.

Although both following and reporting involved finger movements the precise form of these movements differed. For example, during the "follow" condition the finger was dragged across the screen as the subject tracked the target square. During the "report" condition the subject made jabbing movements as the finger intermittently touched one or other of the report buttons. There were also differences in eye movements since, in the "follow" condition, the subjects did not have to look at the report buttons. In order to control for these differences in the form of movement we introduced two additional conditions. These conditions involved the same hand and eye movements, but neither involved reporting. In these conditions the subject controlled the movement of the square. In one condition ("drag" condition) the subject controlled the movement of the square by dragging it from side to side across the screen. The movement in this condition is the same as that in the "follow" condition, with the subject's finger remaining continuously in contact with the screen and no requirement to look at the report buttons. In the second control condition ("move" condition) the subject changed the direction of the movement of the square at will by intermittently touching one or other of the report buttons (Fig. 1). The hand

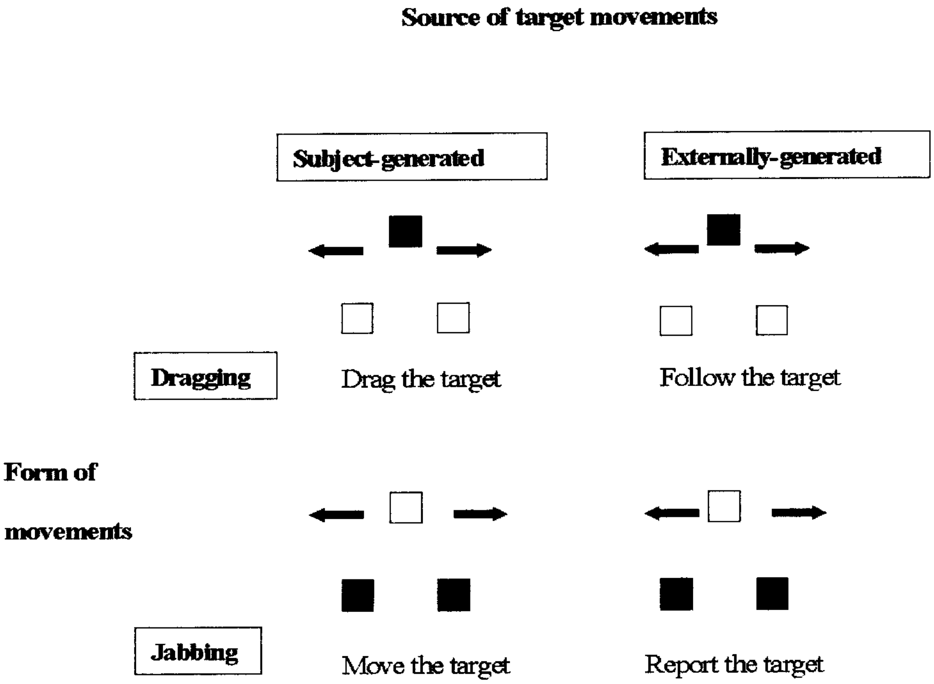


FIG.1. Schema of the stimuli for the four experimental conditions of the factorial design. The three squares were black in the experiment. In this schema, the black squares represent the squares touched by the subjects in the different conditions. In the "dragging" conditions, subjects had to put their finger on the black square and drag it (drag the target) or follow its displacements when it was moving by itself (follow the target). In the "jabbing" conditions, subjects had to move the central square with the two black squares (move the target) or they had to report the displacements of the central square with the same black squares (report the target).

and eye movements in this condition are the same as those in the "report" condition. In order to identify differences between the "report" and the "follow" conditions, which are not simply due to differences in the form of the movement, we looked for those differences which are not also present in the contrast of "move" vs "drag." This is the interaction term in this 2×2 factorial design.

Eye movements were not monitored during the acquisition and the subjects did not receive any instructions with regard to eye movements. However, the interaction term reflects differences between "report" and follow" conditions which are not simply due to differences in the form of hand and eye movements.

Two low-level control conditions were also included: first, a "watch" condition in which the subject had to watch the central square moving by itself without doing anything; second, a "rest" condition in which the subject simply had to watch the screen, which contained only a stationary central box and the report buttons.

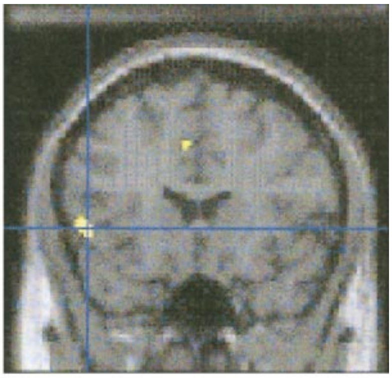
At the beginning of the experiment subjects were required to perform a practice session in all four conditions to familiarize themselves with the equipment and to experience generating random movements.

The PET scanning comprised two blocks of each of the six conditions. Each condition lasted 90 s. The random movements in the "follow" and the "report" conditions were different in the second blocks. The interval between the start time of each condition was 8 min. The order of the conditions within each block was randomized for each subject.

Image Acquisition

The PET images were acquired using an ECAT Exact HR+ PET scanner (CTI Siemens, Knoxville, TN) in the 3-D mode with interdetector collimating septa removed. The total axial field of view was 155 mm, covering the whole brain. Relative regional (r) CBF was measured by recording the regional distribution of cerebral radioactivity using $H_2{}^{15}O$ as a tracer. Nine millicuries of $H_2{}^{15}O$ in 3 ml saline solution was injected over 20 s at a rate of 10 ml/min. Each scan began with background frame duration of 30 s followed by an activation frame duration of 90 s. The trigger contrast for the onset of the activation frame was 30 kcps.

A transmission scan collected before the first emission scan permitted correcting for radiation attenuation. Images were reconstructed by 3-D filtered backprojection (Hanning filter, cut-off frequency 0.5 cycle/pixel) and scatter correction. Sixty-three transverse planes (separation 2.4 mm) were obtained, each with a 128×128-pixel image matrix (size 2.1 mm), giving a resolution of 6 mm at full-width half-maximum (FWHM).



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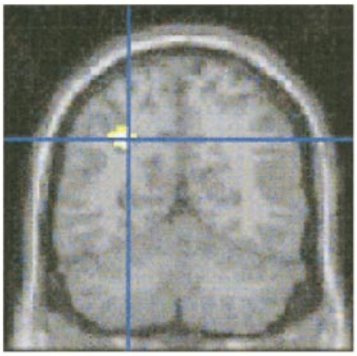

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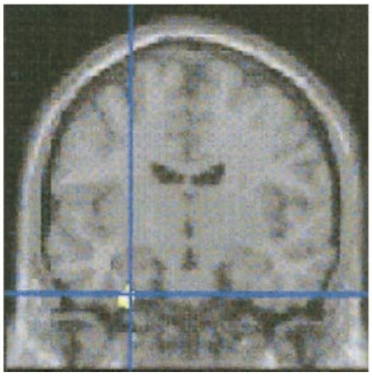

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FIG. 2. Reporting an action activated the left ventral prefrontal cortex (−50, 20, −2). The SPM, thresholded at $P < 0.002$ (uncorrected) and superimposed on a coronal section of the T1 image at $y = 20$ demonstrates this activation.

FIG. 3. Reporting an action activated the left intraparietal cortex (−26, −58, 38). The SPM, thresholded at $P < 0.001$ (uncorrected) and superimposed on a coronal section of the T1 image at $y = -58$ demonstrates this activation.

FIG. 4. Reporting an action activated the left inferior temporal cortex (−28, −12, −34). The SPM, thresholded at $P < 0.001$ (uncorrected) and superimposed on a coronal section of the T1 image at $y = -12$ demonstrates this activation.

All subjects underwent also an MRI scan with a Vision magnetic resonance (MR) scanner operating at 2 T (Siemens, Erlangen, Germany) with a T1 MPRAGE sequence (TE 4 ms, TR 9.5s, TI 600 ms, voxel size 1×1×1.5 mm, 108 axial slices). Those structural images were used for anatomical coregistration.

Data Analysis

Image Analysis: Preprocessing

The data were analyzed with SPM99 (Welcome Department of Cognitive Neurology, London, UK).

Each subject's 12 PET scans were realigned to the first scan of the time series. The estimates extracted from the rigid body transformation (described as three translations (x, y, z) and three rotations about the axes) were used to realign the images. A mathematical adjustment (minimizing the sum of the squares of differences in intensity between each image and the reference) was performed to remove movement-related components. For each subject the structural T1 image was coregistered with the mean rCBF image. The structural image was then spatially normalized into the system of reference of Talairach and Tournoux (1988) using as template a representative brain from the Montreal Neurological Institute series (Evans *et al.*, 1994). The first step of spatial normalization was to determine the optimal affine transformation (correction for the variation in position and size) that would map a brain image to the template (minimization of the sum of the squares of the differences in intensity between those two images and also the squared distance between the parameters and their known expectation). Residual differences between each pair of images were corrected using nonlinear basis functions (Friston *et al.*, 1995). The normalization parameters were subsequently applied to the PET images. Finally PET images were filtered with the use of a low-pass Gaussian filter (FWHM = 12.0, 13.0, 14.0 mm) to reduce noise and maximize signal. The smoothness is achieved by forcing the deformations to consist of a linear combination of predefined smooth spatial basis functions.

Statistical Model and Inference

The data were modeled in order to partition regional CBF of each voxel into components of interest, confounds of no interest, and an error term. The data were first adjusted for the effect of global image signal with the proportional scaling method. We predicted that reporting would be associated with activity in the ventral stream.

The analysis of regionally specific effects was performed using the general linear model. The particular instance of this model in this experiment was a factorial design. It can be framed in terms of a statistical parametric map of a t value SPM(t) and then transformed into a SPM(Z) which was thresholded at $P < 0.05$ corrected for multiple comparisons. The SPM(Z) corresponding to the interaction term was thresholded at $P < 0.001$ uncorrected for multiple comparisons since we had a prior hypothesis about the location of the activity. Finally, statistical inferences about the resulting SPM(Z) were made using distribution ap-

TABLE 1

Significant rCBF Increases during Movement Conditions Compared to No-Movement Conditions

Area	*x*	*y*	*z*	*Z* value	*P* (corrected)
Posterior vermis, cerebellum R	8	−64	−24	11.9	<0.001
Intermediate cerebellar cortex R	20	−52	−20	10.7	<0.001
Striate cortex	−6	−90	4	8.4	<0.001
V5/MT L	−50	−74	2	7.0	<0.001
Parieto-occipital sulcus R	12	−80	38	5.0	0.020
Ventrolateral thalamus L	−12	−14	2	6.1	<0.001
Ventral premotor cortex L	−58	6	24	5.4	0.010

Note. $P < 0.05$ corrected.

proximations from the theory of Gaussian fields. Clusters of activated voxels were characterized in terms of their peak height and spatial extent conjointly.

RESULTS

Movement versus No Movement (Drag, Follow, Report, Move vs Watch, Rest)

The areas showing significantly increased rCBF during conditions in which subjects were required to move their finger compared to conditions of no movement were the right posterior vermis of the cerebellum, the right intermediate cerebellar cortex, the left striate cortex, the left motion area V5/MT, the right parieto-occipital sulcus, the left ventrolateral thalamus, and the left ventral premotor cortex. The coordinates of these areas, the *Z* values, and the probability corrected for multiple comparisons are shown in Table 1.

Areas Related to the Form of Movement

Dragging vs Jabbing (Drag, Follow vs Report, Move)

The areas showing significantly increased rCBF during the dragging conditions compared to the jabbing conditions were the parietal operculum (SII) bilaterally, the right anterior inferior parietal cortex, the prestriate cortex bilaterally, and the left posterior cingulate motor area. The coordinates of these areas, the *Z* values, and the probability corrected for multiple comparisons are shown in Table 2.

Jabbing vs Dragging (Report, Move vs Drag, Follow)

The areas showing significantly increased rCBF during the jabbing conditions compared to the dragging conditions were the right prestriate cortex, the left medial parietal cortex, the left parietal–occipital sulcus, the left anterior cingulate motor area, and the right dorsal prefrontal cortex. The coordinates of these areas, the *Z* values, and the probability corrected for multiple comparisons are shown in Table 3.

Interaction: (Report vs Follow) vs (Move vs Drag)

This interaction term allowed us to identify the specific brain activity associated with “following” or “reporting,” with the differences due to the type of movement removed. The areas showing significantly increased rCBF during reporting were the left ventral prefrontal cortex (Fig. 2), the left intraparietal cortex (Fig. 3), the left inferior temporal cortex (Fig. 4), the left middle temporal gyrus, and the right inferior frontal sulcus. The coordinates of the areas, the *Z* values, and the probability uncorrected are shown in Table 4.

No areas which were specifically associated with following were identified.

TABLE 2

Significant rCBF Increases during Dragging Conditions Compared to Jabbing Conditions

Area	*x*	*y*	*z*	*Z* value	*P* (corrected)
Parietal operculum (SII) L	−50	−26	24	6.5	<0.001
Parietal operculum (SII) R	64	−20	28	4.9	0.050
Anterior inferior parietal cortex R	62	−28	20	4.8	0.060
Prestriate cortex L	−16	−98	0	5.5	0.004
Prestriate cortex R	32	−92	0	5.6	0.003
Posterior cingulate motor area	−2	−14	48	4.6	(<0.001 cluster level)

Note. $P < 0.05$ corrected.

TABLE 3

Significant rCBF Increases during Jabbing Conditions Compared to Dragging Conditions

Area	*x*	*y*	*z*	*Z* value	*P* (corrected)
Prestriate cortex R	6	−82	−4	4.4	(<0.001 cluster level)
Medial parietal cortex L	−10	−54	42	4.3	(<0.001 uncorrected)
Parieto-occipital sulcus L	−14	−78	40	4.1	(0.04 cluster level)
Anterior cingulate motor area	−2	8	52	4.5	(<0.001 uncorrected)
Dorsal prefrontal cortex R	44	38	26	4.1	(0.02 cluster level)

Note. $P < 0.05$ corrected.

DISCUSSION

The aim of this study was to compare directly the brain areas activated when the subject had to guide actions using visual cues with those activated when that subject had to make a report of the same visual cues. We predicted that reporting would elicit activity in the ventral stream.

We first compared the experimental conditions with movement to conditions with no movement. Brain areas typically associated with motor tasks involving the right hand were activated in this contrast (right posterior vermis and right intermediate cerebellar cortex, left ventrolateral thalamus and left ventral premotor cortex) (Fox *et al.*, 1985; Jenkins *et al.*, 1994). In addition activity was observed in the left striate cortex (V1) and left extrastriate cortex (V5/MT). These activations may be explained by a difference in the visual stimulation between these conditions. When the subject has to move his finger on the screen, in the experimental conditions, he sees and must attend to both his own finger and the moving square, whereas during the control condition “watch” he only watches the moving square.

The two main conditions used in our experiment for contrasting reporting with the guidance of movement also differed in the form of the movements they required. It was therefore necessary to identify the brain areas related to the differences in the form of movement. A dragging movement contrasted with a jabbing movement revealed bilateral activation of SII, localized in the parietal operculum (Burton *et al.*, 1993) and the right anterior inferior parietal cortex. The SII activation is not surprising since subjects had to keep their finger on the screen while they dragged or followed the square. Thus they exerted a continuous pressure in this condition in contrast to the brief presses required for jabbing the report buttons. However we did not observe activation of the primary somatosensory cortex (SI) in this comparison or when conditions with movement were compared to the no-movement condition. This is consistent with previous studies which suggest that SI activity may be elicited only by more subtle and complex tactile discrimination tasks than the one used here (Adams and Victor, 1989). Furthermore a number of previous imaging studies have failed to observe SI activity in response to tactile stimulation (see Paulesu *et al.*, 1997). The anterior inferior parietal cortex (AIP) was also activated by dragging movements. The AIP has connections with the SII and has been shown to be involved in a neural network implicated in producing motor responses to visual and somatosensory stimuli (Graziano and Gross, 1993). Our dragging movement clearly has a greater requirement for continuous integration of somatosensory and visual information than the intermittent jabbing movements involved when using the report buttons.

Jabbing at a square contrasted with dragging it involved parietal areas including the left medial parietal cortex and the left parieto-occipital sulcus. This last region activates in object identification tasks (Kosslyn *et al.*, 1995). It was also activated in the shape-matching task of Faillenot *et al.*, (1997). In our study, jabbing at one of two response buttons requires first an identification of the target stimulus, while dragging the

TABLE 4

Significant rCBF Increases during the Interaction (Report vs Follow) vs (Drag vs Move)

Area	*x*	*y*	*z*	*Z* value	*P* (uncorrected)
Intraparietal cortex L	−26	−58	38	3.6	<0.001
Middle temporal gyrus L	−48	−50	10	3.7	<0.001
Inferior temporal cortex L	−28	−12	−34	3.5	<0.001
Inferior frontal sulcus R	52	26	18	3.1	0.001
Ventral prefrontal cortex L	−50	20	−2	3.0	0.002

Note. $P < 0.001$ uncorrected.

square did not need any such identification to be performed. The activation of the parieto-occipital sulcus may reflect such identification process in jabbing movements.

This contrast also revealed activations in the left anterior cingulate cortex and in the right dorsolateral prefrontal cortex. These two regions are shown to be activated when subjects must attend to their actions (Frith *et al.*, 1991; Passingham, 1996; Jueptner *et al.*, 1997). The activation of the dorsolateral prefrontal cortex and of the anterior cingulate cortex in this contrast may be explained by a greater attentional effort required for the jabbing movements than the dragging movements. Greater attentional effort is needed for making the jabbing movements, since this is effectively a dual-task situation. The subject must attend to the action of pressing the response buttons as well to the movements of the square.

Finally, these two movements differ also in the visual processing they required. Different regions of the visual cortex were activated in these two contrasts. In the dragging vs jabbing contrast there was activation in the lateral and posterior part of the visual cortex. In the jabbing vs dragging contrast we observed an activation in a more medial part of the visual cortex localized most likely in the right striate cortex. It is also possible that these different activations are associated with different types of eye movement. For example, dragging is likely to be associated with smooth pursuit eye movements, while jabbing is associated with saccades to the button that is target of the movement.

It is clear that dragging and jabbing movements were associated with activity in different brain areas. However, we are able to discount these differences in our comparison of reporting and following by computing the interaction term. This interaction term reflects specifically the processes involved in reporting over and above differences in the form of the movement made. As we predicted, brain areas involved in the ventral stream such as the left inferotemporal cortex and the left ventral prefrontal cortex were activated in this interaction term. We also found other brain regions activated, such as the left intraparietal cortex, the left middle temporal cortex, and the right inferior frontal cortex. However, these results must be treated with caution since their significance did not survive correction for multiple comparisons.

Inferior Temporal Cortex

Some studies have observed involvement of this brain area in the identification of objects (Milner and Goodale, 1997, for review). Toni *et al.*, (1999) have studied brain areas activated during a visuomotor associative task with an event-related fMRI method. They found that the hemodynamic response in the inferotemporal cortex was associated with the visual cue. In our study when the subject had to report the displacements of the square, he had first to identify the stimulus and its spatial properties. This stage may be processed in the inferior temporal cortex. There are no direct projections in the macaque monkey from the inferior temporal cortex to the premotor cortex (Boussaoud *et al.*, 1996); thus the information processed in this temporal region is likely, in man also, to be relayed via another brain area in order to reach premotor areas.

Ventral Prefrontal Cortex

This region receives projections from the inferotemporal cortex (Webster *et al.*, 1994; Bullier *et al.*, 1996; Pandya and Yeterian, 1998). The ventral prefrontal cortex may provide a link between the cue represented in the inferotemporal cortex and its related motor response. This hypothesis is supported by observation of activation in the ventral prefrontal cortex when subjects had to associate a visual stimulus with a specific movement (Toni *et al.*, 1998). A recent event-related fMRI study by Toni *et al.*, (1999) has revealed a cue-related response in the inferior frontal gyrus. They also found that the evoked hemodynamic response was time locked to the motor response in this region. Thus the ventral prefrontal cortex may constitute part of the circuitry by which associations are formed between arbitrary visual cues and actions (Passingham, 2000). Our observations support the hypothesis that this area is also engaged by the requirement to report a visual stimulus.

Other Regions

Two other areas reached uncorrected levels of significance ($P < 0.0001$) when reporting was contrasted with following. These areas were in the intraparietal cortex and in the middle temporal gyrus close to the superior temporal sulcus. We had not specifically predicted activity in these areas since they are not part of the ventral system. Therefore further studies are needed before we can conclude that these areas are part of a neural system associated with reporting and it is not appropriate to discuss the implications of these observations at length here. Nevertheless, precisely these areas have been observed in previous experiments in which reporting of stimuli was required. A number of recent experiments on the neural correlates of consciousness (see Rees, 2001, for a review) suggest that, while activity in the ventral stream is necessary for consciousness of visual stimuli, it is not sufficient. When subjects are able to report the presence of visual stimulus activity is consistently seen in the intraparietal sulcus, close to the region activated in the present study. Downar *et al.*, (2000) required subjects to report changes in stimuli in any of three different modalities. Independent of modality, activity associated with the report of change was observed in the same region of middle temporal gyrus as in the present study.

Following vs Reporting

Although we found activation of the ventral stream in reporting a stimulus contrasted with following that stimulus, contrasting the following condition with the reporting condition controlling for the differences in the type of movement did not reveal any significant brain activations. One explanation for this absence of activation of the dorsal stream would be that it was involved equally for both following and reporting. Indeed it has been shown that the dorsal stream is involved in the processing of visuospatial cues in goal-directed movements (Jeannerod, 1994; Sakata *et al.*, 1996). Such goal-directed movements are present in the follow condition, but also in the report condition since the subjects had to push one of the two bottom squares.

CONCLUSION

This study has shown that reporting the movement of a stimulus in contrast to simply tracking it elicits additional activation in distinct brain areas even though both following and reporting required only simple finger movements. When reporting the presence of the stimulus, the subjects had to associate a visual cue (direction of displacement of the square) to an arbitrary response. This association may depend upon ventral prefrontal cortex which can link the explicit representation of stimulus identity in the inferotemporal cortex with action systems in the premotor cortex. However, activity in the ventral stream may not be sufficient for reporting. Parietal activity may also be required.

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REFERENCES

Adams, R. D., and Victor, M. 1989. In *Principles of Neurology*. McGraw–Hill, New York.

Boussaoud, D., Ungerleider, L. G., and Desimone, R. 1990. Pathways for motion analysis: Cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *J. Comp. Neurol.* **296:** 462–495.

Boussaoud, D., di Pellegrino, G., and Wise, S. P. 1996. Frontal lobe mechanisms subserving vision-for-action versus vision-for-perception. *Behav. Brain Res.* **72:** 1–15.

Bridgeman, B., Kirch, M., and Sperling, A. 1981. Segregation of cognitive and motor aspects of visual function using induced motion. *Percept. Psychophys.* **29:** 336–342.

Bullier, J., Schall, J. D., and Morel, A. 1996. Functional streams in occipito-frontal connections in the monkey. *Behav. Brain Res.* **76:** 89–97.

Burton, H., Videen, T. O., and Raichle, M. E. 1993. Tactile-vibration-activated foci in insular and parietal–opercular cortex studied with PET mapping the second somatosensory area in humans. *Somatosens. Mol. Res.* **10:** 297–308.

Castiello, U., Paulignan, Y., and Jeannerod, M. 1991. Temporal dissociation of motor responses and subjective awareness: A study in normal subjects. *Brain* **114:** 2639–2655.

Cowey, A., and Stoerig, P. 1995. Blindsight in monkeys. *Nature* **373:** 247–249.

Downar, J., Crawley, A. P., Mikulis, D. J., and Davis, K. D. 2000. A multimodal cortical network for the detection of changes in the sensory environment. *Nat. Neurosci.* **3:** 277–283.

Evans, A. C., Kamber, M., Collins, D. L., and MacDonald, D. 1994. A MRI-based probabilistic atlas of neuroanatomy. In *Magnetic Resonance Scanning and Epilepsy* (S. Shorvon, D. Fish, F. Andermann, G. M. Bydder, and H. Stefan, Eds.), NATO ASI Series A, *Life Sciences*, Vol. 264, pp. 263–274. Plenum, New York.

Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., and Jeannerod, M. 1997. Visual pathways for object-oriented action and object recognition: Functional anatomy with PET. *Cereb. Cortex* **7:** 77–85.

Fox, P. T., Pox, J. M., Raichle, M. E., and Burde, R. M. 1985. The role of cerebral cortex in the generation of voluntary saccades: A PET study. *J. Neurophysiol.* **54:** 348–369.

Friston, K. J., Ashburner, J., Frith, C. D., Poline, J. B., Heather, J. D., and Frackowiak, R. S. J. 1995. Spatial registration and normalisation of images. *Hum. Brain Mapping* **2:** 165–189.

Frith, C. D., Friston, K., Liddle, P. F., and Frackowiak, R. S. J. 1991. Willed action and the prefrontal cortex in man: A study with PET. *Proc. R. Soc. London B.* **244:** 241–246.

Goodale, M. A., and Milner, A. D. 1992. Separate visual pathways for perception and action. *Trends Neurosci.* **15:** 20–25.

Goodale, M. A., Milner, A. D., Jakobson, L. S., and Carey, D. P. 1991. Perceiving the world and grasping it: A neurological dissociation. *Nature* **349:** 154–156.

Graziano, M. S. A., and Gross, C. G. 1993. A bimodal map of space: Somatosensory receptive fields in the macaque putamen with corresponding visual receptive field. *Exp. Brain Res.* **97:** 96–109.

Jeannerod, M. 1994. The hand and the object. The role of posterior parietal cortex in forming motor representations. *Can. J. Physiol. Pharmacol.* **72:** 525–534.

Jenkins, I. H., Brooks, D. J., Nixon, P. D., Frackowiak, R. S. J., and Passingham, R. E. 1994. Motor sequence learning: A study with PET. *J. Neurosci.* **14:** 3775–3790.

Jueptner, M., Stephan, K. M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., and Passingham, R. E. 1997. Anatomy of motor learning. I. Frontal cortex and attention to action. *J. Neurophysiol.* **77:** 1313–1324.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Rauch, S. L., and Anderson, A. K. 1995. Identifying objects seen from different viewpoints: PET investigation. *Brain* **117:** 1055–1071.

Milner, A. D., and Goodale, M. A. 1997. *The Visual Brain in Action*. Oxford Univ. Press, Oxford.

Morel, A., and Bullier, J. 1990. Anatomical segregation of two cortical visual pathways in the macaque monkey. *Visual Neurosci.* **4:** 555–578.

Pandya, D. N., and Yeterian, E. H. 1998. Comparisons of prefrontal architecture and connections. In *The Prefrontal Cortex* (A. C. Roberts, T. W. Robbins, and L. Weiskrantz, Eds.), pp. 51–66. Oxford Univ. Press, Oxford.

Passingham, R. E. 1996. Attention to action. *Philos. Trans. R. Soc. London B* **29:** 1473–1479.

Passingham, R. E, Toni, I., and Rushworth, M. F. 2000. Specialisation within the prefrontal cortex and associative learning. *Exp. Brain Res.* **133:** 103–113.

Passingham, R. E., and Toni, Y. 2001. Contrasting the dorsal and ventral visual systems: Guidance of movement versus decision making. *NeuroImage,* in press.

Paulesu, E., Frackowiak, R. S. J., & Bottini, G. 1997. Maps of somatosensory systems. In *Human Brain Function* (R. S. J. Frackowiak, K. J. Friston, C. D. Frith, R. J. Dolan, and J. C. Mazziotta, Eds.). Academic Press, San Diego.

Rees, G. 2001. Neuroimaging of visual awareness in patients and normal subjects. *Curr. Opin. Neurobiol.* **11:** 150–156.

Sakata, A., Gallese, V., Kaseda, M., and Sakata, H. 1996. Parietal neurones related to memory-guided hand manipulations. *J. Neurophysiol* **75:** 2180–2186.

Talairach, J., and Tournoux, P. 1988. *Coplanar Stereotaxic Atlas of the Human Brain.* Thieme, New York.

Toni, Y., Rushworth, M. F. S., Ramnani, N., and Passingham, R. E. 1998. Visually instructed and visually guided movements. *NeuroImage* **7:** S980.

Toni, Y., Schluter, N. D., Josephs, O., Friston, K., and Passingham, R. E. 1999. Signal, set and movement-related activity in the human brain: An event-related fMRI. *Cereb. Cortex* **9:** 35–49.

Ungerleider, L., and Mishkin, M. 1982. Two cortical visual systems. In *Analysis of Visual Behaviour* (D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield, Eds.), pp. 549–586. MIT Press, Cambridge, MA.

Webster, M. J., Bachevalier, J., and Ungerleider, L. G. 1994. Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cereb. Cortex* **4:** 471–483.

Weiskrantz, L. 1986. *Blindisght: A Case Study and Implications.* Oxford Univ. Press, Oxford.