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# Human inferior parietal cortex ‘programs’ the action class of grasping

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## Abstract

If one writes with a pen grasped between the toes, or a pencil held in the mouth, the handwriting style may be of poor quality but can be identified as belonging to a particular individual. Like other actions, such as grasping or pointing, different body parts can be used to produce the movement. These findings, of reasonably consistent spatial and temporal productions by different effectors, have been used to argue for the concept of motor equivalence and the existence of motor programs abstracted from particular effectors. In this study subjects were required to perform an action (grasping a sweet) with different effectors (the mouth or the hand) while the brain was scanned. Activation of the inferior parietal lobe during real and imagined mouth grasping, and during real hand grasping actions was demonstrated. Primate neurophysiological research has implicated this region in a movement-planning role. Our results confirm the importance of the inferior parietal lobe in integrating converging multimodal sensory information for coding of general action patterns in humans. © 1999 Elsevier Science B.V. All rights reserved.

## 1. Introduction

In its most general sense, a motor program refers to an abstract memory structure of central nervous system origin that specifies or guides movement. Early descriptions placed emphasis on the specificity of a plan to an action, with effector-dependent coding of movement parameters (e.g., specifying the

velocity and sequencing of any movements; Keele, 1968; Adams, 1971). Subsequent conceptual refinement describes the motor program as a mélange of non-specific instructions that codes broadly for a class of motor tasks (such as ‘walk’ or ‘grasp’). The shared higher-order movement elements contained within a representation of each class are said to allow for effector independence in task implementation, and motor equivalence, “the capacity of the motor system to achieve the same end product with considerable variation in the individual components that contribute to them” (Hughes & Abbs, 1976, p. 199).

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Evidence that one representation can be linked to different effectors has come largely from handwriting studies. Bernstein (1947) illustrated surname samples from a single volunteer who wrote with a pencil attached to various body parts (both feet, mouth, etc.). The similar style across samples pointed to the existence of a general coding level that was independent of the specific coding needed for each body segment. Later handwriting studies confirmed qualitative similarities across effectors (Merton, 1972), adding support to the concept that common broad features of some actions were coded (Hughes & Abbs, 1976; Keele, 1968).

The functional hierarchy for motor equivalence and programming is ill defined. Despite similarities in overall shape, performances by different effectors show systematic differences in kinematics, stroke decomposition and fluency for both practiced (name) and unfamiliar (equation) writing tasks (Wright, 1990). In other words, detailed kinematics change from effector to effector (e.g., when comparing right to left hand). Such results suggest that the abstract spatial characteristics of a task class are mapped at one level of the action plan, with coding for effector-specific requirements at other dissociable levels within a coordinated control program hierarchy (Arbib, 1990). The general content at effector-independent levels can change. Castiello & Stelmach (1993) report the case of a left-handed man who had sustained the amputation of his left hand several years previously, and had learnt to write with his previously non-dominant right hand. At the time of kinematic testing of his writing, he had been fitted with a prosthesis for the previously dominant limb. Castiello and Stelmach demonstrated that kinematics of the prosthetically operated handwriting performances were spatially and temporally equivalent to those of the non-dominant right hand. Previously effector-specific levels had entered effector-independent levels.

Complex functions, such as that of grasping, are controlled not by an isolated locus within the brain but by a distributed system of multiple neuronal networks interconnected dynamically (see review in Weisendanger, 1995). Results from behavioural studies imply that the networks activated to achieve motor equivalence include those regions that code for spatial interfacing between the body and environ-

ment (Keele et al., 1990). For example, with learned keyboard sequences, a training effect persists with transfer to alternative effectors but not with transfer to a random sequence, indicating that encoding of the sequence, independent from the system implementing the sequence, incorporates the 'where' of successive signals and/or responses. Keele et al. (1990) proposed that the parietal lobe, with its spatial encoding function, might be a candidate for the underlying neural base of sequence representation.

In particular, the inferior parietal lobe is thought to play an important role in the encoding of general movement features. This site of multimodal sensory convergence from visual, somatosensory and limbic regions (Husain, 1991) shows reciprocal projections with principal motor areas (e.g., frontal eye fields, premotor cortex, striatum) reflecting potential to influence processing in these areas and to receive efference copy. Convergence of information from the inferior parietal cortex to the intraparietal (IP) sulcus points to processing in this region of the 'highest' order (Husain, 1991). As proposed by Arbib (1997), the inferior parietal lobe is well placed to process visual information to extract a variety of affordances for behaviour, and thus to map essential motor features from a perception of the interface between individual and environment.

Neurophysiological studies in primates have confirmed a task-relevant visuomotor transformation function for inferior parietal cortex. Primate parietal cells that fire in relation to eye and upper limb movements have been termed 'command' cells (Mountcastle et al., 1975). Single cells within the monkey lateral IP sulcus encode saccades to behaviourally relevant targets regardless of the modality through which these targets are localised adds further support to a saccade-planning function (Mazzoni et al., 1996). Further, Snyder et al. (1997) located movement direction modulated cells within posterior parietal cortex (including lateral IP) of which 68% were motor-intention specific for either an arm or eye movement. Such reports support contentions of involvement in motor planning networks for this region (Mazzoni et al., 1996; Andersen, 1995).

Because speculation about the function of inferior parietal cortex comes largely from primate studies,

we aimed to determine if this region shows evidence of a role in the coding for effector-independent movement features in humans, and thus to address the functional homology between human and non-human inferior parietal lobule. One means of ascertaining this was to look at activation sites within the brain when a suitable behavioural task is performed. In our study, positron emission tomography (PET) scans were conducted to measure regional cerebral blood flow (rCBF) when participants used either the mouth or the hand for a 'grasp' action. These two effectors were chosen because in a previous study it was demonstrated that mouth 'grasping' shows a kinematic patterning similar to that of reach-to-grasp (Castiello, 1997). Changes in spatial organisation according to target object size, and in the timing of mouth opening and closing, reflected those found with hand use. We reasoned that common features of the grasp action by different effectors should be coded for by brain regions that play a principal role in determining motor equivalence.

Our hypothesis was that the inferior parietal lobule (IPL) should be active irrespective of the effector used to grasp the piece of food. Previous brain imaging studies of humans indicate that the inferior parietal lobe consistently shows activation during both the execution and the imagining of upper limb grasping actions. Left inferior parietal cortex (area 40) is activated when participants imagine grasping either a real (Grafton et al., 1996) or a virtual (Decety et al., 1994) three-dimensional object with the right hand. This same region is activated when actual reach-to-grasp actions are performed with real objects (Rizzolatti et al., 1996).

### 1.1. Methods

*Participants.* Five males (mean age 34 years) gave informed consent and participated in the study. All were right-handed, reported normal or corrected-to-normal vision, and were naïve as to the purpose of the experiment. They attended one experimental session of ~4 h duration.

*Apparatus.* Subjects were scanned using a Siemens/CTI 951/31R PET scanner operated in three-dimensional mode with a 10.8 cm axial field of view. Relative regional cerebral blood flow (rCBF) was measured from the distribution of radioactivity

after slow bolus intravenous injection of  $H_2^{15}O$  (7.0 mCi per scan, each lasting 90 s). Attenuation-corrected data were reconstructed into 31 image planes with a resulting resolution of 6.5 mm at full-width half-maximum. A high-resolution magnetic resonance image (MR; Siemens, Magnatom SP4000) was also acquired for each subject.

*Procedure.* Four relative rCBF measurements were taken during each of the following four conditions: (1) a mouth grasping movement, (2) a finger grasping movement, (3) an imagined mouth grasping movement, and (4) a view-only task. The conditions were administered in a Latin square design that varied for each subject. Subjects lay with eyes open in a quiet, dimly illuminated room fixating on a small red ball (3cm diameter) attached to a stand. The ball acted as a starting position for a fork upon which a piece of food ( $1 \times 1$  cm soft sweet) was impaled. For the real and imagined grasping conditions, subjects were required to fixate on the ball as an experimenter moved the sweet 30 cm toward either the subject's hand or mouth. The task of the subject was to open and close the effector to grasp the sweet. No reaching movement of the head or arm was required (or observed during performance). Head and arm movements were further restrained by comfortable but firm splinting. The subjects' right upper limb was positioned with the hand resting on the chest, and the forearm and wrist within a splint that allowed only thumb and index-finger opposition. The jaw was kept free of a head mask that was fitted to immobilise head movements. For the imagined mouth grasp condition the subject was required to imagine opening his mouth to grasp the object. For this condition the object was moved towards the mouth of the subject as for the mouth grasping movement condition. For the view-only condition, the subject was required to view the sweet being moved approximately 3–5 cm just in front of the fixation ball. Onset of the experimenter's movement was determined by a computer-driven timing program that presented a visual signal at a variable rate (2500–3500 ms). The visual stimulus could not be seen by the subject.

*Data processing and analysis.* An automated image registration algorithm (AIR 3.0; Woods, Grafton, Holmes, et al., 1998; Woods, Grafton, Watson, et al., 1998) was used to align each subject's second

and subsequent PET image to his first PET image. Each subject's MRI image was edited to remove the scalp and other brain coverings and his average PET image was then aligned to his segmented MRI. Each subject's segmented MRI scan was aligned to a standard MRI using a nonlinear algorithm (AIR 3.0). The three alignment transformation matrices generated by AIR 3.0 were then combined and applied as a unique transformation for each PET image. The transformed images were smoothed using a three-dimensional 12 mm FWHM Gaussian smoothing function (AIR 3.0).

Statistical Parametric Mapping (SPM96, Wellcome Department of Cognitive Neurology, London) software was used for statistical analysis (Friston et al.,

1995). Condition-dependent differences in global flow were co-varied out using ANCOVA. Significant activations ( $P_{\text{corr}} < 0.05$ ) were chosen after a Bonferroni-like correction for the number of independent resolution elements (resels) throughout the brain volume. Corrected values refer to correction for the whole brain volume based upon magnitude of the response. The resulting set of  $z$  values constituted a statistical parametric map (SPM $\{z\}$ ). Activation regions having a probability threshold uncorrected for the whole brain volume tested ( $P < 0.001$ ) are also reported. Localizations of maxima are reported within the standard space, as defined by Talairach & Tournoux (1988), and were superimposed on the group average MR image.

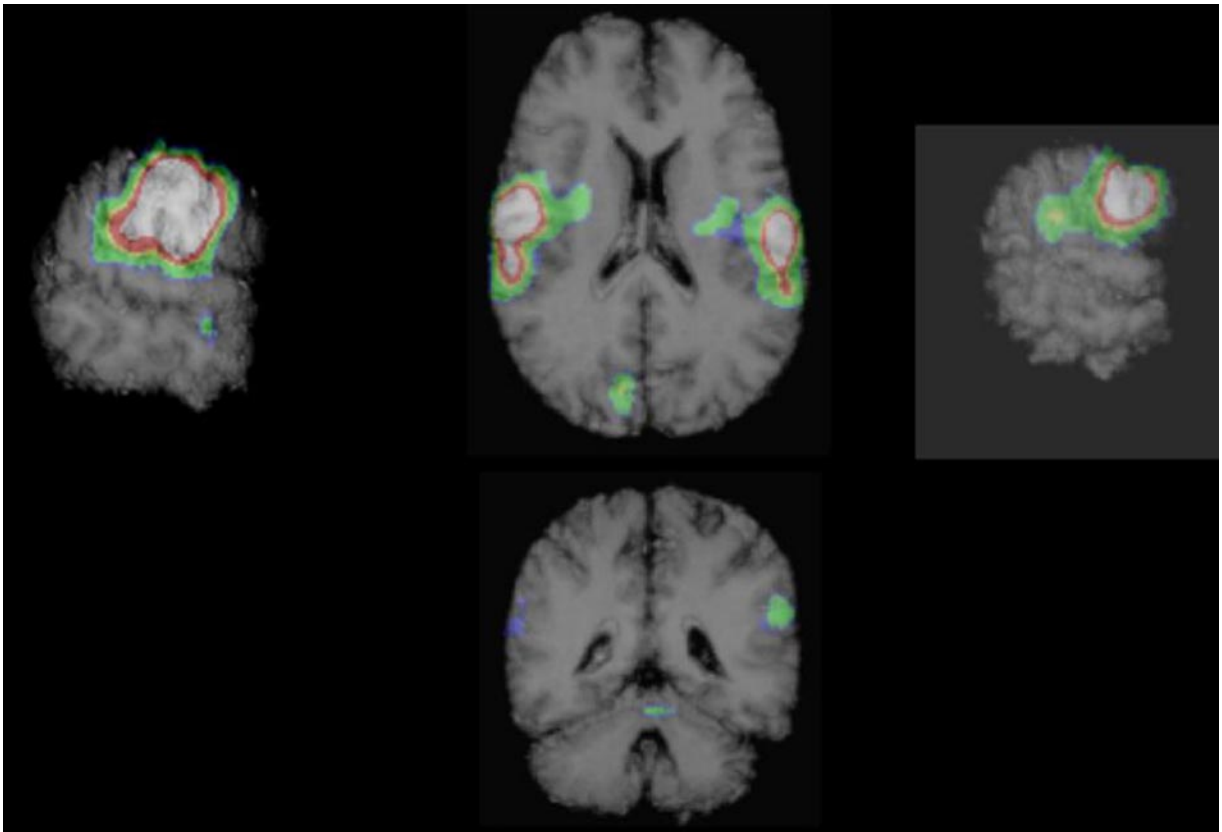


Fig. 1. Orthogonal views of the significant cerebral activations determined for the mouth grasping condition showing the bilateral mouth regions superimposed onto the average MRI image of the subject group. The colour scale depicts the significance of the activation — red:  $Z > 4.3$  ( $P_{\text{corr}} < 0.05$ ); yellow:  $Z > 4.0$  ( $P_{\text{corr}} < 0.10$ ); green:  $Z > 2.33$  ( $P_{\text{uncorr}} < 0.01$ ); blue:  $Z > 1.63$  ( $P_{\text{uncorr}} < 0.05$ ) — where the corrected probability limits are after correction for the multiple non-independent comparisons throughout the brain volume. Activation of the pre-central gyri represented a 10–13% increase in regional cerebral blood flow (rCBF); in the post-central gyri, at least a 10% increase.

## 1.2. Results

We used principles of cognitive subtraction to isolate regions that were more active during the performance of real and imagined grasps by the mouth and real grasps by the hand, than during a condition in which a moving piece of food was viewed. For all conditions we noted bilateral activation of the inferior parietal lobe. When food was grasped using the mouth effector, the pre- and post-central gyri showed significant activation bilaterally. Activation of the right IPL was in the order of a 5% rCBF increase (Fig. 1, Table 1A) and the left IPL showed significant activation with uncorrected  $P$  values. Results for the hand grasping condition confirmed those from previous brain-imaging studies of this action (Rizzolatti et al., 1996). Significant activation was found in the left pre- and post-central gyri, along the midline in the cingulate gyrus, and in the precuneus. Inferior parietal lobule activation was bilateral, with a 7% rCBF increase on the left, and a

4% increase on the right (Fig. 2, Table 1B). The most significant activation for the imagined mouth grasp condition was in the left IPL (5% rCBF increase), and the right IPL showed significant activation with uncorrected  $P$  values. Other activated sites for the imagined mouth grasp condition included the left inferior frontal gyrus and post-central gyrus (Fig. 3, Table 1C). Fig. 4 provides a comparison of the bilateral rCBF activations in the inferior parietal lobule for all three tasks.

## 2. Discussion

The present findings confirm our hypothesis that the inferior parietal lobule would show activation during both real and imagined grasping activities with different effectors. They are also consistent with the idea of posterior/anterior neural circuits for particular action classes. Consistent with the findings of Matsumura et al. (1996), of a grasping network

Table 1

Brain regions associated with significant rCBF increases under each real and imagined grasp condition compared to the view-only condition

Region	Adjusted rCBF (ml (100 g) <sup>-1</sup> min <sup>-1</sup> )		Talairach coordinates $x, y, z$	$z$ score	$P_{\text{corr}} <$
A.	Mouth grasp	View			
Left pre-central gyrus	68	60	-44, -16, 40	7.28	0.001
Left post-central gyrus	63	57	-48, -12, 32	7.21	0.001
Right pre-central gyrus <sup>a</sup>	63	57	56, -16, 32	7.15	0.001
Right inferior parietal lobule	67	64	58, -42, 28	4.71	0.017
B.	Finger grasp	View			
Left inferior parietal lobule <sup>b</sup>	61	57	-46, -30, 40	5.63	.001
Left post-inferior parietal lobule	59	55	-30, -50, 52	5.21	.002
Mid-cingulate gyrus <sup>c</sup>	65	61	-2, -16, 56	5.15	.002
Left precuneus <sup>d</sup>	56	53	-14, -60, 56	4.87	.009
Left post-central gyrus <sup>e</sup>	56	52	-56, -30, 20	4.74	.015
Left pre-central gyrus <sup>f</sup>	60	56	-18, -22, 64	4.68	.02
Right inferior parietal lobule	66.5	64	50, -42, 24	4.52	.038
C.	Imagined mouth grasp	View			
Left inferior parietal lobule <sup>g</sup>	63	60	-46, -36, 32	4.36	0.069
Left inferior frontal gyrus	64.5	62	-42, 2, 32	4.14	0.155
Left post-central gyrus			-50, -20, 40	3.26	0.934

<sup>a</sup> Region includes the post-central gyrus, with maxima within pre-central gyrus.

<sup>b</sup> To validate our findings, corresponding  $x, y, z$  Talairach coordinates for maxima activation areas during a reach-to-grasp action are reported: 36, -28, +32.

<sup>c</sup> Corresponding  $x, y, z$  Talairach coordinates for maxima activation areas during a reach-to-grasp action are reported: -14, -16, +36.

<sup>d</sup> Corresponding  $x, y, z$  Talairach coordinates for maxima activation areas during a reach-to-grasp action are reported: -16, -6, +48.

<sup>e</sup> Corresponding  $x, y, z$  Talairach coordinates for maxima activation areas during a reach-to-grasp action are reported: -22, -22, +48.

<sup>f</sup> Corresponding  $x, y, z$  Talairach coordinates for maxima activation areas during a reach-to-grasp action are reported: -22, -22, +48.

<sup>g</sup> Corresponding  $x, y, z$  Talairach coordinates for a maximum activation area during an imagined hand grasping action: -48, -54, 37.

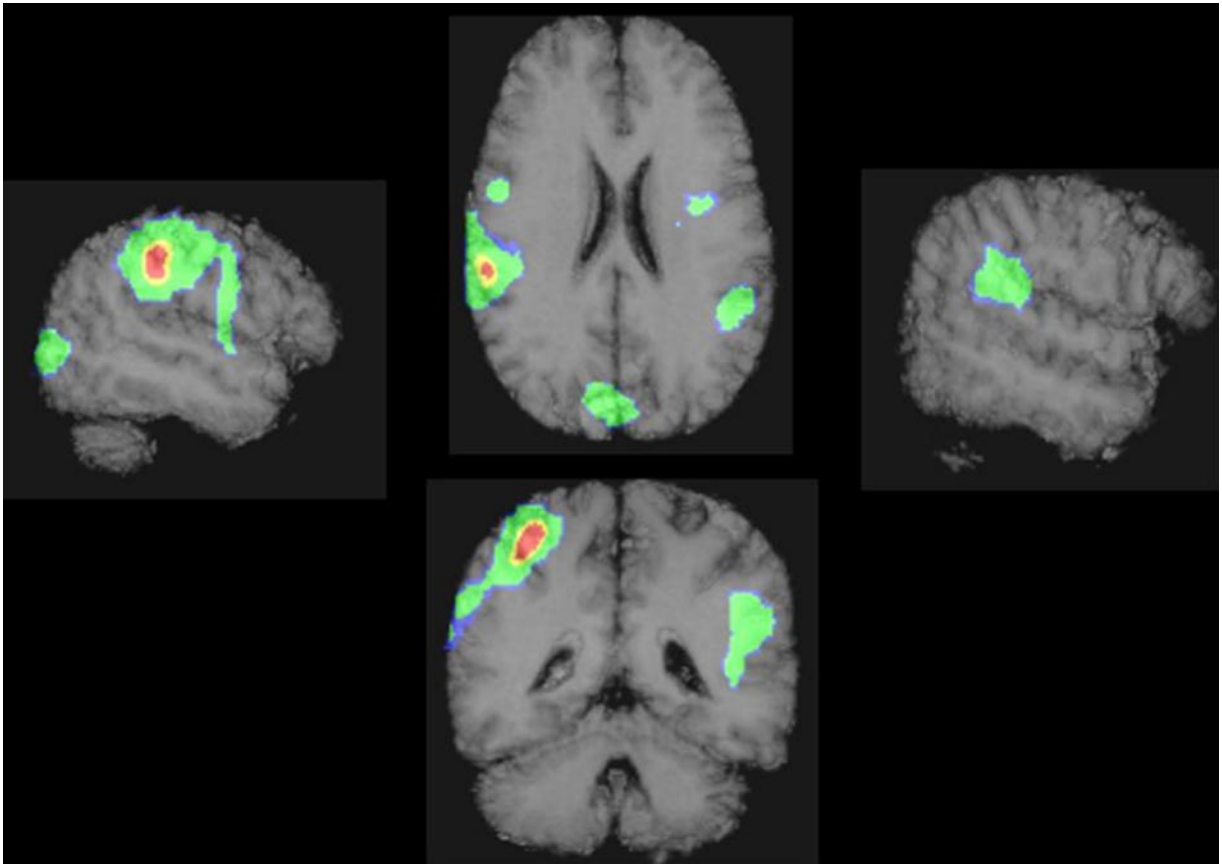


Fig. 2. Orthogonal views of the significant cerebral activations determined for the finger grasping condition compared to the viewing condition showing activations in the left pre- and post-central gyri, and bilaterally in the IPL (colours as in Fig. 1).

that includes parietal, premotor and prefrontal regions, Arbib (1997) proposes that there are parietal–premotor interactions involved in grasping.

Grafton et al. (1996) have also proposed that the inferior parietal lobe forms part of a human hand ‘grasping circuit’ that includes the precentral sulcus. In our study, the precentral gyrus is not additionally activated during imagined mouth grasping as compared to a view-only condition. However, activation of this region is evident during real mouth grasps and during real and imagined hand grasps (see also Grafton et al., 1996; Bonda et al., 1994). In keeping with findings in primates of more segmental coding for grasping in inferior premotor regions (Jeannerod et al., 1995) we suggest that precentral gyrus gives coding that leans more towards effector-dependent

features of the action. In contrast, the consistent activation of the inferior parietal lobe for all real and imagined mouth and hand grasping actions in both this and previous studies makes IPL a good candidate for the coding of effector-independent ‘grasp’ movement features. If inferences can be made from primate analogues (Snyder et al., 1997), there may also be the potential for the encoding of general motor features for motor schemas (Arbib, 1990) of other class actions, and as performed by other body parts.

A possible alternative interpretation for the present data is that they provide evidence for IPL involvement in two modes of grasping, but do not provide evidence for motor programs. In other words, IPL might be involved in the implementation

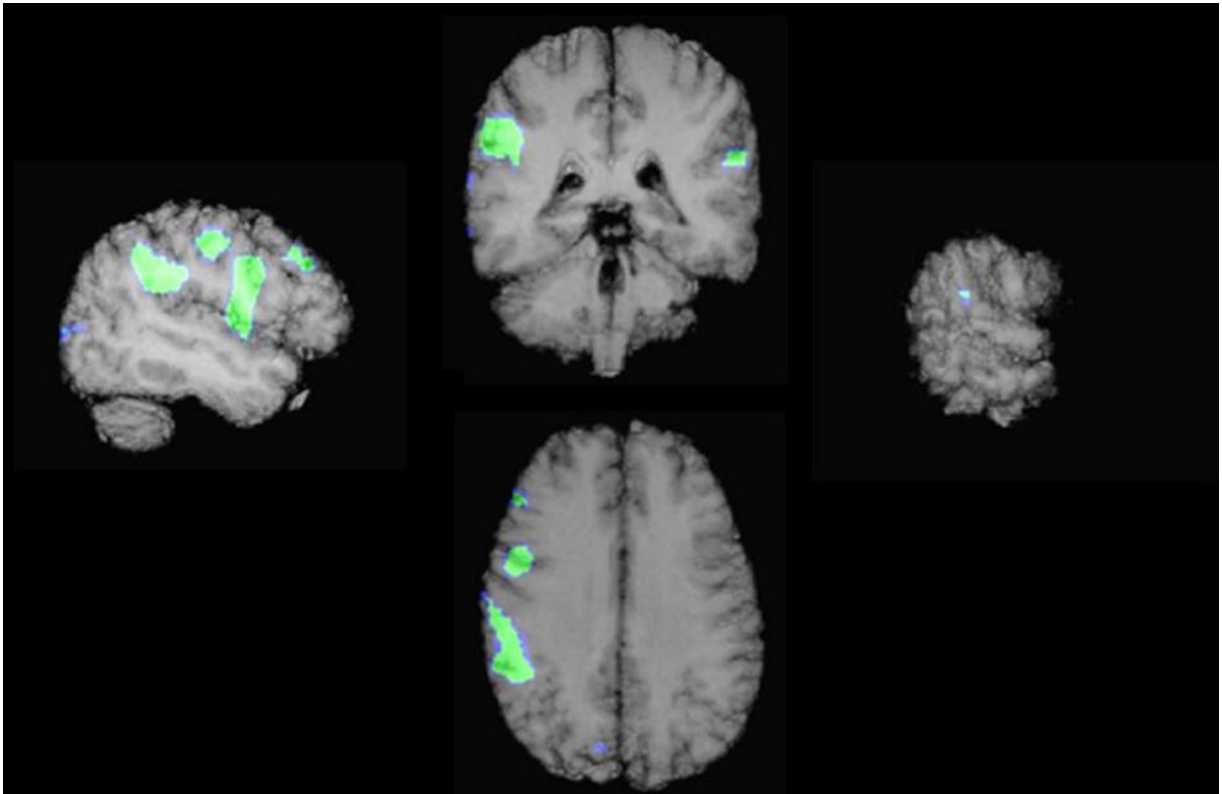


Fig. 3. Orthogonal views of the IPL and inferior frontal gyrus activations for the imagined mouth grasping condition compared to the viewing condition, superimposed on the average MRI image of the subject group (colours as in Fig. 1). Activation in the right parietal lobule was observed at a lower level of significance ( $P_{\text{uncorr}} < 0.01$ ) and is illustrated in this figure.

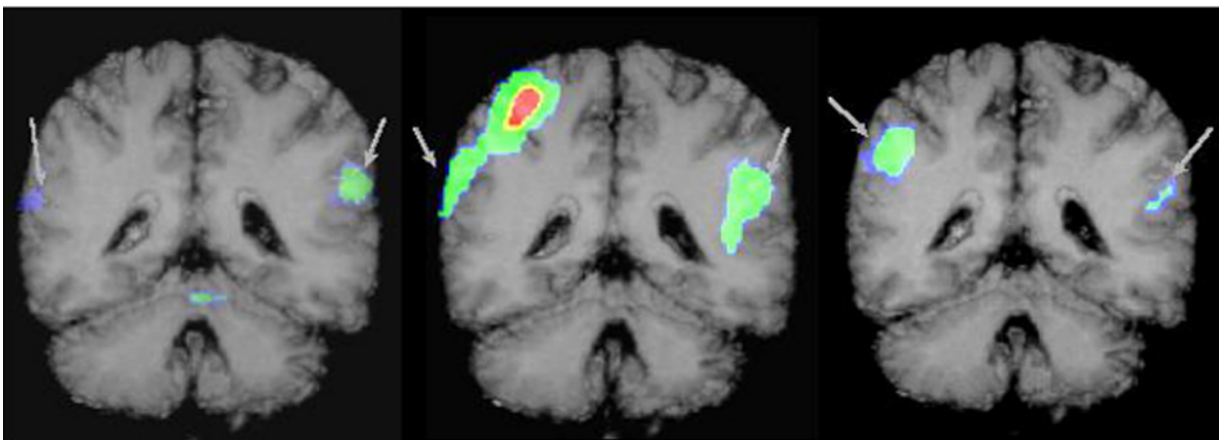


Fig. 4. Coronal views of bilateral rCBF activations in the inferior parietal lobule (arrowed) for three tasks: (a) mouth grasp of an object compared to object viewing only; (b) right-handed thumb and index-finger object grasp compared to view-only; and (c) imagined mouth grasp compared to view-only (colours as in Fig. 1).

of basic units of motor performance rather than specifying how these units are coordinated. In this connection, Gibson (1966) noticed that the movement of features across the retina from moment to moment (optic flow) contains information that could be used to navigate through the environment without prior object recognition. Referring to Gibson's term *affordances* for parameters for motor interactions signalled by sensory cues without the necessary intervention of 'high-level processes' of object recognition, Arbib (1997) suggests that certain regions of the parietal cortex code affordances. That is, various subregions of posterior parietal cortex process visual information to extract a variety of affordances for behavior. Two biologically based models of regions of monkey posterior parietal cortex have been advanced. One of these models is of particular relevance for the present study. The model of the anterior intraparietal area (AIP) addresses parietal–premotor interactions involved in grasping and considers the interaction between the AIP area and the premotor area F5. This model considers the role of various intraparietal areas which work in concert with inferotemporal cortex as well as corollary discharge from F5 to provide and increase the affordance information in AIP. Importantly, this model also suggests how various types of constraints may resolve the action opportunities provided by multiple affordances (Arbib, 1997).

It might be that the IPL activity found in the present study provides evidence for an affordance shared by mouth and hand that routes the information to circuitry specific to the effector set. In this view, it is confirmed that regions of the parietal cortex code affordances. These affordances can thus be seen as a subclass of motor units which express general properties such as 'looking,' 'grasping,' etc., rather than those which depend on more abstract knowledge such as how to peel an apple.

In conclusion, the parietal cortex should be seen as a complex system that subserves a diversity of functions. Specifically, the IPL is subdivided into several areas with specific sensorimotor functions including those for reaching and grasping. The present results suggest motor-planning regions in the IPL that are effector-independent and extend our knowledge of the sensorimotor role played by the IPL.

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