

## The neural basis of selection-for-action

Heidi Chapman<sup>a,b</sup>, Andrea C. Pierno<sup>c</sup>, Ross Cunnington<sup>a</sup>,  
Maria Gavrilesu<sup>a</sup>, Gary Egan<sup>a</sup>, Umberto Castiello<sup>c,d,\*</sup>

<sup>a</sup> Howard Florey Institute, Centre for Neuroscience, University of Melbourne, Melbourne, Australia

<sup>b</sup> Department of Psychology, University of Melbourne, Melbourne, Australia

<sup>c</sup> Department of General Psychology, University of Padua, Italy

<sup>d</sup> Royal Holloway College, University of London, UK

Received 7 November 2006; received in revised form 2 February 2007; accepted 6 February 2007

### Abstract

The selection of objects in the visual environment is important in everyday life when acting in a goal-directed manner. Here we used functional magnetic resonance imaging (fMRI) to investigate brain activity while healthy subjects ( $N = 15$ ) selectively reached to grasp a three-dimensional (3D) target stimulus presented either in isolation or in the presence of 3D non-target stimuli. A pneumatic MRI compatible apparatus was designed to precisely control the presentation of 3D graspable stimuli within the scanner. During scanning subjects were instructed to reach and grasp towards a target presented at an unknown location either in isolation or flanked by two distractor objects. Results indicated that reaching towards and grasping the target object in the presence of other non-target stimuli was associated with greater activation within the contralateral primary motor cortex and the precuneus as compared to the execution of reach-to-grasp movements towards the target presented in isolation. We conclude that the presence of non-targets evokes a differential level of neural activity within areas responsible for the planning and execution of selective reach-to-grasp movement.

© 2007 Elsevier Ireland Ltd. All rights reserved.

**Keywords:** Selection-for-action; Reach-to-grasp; Parietal cortex; Motor cortex

A problem for neuroscience to solve is how perceptual inputs are able to guide actions. For instance, a large body of research has investigated how the hand is directed towards and grasps objects [for a review see 6]. However, in almost all reach-to-grasp studies the experimental environment contains only one object for action, whereas the environments within which we act contain many objects towards which action could be directed. Therefore, to exercise free choice and control it is essential that the system has the capacity to link action selectively with particular objects, a process which has been labelled selection-for-action [1].

Recently, a number of experiments have been reported that were specifically designed to look at changes in reach-to-grasp movement kinematics when multiple objects were introduced into the workspace [for review see 5,23]. In these circumstances

actions appear to be prepared for all potential target objects. That is, objects can evoke actions independent of conscious awareness or conscious intention to act. As an example, Tipper et al. [24] examined transport and grasp kinematics while participants were instructed to selectively reach to grasp a target object in the presence of non-target objects. As participants were not informed in advance about which of the two stimuli was the target object, a visual cue was presented to indicate which stimulus had to be grasped. Results indicated that the spatial trajectory of the arm was affected by the presence of the non-target objects. According to these findings, the authors concluded that the presentation of both target and non-target stimuli evoke competing responses, and that the inhibitory mechanisms resolving this competition are revealed in the affected spatial trajectory of the arm. In other words, the irrelevant non-target objects appear to compete with the target object for the control of action.

In studies of neuronal activity in non-human primates [14,17], it has been shown that cells in motor and parietal cortex code for specific direction of response, firing most when a movement is planned in that direction and less frequently as the movement direction deviates from the preferred direction. As such Tipper

\* Corresponding author at: Dipartimento di Psicologia Generale, Università di Padova, via Venezia 8, 35131 Padova, Italy. Tel.: +39 049 8276659; fax: +39 049 8276600.

E-mail address: [umberto.castiello@unipd.it](mailto:umberto.castiello@unipd.it) (U. Castiello).

et al. [24] proposed that population cells are responsible for the coding of each of the competing movements with the direction of each movement being represented as a vector sum of the firing rates of each population of neurons. Importantly, although the independent and competing responses code for movements to locations in different directions, the response processes may share overlapping neuronal populations within the motor and parietal cortices. When the neurons coding for the competing response are inhibited as selection occurs, the neuronal pools shared by both response processes are affected. Thus, the result of the non-target response inhibition is an overall biased movement trajectory vector that codes for a movement that veers away from the non-target location [16].

By following this line of thought, it is reasonable to assume that the neural network underlying reach-to-grasp actions are likely to represent more than just the target object for action. Therefore, we predict that implementation of parallel motor programs when reaching towards a target presented at an unknown location flanked by distractors would result in an increase in blood oxygenation level dependent (BOLD) signal in contralateral motor and parietal areas concerned with the coding of reach direction. To date, this question remains largely unexplored in humans.

To specifically examine this question, in the present study we compared brain activity during reach-to-grasp movements to a single target with brain activity during reach-to-grasp movements toward a target presented amongst two other objects. A visual cue signalled to the participant the to-be-grasped object.

Fifteen healthy adults (7 F, 8 M; aged 18–38 years) were recruited for the present study. All subjects had normal vision, were right-handed according to the Edinburgh Handedness Inventory [19], and had normal neurological and psychiatric histories. Ethical approval was given by the Ethics Committees of the Howard Florey Institute and the University of Melbourne. Informed consent was obtained from all of the subjects before the testing session in accordance with the declaration of Helsinki.

In order to investigate reach-to-grasp movements towards 3D stimuli a pneumatic apparatus was designed (see Fig. 1). The apparatus allowed the experimenter to precisely control the presentation of the 3D stimulus objects. The stimuli consisted of 3 red balls (each 15 mm in diameter) that were encased within 3 barrels (37 mm in diameter and 228 mm in length) which were in

turn situated behind a plastic mounting panel. Distances between the barrels carrying the stimuli were as follows: 114 mm between the middle and right barrels; 114 mm between the middle and left barrels; and 200 mm between the left and right barrels. The middle barrel was vertically offset 52 mm below the left and right barrels. Above each of the barrels was a green fibre-optic light. The face of the apparatus was mounted on an arch of plastic and placed over the subject's body around the upper thigh region. Such location allowed for a comfortable reach toward the stimuli and proper vision of the stimuli. Each barrel was attached to an 8 m length of pneumatic tubing and all 3 lengths of tubing were connected to a computerised control system which regulated compressed medical air supply (maximum pressure 137 kPa) to the apparatus.

The apparatus worked as follows: the balls extended out of the barrels on the end of pneumatic pistons allowing the balls to be grasped using a precision grip consisting of the opposition between the index finger and the thumb of the right hand. The pistons were spring-loaded so that after each action was performed the balls retracted into the barrels. At the end of the barrels there was a soft plastic frayed curtain which was closed when the piston was inside. When activated the pistons pushed the curtain away. Therefore, participants could not see the stimuli when inside the barrels.

The tasks in this study consisted of reach-to-grasp actions towards a designated target stimulus using only the right-hand thumb and index finger (see Fig. 1). Subjects were told prior to the start of the practice session that combinations of one or three balls would be presented. A fibre-optic light then cued the target ball and indicated subjects to reach towards and grasp the cued item.

There were two experimental conditions: (1) three-objects condition—in which all three balls appeared for 250 ms. The cue light then indicated the target ball (the other two balls remained extended as task-irrelevant objects) and subjects reached-to-grasp the target ball. Therefore, in this condition actions may be prepared to all candidate target objects prior to the cue to respond; (2) one object-three locations condition—in which one ball appeared at any of the three locations (left, right or middle) for 250 ms. The cue light then indicated the target location and served for subjects as a starting signal as to initiate the movement toward the target ball. The sequence

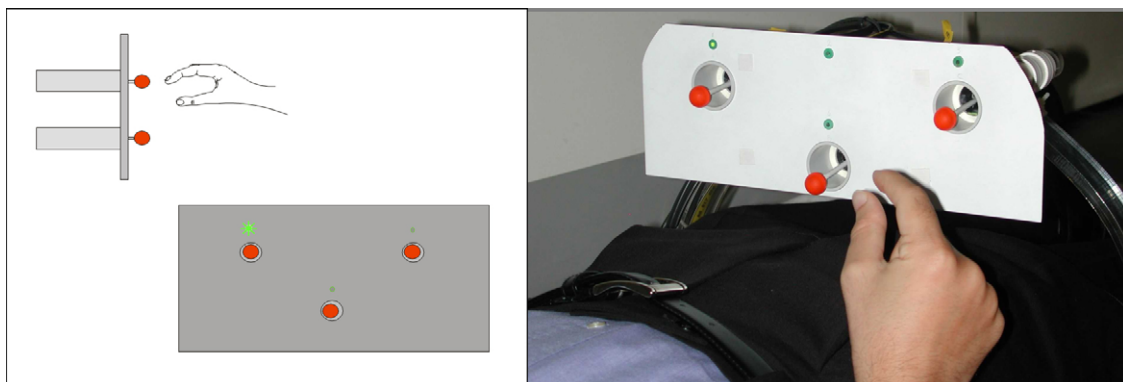


Fig. 1. Diagrammatic representation (left panel) and photograph (right panel) of the pneumatic apparatus (with fiberoptic cue).

of the target location was randomised within condition periods and the likelihood of the target appearing at any of the three locations was equal. For both conditions each trial involved 250 ms of viewing objects for action, followed by 1000 ms for reach-to-grasp, followed by stimuli retracting into their respective barrels creating a blank display for 250 ms.

The functional scans were acquired using a 1.5 T GE scanner (Echospeed, Waukesha, Wisconsin) with echo planar imaging (TR = 3500 ms, TE = 40 ms, FA = 60°, matrix = 64 × 64). Fifteen contiguous 7 mm thick transaxial slices with a 260 mm field of view (FOV) were obtained, yielding a voxel size of 4 mm × 4 mm × 7 mm. With 29 whole brain EPI functional volumes acquired for each experimental run a total of 256 volumes (eight runs) were obtained for each subject. To minimise relaxation artefacts the first two volumes of each run were discarded. Prior to functional imaging, a high-resolution 3D FAST spoiled gradient echo T1 weighted image with an inversion time of 300 ms (FOV = 260 mm, FA = 25°, matrix = 256 × 256, 128 slices, 1.5 mm slice thickness, IR prep SPGR) was acquired in the sagittal plane.

We had two blocks corresponding to our experimental conditions each lasting 10.5 s (3 TRs); the experimental blocks were separated by rest blocks of the same duration. Each run started and ended with a rest block and included two repetitions of each of the experimental block. The order of presentation of each experimental block was randomised within runs. All subjects were given a practice run that included at least two blocks of trials for each condition. In addition, all subjects were videotaped performing the task. Each videotape was later monitored to determine the accuracy of the response for each trial. All subjects performed the task adequately (no mistakes) and so all data was included for analysis. Explicit instructions were given to not make a response until the target was cued.

Scans were pre-processed using SPM99 (Wellcome Department of Cognitive Neurology) by spatial realignment with reference to the first scan, and by normalization to the standard space defined by the Montreal Neurological Institute (MNI) template. Lastly, an 8 mm full-width at half-maximum isotropic Gaussian kernel was applied to spatially smooth all volumes. A high-pass temporal filter was also applied to the time series.

A random effects analysis was conducted on the data. The two experimental conditions ('three-objects' and 'one object-three locations' conditions) were modelled as two separate event types. Regressors were defined based on the timing of presentation of each condition block, and these functions were convolved with a canonical, synthetic haemodynamic response function (HRF) in order to produce the individual models. For each participant, all regressors were incorporated into general linear models (GLM) together with six regressors of no interest comprising the estimated head-motion calculated during the realignment stage of the preprocessing. This was done in order to model residual effects due to head-motion. Individual models were separately estimated and the contrast of interest ('three-objects' condition > 'one object-three locations' condition) was defined for each model. These contrasts were then entered into second-order random-effects analyses (one sample *t*-tests). Areas of significant activation associated with the contrast of interest were identified for the false discovery rate (FDR) [13] corrected *p*-value smaller than 0.05. Group activation results from the random effects analyses were overlaid onto the canonical brain of the Montreal Neurological Institute (MNI) series.

To specifically determine whether there was a different level of activation for key areas when action may be prepared to all candidate target objects, we compared the three-objects condition with the one object-three locations condition. Table 1 and Fig. 2 indicate regions that showed a significant difference in the BOLD contrast signal when these two conditions were compared.

The results showed an increased level of activation within the left pre-central gyrus (primary motor cortex, M1, Fig. 2A) and the left precuneus (PCu, Fig. 2B). The M1 result fits with the concept of directional vector coding in cell populations [14]. In the present study, all objects were presumably attended with the knowledge that a reach-to-grasp response will shortly be required. For all possible responses the requested reach trajectories were very different: one left, one central, and one right. Therefore, specific direction sensitive populations of reach cells might start to fire for each object. Parallel processing of stimuli for action, inducing multiple vectors coding for target and non-

Table 1

Anatomical description, MNI coordinates, probabilistic cytoarchitecture [9], and statistical details for the activations resulting from the contrast 'three-objects condition' > 'one object-three locations condition'

Area	Probabilistic cytoarchitecture	Peak Z value	MNI coordinates: (x, y, z) mm		
Frontal cortex					
Left precentral gyrus (motor cortex)	Area 6 (50%) Area 4a (40%) Area 3b (20%)	4.15	-28	-28	62
Primary somatosensory cortex					
Fundus of the central sulcus	Area 3a (100%) Area 4p (20%)	4.12	34	-22	40
Parietal cortex					
Right postcentral gyrus	Area 2 (70%)	4.80	28	-48	62
Left precuneus		4.36	-12	-58	50
Visual cortex					
Left fusiform gyrus		4.23	-28	-62	-8

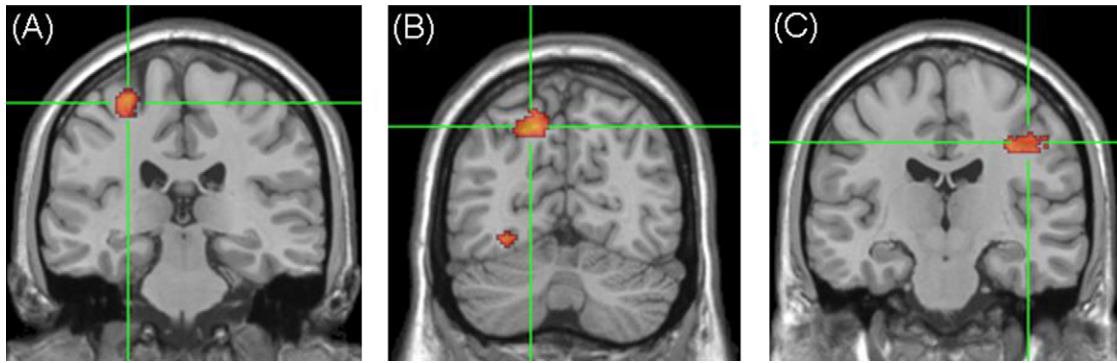


Fig. 2. Three coronal sections representing brain regions activated by the ‘three-objects condition’ > ‘one object-three locations condition’ contrast (FDR corrected  $p < .05$ ). Differential activity is shown for the left primary motor cortex (A), the left precuneus (B) and the fundus of the central sulcus (C, right primary somatosensory cortex).

target stimuli within the motor cortex, may have determined the differential level of activation.

The region of the parietal cortex responsive to the presence of non-target objects was the precuneus (PCu). Given similarity in sulcal landmarks the PCu has been suggested as a putative homologue of the monkey parietal reach reaching area (PRR) [2,8,11,12,22]. This area has been shown to be active during preparation and execution of arm movements and projects to a region of the dorsal premotor cortex that is also involved in the coding of reaching movements [10,21]. Moreover, neurons in this region show activity that is correlated with the direction of the movement the animal intends to make.

We also found right postcentral gyrus activation. This activation may fit, in terms of stereotaxic coordinates, with the medial intraparietal area (mIPS) reported by Prado et al. [20]. In their study this area was activated during a reaching task to a target independent from its location. Here, we add to this literature, showing that in the human brain activity in this region is modulated by the presence of non-target objects eliciting a reaching response.

Reach-to-grasp related activity in our study was different when actions were performed in the presence of non-target objects and when the initial target location was unknown compared with reaching to a single target. Noticeably these results reinforce the notion of functional homology between monkeys and humans. In the non-human primates, Calton et al. [3] reported neurophysiological data of greater preparatory activity within parieto-occipital areas when monkeys were instructed to prepare a reach when the target location was unknown.

Consistent with previous behavioural studies [4,24] these results show that there is specialised neural processing for selecting targets amongst non-target objects. Tipper et al. [24] have already shown that the presence of distractors interferes with reach trajectories to target objects. The current paradigm is similar to Tipper’s in two ways: target location was unknown and the subjects were instructed to perform the action quickly. Further, kinematic analyses of the responses obtained in a situation similar to that used in the present experiment [7,24] show distractor interference on the temporal dynamics of the reach-to-grasp. In particular, the presence of the distractor produced an increase in movement duration, delayed peaks of velocity and acceleration

together with an effect on the time and extent at which the point of maximum spatial trajectories deviation occurred. Thus, previous behavioural evidence and the brain imaging data presented here seem to converge demonstrating parallel processing of target and distractors. Such processing becomes evident through the automatic parallel activation of their associated responses. This seems to occur without the subjects’ intention to act upon the task irrelevant stimuli [18], or even conscious awareness [25].

A final point is concerned with an unexpected activation within the right primary sensory cortex (SI, Fig. 2C and Table 1) with its cluster extending deeply into the central sulcus during the task in which non-target objects were presented. We are inclined to suggest that this activation may be indicative of transcallosal inhibition from the contralateral SI, coupled with sensory suppression [15].<sup>1</sup> If M1 prepares three movements, one might imagine greater sensory suppression effects within the contralateral SI. Consistent with our data no significant activation was found within the contralateral SI when comparing the three objects versus the one object condition.

In summary, this is the first neuroimaging study to show differential activity in M1 and in a region of the posterior parietal cortex (that appears homologous with monkey PRR) during reach-to-grasp movements towards a target stimulus in the presence of non-target objects as compared to reach-to-grasp movements performed towards a single stimulus. The present data represent a step forward in localizing and characterizing the brain areas within which the process of selection for a goal-directed action occurs. However, further studies should be designed as to allow the distinction between brain areas involved in parallel response programming from areas involved in the selection between parallel programs.

### Acknowledgements

This research was supported by an Australian Research Council grant to UC and GE. We thank the Department of

<sup>1</sup> We thank an anonymous reviewer for suggesting this possible explanation for the right SI activation

Radiography, Royal Children's Hospital, Melbourne and Max Rademacher for their technical expertise and support.

## References

- [1] A. Allport, Selection-for-action: some behavioral and neurophysiological considerations of attention and action, in: H. Heuer, A. Sanders (Eds.), *Perspectives on Perception and Action*, Lawrence Erlbaum Associates, Hillsdale, NJ, 1987, pp. 395–419.
- [2] A.P. Batista, C.A. Buneo, L.H. Snyder, R.A. Andersen, Reach plans in eye-centered coordinates, *Science* 285 (1999) 257–260.
- [3] J.L. Calton, A.R. Dickinson, L.H. Snyder, Non-spatial, motorspecific activation in posterior parietal cortex, *Nat. Neurosci.* 5 (2002) 580–588.
- [4] U. Castiello, Grasping a fruit: selection for action, *J. Exp. Psychol. Hum. Percept. Perform.* 22 (1996) 582–603.
- [5] U. Castiello, Mechanisms of selection for the control of hand action, *Trends Cognit. Sci.* 3 (1999) 264–271.
- [6] U. Castiello, The neuroscience of grasping, *Nat. Rev. Neurosci.* 6 (2005) 726–736.
- [7] H. Chapman, C. Bonfiglioli, U. Castiello, Distractor processing during selection-for-action, in: Paper presented at the Cognitive Neuroscience Society, San Francisco, USA, 2004.
- [8] J.D. Connolly, R.A. Andersen, M.A. Goodale, FMRI evidence for a 'parietal reach region' in the human brain, *Exp. Brain Res.* 153 (2003) 140–145.
- [9] S.B. Eickhoff, K.E. Stephan, H. Mohlberg, C. Grefkes, G.R. Fink, K. Amunts, K. Zilles, A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data, *Neuroimage* 25 (2005) 1325–1335.
- [10] P. Fattori, M. Gamberini, D.F. Kutz, C. Galletti, 'Arm-reaching' neurons in the parietal area V6A of the macaque monkey, *Eur. J. Neurosci.* 13 (2001) 2309–2313.
- [11] S. Ferraina, A. Battaglia-Mayer, A. Genovesio, B. Marconi, P. Onorati, R. Caminiti, Early coding of visuomanual coordination during reaching in parietal area PEc, *J. Neurophysiol.* 85 (2001) 462–467.
- [12] C. Galletti, M. Gamberini, D.F. Kutz, P. Fattori, G. Luppino, M. Matelli, The cortical connections of area V6: an occipito-parietal network processing visual information, *Eur. J. Neurosci.* 13 (2001) 1572–1588.
- [13] C.R. Genovese, N.A. Lazar, T. Nichols, Thresholding of statistical maps in functional neuroimaging using the false discovery rate, *Neuroimage* 15 (2002) 870–878.
- [14] A.P. Georgopoulos, Neurophysiology of reaching, in: M. Jeannerod (Ed.), *Attention and Performance XIII*, Lawrence Erlbaum, Hillsdale, NJ, 1990, pp. 849–859.
- [15] Y. Hlushchuk, R. Hari, Transient suppression of ipsilateral primary somatosensory cortex during tactile finger stimulation, *J. Neurosci.* 26 (2006) 5819–5824.
- [16] G. Houghton, S.P. Tipper, A model of inhibitory mechanisms in selective attention, in: D. Dagenbach, T. Carr (Eds.), *Inhibitory mechanisms Inattention, Memory and Language*, Academic Press, Orlando, FL, 1994.
- [17] J.F. Kalaska, The representation of arm movements in postcentral and parietal cortex, *Can. J. Physiol. Pharmacol.* 66 (1988) 455–463.
- [18] F. Lhermitte, "Utilization behavior", and its relation to lesions of the frontal lobes, *Brain* 106 (1983) 237–255.
- [19] R.C. Oldfield, Assessment and analysis of handedness—Edinburgh inventory, *Neuropsychologia* 1 (1971) 97.
- [20] J. Prado, S. Clavagnier, H. Otzenberger, C. Scheiber, H. Kennedy, M.T. Perenin, Two cortical systems for reaching in central and peripheral vision, *Neuron* 48 (2005) 849–858.
- [21] S. Shipp, M. Blanton, S. Zeki, A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: cortical connections of areas V6 and V6A, *Eur. J. Neurosci.* 10 (1998) 3171–3193.
- [22] L.H. Snyder, A.P. Batista, R.A. Andersen, Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex, *J. Neurophysiol.* 5 (1998) 2814–2819.
- [23] S.P. Tipper, L.A. Howard, G. Houghton, Action-based mechanisms of attention, *Philos. Trans. R. Soc. London, Ser. B Biol. Sci.* 1373 (1998) 1385–1393.
- [24] S.P. Tipper, L.A. Howard, S.R. Jackson, Selective reaching to grasp: evidence for distractor interference effects, *Vis. Cog.* 1 (1997) 1–38.
- [25] K. Weiskrantz, *Blindsight: A Case Study and Implications*, Clarendon Press, Oxford, UK, 1986.