

Objects automatically potentiate action: an fMRI study of implicit processing

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Abstract

Behavioural data have shown that the perception of an object automatically potentiates motor components (affordances) of possible actions toward that object, irrespective of the subject's intention. We carried out an event-related fMRI study to investigate the influence of the intrinsic properties of an object on motor responses which were either compatible or incompatible with the action that the object affords. The subjects performed power or precision grip responses based on the categorization of objects into natural or man-made. The objects were either 'small' (usually grasped with a precision grip) or 'large' (usually grasped with a power grip). As expected, the motor responses were fastest to objects that afforded the same grip (congruent) and slowest to objects that afforded the other grip (incongruent). Imaging revealed activations which covaried with compatibility in the parietal, dorsal premotor and inferior frontal cortex. We suggest that the greater the difference in reaction times between congruent and incongruent trials, the greater the competition between the action afforded by the object and the action specified by the task, and thus the greater the activation within this network.

Introduction

Gibson (1979) argued that we perceive objects in terms of the ways in which they can be used. He suggested that objects 'afford' potential actions. Jeannerod (1994) and Arbib (1997) agreed that objects potentiate the appropriate action, but suggested that this process involves motor representations and depends on the intention of the subjects.

There is behavioural literature that provides arguments in favour of the 'automatic' activation of action representations by the observation of objects (Craighero *et al.*, 1996, 1998, 2002; Castiello, 1999; Creem & Proffitt, 2001; de'Sperati & Stucchi, 1997; Gentilucci, 2002). Tucker & Ellis (1998) and Ellis & Tucker (2000) have presented evidence that features of objects such as their location, shape and orientation lead to activation of specific components of a reaching and grasping action. In a series of experiments, the subjects were required to make one of two responses depending on the classification of objects. On some trials, the action potentiated by the object was the same as that required by the classification task (congruent), and on others it differed (incongruent). The results were that, even though the explicit task was not to use the object, the response times differed between congruent and incongruent trials. This was observed for different components of actions, such as the hand used, the direction of wrist rotation and the shaping of the hand (Ellis & Tucker, 2000). These potentiated components of a grasping response are referred to as microaffordances, i.e. motor representations of particular types of interaction with the object. These experiments demonstrated an inter-

action between the action afforded by the object and goal-directed behaviour.

On the basis of their results, Ellis & Tucker (2000) proposed that the representation of a visually presented object includes not only a description of its visual properties but also motor components that are relevant to that object. The present paper follows their account of affordances which diverges from the ecological account (Gibson, 1979) in retaining the notion of representation. Their account claims direct associations between vision and action, which give rise to action potentiation whenever an object is seen, whether or not it is the goal of an intended action.

In the present experiment, we used event-related fMRI to investigate the neural correlates of the behavioural effect demonstrated by Tucker & Ellis (2001). In that experiment the explicit task was to categorize visually presented objects as either natural or man-made by making a precision grip for one category and a power grip for another category. The experiment demonstrated the influence of the implicit processing of affordances on the responses made during the categorization task. We therefore used the same stimuli and the same categorization task to study activations that correlated with the difference between response times on congruent and incongruent trials. On the basis of the single-unit data of Sakata *et al.* (1995) and Murata *et al.* (1997), we predicted that we would find activity related to object affordance in a parieto-premotor circuit.

Materials and methods

Subjects

Twelve right-handed subjects (age range 19–31 years) with no neurological or psychiatric history participated in the imaging study. All

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gave informed consent according to procedures approved by the Joint Ethics Committee of the National Hospital for Neurology and Neurosurgery (UCLH NHS Trust) and Institute of Neurology (UCL).

Stimuli

The subjects viewed colour photographs of real graspable objects and were requested to decide whether the objects presented were natural or manufactured. Within each category, half of the objects were large and would normally be grasped with a power grip (cucumber, hammer), and half were small and would normally be grasped with a precision grip (grape, screw) (See Fig. 1). We used the simple terms 'small' and 'large' to describe the object's compatibility rather than precision-compatible and power-compatible, to avoid confusion with the response terms. It should be borne in mind, however, that the objects within each size category were chosen on the basis of the grip type required to pick them up and not on any absolute physical dimension.

Subjects held two nonmagnetic manipulanda in their hands, and used them to report the appropriate classification. One manipulandum consisted of a plastic cylinder, 7 cm tall and 3 cm in diameter; the other was made of a 2-cm square and 1.5-cm-thick piece of plastic. Both manipulanda contained a switch to record reaction time of grip responses. Subjects grasped the square between their thumb and their index finger, and the cylinder between the fingers and the surface of the palm. The two responses thus mimicked a power and a precision grip. Half of the subjects held the precision manipulandum in their right hand and the power manipulandum in their left hand, and vice versa for the other subjects. Half of the participants made a precision grip if the object was natural and a power grip if it was manufactured, and vice versa for the other subjects. They were instructed to respond as quickly and accurately as possible. The responses were detected by MRI-compatible microswitches in the manipulanda.

All the data, including the behavioural data, were acquired in the scanner. Subjects lay in a supine position in the scanner, held the manipulanda in their hands throughout the experiment and simply squeezed them. The subjects could not see their hands. The stimuli were back-projected onto a mirror mounted on the head-coil ($\approx 1\text{--}2.4^\circ$ of visual angle for 'small' objects, $\approx 5.7\text{--}8.5^\circ$ of visual angle for 'large' objects). Two hundred stimuli (50 trials per condition, each presented for 2.5 s), intermixed with 100 null events were presented in a random order. Stimuli were presented every 3.9 s.

MRI scanning

A 2 T VISION system (Siemens, Erlangen, Germany) was used to acquire 36 $T2^*$ -weighted transverse echoplanar images (EPI; matrix size 64×64 , in-plane resolution of $3 \times 3 \text{ mm}^2$, $T_E = 40 \text{ ms}$) with blood oxygenation level-dependent (BOLD) contrast. EPIs comprised 2.4-mm-thick axial slices taken every 3.6 mm, acquired sequentially in a descending direction and continuously during a 21-min session. An automatic shimming procedure was performed before each session. A total of 445 functional volumes were collected for each subject within the single scanning session with an effective repetition time (T_R) of 2.74 s/volume. The first five volumes were discarded to allow for T1 equilibration effects. T1 anatomical volume images (magnetization prepared rapid gradient echo (MPRAGE) sequence with a high-resolution isovoxel acquisition of $1 \times 1 \times 1 \text{ mm}^3$) were collected for each subject.

Pre-processing

Image processing and statistical were carried out using Statistical Parametric Mapping (SPM99, Wellcome Department of Imaging Neuroscience, London, UK; see <http://www.fil.ion.ucl.ac.uk/spm>)

implemented in MATLAB 5.3 (Mathworks Inc., Sherborn, MA, USA). Images were realigned to the first volume by rigid body transformation, sinc interpolated over time to correct for phase advance during acquisition. They were normalized into standard stereotaxic space using the Montreal Neurological Institute template, and spatially smoothed by a gaussian kernel of full width at half maximum (FWHM) 8 mm (Ashburner & Friston, 1997). Low-pass and high-pass frequency filters were applied to the time series. The anatomical (T1-weighted) images were coregistered with the subject's corresponding mean realigned EPI volume, and normalized with the same deformation parameters.

Data analysis

Data were analysed using SPM99. Population inferences were made through a two-stage procedure. At the first stage, we specified, in a subject-specific analysis, a general linear model including four effects of interest: the events which were congruent with right-hand and with left-hand responses, and the events which were incongruent with right-hand and with left-hand responses. These effects were modelled by convolving a delta function of each event type with the haemodynamic response function to create regressors of interest. For each comparison of interest, for each subject, a contrast of parameter estimates was calculated in a voxel-wise manner to produce a 'contrast image'. In the second stage, the contrast images from all subjects were entered into a one-sample *t*-test (in which participants were treated as random variables) and subsequently transformed into statistical parametric maps (SPMs) of the *Z*-statistic.

We also performed a linear regression analysis to identify regions whose activation (Incongruent vs. Congruent) was positively or negatively correlated with the difference in reaction times (Incongruent and Congruent). The regionally specific differences reported consisted of five or more contiguous voxels surviving the threshold of $Z > 3.09$ ($P = 0.001$ uncorrected, $t > 4.02$). Finally, the correlation coefficient r^2 and its corresponding *P*-value (two-tailed) were calculated for significant voxels detected in the linear regression analysis.

Anatomical identification was performed by superimposing the maxima of activation foci both on the Montreal Neurological Institute template and on the normalized structural images of each subject.

Results

Behavioural results

All error responses were excluded from the analysis, and so were reaction times (RT) > 2 SD from the average RT for each subject. The means from the remaining data were entered into an ANOVA (repeated measures) with within-participant factors of object size ('small' = precision-compatible or 'large' = power-compatible) and response (precision or power). The analysis revealed a significant main effect of object size ($F_{1,11} = 34.238$, $P < 0.0001$, *MSe* (mean square error) = 310); the subjects reacted faster for large objects (mean 561 ms) than for small objects (mean 592 ms). A main effect of response type was also revealed ($F_{1,11} = 6.327$, $P = 0.031$, *MSe* = 358); precision grip responses were faster (mean 569 ms) than power grip responses (mean 583 ms). Finally, there was an interaction between object size and motor responses ($F_{1,11} = 27.750$, $P < 0.0001$, *MSe* = 144); power grip responses were slightly but not significantly faster (mean 558 ms) than precision grip responses (mean 563 ms) when the subjects were viewing large objects (two-tailed *t*-test, $P = 0.52$), and precision grip responses were significantly faster (mean 575 ms) than power grip responses (mean 608 ms) when the subjects were viewing small objects (two-tailed *t*-test, $P < 0.001$). The response times were influenced by the object size (object compatibility), despite

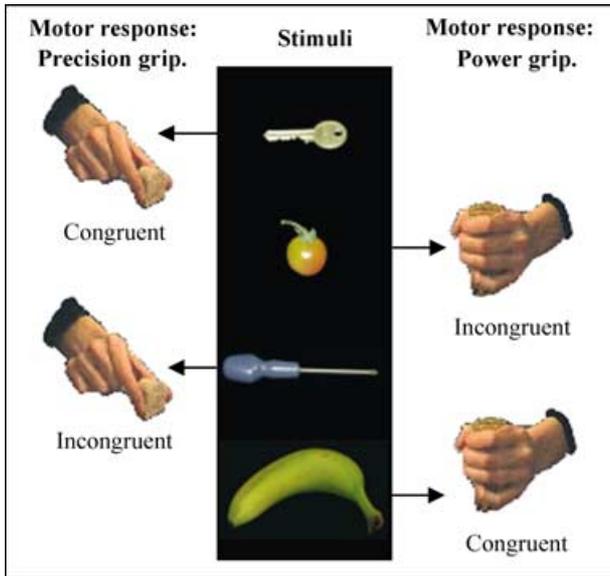


FIG. 1. In this figure, the subject was instructed to perform right-hand responses (precision grip) to manufactured objects and left-hand responses (power grip) to natural objects. Within each category, half of the grip responses were congruent with the actions afforded by the objects and half were incongruent.

the fact that this factor was irrelevant to the task. The interaction is displayed in Fig. 2. It is important to point out that this critical interaction is masked by the presence of two main effects. Both main effects are meaningful and cannot therefore be assumed to arise from the interaction pattern itself. The lack of a significant difference between response types when viewing large objects simply reflects the presence of the overall advantage for large objects and precision responses (see, e.g., Rosnow & Rosenthal, 1989).

Brain imaging results

We looked for brain regions where the difference of activity between incongruent and congruent trials correlated positively with the difference in reaction time between incongruent and congruent trials. Activations were detected in the left hemisphere in the inferior frontal sulcus, in the dorsal premotor cortex and in the supramarginal gyrus, between the Jensen sulcus and the intraparietal sulcus. Activations were also detected in the left posterior superior parietal cortex and the left superior temporal sulcus (horizontal posterior segment) (Table 1 presents the coordinates and correlation coefficients for each region and Fig. 3 shows the plot of the correlation for the dorsal premotor cortex together with the areas in the activity correlated with the reaction time differences.)

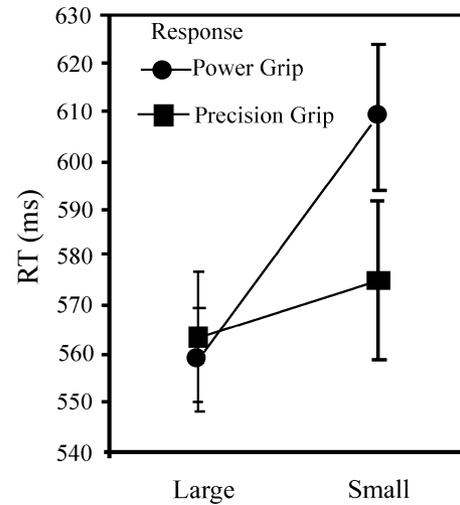


FIG. 2. Mean reaction time (RT) and SEM by response and object compatibility.

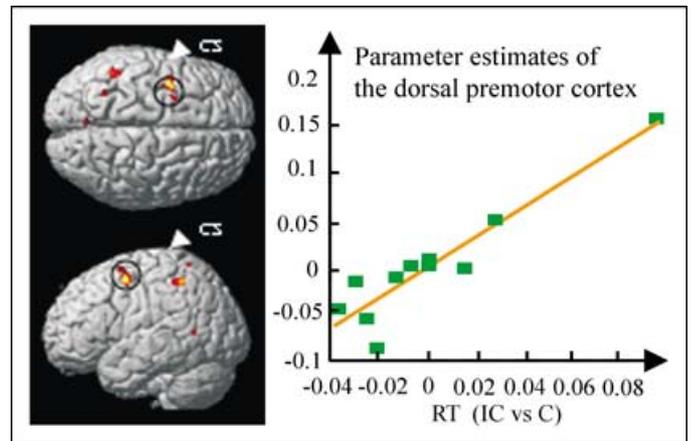


FIG. 3. (Left panel) Brain regions showing magnitude effects for the regression analysis between the parameter estimates of the main effect of congruency and the difference in RT between congruent and incongruent trials. As the difference in RT values were mean-corrected, zero on the x-axis corresponds to the mean of the difference of RT across subjects. Effects are rendered on a canonical normalized brain. The activation in the inferior frontal sulcus is not shown because it lies deep in the sulcus. (Right panel) Parameter estimates at the local maxima of the dorsal premotor cortex [Talairach coordinates (x, y, z): -38, -2, 54 mm] for the main effect of congruency plotted against the difference in RT between congruent and incongruent trials.

TABLE 1. Brain regions showing significant effects for the regression analysis between the parameters estimates of the main effect of congruency and the difference in RT between congruent and incongruent trials; the corresponding correlation coefficients are given for each region of interest

Brain regions	Talairach coordinates			Z-score	Correlation coefficients		
	x	y	z		r ²	F	P-values*
Left inferior frontal sulcus	-32	32	18	3.68	0.7571	31.16	0.0002
Left dorsal premotor cortex	-38	-2	56	4.48	0.8769	71.23	<0.0001
Left anterior parietal cortex	-46	-48	52	4.03	0.8278	48.06	<0.0001
Left superior parietal lobe	-30	-56	66	3.75	0.7699	33.45	0.0002
Left superior temporal sulcus	-50	-60	8	3.55	0.7314	27.23	0.0004

*The P-values are two-tailed.

Discussion

The aim of this experiment was to investigate the neural correlates of the influence of action-relevant object-intrinsic properties (but task-irrelevant) on motor responses that were either compatible or incompatible with the action an object affords. The subjects were required to make power or precision grip responses based on the categorization of visually presented objects into natural or man-made items. Within each category, objects were either 'small' (usually grasped with a precision grip) or 'large' (usually grasped with a power grip).

Behavioural results

It was essential as a basis for our brain imaging results that we be able to replicate the results of Tucker & Ellis (2001) under scanning conditions and using just 12 subjects. We were able to show a compatibility effect between the size and shape of the object and the size of grip required on the classification task. The size and the shape of an object are intrinsic properties which define the opposition space and therefore the type of grip made toward the object, that is, a power or a precision grip. Gentillucci (2002) has demonstrated that object-intrinsic properties influence grasp kinematics; the effect was stronger when subjects grasped familiar objects than geometrical meaningless solids and the author suggests that this is because of stronger affordances with familiar objects.

In the present experiment, motor responses were fastest to compatible objects and slowest to incompatible ones, showing that object affordances were extracted during the categorization task despite being task-irrelevant. This result raises the question as to whether this difference in reaction times between congruent and incongruent trials is due to a facilitation effect for congruent actions or an interference effect with incongruent actions. Using stimulus–response compatibility paradigms (SRC) it has been demonstrated that the response times are shorter on compatible than on neutral trials (Hommel, 1996; Umiltà *et al.*, 1999; Grosjean & Mordkoff, 2002). These authors suggest that, on compatible trials, the automatic response activation facilitates the response demanded by the task. On incompatible trials, on the other hand, the response times are longer than on neutral trials because the automatic response activation competes with the one demanded by the task.

However, the present experiment differs from Simon effect paradigm in that the automatic response was guided not by the spatial location of the stimulus but by the intrinsic properties of the objects. Craighero *et al.* (1996, 1998) carried out an experiment on visuomotor priming in which they required subjects to grip solids of different orientation. If they presented irrelevant drawings on the screen in either the same or different orientation as the object to be grasped, the response times were quicker on congruent than on neutral trials. However, response times were not different in incongruent vs. neutral trials. These experiments demonstrated that actions were facilitated when they were toward an object which had intrinsic properties similar to those of the irrelevant drawings. Because we did not in this experiment include a neutral condition, we are unable to conclude whether the observed difference in RTs between congruent and incongruent trials was a consequence of facilitation or interference or both.

Brain–behaviour correlation

The results revealed a left hemispheric neural network in which the amplitude of the BOLD signal correlated with the behaviour, irrespective of the hand used. These activations were detected in the anterior parietal, dorsal premotor and inferior frontal cortex. These correlations were assessed across subjects. In subjects who showed a

greater difference in reaction times between congruent and incongruent trials, these activations were greater than in subjects showing a smaller difference.

These results raise the question as to why the regression analysis revealed activation in the left hemisphere within the parietal, premotor and frontal cortex. The parietal activation lay on the convexity of the anterior part of the inferior parietal lobule, near to the anterior tip of the intraparietal sulcus. It is not clear whether this includes the anterior intraparietal area (Toni *et al.*, 2001). Activation in this region which correlated with affordances might have been expected on the basis of single-unit studies in monkeys (Murata *et al.*, 2000) and imaging studies in the human brain (Castiello *et al.*, 2000; Grèzes & Decety, 2002). It might have been expected that there would also be a correlation in the ventral premotor area F5. The anterior intraparietal area is interconnected with F5 (Matelli *et al.*, 1986), and these areas are involved in the adjustment of the shape of a grasp to a visually presented object (Fogassi *et al.*, 2001). Arbib *et al.* (2000) have suggested that it is this circuit that extracts object affordances.

However, in the light of the study by Grafton *et al.* (1998), Arbib *et al.* (2000) revised their model. In that study, as in the present one, the activations were in the dorsal rather than the ventral premotor cortex. Arbib *et al.* (2000) therefore proposed that interactions occur between the dorsal premotor cortex and the anterior parietal cortex when actions must be selected on the basis of arbitrary cues. In the present experiment, subjects were required to select between two movements on the basis of their classification of the objects, and thus the selection was made on the basis of arbitrary visual cues. Here, the nature of the object presented (manufactured vs. natural) serves as instructions to determine which of two actions was appropriate. Evidence from lesion and neurophysiological studies in nonhuman primates has suggested a role for the dorsal premotor cortex in associating instruction cues with movements (Halsband & Passingham, 1985; Mitz *et al.*, 1991; Passingham, 1993). Single-pulse transcranial magnetic stimulation (TMS) over the left premotor cortex interferes with a visual choice reaction time performed either with the left or the right hand (Schluter *et al.*, 1998). We also found a correlation in the inferior frontal sulcus. Lesions of the ventral prefrontal cortex in nonhuman primates disrupt the selection of responses on the basis of arbitrary cues (Bussey *et al.*, 2001). Using PET, Schluter *et al.* (2001) have shown activations in this area as well as in the dorsal premotor and parietal cortex when subjects performed visual choice reaction time task. Furthermore, all these activations were in the left hemisphere as in Fig. 3 of the present study.

It remains to be explained why the greater the difference in reaction times between incongruent and congruent trials, the greater the activity in these areas. During incongruent trials, one response was suggested by the object's intrinsic properties and another by the category of the object. The question therefore arises as to whether it is possible to find evidence in these areas that different possible actions could be simultaneously coded in competition with each other. There is evidence for both the premotor and parietal areas.

First, there is direct evidence that two potential actions can be coded for simultaneously in an area. Cisek & Kalaska (2002) have recently demonstrated that, within this area in macaques, directional signals related to multiple alternative actions are simultaneously generated before a decision is taken. When two potential targets are presented, it is possible to record the activity of two distinct subpopulations in the dorsal premotor cortex area cells with different directional preferences. When further information is provided to select the final target, one of the activated populations is suppressed while the discharge of the other is enhanced.

There is also evidence that there can be more activity when one action competes with another. Goldberg & Seagraves (1987) and

Schlag-Rey *et al.* (1997) demonstrated significantly more activity before and during antisaccade trials than before pro-saccades in the supplementary eye field. They suggested that the extra activity observed for antisaccade trials fitted the assumptions that both potential movements were coded for, and that there was competition to be won between the potential saccades in opposite directions. Gottlieb & Goldberg (1999) also observed a similar phenomenon in the lateral intraparietal area LIP. Again they were able to demonstrate an enhancement of the firing rate during antisaccade as compared to saccade trials. These studies provide direct evidence that there can be more activity in premotor and parietal areas when two potential actions compete. That the same could be true in the human brain is suggested by the imaging finding that there is more activation in the frontal eye field associated with antisaccades than with pro-saccades (Doricchi *et al.*, 1997; Connolly *et al.*, 2000; Kimmig *et al.*, 2001).

Transcranial magnetic stimulation over the premotor and parietal cortex also slows a response when an alternative response is potentiated and must be suppressed. Praamstra *et al.* (1999) used a stimulus-response compatibility (SRC) paradigm. They showed that interference over the dorsal premotor cortex with repetitive transcranial magnetic stimulation (rTMS) produced an exaggeration of the compatibility effect, that is, responses were further delayed on incompatible trials. Rushworth *et al.* (2001) applied rTMS over the left anterior parietal cortex. They reported an increase in reaction times on trials on which the instruction cues specified a movement which was the opposite of the one specified by the precues; these trials required the redirection of covert motor intention.

In the current study we found greater activity in parietal, premotor and inferior prefrontal cortex the greater the reaction time difference between incongruent and congruent trials. When the reaction time difference was small the competition between responses was quickly resolved, whereas when this difference was bigger the affordance exerted a greater influence. We therefore suggest that the more the subjects were distracted by affordances the greater the competition between the response evoked by the object and the response required by the explicit task.

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Abbreviations

BOLD, blood oxygenation level-dependent; EPI, echoplanar image; RT, reaction time; rTMS, repetitive TMS; SPM, statistical parametric map; TMS, transcranial magnetic stimulation; T_R , effective repetition time.

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