



Where does your own action influence your perception of another person's action in the brain?

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Activation of premotor cortex during the observation and imitation of human actions is now increasingly accepted, but it remains unclear how the CNS is able to resolve potential conflicts between the observation of another person's action and the ongoing control of one's own action. Recent data suggest that this overlap leads to a systematic bias, where lifting a box influences participant's perceptual judgments of the weight of a box lifted by another person. We now investigate the neural basis of this bias effect using fMRI. Seventeen participants performed a perceptual weight judgment task or two control conditions while lifting a light box, a heavy box or no box during scanning. Brain regions related to perceptual bias were localized by correlating individual differences in bias with BOLD signal. Five regions were found to show correlations with psychophysical bias: left inferior frontal gyrus, left central sulcus, left extrastriate body area, left lingual gyrus and right intraparietal sulcus. The cluster in primary motor cortex was also activated by box lifting, and the cluster in extrastriate body area by the observation of hand actions and the weight judgment task. We suggest that these brain areas are part of a network where motor processing modulates perceptual judgment of observed human actions, and thus visual and motor processes cannot be thought of as two distinct systems, but instead interact at many levels.

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Introduction

An increasing number of behavioral studies demonstrate that perceptual systems and motor systems interact at many levels, but the nature of this interaction remains unclear. In general, observing an action facilitates the performance of similar actions (Brass et al., 2001) and interferes with the performance of different actions

(Kilner et al., 2003), and the existence of direct feed-forward connections from perceptual to motor processes seems well established. However, the results of studies examining how actions influence perceptual processing are more complex. While some studies suggest that performing an action facilitates the perception of related stimuli (Wohlschlaeger, 2001; Craighero et al., 2002), other studies suggest that action biases or impairs perception of related actions (Musseler and Hommel, 1997; Hamilton et al., 2004), and the locus of either effect is unknown.

The principal purpose of the current study was to locate brain regions involved in the interaction of perceptual and motor processes. Many previous studies have used tasks such as imitation, where both actor and observer are performing in a similar fashion, to investigate the overlap of motor control and action understanding (Iacoboni et al., 1999; Decety et al., 2002). However, in daily life, people do not often directly imitate, but instead are able to interpret other people's actions while continuing to perform their own. Hamilton et al. (2004) investigated such a situation, and showed that performing an action, specifically holding a box, systematically biases observers' psychophysical judgments of the weight of a box lifted by another person. They demonstrated that if an observer holds a light box while judging the weight of a box lifted by another person, the observer judges the other's box to be heavier, and vice versa when the observer holds a heavy box. This result, demonstrating that action biases perceptual judgments, was interpreted in terms of a functional overlap between modular perception and action systems where modules could not contribute to both the action task and perceptual task simultaneously, so the dual task situation resulted in a perceptual bias. The aim of the present study was to localize the brain regions responsible for the bias effect, and thus gain insight into the interaction of perceptual and motor processes.

In order to localize the weight judgment bias in the brain, we asked subjects in an fMRI scanner to observe a hand lifting a small box, and to judge the weight of the box. This task will be referred to as the judge-hand condition, to distinguish it from control conditions where subjects judged the weight of a bouncing ball. The judgment task was performed under three different conditions:

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no lifting, lifting a light box or lifting a heavy box, similar to Hamilton et al. (2004). Brain activity under each of these conditions was compared to activity in two control conditions. In the animacy control, subjects judged the weight of an object that was not moved by another person, that is a bouncing ball. In the task control, judgment was not of the weight, but of the number of flickers of a square imposed on the hand and ball videos. These conditions made up a fully factorial design (Fig. 1A). Furthermore, a correlation analysis across subjects was used to relate individual differences in the psychophysical bias observed in the judge-hand conditions to brain activity, and thus to localize the influence of motor activity on perceptual judgment in the brain.

To our knowledge, there are no previous human functional imaging studies which specifically examine either the biasing effect of action on the perception of human actions or the brain regions involved in weight judgment by action observation, though the task has been used as a tool to examine deception and false belief (Grezes et al., 2004a,b). Thus, the present study is an exploratory one and strict hypotheses for where activations should be found cannot be formed a priori. However, some possibilities can be distinguished.

The first prediction is based on the hypothesis that motor control structures are involved in the interpretation of observed human actions, and that the bias arises from the overlap of motor and perceptual processing when subjects both lift a box and judge the weight of an observed box lifted by another person. In this case, the bias is considered to be a motor effect, and activations related to bias could be expected in motor regions which have previously been shown to be involved in the observation of human actions. This include the inferior frontal gyrus (Decety et al., 1997; Johnson-Frey et al., 2003; Saygin et al., 2004), superior and inferior parietal regions (Grezes et al., 1998; Buccino et al., 2001), the supplementary motor area (Grafton et al., 1996) and the lateral premotor cortex (Grezes et al., 2003b; Manthey et al., 2003; Schubotz and von Cramon, 2004). These areas encompass functional homologues of nonhuman primate cortex known as the

mirror system, which are activated by both the perception of human action and by motor tasks (Rizzolatti and Craighero, 2004). In previous behavioral work (Hamilton et al., 2004), the bias was also interpreted in terms of the MOSAIC model of motor control (Haruno et al., 2001), which has been particularly associated with the cerebellum (Imamizu et al., 2003), so cerebellar activation in the bias conditions would also support the motor hypothesis.

Second, the bias might be principally a perceptual effect, occurring in regions involved in the processing of visual motion and observed human actions. These include V5, a motion area, the extrastriate body area (EBA), which is selective for observed human body parts (Downing et al., 2001) and the superior temporal sulcus (STS) which is activated by the observation of biological motion (Grossman et al., 2000; Beauchamp et al., 2003). There is evidence that these regions can be modulated by attention and by the task a subject is engaged in (Friston and Buchel, 2000; Luks and Simpson, 2004). Recent data also demonstrate that EBA is modulated by motor activity, with a decrease in BOLD signal in this region during hand movements (Astafiev et al., 2004). Such modulations might be responsible for the bias effect.

A third possibility is that bias is not specific to human actions, but arises from a general cognitive or comparative mechanism, for example if subjects take the lifted box as a standard and judge the weight of the observed object by comparison. Biases induced by comparative judgments have been found in a wide range of judgment tasks, including lifted weight, time interval, height, color and even the aesthetic value of works of art (Helson, 1964). This hypothesis makes two predictions. First, a general mechanism should apply to both judgments of the weight of a box lifted by an actor and judgments of the weight of a bouncing ball, so equivalent psychophysical biases should be seen in each case. Secondly, similar neural activations should be seen in both judgment conditions, with activations predicted in regions associated with decision making and comparison. Decision making has been associated with a variety of regions, in particular the dorso-lateral prefrontal cortex (Miller and Cohen, 2001; Heekeren et al., 2004),

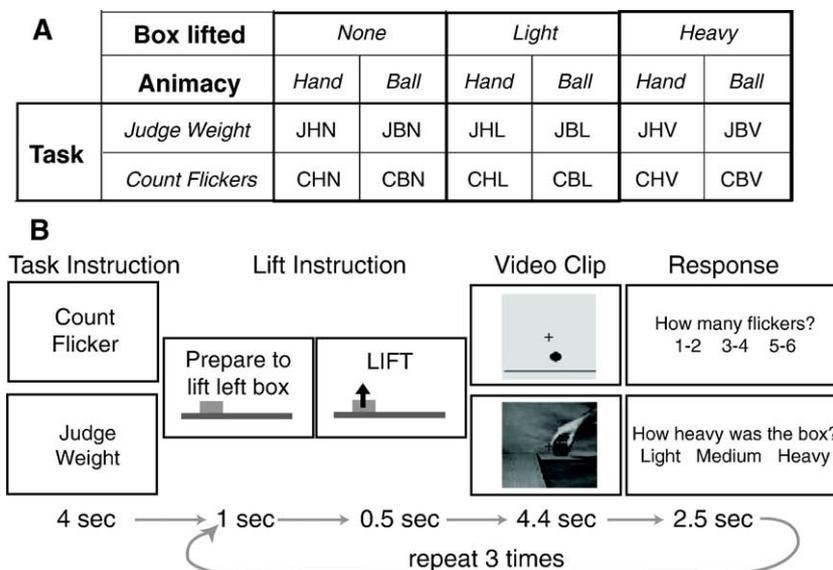


Fig. 1. (A) Experimental design. A $2 \times 2 \times 3$ fully factorial design was used, this figure summarizes the labels given to each cell in the design. (B) Event sequence in a block. Subjects saw an instruction for 4 s, with a red background for the Count task and a blue background for the Judge task. Then subjects saw the lift instruction for 1.5 s, followed by the video clip of a hand lifting a box or bouncing ball and a response screen for 2.5 s. This sequence was repeated three times in each block. An additional 2.3 s of rest were given at the end of the block (not shown).

and also the anterior cingulate (Paus, 2001). Activations in these regions, but not in any motor areas, would be expected if the bias arises from a general comparative mechanism.

Methods

The primary task used in this study was a box weight judgment task, where the participant observes a movie of an actor's hand lifting a box and placing it on a shelf, and is required to judge the weight of the box. Two control conditions were used to account for the task of weight judgment and the observation of hand actions. Furthermore, to examine the effect of the participant's action on judgment, the participant lifted a light or heavy box on some trials. These trials were arranged in a $2 \times 2 \times 3$ factorial blocked design, giving 12 unique conditions (Fig. 1A) which are described in detail below. The factors were: *Animacy* (hand or ball), *Task* (judge weight or count flickers) and *Lifting* (no box, light box or heavy box). To make the contrast calculations explicit, the 12 conditions will sometimes be referred to by three letter codes, given in Fig. 1A.

Animacy

The factor *Animacy* had two levels: Hand and Ball. Hand videos were short clips showing a hand lifting a box and placing it on a shelf. Ball videos showed a bouncing ball, such that subjects could also determine the weight of the object by observation alone, but no human agent was present in the clip. The conditions are matched in the observation of a moving object and the judgment of weight, but differ in the presence of a human hand and the importance of the behavior of the hand for the judgment task. Sample frames from each video are shown in Fig. 1B.

The hand videos were generated by filming an actor lifting a small black box and placing it on a shelf, using a high-speed camera at 250 frames per second (fps). This frame sequence was then downsampled to 25 fps, and the duration of the grasping and lifting movement was manipulated to give the percept of different box weights, while the durations of the reach and leave phases of the movement were held constant. Kinematic studies (Weir et al., 1991; Hamilton et al., in press) show that when people lift heavier boxes, their grasp and lift movements are prolonged, and psychophysical data (Hamilton et al., in press) demonstrate that observers use the durations of grasp and lift to judge box weight. For the current study, our video manipulations generated a single prototypical lift of each box weight, using a grasp–lift duration of 425 ms for the light box, 527 ms for the medium box and 602 ms for the heavy box. Because all three clips were created from the same high-speed recording, they all show the same hand form grasping the same object with the same finger configuration. The only differences between them were the durations of grasp and lift phases, and thus the velocity of the hand in these stages. Subjects must be sensitive to these kinematic parameters to make correct judgments of box weight. Although the videos are not entirely natural, they avoid the normal movement variability which might confound natural video clips, and thus they provide tightly controlled stimuli. None of the videos are explicitly perceived as being temporally manipulated by subjects.

To make an equivalent stimulus set which did not involve a hand performing a biological movement, Matlab was used to generate a movie of a bouncing ball with physically realistic

properties. The ball fell from the top of the screen and bounced three or four times before coming to a halt, and both the height and duration of the first bounce provided the principal cue to the weight of the ball. These parameters were 90 pixels over 1400 ms for the light ball, 65 pixels over 1200 ms for the medium ball and 35 pixels over 1000 ms for the heavy ball. Each hand and ball videos was 4.4 s long and included a fixation cross in the center of the screen.

Task

The factor *Task* had two levels: weight judgment and flicker counting. For the weight judgment task, subjects were asked to watch one of the video clips and to judge the weight of the object shown; judgments were made after the clip ended by pressing one of three keys with the left hand to indicate Light, Medium or Heavy. For the flicker counting task, subjects were asked to count the number of times a red square appeared at the fixation point. The red square appeared for one frame at a time, between one and six times in each video clip at a random interval, and subjects responded with the left hand, pressing one of three keys to indicate 1 or 2, 3 or 4, or 5 or 6 appearances of the square. This control task is useful because it requires subjects to pay close attention throughout the video clip, but not to focus on the hand or ball stimuli. Exactly the same set of videos was used for both the weight judgment task and the flicker counting task, only the instructions given to the participant, and thus presumably their attentional and cognitive state, differed.

Box lifting

At the same time as performing the weight judgment or flicker counting tasks, on some trials, subjects were asked to lift a small box and hold it in mid air. Two black plastic boxes were provided, each measured $82 \times 55 \times 32$ mm, and the light box weighed 150 g while the heavy box was filled with lead shot to the weight of 750 g. The boxes were placed on a platform above the response keys, which lay on the participant's chest and stomach as he/she lay in the scanner. The location of the heavy and light box on the left or right side of the platform was counterbalanced across subjects.

On seeing an instruction (Fig. 1B), subjects lifted one of the boxes, held it still in the air for the duration of the video clip and replaced it on the platform before responding to the question. Lift-off occurred before the video started, so the participant was statically holding the box during the video. This means that the participant's action preceded the observed action by approximately 2 s, similar to the timing used in Hamilton et al. (2004). On no-lifting trials, subjects just watched the video without moving their right hand. All subjects used their right hand for box lifting and their left hand for responding to the psychophysical task by pressing one of three buttons.

Experiment time course

Trials were arranged in blocks of three, and within a block, subjects performed the same task on the same stimulus type and lifted the same box. At the start of a block, subjects first saw the task instruction ('Judge weight' or 'Count Flicker') for 4 s, followed by a 'prepare to lift the left (or right) box' instruction for 1 s and a 'lift' instruction for 0.5 s. Compliance with the

lifting instructions was monitored by the experimenter in the scanner control room. While holding the box static in the air, participants saw the video for 4.4 s, followed by a response interval lasting up to 2.5 s. During this time, the participant replaced the lifted box on the platform and responded to the question by pressing a key with the left hand. As soon as the participant responded, the screen turned black until the next trial began. To remind subjects of their task, a dark red border was present on the screen throughout the counting trials, and a dark blue border was present on the judgment trials. The time course and frames from the videos are illustrated in Fig. 1B, and each block lasted 32.5 s in total. Short rest periods were included between each block and a longer 20 s rest at the end of each run to safeguard against timing delays in the presentation software during scanning, but delays were not found in practice.

Within a block, the order of the video clips was pseudo-randomized such that subjects could not predict the correct response on any clip from the previous responses. Over the whole experiment, there were six clips of each type (light–medium–heavy or number of flickers) in each condition, such that a participant who performed perfectly would press each response key equally often in each condition over the whole experiment. Because clip type was balanced across conditions, any small differences in the duration of movement on the screen in the different videos could not make a difference to the imaging results.

The 12 different types of block, one for each condition of the $2 \times 2 \times 3$ factorial design, were performed once each in a run, ordered according to a Latin square. A rest block of 32.5 s was included after block 6. Each participant performed six runs with short breaks in between, giving 6 entries in each cells of the design over the whole experiment.

Subjects

19 right handed subjects aged between 18 and 35 gave their informed consent to take part in accordance with the guidelines of the local ethics committee. They each performed at least one full block of practice outside the scanner and then performed six functional runs in the scanner.

Psychophysics analysis

For the purposes of analysis, responses on the weight judgment task were summarized by coding a response of *light* as 1, *medium* as 2 and *heavy* as 3. To determine if the action of lifting a box biased the perceptual judgment of observed box weight, judge-hand bias was defined as the mean of a participant's box weight judgments while lifting a light box (condition JHL) minus their mean box weight judgment while lifting a heavy box (condition JHV). An equivalent measure was calculated for judge-ball conditions; this was the mean ball weight judgment while lifting a light box (condition JBL) minus mean ball weight judgment while lifting a heavy box (condition JBV). This definition of bias compares judgment during light and heavy lifting directly (rather than to judgment with no-lifting, as in Hamilton et al., 2004), and gives a single bias value for each participant. Biases were calculated separately for each participant so that individual differences in bias could be examined. A positive bias indicates that the participant judges the observed box or ball to be heavier when lifting a light box, and lighter when lifting a heavy box, equivalent to the contrast effect

observed previously (Hamilton et al., 2004). A negative bias indicates that the participant judges the box or ball to be lighter when lifting a light box and heavier when lifting a heavy box, that is an assimilation effect.

Magnetic resonance imaging

Imaging was performed with a General Electric Horizon echospeed whole body 1.5 T MRI scanner using a standard birdcage head coil. Head movements were minimized by using a foam pillow and padding, including a folded blanket to support the right arm during box lifting. For each functional run, an echo planar gradient echo imaging sequence sensitive to blood oxygenation-level-dependent (BOLD) contrast was used to acquire 25 slices per TR (4.5 mm thickness, 1 mm gap), with a TR of 2500 ms, TE of 35 ms, a flip angle of 90° , a field of view of 24 cm and a matrix 64×64 . The first four volumes of each functional run were discarded to allow magnetization to approach equilibrium, and a further 177 whole brain images were collected in each run. A high-resolution T1 weighted axial fast spin echo sequence was used to obtain 25 slices coplanar to the BOLD images (TE = 6.3 ms, TR = 650 ms, FOV = 24 cm, matrix = 192×192). After all the functional runs, a high-resolution T1 weighted image of the whole brain was acquired using a spoiled gradient recalled 3D sequence (TR 7.7, TE min full, flip angle 15° , FOV 24, slice thickness 1.2, matrix 256×192).

Image processing

All analysis was carried out in SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>). First, functional images were realigned to correct for head movement. Data from two subjects were rejected for excessive head movement, and the data from the remaining 17 subjects were coregistered to their high-resolution scans and normalized to a standardized stereotaxic space. Data were smoothed with an isotropic Gaussian kernel (6 mm full width half maximum) to give images with 25 axial slices of $2 \times 2 \times 2$ mm voxels.

For each participant, a fixed effects analysis was carried out on the data for all runs together, with one regressor for each of the 12 conditions, as well as fixed, linear and quadratic regressors to account for global signal changes over each run. The duration of each experimental block was 32.5 s, but as the first 5 s were instructions rather than the actual task, block duration was set as 27.5 s and block onset to the time of the first video clip in a block. The experimental blocks were modeled as a box car convolved with an HRF, and the rest block was not modeled. The design matrix was fit to the data for each participant individually, and the parameter estimates taken to the second level for random effects analysis.

Data analysis

Our first analysis aimed to identify brain regions preferentially activated by the weight judgment task and by the observation of human actions, without any action by the participant. We used a random effects analysis to find the effects of Task (Judge > Count) and Animacy (Hand > Ball), using only data from the conditions when participants were not lifting any box. Second, we aimed to identify brain regions preferentially involved in lifting a light or heavy box without any observation of action. Thus, we excluded

all data from the Hand conditions and calculated a lifting contrast based on the remaining conditions, that is $(JBL + CBL + JBV + CBV) > 2 \times (JBN + CBN)$, using the condition names given in Fig. 1. Voxels which were significant at $P < 0.001$ uncorrected and in clusters of more than 10 voxels are reported in MNI coordinates. The anatomical locations of all voxel clusters were identified by careful comparison of the results with a brain atlas (Duvernoy, 1999).

The second stage of analysis examined how brain activity related to individual differences in the box weight judgment task. As described above, a single measure of psychophysical bias was obtained for each participant as the difference between their box weight judgments when lifting a light box (condition JHL) and when lifting a heavy box (condition JHV). To link this bias measure to BOLD signal, a contrast image was calculated for each participant to reveal the difference in BOLD between judging box weight while lifting a light box (condition JHL) and judging box weight while lifting a heavy box (condition JHV). Regression across subjects was used to find brain areas where the magnitude of this bias contrast covaried with the magnitude of the psychophysical bias observed in each participant. This regression effectively searches for brain regions where the difference in the fMRI signal between lifting a light and heavy box while judging observed box weight (conditions JHL and JHV) correlates with the difference in psychophysical judgment between these same two conditions. As a simple regression with only 17 subjects can be susceptible to outliers, we used a robust regression which iteratively re-weights least squares according to a bi-square weighting function until convergence (Matlab Statistics toolbox 5.0.1). When outliers are absent, the robust regression gives results which are almost identical to a standard regression. Voxels which were significant at $P < 0.001$ uncorrected and in clusters of more than 10 voxels are reported in MNI coordinates. To provide a comparison data set, an equivalent analysis was performed on bias for the ball weight judgment task.

The third stage of analysis focused solely on the clusters revealed by the bias analysis, and aimed to determine if these regions were also involved in the primary task-judgment of the weight of a box lifted by another person. We calculated the main effects of Animacy, Task and Lifting within each cluster found in the bias analysis. Results are reported at $P < 0.05$, Bonferroni corrected for multiple comparisons. Again, an equivalent analysis was conducted on the ball data set, testing for main effects of Ball > Hand, and also the main effects of Task and Lifting.

Results

Psychophysical performance

Subjects' responses on every trial were recorded for analysis. Responses on the flicker counting task had a 97.5% accuracy rate, which did not differ between conditions, so these results were not analyzed further. In the no-lifting condition of the weight judgment task, every participant was able to judge the weight of the box or ball at levels above chance. Performance of all subjects is illustrated in Fig. 2A for the hand and Fig. 2B for the ball, and the linear fits in each case were significant at $P < 0.001$.

As a measure of the systematic effect of action on perception, bias was calculated as the difference between mean box weight judgment when a participant lifted a light box (condition JHL) and

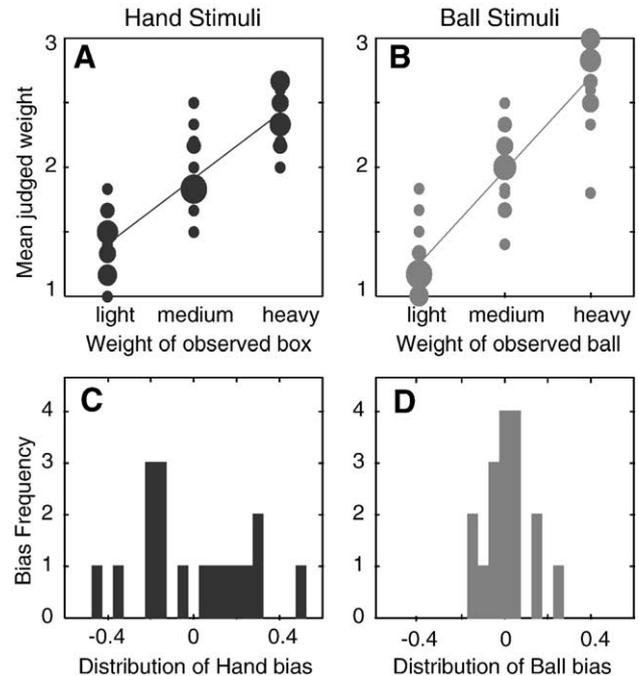


Fig. 2. Psychophysical performance during scanning. (A) Mean judged box weight for observation of the hand stimuli when participants were not lifting any box (condition JHN). Means are shown for each participant, with larger bubbles indicating overlapping data points. (B) Mean ball weight judgment without box lifting (condition JBN). (C) Distribution of biases observed in hand judgment responses when subjects lifted a light or heavy box. Positive bias means subjects judged the observed box as heavier when lifting a light box and vice versa. (D) Distribution of biases observed in the ball judgment task during lifting.

mean judgment when the participant lifted a heavy box (condition JHV) for each participant. An equivalent bias was calculated for the ball weight judgment conditions (see Methods). The distribution of biases obtained when judging box weight from watching a hand is shown in Fig. 2C. Hand bias ranged from -0.44 to 0.50 and did not appear to be normally distributed. Using the Lilliefors modification of the Kolmogorov–Smirnov test of normality (Lilliefors, 1967), the probability that the distribution of hand biases was not normal was $P < 0.0729$. At a single subject level, bias direction was consistent for all three observed box weights in eight participants, five with positive bias and three with negative bias. The distribution of biases obtained when judging the weight of a bouncing ball is shown in Fig. 2D. Bias during the ball trials was normally distributed ($P > 0.20$ Lilliefors test) and had a narrow range (-0.167 to 0.239) with a mean very close to zero. A Kolmogorov–Smirnov test did not reveal significant differences between the distributions of hand and ball bias ($P = 0.19$). There was no correlation across subjects between ball and hand bias scores ($r^2 = 0.126$, $P = 0.16$), suggesting that there is not a common judgment mechanism generating bias in the different conditions.

Analysis of main effects and interactions

The main effect of viewing a movie of a hand lifting a box compared to viewing a movie with a bouncing ball, without any concurrent box lifting, results in a significant activation in several occipital and frontal areas. The activations are illustrated in Fig. 3

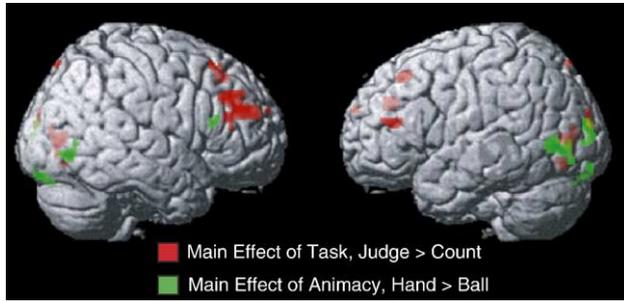


Fig. 3. Main effects without box lifting. Red indicates greater activation for judging weight compared to counting flickers. Green indicates greater activation for observing a hand compared to observing a ball.

(green) and listed in the top part of Table 1. Occipital activations included the extrastriate body area, which is known to be preferentially activated by viewing of the human body (Downing et al., 2001; Astafiev et al., 2004). Activation was also found in the superior and inferior occipital gyrus, where activity is commonly found on visual tasks including attentional or search tasks (Buchel et al., 1998; Gitelman et al., 2002), and in the right inferior frontal gyrus, an area associated with the observation of human actions (Leslie et al., 2004; Schubotz and von Cramon, 2004; Iacoboni et al., 2005).

The main effect of judging the weight of a moving object compared to counting the number of times a square flickers at the center of the screen also results in occipital and frontal activations,

Table 1
Main effects of animacy and task

| Region | Number of voxels | MNI coordinates | | | <i>t</i> statistic |
|--|------------------|-----------------|----------|----------|--------------------|
| | | <i>x</i> | <i>y</i> | <i>z</i> | |
| <i>Main effect of animacy: hand > ball (JHN + CHN > JBN + CBN)</i> | | | | | |
| Superior occipital gyrus (left) | 50 | -26 | -92 | 14 | 10.28 |
| | | -24 | -94 | 6 | 4.47 |
| | | -28 | -88 | 2 | 3.96 |
| Extrastriate body area (left) | 81 | -50 | -68 | 0 | 7.06 |
| | | -48 | -80 | 0 | 4.40 |
| | | -46 | -82 | -8 | 4.02 |
| Extrastriate body area (right) | 41 | 44 | -72 | -6 | 5.56 |
| | | 48 | -68 | 2 | 4.22 |
| Inferior frontal gyrus (right) | 15 | 56 | 24 | 16 | 5.03 |
| Inferior occipital gyrus | 25 | 22 | -92 | -18 | 4.72 |
| | | 18 | -82 | -24 | 4.01 |
| Inferior occipital gyrus | 10 | -28 | -94 | -12 | 4.41 |
| <i>Main effect of task: judge > count (JHN + JBN > CHN + CBN)</i> | | | | | |
| Middle frontal gyrus (right) | 231 | 44 | 42 | 24 | 6.29 |
| | | 46 | 34 | 32 | 6.27 |
| | | 44 | 52 | 22 | 5.67 |
| Anterior cingulate cortex | 55 | 8 | 38 | 30 | 6.01 |
| Inferior frontal sulcus (left) | 50 | -44 | 38 | 16 | 5.31 |
| Calcarine sulcus | 55 | -8 | -76 | 4 | 5.30 |
| | | -8 | -84 | 10 | 4.62 |
| Middle frontal gyrus (right) | 26 | 38 | 24 | 56 | 5.04 |
| Calcarine sulcus | 28 | 6 | -78 | 4 | 4.97 |
| | | 8 | -80 | -6 | 3.78 |
| Superior occipital gyrus | 13 | -26 | -92 | 22 | 4.78 |
| Superior frontal gyrus | 53 | 2 | 30 | 46 | 4.75 |
| Lingual gyrus | 20 | -12 | -76 | -12 | 4.74 |
| Superior frontal gyrus | 12 | 30 | 64 | 24 | 4.71 |
| Superior parietal gyrus | 12 | 14 | -82 | 54 | 4.65 |

Table 2
Main effects of lifting and interactions

| Region | Number of voxels | MNI coordinates | | | <i>t</i> statistic |
|---|------------------|-----------------|----------|----------|--------------------|
| | | <i>x</i> | <i>y</i> | <i>z</i> | |
| <i>Main effect of lift > no lifting (JBL + CBL + JBV + CBV > 2 * (JBN + CBN))</i> | | | | | |
| Right cerebellum | 1129 | 8 | -60 | -14 | 12.88 |
| | | 28 | -48 | -30 | 12.25 |
| | | 8 | -54 | -26 | 6.55 |
| Left sensorimotor cortex | 7965 | -52 | -28 | 20 | 12.31 |
| | | -34 | -10 | 54 | 10.92 |
| | | -27 | -22 | 64 | 10.37 |
| Thalamus | 310 | -12 | -20 | 6 | 8.16 |
| | | -22 | -24 | 14 | 4.59 |
| Basal ganglia | 182 | -30 | -2 | 0 | 6.07 |
| Caudate | 58 | -24 | -4 | 26 | 5.87 |
| | | 41 | 36 | -50 | 70 |
| Intraparietal sulcus | | 24 | -44 | 66 | 4.08 |
| Thalamus | 17 | 0 | -32 | 10 | 5.55 |
| Insula | 54 | -34 | -22 | -2 | 4.93 |
| | | -30 | -18 | 6 | 4.43 |
| Cerebellum | 13 | 26 | -84 | -24 | 4.87 |
| Cerebellum | 14 | 36 | -66 | -30 | 4.51 |
| Cuneus | 13 | 16 | -76 | 6 | 4.09 |
| Intraparietal sulcus | 36 | -18 | -66 | 58 | 4.09 |
| <i>Interaction of animacy and task without lifting (JHN-CHN < JBN-CBN)</i> | | | | | |
| Intraparietal sulcus | 42 | 44 | -36 | 44 | 5.19 |
| | | 40 | -40 | 34 | 3.94 |
| Cingulate cortex | 11 | 10 | 4 | 32 | 4.40 |
| <i>Interaction of animacy and task without lifting (JHN-CHN > JBN-CBN)</i> | | | | | |
| Posterior cingulate cortex | 11 | -10 | -48 | 4 | 5.35 |

as show in Fig. 3 (red). Activity was strongest in the middle frontal gyrus, which is an area that has been associated with decision making (Monchi et al., 2001; Bunge et al., 2003; Pernet et al., 2004). Activations were also seen in several occipital areas including the calcarine sulcus and superior and middle occipital gyrus, which may be related to either judgment itself (Pernet et al., 2004), or to the different focus of attention in the judgment and flicker counting tasks.

The main effect of lifting a box with the right hand and holding it still in the air compared to no lifting resulted in activity in motor areas as expected. Left primary motor cortex and right cerebellum were activated by lifting, and smaller activations were also seen in the intraparietal sulcus, basal ganglia and inferior frontal gyrus. The coordinates of these activations are given in Table 2.

An interaction analysis was used to examine areas with nonadditive responses to combinations of the tasks and stimuli, and the coordinates of the regions found are listed in the lower part of Table 2. The interactions identified regions in the intraparietal sulcus, posterior cingulate and middle cingulate cortices. Examination of the parameter estimates in these regions revealed that the intraparietal sulcus showed greatest activity in the judge-ball condition, while posterior cingulate cortex was selectively activated by the count-ball condition and cingulate by both the judge-ball and count-hand conditions, but no regions were found to show a preferential activation or deactivation in the judge-hand condition alone. For this reason, these regions will not be considered further.

Table 3
Brain–behavior correlations

| Region | Number of voxels | MNI coordinates | | | <i>t</i> statistics | | | |
|---|------------------|-----------------|----------|----------|---------------------|-------------|---------------|----------------|
| | | <i>x</i> | <i>y</i> | <i>z</i> | Bias regression | Hand > Ball | Judge > Count | Lift > no lift |
| <i>Negative robust regression for judge-hand conditions</i> | | | | | | | | |
| Inferior frontal gyrus | 19 | −42 | 10 | −4 | 7.62 | 0.84 | 1.36 | 0.47 |
| Precentral gyrus | 50 | −44 | −20 | 52 | 6.92 | 1.70 | 2.63 | *5.98 |
| <i>Positive robust regression for judge-hand conditions</i> | | | | | | | | |
| Intraparietal sulcus | 28 | 26 | −58 | 64 | 7.21 | 0.05 | 1.56 | 0.23 |
| Extrastriate body area | 11 | −48 | −74 | −6 | 6.18 | *2.96 | *3.11 | 1.30 |
| Lingual gyrus | 11 | −10 | −78 | −4 | 5.41 | 1.88 | 1.95 | 0.21 |
| <i>Negative robust regression for judge-ball conditions</i> | | | | | | | | |
| Lingual gyrus | 69 | −2 | −74 | 8 | 12.42 | 2.65 | *3.42 | 0.43 |
| Cingulate | 13 | −16 | −20 | 40 | 7.98 | 1.90 | 1.51 | 2.00 |
| Posterior cingulate | 67 | −2 | −48 | 38 | 7.22 | 1.89 | 1.49 | 0.72 |
| Intraparietal sulcus | 25 | 22 | −84 | 38 | 6.68 | 0.26 | 1.57 | 0.41 |
| Superior occipital gyrus | 13 | 14 | −88 | 16 | 6.58 | 1.61 | 2.14 | 0.70 |
| Lingual gyrus | 30 | −16 | −66 | −4 | 6.03 | 1.95 | 2.85 | 0.12 |
| <i>Positive robust regression for judge-ball conditions</i> | | | | | | | | |
| Supplementary motor area | 11 | −8 | −8 | 66 | 6.14 | 0.62 | 2.12 | *5.00 |
| Thalamus | 17 | 18 | −22 | 16 | 6.06 | 1.75 | 1.64 | 1.28 |
| Superior frontal gyrus | 17 | 4 | 40 | 4 | 5.81 | 0.65 | *3.53 | *5.40 |
| Anterior insula | 19 | 30 | 24 | −10 | 5.28 | 0.83 | 0.48 | 2.74 |
| Caudate | 11 | −10 | 18 | 18 | 5.10 | 2.02 | 0.62 | 1.40 |

Regions showing a significant correlation between BOLD and psychophysical bias are listed. *t* statistics are given for the peak voxel in each cluster for the bias regression at $P < 0.001$ uncorrected. *t* statistics are also listed for three tests on the mean activation in each cluster: (1) Hand > Ball with no box lifting, (2) Judge > Count with no box lifting and (3) Lift > no lifting. Values marked with * are significant at $P < 0.05$ corrected for multiple comparisons.

Analysis of brain–behavior correlation

In order to identify brain regions associated with the effects of action on perceptual judgment, a robust regression analysis across subjects was used to locate regions with a significant correlation between psychophysical bias in the judge-hand conditions when lifting a box and the difference in SPM parameter estimates between these conditions. The brain–behavior correlation analysis was performed first over the whole brain with a threshold of $P < 0.001$ uncorrected and 10 voxels. The coordinates of all the regions found are listed in the top part of Table 3. Within each cluster, the main effects of Animacy, Task and Lifting were tested, and the *t* statistics for these tests are also listed in Table 3.

Significant negative correlations were found in two motor regions, the inferior frontal gyrus and the central sulcus (Figs. 4A and B). The cluster in central sulcus also showed a main effect of lift, confirming that this is truly a motor region. No other main effects were found in the inferior frontal gyrus. Positive brain–behavior correlations were found in the intraparietal sulcus and the lingual gyrus. A positive correlation was also found in the extrastriate body area, as illustrated in Fig. 4D. In this region, main effects of Task and Animacy were also found, and the coincidence of these three effects strongly implicates the extrastriate body area in the box weight judgment task and the psychophysical bias.

For the purposes of comparison, a robust regression between bias in the judge-ball conditions and the difference in BOLD between these conditions was also carried out, and regions with significant correlations are listed in the lower part of Table 3. The validity of these correlations is limited by the narrow range of biases observed, but a highly significant effect was obtained in the

lingual gyrus, where there was also a main effect of task. Negative correlations were also found in the cingulate, intraparietal sulcus and superior occipital gyrus. Positive correlations were found in the supplementary motor area, superior frontal gyrus and anterior insula, and subcortically in the thalamus and caudate.

Discussion

The pattern of activation described above includes many of the regions predicted by the hypotheses described in the Introduction. To understand the implications of these activations, we first consider what evidence is necessary to say that a brain region is a site where perceptual and motor processing interacts and a bias occurs. One approach to link brain activity to bias might be to calculate contrast images between the conditions where bias is present and those where it is not. However, in the current study, there is no single subtraction which would reveal an overall bias without the concurrent effects of observed Animacy or box lifting. Another possibility might be to relate bias on individual trials to BOLD, but this is not practical in a block design, though an event related design with jittering would allow this in a future study. Instead, we have used a correlation approach which localizes brain regions in which individual differences in psychophysical bias are significantly related to individual differences in BOLD signal in the conditions where bias occurs. Note that this approach captures brain–behavioral correlations unbiased by intersubject variability of task related BOLD responses. We do not place any particular importance on whether a correlation was positive or negative, because the relationship between BOLD and excitation or inhibition of

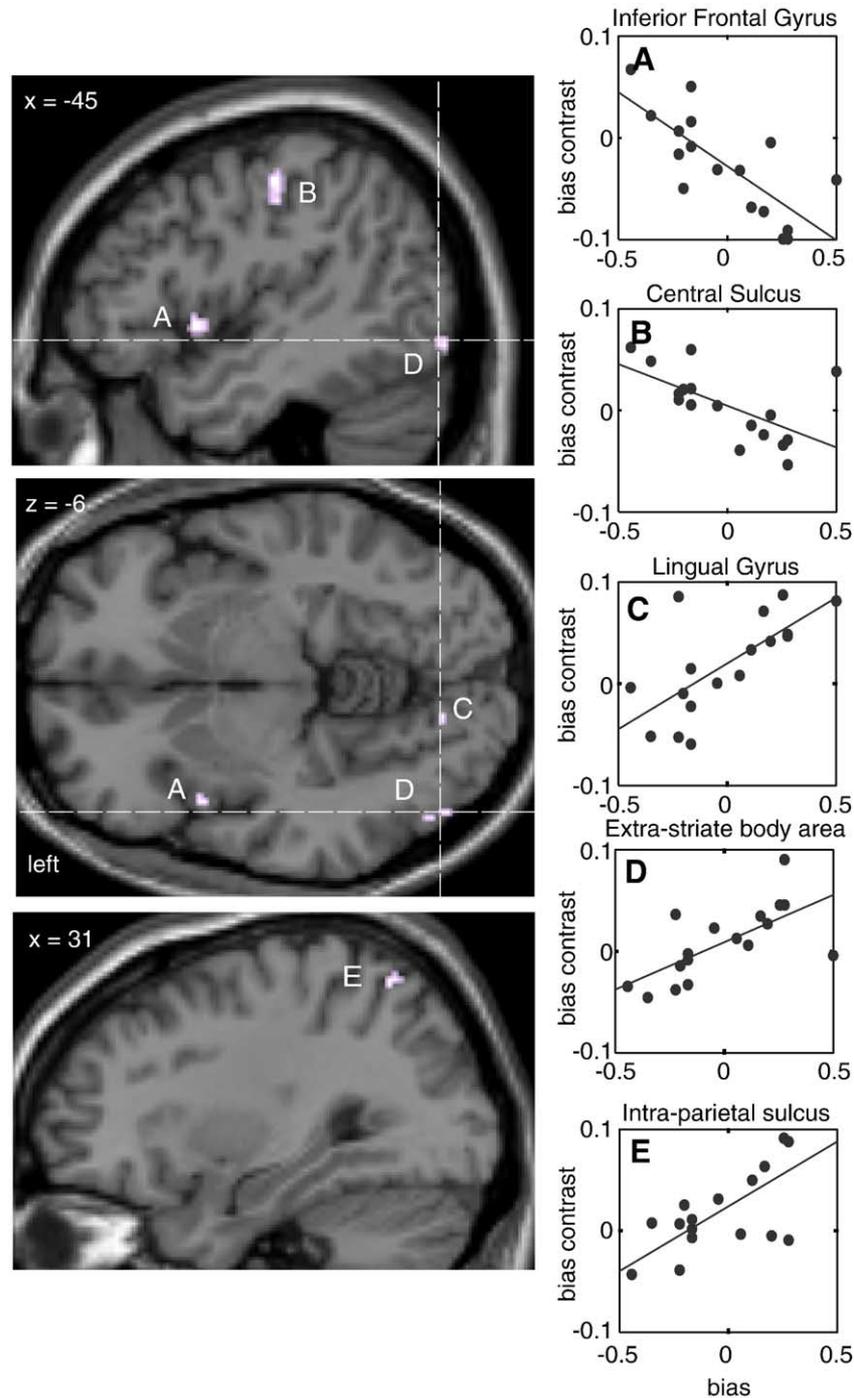


Fig. 4. Regions showing a brain–behavior correlation. The correlation between psychophysical bias and BOLD signal is shown on the right for five clusters. The top panel illustrates clusters in the left inferior frontal gyrus (A), left central sulcus (B) and left extrastriate body area (D). The middle panel again shows the clusters in left IFG (A) and left EBA (D) as well as the left lingual gyrus (C). The lower panel illustrates the cluster in the right intraparietal sulcus (E). Coordinates of all of these clusters are given in the top part of Table 3.

neurons is not clearly defined (Attwell and Iadecola, 2002). Furthermore, this correlation method compared differences in BOLD and differences in performance between conditions, rather than absolute values, so positive and negative correlations define only the relative values of weight judgment and BOLD signal. Although interpreting the direction of the signal is not straightforward, the presence of a robust correlation is a clear demonstration of a link between a brain region and the bias

effect. To assist the interpretation of the brain–behavior correlation, we also tested within the bias clusters for main effects of observing a hand lifting a box and of judging weight, without any lifting behavior, and for lifting without the observation of a hand.

The brain–behavior correlation for the judge-hand task revealed a network of five regions with a significant correlation, that is, inferior frontal gyrus (IFG), central sulcus, intraparietal

sulcus (IPS), lingual gyrus and extrastriate body area (EBA). We consider now the potential contributions and implications of each of these regions.

A cluster in the frontal operculum of the inferior frontal gyrus was found to show a significant brain–behavior correlation. This location is close to activations previously reported in studies of action observation (Buccino et al., 2001; Hamzei et al., 2003; Johnson-Frey et al., 2003). Given these previous action observation studies, it might seem surprising that within this IFG cluster, there were no reliable effects of either lifting and holding a box (while observing a ball) or observing hand motion (without any concurrent movement). Though inferior frontal gyrus is closely connected to motor regions, it is not strongly activated by simple motor tasks (Colebatch et al., 1991; Ehrsson et al., 2000), but seems to require more complex tasks such as imitation (Iacoboni et al., 1999; Buccino et al., 2004). Similarly, not all studies of action observation have found activation of IFG (Grafton et al., 1996; Grezes et al., 2003b), and studies which did find these activations often required subjects to remember configural arrangements (Johnson-Frey et al., 2003) or to infer intentionality (Iacoboni et al., 2005). In contrast, our study emphasized perceptual judgment of a single motor act with constant intentionality and it did not require action memory or subsequent motor imitation. Instead, we used an attentional control where subjects observe the same videos but attended to different features of the stimulus. It is known that unattended objects and actions can draw attention (Handy et al., 2003; Downing et al., 2004), and it is possible that the processing of any observed action automatically recruits some brain areas such as IFG (Iacoboni et al., 2005). The presence of the bias effect in IFG provides strong evidence for the importance of this region in the perceptual judgment of action. It has been suggested that involvement of motor systems in action observation tasks is evidence that an observer interprets other people's actions by simulating them in her own motor system (Gallese and Goldman, 1998). The finding that IFG is involved in the bias effect supports the hypothesis that this is an important site for the interaction of perceptual and motor processes, and that the bias effect is a behavioral consequence of the use of the motor system to interpret actions, as previously proposed (Hamilton et al., 2004).

A cluster of voxels showing an effect of bias was also found in central sulcus, the hand region of primary motor cortex, and this area also had a strong main effect of box lifting, confirming its motor role. There is fMRI evidence for modulation of primary motor cortex by gaze (Baker et al., 1999), by attention to one's own action (Binkofski et al., 2002) and by imagined action (Decety et al., 1994) but activation in primary motor cortex has not previously been reported in fMRI studies of action observation. Other methods of measuring cortical activation have, however, shown changes in this region during action observation. Enhancement of primary motor cortex excitability when subject's watch another person move has been demonstrated using TMS (Fadiga et al., 1995; Strafella and Paus, 2000) and MEG studies also show modulation of this area during the observation of human actions (Nishitani and Hari, 2000). It is important to note that the correlation related to psychophysical bias was seen in this area even though the visual stimuli and the action performed were balanced across all conditions.

Data from macaques demonstrate functional connections between the hand region of primary motor cortex and area F5 (Shimazu et al., 2004), and connections between primary motor cortex and inferior frontal gyrus have been shown for facial

muscles (Greenlee et al., 2004). Thus, it seems plausible that the hand representation in human primary motor cortex and IFG is closely connected and may form a motor network which gives rise to the observed bias. We suggest that this loop may simulate observed actions, in order to interpret them. The fact that this bias network extends to primary motor regions suggests that simulation of observed action can be a detailed motor process, rather than visual or conceptual pattern matching. In our task, subjects had to use subtle changes of hand speed to infer object weights. This specificity is also compatible with Buccino et al.'s (2001) findings of somatopy in the premotor cortex during the observation of actions, and their suggestion that this is evidence for motor simulations.

Moving caudally, a significant correlation between judge-hand bias and BOLD was found in a small region of the right intraparietal sulcus. Close but not overlapping activations along this sulcus were also found for the main effect of task (see Fig. 3) and for the ball bias. Interpreting the IPS focus in the judge-hand bias conditions is not straightforward, because this brain region has been linked to a wide range of processes. Both imitating actions and pantomiming actions activate sites along the intraparietal sulcus (Muhlau et al., 2005), as does the observation of human actions (Bonda et al., 1996; Buccino et al., 2004; Leslie et al., 2004). The inferior parietal area is considered to be part of the mirror neuron system by Rizzolatti and Craighero (2004), and this region is known to be connected to the inferior frontal gyrus and to visual systems, and is thus a plausible link in the bias network. However, the IPS activation was in the right hemisphere rather than the left where all the other bias related activations were found, and it did not overlap with any of the main effects. Thus, we can conclude that it is possible that IPS is part of the bias network, but that the evidence for this area's involvement is weaker.

The fourth region revealed by the brain–behavior correlation analysis was the lingual gyrus, which was close to another lingual gyrus cluster activated by the ball-bias correlation. However, the two clusters did not overlap and the regressions were in opposite directions. This supports the hypothesis that different mechanisms are responsible for the bias for the two different stimulus sets. As lingual gyrus was not among our hypothesized regions and has not been strongly linked to action observation, we do not consider this region to be particularly important.

The final noteworthy region is an occipital region centered on $x = -48$, $y = -74$, $z = -6$, which showed a correlation with bias in the opposite direction to that found in motor and premotor regions. This location is close to both area V5, well defined as a visual motion area, and extrastriate body area (EBA), a region which shows a preference for the observation of body parts (Downing et al., 2004). Many studies of action observation have found activation spanning these adjacent regions, and most do not distinguish between them or comment in detail on these areas. The activation we report is very close to the published coordinates of EBA, and this cluster also showed a main effect of Animacy, with greater activation for the observation of a lifting hand compared to a bouncing ball, suggesting that it is mostly likely EBA. There is ample evidence in humans and monkeys for modulation of visual regions by attention or task demands or motor tasks. In particular, a recent fMRI study demonstrates that activation in EBA is modulated by motor activity, with a decrease in BOLD in EBA during actions (Astafiev et al., 2004). This result remains controversial (Astafiev et al., 2005; Peelen and Downing, 2005), but the current data support the hypothesis that EBA is modulated

by motor activity and further suggests that it may be a component of the network giving rise to the biasing effect of action on perception. Our data support idea that motor control modulates EBA and suggest that this modulation has behavioral consequences in terms of the bias effect.

Based on the results discussed above, we suggest that the psychophysical bias observed in the judge-hand conditions arises principally from the interaction of three areas—the IFG, central sulcus and EBA, and there is weaker evidence for IPS involvement. This network of regions corresponds well with the activations reported in a range of studies of action observation (Buccino et al., 2001) and in particular with studies using MEG (Nishitani and Hari, 2000) which have shown the involvement of primary motor cortex, inferior frontal gyrus and V5 in the observation of actions. The same three regions form the bias network we have observed.

One possible difficulty with the conclusions outlined above is the discrepancy between the current psychophysical results and the data reported previously in a similar task (Hamilton et al., 2004). In the current study, subjects showed a range of individual difference in bias, with 9/17 subjects showing a negative bias and 8/17 showing a positive bias. The bias was consistent at the single subject level in 3 participants with negative bias and 5 with positive bias. In contrast, our previous study with similar stimuli and instructions found a positive bias in all 12 participants (Hamilton et al., 2004), which was significant in 9 at the single subject level. Though this might seem problematic, there are two likely causes of the differences. First, compared to our previous psychophysical studies, the current study is limited by lower statistical power, fewer response keys and less control of relative timing of action and video. This is due to the constraints of the scanning environment. Second, we have reason to believe that the modulation of weight judgment by motor activity is a subtle effect which could be altered by context (for example, being in the scanner) or by differences in how subjects approach the task and interpret the instructions. Several studies of interactions between perceptual and motor processes have failed to find effects in a consistent direction. For example, some researchers have found that performing an action can prime or enhance the perception of similar stimuli (Craighero et al., 1999, 2002; Wohlschlagel, 2000), equivalent to a negative bias in the current task. Others have found that action reduces the likelihood of perceiving a related stimulus (Muesseler and Hommel, 1997) equivalent to a positive bias in the current task. One recent study demonstrates that the direction of bias changes according to whether subjects interpret triangular stimuli as arrows or as headlights (Kunde and Wuhr, 2004). These results all indicate that the direction of the biasing effect of action on perceptual processing is highly flexible depending on the precise circumstances of the task.

Despite these limitations, the range of individual differences in bias provides a powerful method for relating bias to brain areas, in a manner which would not have been possible if all subjects showed the same bias. An increasing number of studies use individual differences in performance to obtain functional localizations (for example: Lane et al., 1998; Canli et al., 2001; Grezes et al., 2003a; Osaka et al., 2003; Singer et al., 2004; Baird et al., 2005) and this approach can provide information unobtainable by conventional subtraction methods. Most previous studies have correlated the percent signal change compared to rest with an absolute measure of individual differences. For this study, we used relative measures at the second level, that is, the difference in

BOLD between two very similar tasks and the difference in performance between these two conditions. However, the underlying principle remains the same.

Our analysis of both positive and negative bias together by the regression method makes the assumption that both biases arise in the same brain regions, which may be modulated to cause a positive or negative bias in judgment. This assumption is compatible with studies showing different biases can arise from the same stimuli in different circumstances (Kunde and Wuhr, 2004). It is possible that there are also brain regions which show activity only in participants with a positive bias, or only in those with a negative bias, but further experiments will be required to identify such areas. Such work may also define more precisely what causes some subjects to show a positive bias while others show a negative bias. In the current data set, the correlation analysis remains a useful mechanism to reveal the brain regions underlying the bias. By using the individual differences in psychophysical bias, we have been able to define a network of regions involved in the interaction of visual and motor processing, namely the IFG, central sulcus and EBA. What are the implications of these findings for our understanding of action observation in humans?

Many previous studies have examined the brain networks involved in the observation of human action without any concurrent action (Decety, 1996; Grafton et al., 1996; Buccino et al., 2001) or during imitation of human actions (Iacoboni et al., 1999; Decety et al., 2002; Grezes et al., 2003b), which involves an explicit encoding of the observed action and deliberate mimicry. In contrast, the situation in the current task bears more similarity to daily life, where we can see and interpret other people's actions while doing something different. The bias effects we observe are entirely implicit and automatic, yet the imaging data suggest that a similar network of regions is involved to that found in explicit imitation or action observation tasks. This adds further evidence to the theory that this network of regions is automatically involved in interpretation of observed actions. The IFG and primary motor cortex activations particularly suggest that this interpretation involves an element of motor simulation, where the observers own motor system is used to process visual information about another person's behavior (Gallese and Goldman, 1998). These data are compatible with the mirror system hypothesis (Rizzolatti and Craighero, 2004), but go further in suggesting that the mirror system is not just a passive recipient of visual information, but actively shapes visual judgment. The finding that such a wide network is involved in the bias effect suggests that the interaction of perceptual and motor processing does not have a single locus, but occurs throughout the brain across many areas which are concerned with both the visual recognition of actions and the control of actions. In particular, the fact that motor performance has a detectable impact on perceptual judgment demonstrates that the links between these regions cannot be only feedforward, but must include a significant backwards influence of the motor regions on the visual regions. Further exploration of the dynamics of this system and the circumstances which give rise to different types of bias would be helpful to understand these interactions.

To conclude, we have demonstrated that the biasing effect of lifting a box on subject's perceptual judgment of box weight can be linked to a network of brain regions spanning the perceptual and motor systems. The specific areas involved in the bias are the extrastriate body area, inferior frontal gyrus and central sulcus in the left hemisphere. These data support the idea that

motor processing has a modulatory influence on perceptual processing and thus visual and motor processes cannot be thought of as two distinct systems, but instead interact at many levels.

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