Your Own Action Influences How You Perceive Another Person's Action

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Summary

A growing body of neuroimaging and neurophysiology studies has demonstrated the motor system's involvement in the observation of actions [1–5], but the functional significance of this is still unclear. One hypothesis suggests that the motor system decodes observed actions [6, 7]. This hypothesis predicts that performing a concurrent action should influence the perception of an observed action. We tested this prediction by asking subjects to judge the weight of a box lifted by an actor while the subject either lifted or passively held a light or heavy box. We found that actively lifting a box altered the perceptual judgment; an observed box was judged to be heavier when subjects were lifting the light box, and it was judged to be lighter when they were lifting the heavy box. This result is surprising because previous studies have found facilitating effects of movement on perceptual judgments [8] and facilitating effects of observed actions on movements [9], but here we found the opposite. We hypothesize that this effect can be understood in terms of overlapping neural systems for motor control and action-understanding if multiple models of possible observed and performed actions are processed [10–12].

Results

Although perception and action have traditionally been considered to be separate domains, there is increasing evidence of complex interactions between these systems. Observing actions facilitates, or speeds up, the production of similar actions [9, 13–16], but it interferes with the production of different actions [17]. These effects are believed to reflect common neural activations that occur during the performance and observation of action. Neurophysiological studies of the macaque monkey have demonstrated the existence of "mirror neurons," which respond both when the monkey performs a particular action and when he watches or hears another individual performing the same action [1, 5, 18]. Neuroimaging studies have provided support for the existence of a similar system in the human brain [2, 3], and transcranial magnetic stimulation studies have shown increased excitability of the part of primary motor cortex that controls a particular body part during observation of an action involving that body part [19, 20]. Based on these results, it has been proposed that when an individual observes another person performing an action, the observer's motor system may simulate the other person's behavior and that this simulation contributes to the observer's understanding of that person's movement, intentions, and goals [6, 7]. If the motor system has a functional role in understanding observed actions but is also required to perform movements, it is possible that performing an action will interfere with or bias the processing of observed actions, and thus might also interfere with or bias the interpretation of other people's movements. The purpose of this present study is to test the hypothesis that the motor system has a functional role in interpreting observed actions and to define how this role coexists with the ongoing control of movement.

We examined the subjects' perceptual judgments of an observed action while they performed different motor tasks. Subjects performed a visual weight judgment task [21, 22], in which they were required to judge the weight of a box while watching a video clip of an actor's hand lifting the box and placing it on a shelf (see Figure 1 and Experimental Procedures for details). In order to accurately assess the box's weight, subjects had to continually assess the kinematics of the observed movement. The task performances of normal, unskilled observers showed neither floor nor ceiling effects. Observers made weight judgments while lifting actively, holding passively, or maintaining a neutral (no action) condition. The results are expressed in terms of the bias or difference between the experimental and neutral conditions. For each subject and each video clip shown, we calculated the mean judged weight of the box on all the neutral trials. We defined response bias for active and passive trials as the judgment given in a trial minus the mean neutral response; a positive bias meant that the weight was judged to be heavier than in the neutral condition.

If the perceptual system required the use of motor resources, we predicted that the observers' action would affect the perceptual task and that this effect could occur in one of two directions. In the case of a compatibility effect, the observed action would be judged to be similar to the performed action (Figure 2A); for example, when lifting a heavy box, subjects would judge the observed box to be heavier than neutral and thereby show a positive bias (represented by the solid line in Figure 2A) and vice versa. Several studies have found that movements are found to be facilitated by or similar to observed actions [9, 13, 14] and these results predict the compatibility effect for weight judgment. An alternative possibility is a contrastive effect, in which
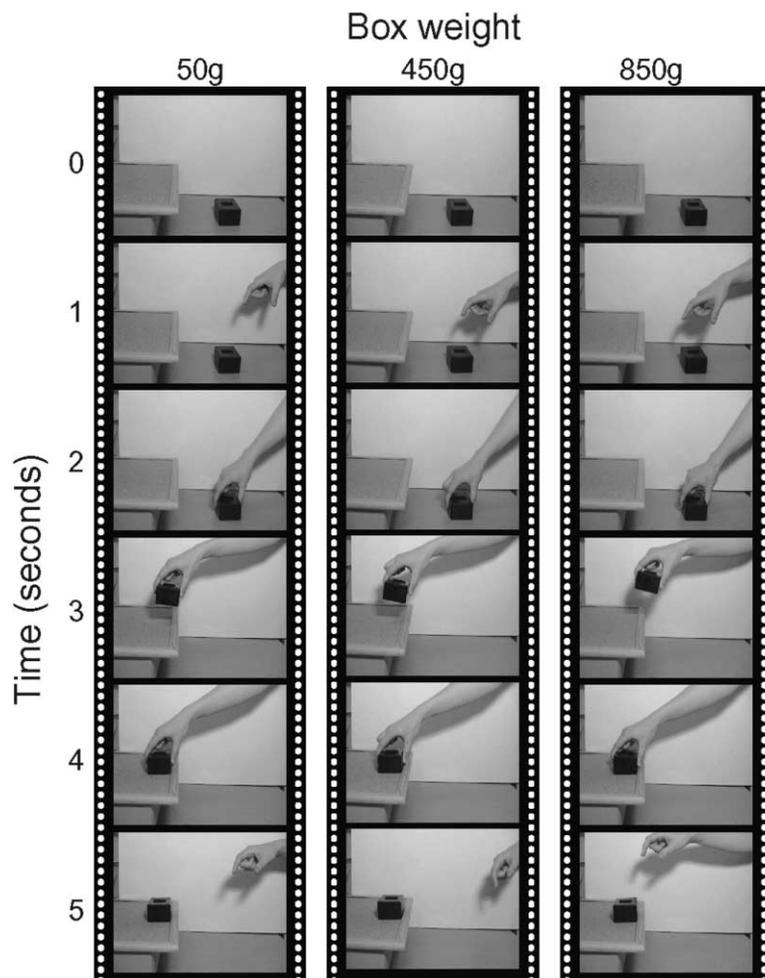
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Box weight

50g · 450g · 850g

Time (seconds)

the observed action is judged to be unlike the performed action (Figure 2B). In this case, when lifting a light box, subjects would judge the observed box to be heavier than neutral (represented by the dashed line in Figure 2B) and vice versa. This is not specifically predicted by previous results and would imply that the motor system has a role in the perception of action, but not necessarily a role that involves simple facilitation of similar representations.

When subjects rated the weight of the observed box without performing a motor task (neutral condition), the ratings increased as the true box weight increased (Figure 2C). The best fit to the data was a quadratic regression, which gave a mean r^2 of 0.38 (range 0.198–0.62), and t tests on each regression term for the subjects found the terms to be significantly different from zero ($p < 0.0001$). This performance indicates that the task was tractable but not trivially easy.

Figures 2D and 2E plot the mean and standard errors of the response bias for all 12 subjects for the active and passive conditions. When subjects actively lifted a heavy weight while making a perceptual judgment about the observed weight, they showed a significant negative bias (Figure 2D, solid line). This means that while lifting a heavy weight, subjects tended to report the observed weight as being lighter than they had reported it to be

in the neutral condition. Similarly, when lifting a light weight, subjects showed a significant positive bias. These biases correspond to a 61 g underestimation when subjects lifted a heavy mass and a 47 g overestimation when subjects lifted a light mass. This pattern of data (Figure 2D) is consistent with the contrastive hypothesis (Figure 2B). When subjects passively held a heavy weight while making a perceptual judgment about the observed weight, they also showed a small negative bias (25 g overestimation). Similarly, when holding a light weight, subjects showed a small positive bias (20 g underestimation). The direction of the bias is consistent with the contrastive hypothesis, but the bias was slightly greater when subjects watched heavy boxes being lifted (Figure 2E), which was not predicted by either hypothesis.

A two-way, repeated-measures ANOVA (Figure 2F) on the bias, with the factors of 1) the box weight held in the hand (heavy/light) and 2) trial type (active/passive), showed a significant effect of box weight (F = 36.37, df = 1,11, $p < 0.001$) and no effect of trial type (F = 2.82, df = 1, 11, $p = 0.12$). The interaction between box weight and trial type was significant (F = 9.11, df = 1,11, $p = 0.012$), confirming a contrastive effect that was greater for the active condition than for the passive condition.
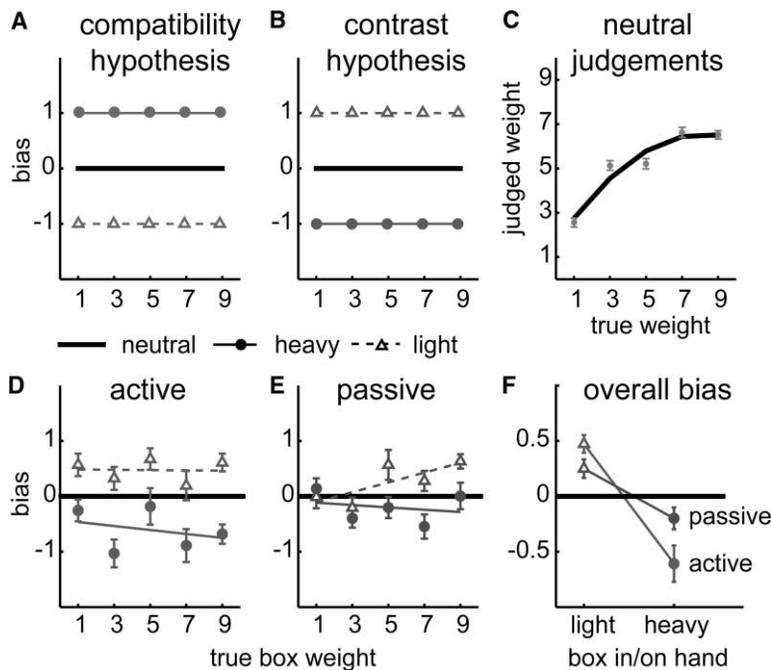
Figure 2. Hypotheses and Experimental Results

(A) Compatibility hypothesis. This predicts that when lifting a light box, subjects will judge the observed box to be lighter than they had judged it to be on neutral trials, thereby leading to a negative bias (dashed line) and when lifting a heavy box, subjects will judge the observed box to be relatively heavier, thereby leading to a positive bias (solid line).
(B) Contrast hypothesis. This predicts that when lifting a light box, subjects will judge the observed box to be heavier, thereby leading to a positive bias (dashed line), and when lifting a heavy box, subjects will judge the observed box to be relatively lighter, thereby leading to a positive bias (solid line).
(C) Neutral judgments. The mean (± standard error [± SE]) judged weight in the neutral condition across all twelve subjects is plotted against the true box weight, demonstrating that the subjects were able to perform the task at levels well above chance performance. The heavy black line gives the mean quadratic fit to the data for each subject.
(D) Active conditions. The mean (± SE) biases observed across all twelve subjects in the active-heavy (solid circles and line) and active-light (hollow triangles and dashed line) conditions are plotted against the true box weight.
(E) Passive conditions. The mean (± SE) biases observed across all 12 subjects in the passive-heavy (solid circles and lines) and passive-light (hollow circles and dashed line) conditions are plotted against true box weight.
(F) Summary of bias. The mean and standard error of the bias in each of the four conditions for all subjects is plotted. A repeated-measures ANOVA was performed on this data as described in the Results. A significant effect of weight and a significant interaction between the active and passive conditions were revealed.

Discussion

Overall, the analysis clearly demonstrates a contrastive effect of action upon perception—that is, during action upon a heavy box, subjects judged the observed box as being lighter, and during action on a light box, they judged the observed box as being heavier. The presence of a small contrast effect in the passive condition was unexpected, but there are two possible explanations. First, it is known that the sight of a graspable object can engage the neural systems involved in acting on that object [23, 24]. A box resting on the palm of the hand is clearly graspable and could induce low levels of activity in the systems we were studying, thereby resulting in a small contrast effect even in the passive-holding condition. Second, the motor system can be influenced by contextual information from the visual and proprioceptive systems [25]. In the passive condition, proprioceptive information defining the weight of the held box is present and could lead to a small contrast effect within the motor system.

The contrast effect was significantly smaller during passive holding of the box, thereby suggesting that action affects perceptual judgment and that this effect is not mediated purely by the proprioceptive experience of the weight of the held box. These results showed that concurrent action can influence the perception of an observed action, as the simulation hypothesis predicted [6, 7]. However, this result was surprising because the effect was contrastive, despite the fact that previous studies on the influence of perception on action had suggested a compatibility effect.

We can compare the contrast effect found in this study to effects found in other studies of the influence of action upon perception (as opposed to perception upon action). Long-term facilitating effects of motor experience on action perception have been demonstrated; for example, subjects are able to predict the next stroke in their own handwriting better than the next stroke in another person's handwriting [26], and subjects can predict the landing position of darts they have thrown [27]. Enhancement of perception by simultaneous action has been shown for abstract tasks, including mental rotation and the perception of bistable motion stimuli [8, 28, 29]. In these experiments, subjects were more likely to perceive a stimulus moving in the same direction as their action and were less likely to perceive a stimulus moving in the opposite direction. Hand action preparation has also been shown to prime responses to pictures of graspable objects [30, 31], and grasp reaction times are faster when the go signal is an image of a hand grasping, which is compatible with the prepared action [32]. These results all suggest that actions enhance congruent perceptions or mental operations and impair incongruent ones; their effect is thus unlike the contrast effect found in the weight judgment task. However, there are several important differences between these studies and the weight judgment task. First, the stimulus sets in several of these tasks were geometric figures such as arrays of dots and cubes [8, 28, 29], and it is not

clear if the same effects would also be seen in judgments made about biological motion such as human body movement. The observation of biological motion is known to activate different neural systems from observations of nonbiological motion [33–35], and thus it should not be surprising that the effects of action on the perception of biological and non-biological motion are different. In the studies using biological stimuli, either long-term effects were studied [26, 27], or hand images and hand movement responses were confounded [30–32], so it is hard to discriminate the effects of action on perception from the effects of perception on action.

However, one set of studies of the influence of action on perception is coherent with the weight judgment results. Action-effect blindness is elicited when subjects are impaired at detecting a stimulus compatible with their current response while planning or making the response. For example, they are more likely to fail to detect a right-pointing arrow presented during a righthand movement [36, 37]. This is a contrastive result similar to the weight judgment effect because, in both cases, subjects show a disinclination to judge the visual stimulus as being similar to their action. Although action-effect blindness studies typically use abstract stimuli, compared to stimuli in the current weight judgment study, in all cases the property of the observed stimulus to be judged (the arrow direction or box weight) was directly related to a current motor plan or act (the movement direction or grip parameters). Action effect blindness has been interpreted as evidence for a "common coding" system for both perception and action [38, 39]. The blindness arises because a code that is involved in an action plan is occupied and unavailable for perception [37]. It is possible that a similar mechanism, in which lifting a box occupies the code for a particular weight and prevents its contribution to the perceptual judgment, is responsible for the contrastive weight judgment results.

However, occupation of a cross-modal weight representation alone cannot explain why there is a systematic bias in weight judgment performance rather than a general decrement in weight discrimination. Here, we consider a model that can explain the contrastive results, based on the framework of MOSAIC [10, 11]. Although there may be many possible cognitive models that could fit the data, we have chosen to base ours on MOSAIC because this is a well-specified model that has previously been described in detail for the control of human movement, and because it has recently been proposed that MOSAIC could also be involved in interpreting other people's actions [12].

The MOSAIC framework suggests there are multiple brain modules that play a role in both the perception and production of actions (in this case, lifting boxes). Lifting objects is a task well suited to a modular control structure because we interact with many different individual objects in daily life, and the motor system is able to learn the appropriate grip pattern for each one [40, 41]. Thus, a MOSAIC for box lifting might have a module for each possible box (see the left side of Figure 3), and each module would specify the grip force and lift kinematics required to lift a box of that particular weight.

When a subject observes another person lifting a box, each module predicts the kinematic pattern that one would expect if that module's particular weight were lifted, and the predicted kinematics can be compared to the observed kinematics for calculation of each module's responsibility. A module's responsibility is high if the module provides a good prediction of the observed movement, so we would expect that the highest responsibility would be for the module representing the true weight of the observed box. However, given typical noise in sensory information, we would also expect neighboring modules to have nonzero responsibilities, such that the true weight is represented in a distributed form across all the modules (black horizontal bars on the right of Figure 3). When the module activities multiplied by the weights they represent are summed, the result is the judged weight of the observed box.

This model is similar to the action observation MOSAIC previously described [12]. We can extend it to account for the weight judgment results if we assume that during action on a particular object, the module responsible for that action is unavailable to the perceptual system. For example, in the case of lifting a light box, the "150 g" module is unavailable (Figure 3, gray box), so proportionally more "medium weight" and "heavy weight" modules will contribute to the judgment (Figure 3, gray bars). This will result in the observed box being judged as slightly heavier than neutral and give a positive bias as observed experimentally. The converse pattern of results is predicted when a heavy box is lifted, and this is the pattern observed.

Two critical assumptions are necessary for MOSAIC to provide an explanation for the weight judgment results. First, it requires a distributed representation of many possible box weights, where the true weight is encoded in the activity pattern distributed over all the units. Multiple representations have proved to be a successful strategy in the motor control MOSAIC [12], and there is evidence that the visual and motor properties of multiple objects can be accurately learned [40, 41]. Similarly, distributed representations have been shown to have useful computational properties in connectionist models of cognitive processing [42], so it does not seem implausible to suggest that a distributed representation could be used in action observation. Second, modules must be able to contribute to either perceptual judgment or action but not both, with priority given to action. Thus, modules that are involved in controlling an ongoing action must be inhibited or "gated out" from contributing to perceptual judgment. Recent work suggests that activity in higher visual areas is attenuated by concurrent action [43].

This MOSAIC explanation of the weight judgment task has conceptual similarities with the common-coding explanation of action effect blindness. Both MOSAIC and common coding suggest that motor and perceptual processes can make use of the same neural mechanisms but that action plans take priority over perceptual judgment. However, we do not want to suggest that there is a specific correspondence between MOSAIC modules and common codes, and the questions of whether action plans simply occupy codes [37] or actively inhibit modules remains to be tested.
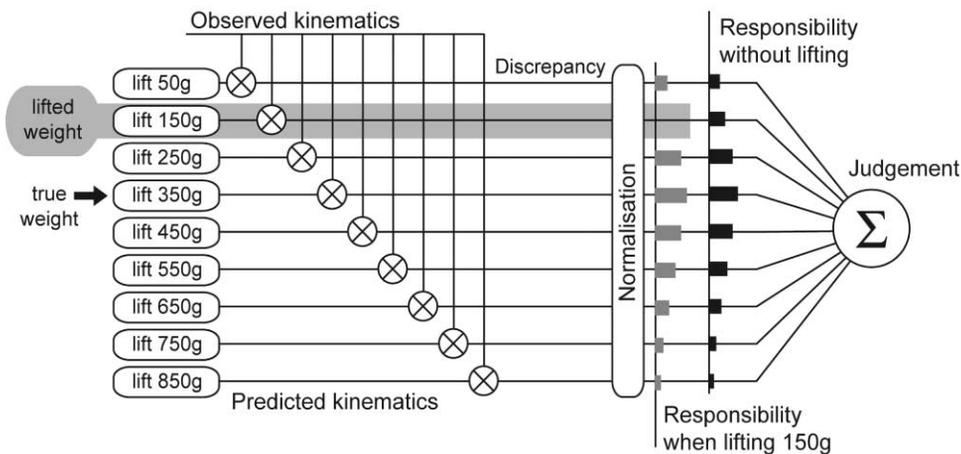
Figure 3. MOSAIC Model for Weight Judgment

The basic structure of MOSAIC for weight judgment is shown with nine modules (left), each of which predicts the kinematic pattern for lifting its weight. The predicted kinematics are compared to the observed kinematics, and the resultant discrepancy is normalized to obtain the responsibility of each module. For example, when no weight is lifted and the true observed weight is 350 g, as indicated by the arrow on the left, the responsibility is highest for the 350 g module and is distributed across the other modules, illustrated by the black bars on the right. Multiplying the responsibilities by the weights of the units and then summing the results gives the judgment of the model under neutral conditions. However, when a 150 g weight is lifted, this module is unable to contribute to the judgment (indicated by the gray box) and has zero responsibility. The responsibilities of the remaining modules (gray bars) are used for making the judgment, which will have a positive bias, as observed experimentally.

We do not claim that the MOSAIC architecture provides a full or exclusive explanation for the range of action-perception interactions that have been demonstrated here and in other studies [9, 13, 14, 36, 37]. However, MOSAIC can provide a qualitative account of how a simple mechanism, grounded in the motor system, is able to produce a contrastive effect of action on perception. Further work will be necessary for determining if this model provides the best description of the information processing that occurs during action observation and concurrent action. Independent of the model, the experimental results make it clear that performing an action has a systematic and contrastive effect upon the interpretation of another person's action. This provides psychophysical evidence for the functional role of the motor system in the perception of action, as imaging studies have previously suggested [2, 3]. Understanding the computational abilities and limits of this system will be an important step toward unravelling the cognitive structures involved in comprehending other people's actions and ultimately in a range of social interactions.

Experimental Procedures

Twelve right-handed, naïve subjects (six male and six female, aged 20–37) gave their informed consent to take part. A set of nine black boxes (all 82 × 55 × 32 mm) with weights ranging from 50 g to 850 g in 100 g steps were prepared. Subjects were asked to lift each box and were told that the box weights made a linear scale from 1 to 9, e.g., the 50 g box had a weight of 1, the 150 g box had a weight of 2, etc. They were then informed that they would see videos of the same boxes lifted by another person, and they were asked to judge the weight of the observed box on the 1–9 scale defined by the nine boxes that they had lifted. Responses were made verbally and without time pressure, so that planning or preparing a response did not influence judgment or lifting performance. Boxes 1, 3, 5, 7, and 9, which evenly spanned the range from 50 g to 850 g, were used in the preparation of the video clips (details in the legend of Figure 1), and none of the subjects noticed that some boxes were not used in clips. All stimulus ordering and presentation was controlled by Cogent running in Matlab 6.5, and all video clips were displayed at 25 frames/s and at full resolution (720 × 576 pixels) and filled the screen of a 19 in computer monitor.

After ten practice trials, each subject performed 240 weight judgment trials under five task conditions. On neutral trials, subjects performed only the judgment task and kept their hands in their laps. In the active condition, subjects lifted a light (150 g) or heavy box (750 g) with a precision grip as the video clip started and held it approximately 3 cm above the desk for the duration of the clip. In the passive condition, the experimenter placed the light or heavy box on the subject's palm, which rested on the desk, before the video clip started. In all conditions, subjects reported their judgment of the weight of the observed box as a number from 1 to 9 after the video ended. Each subject performed 80 neutral trials, 40 active trials, and 40 passive trials for each of the heavy and light boxes. Trials were ordered in triplets of the type A-A-N, where A is an active or passive trial at one particular box weight and N is a neutral trial. The ordering of the triplets was randomized. Each clip was paired with each trial type equally often over the whole experiment, and each box weight and each trial type were presented equally often in each block of 30 trials. No feedback was given after individual trials, but at the end of each block, subjects were told a score based on the r^2 of the correlation between their responses and the true box weight and were encouraged to aim for a high score. They were also informed of the number of times they gave each possible response and were encouraged to use the whole range of available responses evenly. This instruction was intended to prevent subjects from responding "five" on every trial, but, in fact, subjects did not find it hard to use the full range of answers. Five trials over all the subjects were lost because of experimenter error and were excluded from analysis, but a total of 240 judgments were collected from each subject.

Acknowledgments

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