doi:10.1093/scan/nsr057 SCAN (2012) 7, 841–849

Attitudes trigger motor behavior through conditioned associations: neural and behavioral evidence

Cade McCall, Christine M. Tipper, Jim Blascovich, and Scott T. Grafton

¹Department of Social Neuroscience, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany and

It has long been argued that attitudes prepare the body to act. While early evidence suggested that evaluations (positive or negative) are rigidly linked to specific motor behaviors (approach or avoidant), recent behavioral evidence suggests that this linkage is context dependent. Here, we report that the neural circuitry mediating the relationship between evaluations and motor responses promotes flexibility in our embodiment of attitudes. In a behavioral study, stimulus—response relationships between evaluations and actions were rapidly conditioned. In a neuroimaging (functional magnetic resonance imaging) study, repetition suppression demonstrated that these relationships are formed in neural systems traditionally implicated in arbitrary sensorimotor mappings (i.e. the dorsal premotor cortex and posterior superior parietal lobule). These data provide the first neurophysiological evidence for attitude embodiment and demonstrate that relationships between evaluation and action are inherently malleable.

Keywords: attitudes; embodiment; social cognition; social neuroscience; motor behavior; action

INTRODUCTION

Researchers have long argued that attitudes prepare our bodies to act (Darwin, 1872; James, 1890; Cacioppo et al., 1993; Chen and Bargh, 1999). Direct relationships between positive or negative evaluations and motor behavior, the reasoning goes, allow us to respond quickly and without conscious deliberation to the desirable and undesirable features of the environment. Traditionally, research on this form of attitude embodiment has demonstrated apparently rigid associations between evaluations and specific motor behaviors (Solarz, 1960; Chen and Bargh, 1999). Recent findings, however, draw this rigidity into question with evidence that the associations are context dependent (Markman and Brendl, 2005; Lavender and Hommel, 2007; Bamford and Ward, 2008; Eder and Rothermund, 2008). These findings raise fundamental questions regarding the phenomenon. How are general evaluations (positive vs negative) linked with specific motor behaviors? Do these relationships adapt over time and across situations? If so, what neural mechanism can account for this plasticity? In a pair of studies, we used behavioral and neuroimaging techniques to demonstrate that evaluation triggers action through conditioned stimulus-response relationships equivalent to arbitrary sensorimotor mappings. In doing so, we provide the

Received 12 November 2010; Accepted 25 August 2011 Advance Access publication 23 September 2011

Supported by the Institute for Collaborative Biotechnologies through contract no.W911NF-09-D-0001 from the US Army Research Office. The authors thank Masaki Miyanohara for assisting with software development and Brendan McHugh for assisting with data collection.

Correspondence should be addressed to Cade McCall, Department of Social Neuroscience, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. E-mail: mccall.cade@gmail.com

first neurophysiological evidence for attitude embodiment and illustrate its inherent malleability.

In the classic demonstration that evaluations facilitate motor behavior, participants are instructed to either pull or push a lever while looking at negatively or positively valenced targets (Solarz, 1960; Chen and Bargh, 1999). Typically, participants pull the lever more quickly when the target is positive and push the lever more quickly when the target is negative, regardless of whether or not the task has evaluative goals (Chen and Bargh, 1999). Early accounts of this phenomenon attributed these embodied patterns to conditioned associations between specific muscle activations and specific evaluations (Cacioppo et al., 1993). The theory proposed that a lifetime of pulling desirable objects toward ourselves links positive evaluation with arm flexion and a lifetime of pushing undesirable objects away from us links negative evaluation with arm extension. Specific motor behaviors, then, become an integral part of the cognitive representation of attitudes (Niedenthal et al., 2005).

A more flexible account of embodied social cognition proposes that motor facilitation varies in different situations. Indeed, such flexibility ensures behavioral adaptiveness to a continuously changing environment. Along these lines, several recent studies suggest that positively valenced stimuli facilitate actions that lead to approach while negatively valenced stimuli facilitate actions that lead to avoidance, regardless of the specific motor behavior employed (Wentura *et al.*, 2000; Markman and Brendl, 2005; van Dantzig*et al.*, 2008). Other data suggest that, more generally, actions with

²Department of Psychology, University of California, Santa Barbara, CA, USA

rewarding *vs* punishing outcomes (regardless of target valence) are facilitated (Bamford and Ward, 2008). Still more findings suggest that a specific motor behavior can be assigned a positive or negative semantic label (i.e. through instruction sets or aversive conditioning) and that subsequent use of that motor behavior is facilitated by exposure to stimuli of matching valence (Beckers *et al.*, 2002; Eder and Rothermund, 2008). These studies provide mounting evidence that the influence of evaluation on action is driven by malleable processes that can adapt to experience and situational constraints.

One obvious way in which motor behavior, more generally, shows malleability is in the degree to which arbitrary linkages form between sensory cues and actions. This conditional motor learning allows for action to be triggered without any reference to spatial relationships. A colored plaque (e.g. Halsband and Freund, 1990) or a blinking LED (e.g. Grafton et al., 1998) can act as a cue, despite the fact that its appearance and its mapping to the behavior are arbitrarily assigned. This capability affords a broad action repertoire driven by signaling and symbolically guided action (e.g. Wise and Murray, 2000). We hypothesized that evaluation can cue action in a similar fashion such that stimulus-response relationships between a specific evaluation (positive vs negative) and a specific motor behavior can be conditioned quickly and arbitrarily (and with no necessary relationship to physical approach and avoidance). We further hypothesized that neural representations of these relationships between implicit evaluation and action operate much the same as arbitrary sensorimotor mappings between explicit stimuli and motor responses.

Existing research suggests that the dorsal premotor cortex (PMd) and superior parietal cortex are directly involved in conditioned motor responses (Wise et al., 1996; Grol et al., 2006) and are partly responsible for the flexible nature of action repertoires (Wise and Murray, 2000). Non-human primate data from lesion studies (Halsband and Passingham, 1982), single cell recordings (Mitz et al., 1991; Hoshi and Tanji, 2006) and muscimol injections (Kurata and Hoffman, 1994), as well as human lesion (Halsband and Freund, 1990) data suggest that the PMd is necessary for the execution of behaviors cued by non-spatial stimuli. Human functional imaging studies have further shown this region to be active in motor planning cued by arbitrarily associated visual (Grafton et al., 1998; Toni et al., 2001), audio, and sensorimotor stimuli (Weeks et al., 2001). Recent work using repetition suppression paradigms has also implicated this region in stimulus-response mappings that are independent of spatial or sensory properties of a given target (Majdandzic et al., 2009).

Imaging work (Grafton *et al.*, 1998) also suggests that the superior parietal lobe is specifically involved in the conditional selection of grasp (as compared to non-conditional motor tasks). Furthermore, blood oxygen level-dependent (BOLD) activity in the posterior parietal cortex has been

shown to increase with overlearning of arbitrary sensorimotor relationships (Grol *et al.*, 2006). Although we did not limit our analyses to specific areas of the brain, given our hypothesis that evaluations are comparable to non-spatial cues for action, we were particularly interested in whether or not the influence of evaluation on action would modulate recruitment of the PMd and posterior superior parietal areas during response selection.

To test these hypotheses, we first had participants complete a task in which they moved a joystick to rate the positivity or negativity of a series of images. We then tested reaction times and neural responses when those same movements were used in non-evaluative tasks involving valenced words. We predicted that implicit relationships between evaluation and action formed during the rating task would lead to a valence-specific facilitation of motor behaviors and their neural representations in the subsequent tasks.

METHODS

Participants

Sixty-seven undergraduate students (47 women) participated in Experiment 1 (a behavioral experiment) for course credit. Twenty-five participants (10 women) participated in Experiment 2 [an functional magnetic resonance imaging (fMRI) experiment] for pay.

Materials

Both experiments included training and testing phases. The images used in the training phase were taken from the International Affective Picture System (IAPS; Lang *et al.*, 1990). The words used in the testing phase were taken from the set used in Chen and Bargh (1999) and from the Affective Norms for English Words (ANEW; Bradley and Lang, 1999). All experimental tasks were created with Python 2.4. In Experiment 2, both tasks were completed in a Siemens Magnetrom Trio 3T MR scanner.

Training task

The training task was the same for both experiments. Participants spent $\sim \! 10 \, \mathrm{min}$ rating a series of images on a visually vertical scale from 'extremely positive' to 'extremely negative' (Figure 1). To record their ratings, participants moved an indicator (i.e. a 'tic') up and down the scale using a joystick. The mapping of joystick movement to valence was counterbalanced between participants such that for half of the participants, movement of the joystick in one direction moved the tic toward the positive end of the scale and movement of the joystick in the other direction moved the tic toward the negative end of the scale. For the other half of the participants this valence-direction mapping was reversed. For Experiment 1, the two movements used were clockwise and counterclockwise movement of the joystick. For Experiment 2, leftward and rightward movements



Fig. 1 Screenshot of the training task. Participants rated a series of images using the scale on the right side of the screen. Participants moved the indicator up and down the scale using a joystick. Movement of the joystick in one direction moved the tic up while movement of the joystick in the other direction moved the tic down. The specific valence-direction pairing was counterbalanced between participants.

were used 1 . The training task took participants \sim 10 min to complete.

The instructions for the training task did not explicitly link the direction of movement with valence. Instead, participants were simply told to 'use the scale on the right to rate the image from extremely positive (+5) to extremely negative (-5). Move the scale by twisting [or moving] the joystick'. The scale itself was arranged vertically on the screen. As a result, there was also no visual feedback linking clockwise/counterclockwise or rightward/leftward with valence.

Testing task: Experiment 1

In Experiment 1, the training task was followed by an ostensibly unrelated testing procedure modeled on one used in the past to investigate the influence of evaluation on motor behavior (Chen and Bargh, 1999). In this task, words appeared at random time intervals on a computer screen. Participants were instructed to move a joystick as soon as they saw a word appear. The words on these trials were either positively or negatively valenced (e.g. 'cake', 'cancer'). There were two blocks of trials in this task and within each block participants moved the joystick in the same direction for every trial. The joystick movements used for these two blocks of trials were the two movements used in the training task. As such, the word on a given trial could either be affectively congruent or incongruent with the hypothetically trained valence of the joystick movement for that block of trials. Importantly, valence and movement were completely crossed to produce

¹The specific motor movements used in the two studies differed for practical reasons, but with theoretically justification. The joystick used in Experiment 2 did not have the twist feature of the joystick used outside of the scanner. However, varying the movement between experiments emphasizes the arbitrary nature of the assignment of a given movement to a valence.

congruent and incongruent trials such that each trial type included both valences and movement types.

Testing task: Experiment 2

The testing phase of Experiment 2 was designed to tease apart the presentation of the valenced stimuli from their corresponding actions such that they occurred at two separate events. Participants completed two runs of 80 coupled trials. For each trial, a word appeared for 2 s, disappeared, and then an arrow appeared for an additional 2 s. Participants were given two separate goals and these instructions were repeated at the beginning of each run of trials. For the word portion of a trial, they were instructed to press a button on top of the joystick if they saw a nonsense word (e.g. 'vaseball'). The nonsense word detection was included to ensure that participants would attend to the words. Two nonsense words appeared per run such that participants saw 78 words per run and 2 non-words. Because they do not pertain to the hypotheses tested here, the nonsense word trials were excluded from all analyses. For the arrow portion of a trial, participants were instructed to move the joystick in the direction cued by the arrow. The direction of the arrow varied randomly from trial to trial and the order of each participant's trials was unique.

The words presented on these trials were either positively or negatively valenced. Because the required movement on a given trial had been paired with a valence during in the training task, joystick movements could either be congruent or incongruent with the preceding word's valence (Figure 2). As in the Testing Task for Experiment 1, both incongruent and congruent trials included both valences and movement types.

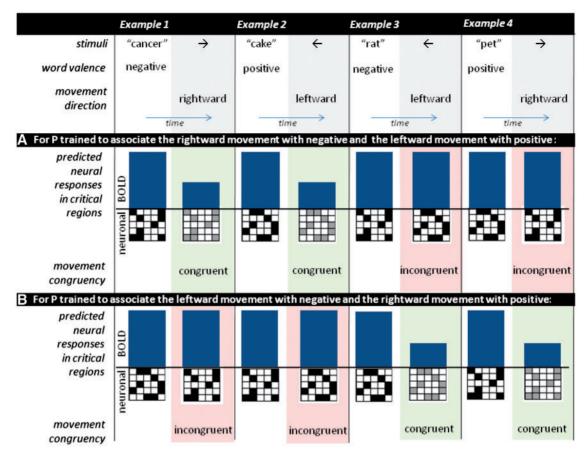


Fig. 2 Four example trials from the testing portion of the imaging experiment. Row A depicts predictions for a participant trained to associate the rightward movement with negative valence and the leftward movement with positive valence during the image rating task. Row B depicts the converse. By crossing word valence (negative vs positive) and movement direction (leftward vs rightward) we defined two congruency conditions. On a given trial, a movement was considered congruent if its trained valence matched the valence of the preceding word. As such, congruent and incongruent trials included both valences and both movements. Based on the logic of repetition suppression, we expected reduced BOLD responses in areas representing the triggered movement during the movement portion of congruent trials (shaded in green) but not incongruent trials (shaded in pink).

fMRI data acquisition and analysis

Functional images were acquired during Experiment 2 s runs using an EPI pulse sequence (37 slices, TR = 2). All analysis procedures were carried out using SPM5 (http://www.fil.ion .ucl.ac.uk/spm). Slice timing correction was applied to correct for the temporal discrepancy between the acquisitions of multiple two dimensional slices comprising each three dimensional brain volume. Functional images were aligned with the first image from each scanning run to correct for head movement. The images from each run were then coregistered to the given participant's high resolution anatomical T1 image and normalized to the standardized Montreal Neurological Institute (MNI) stereotaxic template and resliced at a $2 \times 2 \times 2$ voxel resolution. Images were then spatially smoothed with an isotropic Gaussian kernel (8 mm full width half maximum). One participant was excluded from analyses because of a structural abnormality revealed in the anatomic scan. One other participant was excluded from analyses because he rotated the joystick between the training and testing phases (thereby

undermining the effects of the training phase on the testing phase). One run from one other participant was excluded because he fell asleep during the run.

A fixed-effects analysis was conducted for each participant, using a general linear model to assess the BOLD response at each voxel for each moment of interest: congruent movements and incongruent movements. The word presentation events were not modeled. The nonsense word trials were excluded from analysis. The model contained one regressor for each condition, plus its temporal and dispersion derivatives, as well as a constant for each scanning run. Linear contrasts were constructed to estimate both BOLD activity uniquely associated with the condition and the difference in BOLD activity between congruent and incongruent conditions. The images of the incongruent vs congruent contrast (one for each condition, for each subject) were submitted to a random-effects (second-level) analysis in order to identify significant group effects.

The trials were designed to reveal patterns of repetition suppression (RS) created by the congruency between the

response triggered by a valenced word and an action (Figure 2). RS paradigms (e.g. Kourtzi and Kanwisher, 2000; Grill-Spector and Malach, 2001; Grafton and Hamilton, 2007) are based on the observed tendency for a stimulus to produce reduced neural responses when presented repeatedly. It follows from this observation that if the processing of two related stimuli relies on the same neural mechanisms, neural populations associated with those mechanisms should show suppression of the BOLD signal when the two stimuli are presented in succession. As such, RS can be used to reveal the overlap in functional neuroanatomy for two cognitive processes based on their similarity. Along these lines, RS has been used to study the neural representations of motor responses. For example, Dinstein et al. (2007, 2008) showed RS for repetitions of observed and executed actions (as well as for cross-modal repetitions). Hamilton and Grafton (2009), furthermore, showed RS in motor-relevant areas for repetitions of text-instructed actions. Following this logic, we predicted RS for actions when they were preceded by the presentation of an evaluatively congruent word. In other words, when participants read a negative or positive word and then executed a motor behavior that had been conditioned to be associated with that valence, then the areas involved in representing that action should show a weaker BOLD signal than they would during movements preceded by a word with an incongruent valence. As such, the critical contrast in this experiment was between trials in which the given movement was preceded by an incongruently vs a congruently valenced word (the conceptual equivalent of the novel vs repeat contrast in a traditional RS paradigm).

Importantly, congruent and incongruent trials included both valences and movements (Figure 2). Because of this fact, congruency was not determined on a given trial until the movement cue was revealed. Differences between congruency conditions, then, must necessarily emerge during the movement portion of the trials and as a consequence of the relationship between word valence and the movement.

To hone in on areas that were involved in both trial types and to look at relative differences in activity during the movement portion of trials, we used a mask based on all the areas activated during the movement portion of all of the trials (at a threshold of P < 0.05).

RESULTS

Experiment 1

If a given valence facilitates a specific motor behavior, then participants should be faster at executing that behavior when a word of that valence is used as a cue for action (i.e. when the word and the action are evaluatively congruent). As such, the critical-dependent variable in Experiment 1 was reaction time (RT). RTs were log-transformed and aggregated by word valence and the evaluative congruency of the movement. RTs two standard deviations above or

below the mean were omitted from analyses (Ratcliff, 1993). An ANOVA with one between-subjects variable (training group) and two within-subjects variables (congruency and word valence) was performed. This ANOVA revealed the predicted influence of congruency whereby participants were faster on congruent vs incongruent tri [F(1,65) = 8.82, P = 0.004, log transformed RT meansand SEs: $M_{\text{congruent}} = -0.865 + -0.016$, $M_{\text{incongruent}} =$ -0.852 + -0.017, RT means and SEs: $M_{congruent} =$ 0.430 + -0.00, $M_{\text{incongruent}} = 0.437 + -0.008$]. No other factors or interactions were significant in this analysis, all F's < 3.05, P's > 0.09. More importantly, the interaction between congruency and training group was far from significant, F(1,65) = 0.04, suggesting that the congruency pattern held for both training groups (i.e. both clockwise and counter-clockwise twisting movements were successfully associated with either valence).

The initial rating task conditioned associations between valence and action such that during the testing task valenced words facilitated their actions. Importantly, this effect emerged despite the fact that the training phase used images and the testing phase used words, highlighting the fact that evaluated valence (and not some other feature of the stimuli) was the common factor facilitating action.

Experiment 2

The contrast of BOLD activity between the incongruent and congruent trials was significant (at $P_{uncorrected} < 0.001$) in several areas (Figure 3, Table 1). Of particular interest was greater activity in the PMd (x = -28, y = 12, z = 40, $t_{\text{max}} = 4.54$) and the posterior superior parietal lobule $(x=-20, y=-48, z=41, t_{max}=4.57)$. Conversely, no areas emerged with significantly greater activity in the reverse contrast (congruent vs incongruent trials). These patterns support our hypothesis that RS occurred in congruent, but not incongruent trials. Furthermore, the stronger BOLD response for incongruent trials in these critical areas, irrespective of the particular movement paired with a given evaluation, is consistent with our hypothesis that attitudes trigger action via conditioned stimulus-response associations instantiated by neural mechanisms responsible for arbitrary (and inherently flexible) sensorimotor mechanisms.

Although Experiment 2 was not designed to look at reaction time differences, we conducted an ANOVA on these data with one between-subjects variable (training group) and two within-subjects variables (congruency and word valence). This analysis revealed no significant effects (all P's>0.40). The fact that there were no significant RT differences between incongruent and congruent trials was not particularly surprising given that the experimental task included two separate events (presentation of the word and then the movement cue). Moreover, participants were instructed to move the joystick in the direction of the arrow and were not told (as in Experiment 1) to move as quickly as possible, a fact reflected in the relatively slow reaction times

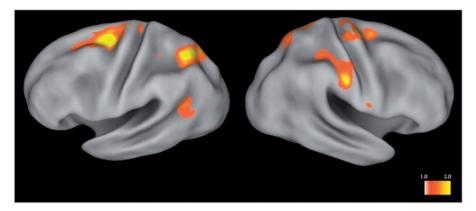


Fig. 3 Areas showing repetition suppression for attitude-primed action. The contrast shown here is between trials that were preceded by an evaluatively incongruent vs congruent word. These analyses used a mask based on areas active during the movement portion of all trials.

Table 1. Significant voxels ($P_{uncorrected} < 0.001$) emerging from the incongruent vs congruent movement contrast from Experiment 2

Region	Voxels	Peak voxel	Talaraich coord		
			Х	у	Z
Left middle frontal gyrus and superior frontal sulcus, BA 6,8	56	4.54	-28	12	40
Left parietal cortex, superior parietal lobule, BA 7	52	4	-20	-48	41
Right parietal cortex, post-central gyrus, BA 2	41	5.07	57	-22	36
Right inferior parietal lobule, BA 40	19	4.22	50	-35	42
Right middle frontal gyrus and superior frontal sulcus, BA 6,8	29	3.97	30	— 5	61
	24	4.21	24	-2	42

(M=700 ms). As such, the movements in Experiment 2 were slower and likely more controlled responses.

DISCUSSION

These data provide the first neural evidence for the direct influence of attitudes on motor behavior. Moreover, they demonstrate that general categories of evaluation (positive *vs* negative) trigger specific actions through flexible associations that are comparable to the kinds of mappings described in the literature on non-spatial motor conditioning.

In these experiments participants were first unobtrusively trained to associate positive or negative evaluations with specific motor behaviors through a task in which they rated a series of images. These pairings affected reaction times in a subsequent task in which participants' only goal was to respond when a word appeared on the screen. Participants were faster to respond to words with a specific movement when the word's valence matched the conditioned valence of that movement. In the testing phase of the fMRI experiment, participants repeatedly executed the same behaviors that had been used in the rating task. When behaviors were preceded by words of a congruent valence, motor-relevant areas of the brain showed relatively suppressed activity, notably in the PMd and posterior

superior parietal areas. Evaluations of the words apparently activated associated motor representations, facilitating action and resulting in repetition suppression in those areas. The fact that participants were trained on images and tested on words underscores our claim that the valence of the stimuli drove these effects.

Together these data provide one neurophysiological mechanism by which attitudes become embodied. This mechanism is inherently plastic: automatized relationships between attitudes and motor behaviors emerge as a consequence of conditioning such that experience helps determine how attitudes are embodied by the individual in the moment. The functional benefits of this flexibility are clear. We adapt to respond appropriately to the positive or negative features of our environment.

In addition to providing one explanation for the contradictory evaluation-to-behavior patterns demonstrated in the behavioral literature, these findings argue strongly for a conceptualization of this form of embodied social cognition not as rigid sets of mappings, but as flexible relationships that adapt and change with experience. Of course common patterns in attitude embodiment occur across individuals. Prime examples are the classic negative valence/arm extension and positive valence/arm flexion patterns described repeatedly in the literature (Solarz, 1960; Chen and Bargh, 1999). But while these and other findings tie the influence

of evaluation on motor behavior to approach and avoidance, the current findings demonstrate that the link between an evaluation and an action can be totally arbitrary, with no reference to physical or symbolic approach or avoidance. Clearly, avoiding negative targets and approaching positive targets are beneficial patterns to learn, but they are not the limit of evaluation's influence on action.

While the current data focus on the effects of evaluation on specific motor behaviors, recent studies have demonstrated that evaluation facilitates approach/avoidance action outcomes regardless of the motor behaviors used to facilitate those outcomes (Markman and Brendl, 2005; Bamford and Ward, 2008). We do not consider the findings reported here to be at odds with those data. Given that action planning is organized and represented hierarchically, from low-level kinematics to higher level outcomes (Grafton and Hamilton, 2007), we suggest that evaluation influences action at multiple levels of this hierarchy. The current findings illustrate the effects of evaluation on action kinematics, while the above-referenced findings address evaluation's influence on action outcomes. This multi-leveled facilitation of action by evaluation would support optimal responses across a broad range of circumstances.

The neuroimaging data presented here implicate the doral premotor cortex and posterior superior parietal areas in the influence of evaluation on motor behavior. Because existing research has also implicated these areas in arbitrary sensorimotor mapping (Halsband and Passingham, 1982; Halsband and Freund, 1990; Mitz et al., 1991; Kurata and Hoffman, 1994; Wise, et al., 1996; Grafton et al., 1998; Toni et al., 2001; Weeks et al., 2001; Grol et al., 2006; Hoshi and Tanji, 2006; Majdandzic et al., 2009), we interpret these data to support our claim that attitudes influence action through comparable stimulus-response relationships. However, because the present work focused exclusively on the influence of evaluation on action, we cannot conclude from these data that the mechanisms involved are the same. In fact, given the dramatically different nature of sensory cues vs valenced evaluations (a subjective, affective, and relatively abstract response to a target), it would be surprising if their respective influences on action were not significantly different. Along these lines, further research will need to identify the shared and distinct neural mechanisms that underlie attitude embodiment vs more traditional sensorimotor mappings. The design and interpretation of the neuroimaging experiment rely upon the logic of repetition suppression. We honed in on differences in BOLD activity for movements that were either preceded by a word whose valence was congruent or incongruent with the given movement's hypothetically trained valence. Based on the logic of RS, decreased activity in critical regions during the congruent vs incongruent trials indicates shared activation within subpopulations of neurons responsible for the movement's representation (for a discussion of RS interpretations of the BOLD signal during motor behavior, see Grafton and Hamilton, 2007; Hamilton and Grafton, 2009). Importantly, both trial types included both types of movement so that the only difference between them was their congruency, a difference that was only determined once the movement cue was revealed. As such, although the word and movement events are relatively close together in time, we interpret the differences in the BOLD signal as driven by the congruency of the motor behavior. Although we cannot test for RS directly, we believe that it provides a parsimonious account of this congruency effect. However, we do not necessarily assume that RS, *per se*, is the mechanism by which evaluation facilitates action. Instead, it provides evidence for a stimulus–response relationship between the two. (For more general discussions of RS and behavioral facilitation see Maccotta and Buckner, 2004; Wig *et al.*, 2005; Grafton and Hamilton, 2007; Schacter *et al.*, 2007).

The critical contrast presented in the analyses of the neuroimaging data, between evaluatively incongruent and congruent trials, leaves open an alternative interpretation of the results. It is possible that the demonstrated effects are not just driven by RS in congruent trials but also by the recruitment of additional neural mechanisms in the incongruent trials. For example, if attitudes indeed trigger motor behaviors then additional mechanisms may be necessary to override those behaviors when they are inappropriate. In the context of our experiment, participants may have needed to recruit areas responsible for handling response conflict when moving the joystick in the opposite direction of the direction cued by the previously presented word. To address this possibility, our analyses honed in exclusively on areas that showed activity both for incongruent and congruent trials. This activation-based masked contrast should highlight the relative differences between areas that were active during both conditions and not areas that were exclusively active during the incongruent condition. As such, it seems less likely (but still possible) that the areas emerging as significant are driven entirely by the incongruent condition.

Another alternative explanation for these results is that the training task's instructions generalized to the testing phases of the experiments such that participants responded to the test stimuli as though they were still rating them with the joystick. While we cannot rule out this possibility, the testing tasks were significantly different from the training task in several ways. Participants in the training task consciously evaluated images and took their time to express those evaluations. In the testing tasks, however, participants were not instructed to evaluate anything. Instead, they merely responded to various stimuli with specific motor behaviors. In Experiment 1, they used the same movement repeatedly for each block of words. In Experiment 2, they did not respond to valenced targets at all, but to arrows. Although the task goals and demands could still have carried over to the testing portions of the experiments, the fact that the pattern of neural activity presented here corresponds to patterns found in the research on sensorimotor mappings argues more strongly for the interpretation of our data as

illustrating S–R relationships between attitudes and motor movements.

Nevertheless, these findings parallel research on the creation of automatic stimulus-response compatibility effects through instruction sets (De Houwer, 2004; De Houwer et al., 2005) and on the facilitation of evaluatively congruent responses through the explicit labeling of actions as positive or negative (Eder and Rothermund, 2008). On the one hand, the instructions in the present study never explicitly linked movement in any given direction with any specific valence. Participants were simply told to 'use the scale to rate the images' and to 'move the joystick' to do so. The links between movement and valence in our studies, then, were formed experientially. We would still argue, however, that although the formation of these associations may have had different origins from the formation of pairings in the instruction set literature, the resulting S-R relationships are comparable.

We all have different bodies with different capabilities and a different history of experiences. Moreover, we possess a tremendous range of possible actions at any given moment. The neural systems that support motor behavior accommodate for this range and for the dynamic nature of the physical world (Wise and Murray, 2000; Grafton and Hamilton, 2007). Attitude embodiment taps into this flexibility, allowing us to respond quickly and appropriately to a highly valenced and constantly changing environment.

REFERENCES

- Bamford, S., Ward, R. (2008). Predispositions to approach and avoid are contextually sensitive and goal dependent. *Emotion*, 8(2), 174–83.
- Beckers, T., De Houwer, J., Eelen, P. (2002). Automatic integration of non-perceptual action effect features: The case of the associative affective Simon effect. *Psychological Research*, 66(3), 166–73.
- Bradley, M.M., Lang, P.J. (1999). Affective norms for English words (ANEW): Stimuli, instruction manual and affective ratings. Technical report C-1, Gainesville, FL. The Center for Research in Psychophysiology, University of Florida.
- Cacioppo, J.T., Priester, J.R., Berntson, G.G. (1993). Rudimentary determinants of attitudes: II. Arm flexion and extension have differential effects on attitudes. *Journal of Personality and Social Psychology*, 65, 5–17.
- Chen, M., Bargh, J.A. (1999). Consequences of automatic evaluation: Immediate behavioral predispositions to approach or avoid the stimulus. *Personality and Social Psychology Bulletin*, 25(2), 215–24.
- Darwin, C. (1872). The expression of emotions in man and animals. Appleton: New York.
- De Houwer, J. (2004). Spatial Simon effects with nonspatial responses. Psychonomic Bulletin and Review, 11, 49–53.
- De Houwer, J., Beckers, T., Vandorpe, S., Custers, R. (2005). Further evidence for the role of mode-independent short-term associations in spatial Simon effects. *Percept Psychophys*, 67, 659–66.
- Dinstein, I., Gardner, J.L., Jazayeri, M., Heeger, D. (2008). Executed and observed movements have different distributed representations in human aIPS. *The Journal of Neuroscience*, 28, 11231–9.
- Dinstein, I., Hasson, H., Rubin, N., Heeger, D.J. (2007). Brain areas selective for both observed and executed movements. *Journal of Neurophysiology*, 98, 1415–27
- Eder, A.B., Rothermund, K. (2008). When do motor behaviors (mis)match affective stimuli? An evaluative coding view of approach and avoidance reactions. *Journal of Experimental Psychology: General*, 137(2), 262–81.

Grafton, S.T., Hamilton, A.F. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human Movement Science*, 26(4), 590–616.

- Grafton, S.T., Fagg, A.H., Arbib, M.A. (1998). Dorsal premotor cortex and conditional movement selection: A PET functional mapping study. *Journal of Neurophysiology*, 79, 1092–7.
- Grill-Spector, K., Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, 107, 293–321.
- Grol, M.J., de Lange, F.P., Verstraten, F.A.J., Passingham, R.E., Toni, I. (2006). Cerebral changes during performance of overlearned arbitrary visuomotor associations. *The Journal of Neuroscience*, 26, 117–25.
- Halsband, U., Freund, H.J. (1990). Premotor cortex and conditional motor learning in man. *The Brain*, 113, 207–22.
- Halsband, U., Passingham, R. (1982). The role of premotor and parietal cortex in the direction of action. *Brain Research*, 240, 368–72.
- Hamilton, A.F., Grafton, S.T. (2009). Repetition suppression for performed hand gestures revealed by fMRI. Human Brain Mapping, 30, 2898–906.
- Hoshi, E., Tanji, J. (2006). Differential involvement of neurons in the dorsal and venral premotor cortex during processing of visual signals for action planning. *Journal of Neurophysiology*, 95, 3596–616.
- James, W. (1890). The Principles of Psychology, Vol. 2, New York: Dover Publications.
- Kourtzi, Z., Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience*, 20, 3310–18.
- Kurata, K., Hoffman, D.S. (1994). Differential effects of muscimol microinjection intro dorsal and ventral aspects of the premotor cortex of monkeys. *Journal of Neurophysiology*, 71, 1151–64.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N. (1990). Emotion, attention, and the startle reflex. *Psychological Review*, 97(3), 377–95.
- Lavender, T., Hommel, B. (2007). Affect and action: towards an event-coding account. *Cognition and Emotion*, 21(6), 1270–96.
- Maccotta, L., Buckner, R.L. (2004). Evidence for neural effects of repetition that directly correlate with behavioral priming. *Journal of Cognitive Neuroscience*, 16, 1625–32.
- Majdandzic, J., Bekkering, H., van Schie, H.T., Toni, I. (2009). Movement-specific repetition suppression in ventral and dorsal premotor cortex during action observation. *Cerebral Cortex*, 19(11), 2736–2745.
- Markman, A.B., Brendl, C.M. (2005). Constraining theories of embodied cognition. *Psychological Science*, 16(1), 6–10.
- Mitz, A.R., Godschalk, M., Wise, S.P. (1991). Learning-dependent neuronal activity in the premotor cortex: activity during the acquisition of conditional motor associations. *Journal of Neuroscience*, 11, 1855–72.
- Niedenthal, P.M., Barsalou, L.W., Winkielman, P., Krauth-Gruber, S., Ric, F. (2005). Embodiment in attitudes, social perception, and emotion. Personality and Social Psychology Review, 9(3), 184–211.
- Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychological Bulletin*, 114(3), 510–32.
- Schacter, D.L., Wig, G.S., Stevens, W.D. (2007). Reductions in cortical activity during priming. *Current Opinion in Neurobiology*, 17(2), 171–6.
- Solarz, A.K. (1960). Latency of instrumental responses as a function of compatibility with the meaning of eliciting verbal signs. *Journal of Experimental Psychology*, 59(4), 239–45.
- Toni, I., Rushworth, M.F., Passingham, R.E. (2001). Neural correlates of visuomotor associations. Spatial rules compared with arbitrary rules. *Experimental Brain Research*, 141, 359–69.
- van Dantzig, S., Pecher, D., Zwaan, R.A. (2008). Approach and avoidance as action effects. *Quarterly Journal of Experimental Psychology*, 61, 1298–306.
- Weeks, R.A., Honda, M., Catalan, M.J., Hallett, M. (2001). Comparison of auditory, somatosensory, and visually instructed and internally generated finger movements: a PET study. *NeuroImage*, *14*, 219–30.
- Wentura, D., Rothermund, K., Bak, P. (2000). Automatic vigilance: The attention-grabbing power of approach- and avoidance-related social information. *Journal of Personality and Social Psychology*, 78(6), 1024–037.

Wig, G.S., Grafton, S.T., Demos, K.E., Kelley, W.M. (2005). Reductions in neural activity underlie behavioral components of repetition priming. *Nature Neuroscience*, *8*, 1228–33.

Wise, S.P., Murray, E.A. (2000). Arbitrary associations between antecedents and actions. *Trends in Neuroscience*, 23, 271–6.

Wise, S.P., di Pellegrino, G., Boussaoud, D. (1996). The premotor cortex and nonstandard sensorimotor mapping. *Canadian Journal of Physiology* and Pharmacology, 74, 469–82.