Brain and Cognition 72 (2010) 306–309

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

The mirror reflects both ways: Action influences perception of others

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ARTICLE INFO

Article history:
Accepted 3 October 2009
Available online 14 November 2009

Keywords:
Mirror neuron system
Embodied cognition
Facial expression
Action–perception link

ABSTRACT

Substantial evidence links perception of others' bodies and mental representation of the observer's own body; however, the overwhelming majority of this evidence is unidirectional, showing influence from perception to action. It has been proposed that the influence also runs from action to perception, but to date the evidence is scant. Here we report that ordinary motor actions performed by the subject affect concurrent psychophysical judgments of human-body stimuli. Subjects remained unaware of the connection between the action and the main task. The results show that perception can change as a result of the observer's ongoing actions.

1. Introduction

It is now widely accepted that perception of human body postures and actions triggers representations in the observer of performing those same postures and actions, via the mirror system in the brain. The converse, that the observer's motor and somatosensory systems can influence perception of others' bodies, is not well established, although variations of this claim have been advanced several times (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005).

The strongest evidence of action influencing perception lies in a handful of studies showing that expertise in specialized motor skills – athletics, artificial movements learned in the laboratory, or the subject's own idiosyncratic movement patterns – results in greater perceptual accuracy for observing those same skills than is found in non-experts (Aglioti, Cesari, Romani, & Urgesi, 2008; Casile & Giese, 2006; Daprati, Wriessnegger, & Lacquaniti, 2007; Hecht, Vogt, & Prinz, 2001; Knoblich & Flach, 2001; Loula, Prasad, Harber, & Shiffrar, 2005; see also Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006).

These studies are vulnerable, to varying degrees, to questions regarding the source of the perceptual effects. For example, studies that employ real-world skills such as sports or dance must address the visual expertise that accompanies motor expertise when participating in a discipline. The strategy adopted by researchers has been to match for visual expertise without motor expertise, by comparing basketball players to sports journalists and coaches (Aglioti et al., 2008) or by comparing male and female ballet dancers on gender-specific ballet moves (Calvo-Merino et al., 2006). However, it is unclear that non-performer observers watch these movements with the same orientation to detail that performers do.

One study, that by Casile and Giese (2006), is not vulnerable to this criticism, because subjects were taught a novel movement pattern while blindfolded. However, the key component of this movement pattern was a syncopated rhythm (while walking, the arms swung 270° out of phase with the legs instead of the usual 180°). The final test consisted of same/different matching for point-light walkers at various phase shifts. Thus, it is possible that transfer to a perceptual task was due to greater sensitivity to this rhythm, perhaps represented amodally. To address this possibility, the authors included a control group trained on a purely visual, non-body version of this same syncopated rhythm (pairs of sliding squares 270° out of phase), and this group showed no heightened sensitivity to point-light walkers at 270°. However, since the visual system is not as adept at temporal processing as other modalities, it is quite possible that the rhythm was not learned as well from visual input as from bodily movement.

In general, all of the studies mentioned above raise questions about how the motor acquisition process affects stored representations (both perceptual and amodal), before the time of stimulus presentation. More broadly, these studies only show that perceptions can differ depending on level of expertise, and rely on presumed (but not demonstrated) activation of stored motor programs. They do not show a dynamic relationship between action and perception, wherein a change of action results in a change of perception.

A few studies have used on-line judgments of visual stimuli during performance of an action. One study (Jacobs & Shiffrar, 2005) showed that walking interfered with judging the speed of point-light walkers, but this finding is also vulnerable to a rhythm

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doi:10.1016/j.bandc.2009.10.001

hypothesis. Cycling caused no interference, which might seem to control for a rhythm explanation; however, subjects cycled at a speed that matched heart-rate in the walking condition, not pace. Thus, the pace of walking may have been much more similar to the stimulus walkers than was the pace of cycling. In a different study, subjects predicted future movement trajectories by a model whose posture either matched the observer's own or did not (Fischer, 2005). That study found no effect of observer's posture; however, the observers held their postures continuously for blocks of 96 trials, and other findings show that postural-feedback effects fade after approximately a minute (e.g. Tops & de Jong, 2006).

Other studies that might suggest an action–perception influence are even more indirect. For example, several studies show effects of action on short-term memory for body postures (Reed & Farah, 1995; Reed & McGoldrick, 2007; Wilson & Fox, 2007), but do not directly demonstrate an effect on the perceptual encoding of the stimuli.

In contrast to the studies reviewed above, the present study used ordinary actions that did not require special expertise – smiling, opening a pair of scissors – and that were overtly performed during the experimental session. The perceptual judgment concerned posture, not rhythm, and the observer's movements were repeatedly re-initiated.

One concern with the present approach is that asking subjects to perform an action can make them consciously aware of that action, and psychophysical judgments could then be mediated by conceptual activation or even a conscious attempt to produce the expected answer. To circumvent this, we began with a manipulation that has been previously demonstrated to engage certain muscles without cuing subjects as to the actual targeted behavior. Strack, Martin, and Stepper (1988) showed that holding a pen in one's teeth engages the muscles used for smiling, but subjects are generally unaware that they are being manipulated to producing a smile. This tactic was used by Strack et al. (see also Ito, Chiao, Devine, Lorig, & Cacioppo, 2006; Soussignan, 2002) to demonstrate an effect of muscle engagement on emotion (the facial feedback hypothesis); here we use it to demonstrate an effect of muscle engagement on perception.

2. Experiment 1

2.1. Method

2.1.1. Participants

Twenty-eight UCSC students participated for course credit. Three of these were excluded from the analysis because they correctly guessed the purpose of the manipulation.

2.1.2. Stimuli

Eleven pictures of the same face on a continuum from smiling to frowning were used as stimuli (Fig. 1A), originally created for a categorical perception study (McCullough & Emmorey, 2009). These were created from two photographs at the smiling and frowning ends of the continuum. The nine intermediate stimuli were created by digital morphing in 10% increments (see McCullough and Emmorey (2009), for details).

2.1.3. Design

Two conditions were compared in a within-subjects design. In the Pen condition, subjects were instructed to hold a pen horizontally with their teeth, without touching the pen with their lips. No mention was made of smiling, and subjects were told that the purpose of the study was to test their ability to multitask. In the No Pen condition, subjects were given no special instructions.

2.1.4. Procedure

Each trial was preceded by a screen prompting the subject with the words "Pen" or "No Pen" to either place the pen between their teeth or not. When ready, the subject initiated the trial with a keypress. Each trial began with a blank interval of 500 ms, followed by a stimulus face presented for 750 ms. Subjects indicated whether the face was "happy" or "sad." Pen and No Pen trials were alternated, in order to avoid habituation to the motor action. The 11 stimulus faces were presented in pseudo-random order, in blocks of 22 trials containing all 11 stimuli twice in two random orderings, interleaved for the two conditions. Each stimulus was shown 15 times in each of the two conditions, for a total of 330 trials. After completion of the experiment, subjects filled out a debriefing form in which they were asked to speculate on the purpose of the experiment. Any subject whose responses suggested a connection between the pen manipulation on the one hand, and the act of smiling or the facial expressions shown on the screen, on the other hand, were eliminated from the analysis.

2.2. Results

For each subject, the percentage of "happy" responses for each of the eleven stimuli was tabulated separately for the Pen and No Pen conditions. Threshold for perceiving the face as happy was defined as 50% "happy" responses. The location of this threshold along the stimulus continuum was determined for each subject using a Probit analysis, with stimulus number (1–11) as the independent variable (Fig. 2). The result in each case was a number representing what point along the stimulus continuum represented the 50% threshold. These threshold points for the Pen and No Pen conditions for each subject were compared with a paired-samples *t*-test. The difference in threshold between the Pen condition ($M = 5.22$, $SE = 0.18$) and the No Pen condition ($M = 5.33$, $SE = 0.16$) was significant ($t(24) = 2.35$, $p = .028$). The difference was in the predicted direction, with subjects showing a lower threshold to perceive a happy expression when they themselves were smiling.

The results show that unconsciously engaging the smiling muscles alters psychophysical judgments of facial expression. We must consider, though, whether this influence is a result of a direct action-to-perception link, or whether it might be mediated by the emotional state of the subject. Studies show that the pen manipulation does influence the subject's emotional state (Ito et al., 2006; Soussignan, 2002; Strack et al., 1988), and that the subject's emotional state can influence judgment of others' expressions (Niedenthal, Halberstadt, Margolin, & Innes-Ker, 2000). In order to demonstrate a direct action–perception link, it is therefore necessary to eliminate emotion as a possible mediator. For this purpose, a hand-posture manipulation was used.

3. Experiment 2

3.1. Method

3.1.1. Participants

Twenty-two students participated for course credit. One subject was excluded for not following instructions. No subjects guessed the connection between the stimuli and the postures of their own hands. All were right-handed, as determined by self-report.

3.1.2. Stimuli

Stimuli were 11 computer-generated pictures of a hand, originally created for a categorical perception study (Emmorey, McCullough, & Brentari, 2003). The pictures were created with MetaCreations Poser software, and showed a continuum from

Fig. 1. Sample stimuli from the facial expression continuum used in Experiment 1 (A) and the handshape continuum used in Experiment 2 (B). In each case, stimulus numbers 1, 6, and 11 of the 11 stimuli are shown.

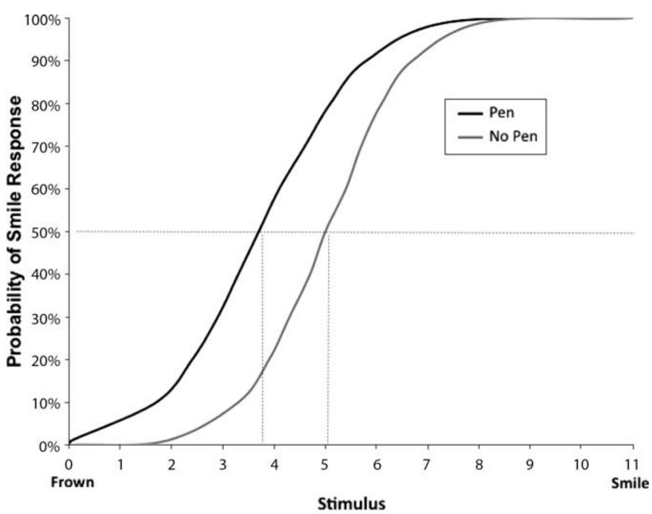

Fig. 2. Sample data from Experiment 1, showing one subject's fitted curves from a Probit analysis for the Pen and No Pen conditions. Vertical dotted lines show the point on the stimulus continuum that corresponds to the 50% threshold.

three fingers extended (thumb, index and middle fingers, with the ring and pinkie fingers curled into the palm) to all five fingers extended (Fig. 1B). The nine intermediate stimuli showed the ring and pinkie fingers partially curled in 10% increments (see Emmorey et al. (2003) for details).

3.1.3. Design

Two conditions that manipulated the subjects' hand-postures were compared in a within-subjects design. In the Small Scissor condition, subjects held a pair of scissors with a small loop opposite the thumb, which only allowed insertion of the index and middle finger, thus employing only three fingers. In the Large Scissor condition, subjects held a pair of scissors with a large loop, thus employing all five fingers. Subjects held the scissors in the right hand, which matched the hand shown in the pictures. Small Scissor and Large Scissor trials were presented in separate blocks. Subjects were instructed to quickly open the scissors at the appearance of the fixation cross, and to close the scissors after the disappearance of the stimulus hand. As in Experiment 1, subjects were told that the purpose of the study was to test their ability to multitask. No subjects guessed the connection between the stimuli and the scissor manipulation.

3.1.4. Procedure

Each trial began with a fixation cross presented for 750 ms, followed by a stimulus hand presented for 750 ms. After opening and closing the scissors, subjects indicated by key press with the left hand whether the stimulus hand was the three-fingered posture or the five-fingered posture. Response keys were indicated with small pictures of the two postures, and verbal labels were never used to describe these. In all other respects, the procedure was identical to that of Experiment 1.

3.2. Results

Mean thresholds for categorizing the stimulus as the three-fingered posture were 3.73 ($SE = 0.21$) for the Large Scissor condition and 3.38 ($SE = 0.17$) for the Small Scissor condition, a statistically significant difference ($t(20) = 2.6$, $p = .018$). The difference was in the predicted direction, with subjects showing a lower threshold to perceive the three-fingered posture when opening the small (three-fingered) scissors.

4. Discussion

These findings support a bidirectional account of the mirror system. Motor activation as a result of seeing others' actions (see Wilson and Knoblich (2005), for review) implies the existence of a common code (Hommel, Musseler, Aschersleben, & Prinz, 2001) for representing one's own body and others' bodies. It is highly plausible, then, that influence would run in the other direction as well – that information about one's own body would influence perceptual representations of others' bodies. This is plausible both on grounds of neurological wiring, since connected systems are likely to communicate in both directions; and on grounds of adaptive functionality, since one's own body representation could be usefully employed as an internal model for predicting and constraining the perception of how another body will move (Wilson & Knoblich, 2005).

This finding has important implications for our understanding of the mirror system. Most current accounts emphasize the role of this system in social and emotional processes, hypothesizing a flow of causality from perception, to motor activation and imitation, to higher-level representations involved in empathy, theory of mind, and social learning (e.g. Gallese, Rochat, Cossu, & Sinigaglia, 2009; Iacoboni et al., 2005; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007). The present results indicate that the mirror system serves another function as well, which is to provide top-down support for visual perception. Just as with other top-down effects, this would have the advantage of making perception faster, more fluent, and in most cases more accurate, allowing rapid, appropriate responses to a changing environment (Nijhawan, 2008). Thus, the mirror system may be a multi-function system, perhaps originally selected for in partial form to serve one particular function. Additional serendipitous advantages of this proto-system could then have driven its further refinement and elaboration, resulting in the complex functionality that we see today.

Acknowledgments

We thank Karen Emmorey and Steven McCullough for the use of their stimuli, and Sondra Bitonti, Erin Buonocore, Andrea Frick, Jessy Lancaster, Kristy Lindemann, and Stefan Mangold for their assistance with this project.

References

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience, 11*(9), 1109–1116.

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An FMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243–1249.

Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905–1910.

Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology, 16*(1), 69–74.

Daprati, E., Wriessnegger, S., & Lacquaniti, F. (2007). Knowledge of one's kinematics improves perceptual discrimination. *Conscious Cognition, 16*(1), 178–188.

Emmorey, K., McCullough, S., & Brentari, D. (2003). Categorical perception in American sign language. *Language and Cognitive Processes, 18*(1), 21–45.

Fischer, M. H. (2005). Action simulation for others is not constrained by one's own postures. *Neuropsychologia, 43*(1), 28–34.

Gallese, V., Rochat, M., Cossu, G., & Sinigaglia, C. (2009). Motor cognition and its role in the phylogeny and ontogeny of action understanding. *Developmental Psychology, 45*(1), 103–113.

Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: A case for action–perception transfer. *Psychological Research Psychologische Forschung, 65*(1), 3–14.

Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences, 24*(5), 849–878 (discussion 878–937).

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology, 3*(3), e79.

Ito, T. A., Chiao, K. W., Devine, P. G., Lorig, T. S., & Cacioppo, J. T. (2006). The influence of facial feedback on race bias. *Psychological Science, 17*(3), 256–261.

Jacobs, A., & Shiffrar, M. (2005). Walking perception by walking observers. *Journal of Experimental Psychology: Human Perception and Performance, 31*(1), 157–169.

Knoblich, G., & Flach, R. (2001). Predicting the effects of actions: Interactions of perception and action. *Psychological Science, 12*(6), 467–472.

Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review, 74*(6), 431–461.

Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology: Human Perception and Performance, 31*(1), 210–220.

McCullough, S., & Emmorey, K. (2009). Categorical perception of affective and linguistic facial expressions. *Cognition, 110*.

Niedenthal, P. M., Halberstadt, J. B., Margolin, J., & Innes-Ker, Å. H. (2000). Emotional state and the detection of change in facial expression of emotion. *European Journal of Social Psychology, 30*(2), 211–222.

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and Brain Sciences, 31*, 179–239.

Reed, C. L., & Farah, M. J. (1995). The psychological reality of the body schema: A test with normal participants. *Journal of Experimental Psychology: Human Perception and Performance, 21*(2), 334–343.

Reed, C. L., & McGoldrick, J. E. (2007). Action during body perception: Processing time affects self-other correspondences. *Social Neuroscience, 2*(2), 134–149.

Schulte-Rüther, M., Markowitsch, H. J., Fink, G. R., & Piefke, M. (2007). Mirror neuron and theory of mind mechanisms involved in face-to-face interactions: A functional magnetic resonance imaging approach to empathy. *Journal of Cognitive Neuroscience, 19*(8), 1354–1372.

Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences, 11*(8), 349–355.

Soussignan, R. (2002). Duchenne smile, emotional experience, and autonomic reactivity: A test of the facial feedback hypothesis. *Emotion, 2*(1), 52–74.

Strack, F., Martin, L. L., & Stepper, S. (1988). Inhibiting and facilitating conditions of the human smile: A nonobtrusive test of the facial feedback hypothesis. *Journal of Personality and Social Psychology, 54*(5), 768–777.

Tops, M., & de Jong, R. (2006). Posing for success: Clenching a fist facilitates approach. *Psychonomic Bulletin & Review, 13*(2), 229–234.

Wilson, M., & Fox, G. (2007). Working memory for language is not special: Evidence for an articulatory loop for novel stimuli. *Psychonomic Bulletin & Review, 14*(3), 470–473.

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*(3), 460–473.