

# Action observation modulates auditory perception of the consequence of others' actions

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Received 6 October 2007

Available online 4 March 2008

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## Abstract

We can easily discriminate self-produced from externally generated sensory signals. Recent studies suggest that the prediction of the sensory consequences of one's own actions made by forward model can be used to attenuate the sensory effects of self-produced movements, thereby enabling a differentiation of the self-produced sensation from the externally generated one. The present study showed that attenuation of sensation occurred both when participants themselves performed a goal-directed action and when they observed experimenter performing the same action, although they clearly reported that the tones were produced by other during action observation and by themselves during their own action. These results suggest that sensory prediction of action modulates ongoing auditory processing irrespective of who produces the sounds and that the explicit judgment of agency does not necessarily rely on the same mechanisms on which implicit perceptual measures such as sensory attenuation rely.

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*Keywords:* Action observation; Forward model; Motor awareness; Sense of agency; Authorship processing; Self-recognition; Action perception

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## 1. Introduction

Normally, we can easily discriminate self-produced from externally generated sensory signals. It has been proposed that an internal predictor, or a forward model, enables this distinction between self-produced and externally produced sensory events (Wolpert, Ghahramani, & Jordan, 1995; Wolpert, Ghahramani, & Jordan, 2001). Forward models use an “efference copy” of the motor command to make a prediction of the consequences of the actions. A forward dynamic model makes predictions about the next state of the system and compares this with the desired state. This comparison enables rapid error correction before sensory feedback is available. A forward output (sensory) model makes predictions about the sensory consequences of a movement. This predictable component is removed from the incoming sensory signals, thereby attenuating the

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sensory effect of self-generated movement and increasing the relative salience of sensations with an external cause (Bays, Flanagan, & Wolpert, 2006).

Previous studies support the notion that sensory prediction can be used to attenuate the sensory effects of self-generated movement. For instance, participants rated the self-administered tactile stimulus as less tickly than the same tactile stimulus generated externally (Weiskrantz, Elliott, & Darlington, 1971). A functional magnetic resonance imaging study showed a reduction in activity of the secondary somatosensory cortex and the anterior cingulate cortex when the tactile stimulus was self-produced relative to when it was externally produced (Blakemore, Wolpert, & Frith, 1998). Moreover, the tickliness rating increased significantly as the discrepancy between predicted and actual sensory feedback increased even if the tactile sensation was self-produced (Blakemore, Frith, & Wolpert, 1999). Similar sensory attenuation is also observed in other modalities. For example, the magnetoencephalographic responses from the human auditory cortex are smaller to self-generated sounds than to externally produced sounds irrespective of whether or not the sounds involved were made by using a tool (Houde, Nagarajan, Sekihara, & Merzenich, 2002; Martikainen, Kaneko, & Hari, 2005). Recently, it was reported that this predictive attenuation of self-generated sensation mainly relies on central signals related to the preparation for movement and that it occurs in the absence of movements (Voss, Ingram, Haggard, & Wolpert, 2006).

Sensory prediction made by forward model also contributes to the experience of agency. For instance, using explicit judgment of agency Sato and Yasuda (2005) showed that the sense of agency, that is the sense that “I am the one who is causing or generating an action” (Gallagher, 2000), largely depends on the degree of discrepancy resulting from a comparison between the predicted and actual sensory consequences. In their experiments, participant first learned that their action consistently produced a particular auditory effect (tone) at particular time. In the subsequent test phase, the degree of congruency between the predicted and actual sensory consequences was manipulated in terms of the action–effect mapping and the temporal delay between action and effect. The results showed that the self-reported degree to which participants felt that the tone was a consequence of their own action was reduced when the effect tones were inconsistent with the acquired the action–effect mapping. Moreover, the sense of agency diminished as the temporal delay between an action and predicted consequence increased, although in fact the tone was self-produced in all cases. The higher the congruency between the predicted and actual sensory consequences was, the more intense participants experienced the sense of agency. These findings fit well with the forward model theory of agency.

As mentioned above, much evidence has supported the hypothesis that sensory predictions based on forward models play a key role in differentiating the self as an agent from the surrounding environment. However, it remains unknown whether or not a forward model would be activated by observation of an action made by others. Previous studies have reported that there are a set of neurons that respond both when the monkey performs a particular goal-directed action, and when it observes another individual performing a similar action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). These “mirror neurons” or “mirror neuron system (MNS)” respond even when the final part of the action, crucial in triggering the response in full vision, is hidden and can only be inferred (Umiltà et al., 2001), and this system also appears to code actions independently of the modality through which a given action is inferred (Kohler et al., 2002). The MNS does not respond during perception of impossible biomechanical motion, thus suggesting that it is selectively activated to process actions that conform to the capabilities of the observer (Stevens, Fonlupt, Shiffrar, & Decety, 2000). The extent of activation of this system seems to depend on the congruency between the observer’s own motor repertoire and perceived actions performed by others irrespective of whether or not actions are performed with tools (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Järveläinen, Schürmann, & Hari, 2004). Rizzolatti, Fogassi, and Gallese (2001) proposed that these mirror neurons are a core part of the system that automatically matches the agent’s action onto its own motor repertoire without executing it, thus allowing us to directly understand the meaning of actions by internally replicating them without any explicit reflective mediation. If there is a system like the MNS that codes a bidirectional association between the motor pattern that a movement was generated by and the sensory effects that it produces (Hommel, Müssele, Aschersleben, & Prinz, 2001; Knoblich & Flach, 2003), the observation of well-learned actions should activate a forward model through the MNS, thus attenuating or modulating ongoing perception of the sensory consequence of action made by others, which may lead to the confusion as to who is the author of the action. The purpose of the present studies was to test this possibility.

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