

- shares functions with WASp. *J. Cell Biol.* 151, 789–799.
17. Sirotkin, V., Beltzner, C.C., Marchand, J.-B., and Pollard, T.D. (2005). Interactions of WASp, myosin-I, and verprolin with Arp2/3 complex during actin patch assembly in fission yeast. *J. Cell Biol.* 170, 637–648.
18. Sun, Y., Martin, A.C., and Drubin, D.G. (2006). Endocytic internalization in budding yeast

- requires coordinated actin nucleation and myosin motor activity. *Dev. Cell* 11, 33–46.
19. Cramer, L.P. (1997). Molecular mechanism of actin-dependent retrograde flow in lamellipodia of motile cells. *Front. Biosci.* 2, d260–d270.
20. Cramer, L.P. (1999). Organization and polarity of actin filament networks in cells: implications for the mechanism of myosin-based cell motility. *Biochem. Soc. Symp.* 65, 173–205.

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## Action Recognition: Is It a Motor Process?

**A new study has found that brain-damaged patients impaired in the production of an action also find it difficult to recognize the sound of the same action, providing new insights into the complex relationship between action production and action recognition.**

**Bradford Z. Mahon**

How do we recognize the actions of other individuals? Motor theories of perception argue that motor processes play an active and necessary role in the recognition of familiar actions. The basic claim of this class of theories is that perceived actions are mapped onto the motor routines that would be required in order to produce those same actions. Through the activation of those motor routines, the observer is then able to recognize, and meaningfully interpret, the observed action. A central prediction of motor theories of action recognition is that when motor processes are compromised, recognition processes should be similarly affected. In this issue, Pazzaglia *et al.* [1] report new neuropsychological evidence suggesting a close link between impairments for producing actions and impairments for recognizing the sounds of actions.

The motor theory of perception was initially developed in the domain of speech perception by Liberman *et al.* [2]. The theory has since been expanded and applied to visual and auditory action recognition [3], object recognition [4], but see [5], and even mental state attribution [6], but see [7]. These extensions of the motor theory of perception were spurred by Rizzolatti and colleagues' observation that some neurons in frontal and parietal motor structures of the macaque monkey brain discharge during both the execution and observation of actions — these are the so-called 'mirror' neurons. A growing

literature using a range of methods — such as functional magnetic resonance imaging and transcranial magnetic stimulation — has described the putative human homologues of the macaque mirror neuron system (for review, see [3]; and see Dinstein *et al.* [8] for healthy skepticism about the empirical basis of the mirror neuron system).

The motor theory of action recognition faces two major challenges. First, it is difficult to determine whether the motor system is activated during perception because motor processes are necessary for perception, supportive but not necessary, or merely connected to, but not functionally relevant for, perception. Experiments that demonstrate that the motor system is automatically engaged during action perception do not distinguish among these interpretations. This is because a theory is lacking about the dynamics of how information is exchanged among (potentially distinct) perceptual and motor processes [9].

The second challenge faced by the motor theory of action recognition comes from neuropsychological studies of patients with apraxia. Apraxia is an impairment for action production that cannot be explained by low-level muscle or motor disturbances, nor by an inability to comprehend the task (as, for example, because of problems with perception or language understanding). For instance, apraxic patients may be impaired at demonstrating the use of objects (transitive actions, such as using a hammer), and/or performing

familiar gestures that do not involve objects (intransitive gestures, such as waving goodbye). Several studies [10–12] have reported correlations across groups of patients between their ability to produce actions and their ability to recognize and/or imitate visually presented actions (performed with the hand/arm). These data are consistent with the motor theory of action recognition. But a number of studies have shown that patients with apraxic impairments may be relatively unimpaired for recognizing the same actions that they cannot produce ([11–17]; see also Table S2 in [1]). This means that successful action recognition does not require the normal functioning of the action production system, and is at variance with the central prediction made by the motor theory of action recognition [18,19].

Pazzaglia *et al.* [1] now report new data in the auditory domain that address the two major challenges faced by the motor theory of action recognition. The authors defined different groups of patients on the basis of their ability to imitate the actions of another individual. One group of patients, with buccofacial apraxia, were differentially impaired at imitating actions involving the mouth; another group, with limb apraxia, were differentially impaired at imitating actions performed by the hand/limb [1]. All of the patients were then tested on their ability to match sounds to pictures. The sounds were the canonical sounds that are produced either by mouth actions (for example, slurping soup), limb actions (for example, using scissors), or non-human related environmental sounds (for example, airplane flying). The authors found that patients with (selective) buccofacial apraxia were differentially impaired for the sound-picture matching task for mouth-related actions. In contrast, patients with (selective) limb apraxia were differentially impaired for sound-picture matching for

limb-related actions. In a further analysis, they showed that, while frontal and parietal motor regions, as well as the insula, were reliably damaged in both groups of patients, there was differential frontal involvement for patients with buccofacial apraxia. While the lesion data do not cleanly map onto the somatotopic organization of motor structures, they do demonstrate dissociable neural substrates for buccofacial and limb apraxia.

Pazzaglia *et al.*'s [1] findings elegantly show that action production and action recognition impairments can be associated at the level of specific effectors. Their study has a number of virtues. It is the first detailed study of the ability of apraxic patients to recognize action-related sounds. Another advantage of the study is that, while the patients were selected for enrollment on the basis of their ability to imitate different types of actions, the patients were included on a consecutive basis. Thus, the different groups of patients were established independently of their performance on the critical test of sound-picture matching. The pattern of empirical results is particularly strong because of the presence of a double dissociation over the same materials, thus ruling out alternative explanations in terms of differential difficulty for the mouth- or limb-action tests.

This new study [1] sheds light on several issues for future research. For instance, research on the 'mirror neuron system' has generally not considered the potential role of those same neurons/regions in monitoring actions performed in the first person (see [20] for relevant findings). Do mirror-like properties of the motor system piggy-back on a more basic system that has developed in order to keep track of one's own actions? Future work will also need to address whether the associations of impairment that Pazzaglia *et al.* [1] report are due to damage to motor structures *per se*, or rather to structures that are immediately adjacent to the motor system and which process and represent more abstract knowledge

of actions. Another important issue is whether motor simulations would be able, in principle, to distinguish between different actions that are highly similar in terms of their kinematic properties but radically different in terms of their meaning and/or goals [7].

More generally, the study by Pazzaglia *et al.* [1] highlights an important theoretical vacuum: as a field, we are lacking a theory that can explain both the dissociations between action production and recognition, and the associations of impairments in action production and recognition [9]. Strong forms of the motor theory of action recognition can explain the associations of impairment, but fail to explain dissociations. Theories at the other end of the hypothesis space, which assume a strict separation between action recognition processes and action production processes (for example, [19]), can explain the dissociations but have difficulty explaining the associations (at least, as arising from damage to a single process/mechanism). Ultimately, we will need an account that can explain both types of neuropsychological evidence. The most likely hypothesis occupies a middle ground between the two extremes: action recognition is 'grounded' in the action production system, not because motor processes are constitutive of recognition processes, but because perception and production are heavily interactive. Such a framework would shift the focus of study away from demonstrating the existence of perceptually-driven neural responses within the motor system, and toward an understanding of how information is communicated between perceptual and motor systems.

#### References

1. Pazzaglia, M., Pizzamiglio, L., Pes, E., and Aglioti, S.M. (2008). The sound of actions in apraxia. *Curr. Biol.* 18, 1766–1772.
2. Liberman, A., Cooper, F., Shankweiler, D., and Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychol. Rev.* 74, 431.
3. Rizzolatti, G., and Craighero, L. (2004). The mirror neuron system. *Annu. Rev. Neurosci.* 27, 169.
4. Martin, A., Ungerleider, L.G., and Haxby, J.V. (2000). Category specificity and the brain: the sensory/motor model of semantic representations of objects. In *The New*

Cognitive Neurosciences, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).

5. Johnson-Frey, S.H. (2004). The neural basis of complex tool use in humans. *Trends Cogn. Sci.* 8, 71–78.
6. Gallese, V., and Goldman, A.I. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 2, 493–501.
7. Jacob, P., and Jeannerod, M. (2005). The motor theory of social cognition: a critique. *Trends Cogn. Sci.* 9, 21–25.
8. Dinstein, I., Thomas, C., Behrmann, M., and Heeger, D.J. (2008). A mirror up to nature. *Curr. Biol.* 18, R13–R18.
9. Mahon, B.Z., and Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J. Physiol.* 102, 59–70.
10. Buxbaum, L.J., Kyle, K.M., and Menon, R. (2005). On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. *Cogn. Brain Res.* 25, 226–239.
11. Negri, G.A.L., Rumiati, R.I., Zadini, A., Ukmar, M., Mahon, B.Z., and Caramazza, A. (2007). What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cogn. Neuropsychol.* 24, 795–816.
12. Pazzaglia, M., Smania, N., Corato, E., and Aglioti, S.M. (2008). Neural underpinnings of gesture discrimination in patients with limb apraxia. *J. Neurosci.* 28, 3030–3041.
13. Cubelli, R., Marchetti, C., Boscolo, G., and Della Sala, S. (2000). Cognition in action: Testing a model of limb apraxia. *Brain Cogn.* 44, 144.
14. Frey, S.H., Funnell, M.G., Gerry, V.E., and Gazzaniga, M.S. (2005). A dissociation between the representation of tool-use skills and hand dominance: Insights from left- and right-handed callosotomy patients. *J. Cogn. Neurosci.* 17, 262–272.
15. Halsband, U., Schmitt, J., and Weyers, M. (2001). Recognition and imitation of pantomimed motor acts after unilateral parietal and premotor lesions: a perspective on apraxia. *Neuropsychologia* 39, 200.
16. Rumiati, R.I., Zanini, S., Vorano, L., and Shallice, T. (2001). A form of ideational apraxia as a selective deficit of contention scheduling. *Cogn. Neuropsychol.* 18, 617.
17. Rapcsak, S.Z., Ochipa, C., Anderson, K.C., and Poizner, H. (1995). Progressive ideomotor apraxia: Evidence for a selective impairment in the action production system. *Brain Cogn.* 27, 213–236.
18. Mahon, B.Z., and Caramazza, A. (2005). The orchestration of the sensory-motor systems: Clues from neuropsychology. *Cogn. Neuropsychol.* 22, 480.
19. Rothi, L.J., Ochipa, C., and Heilman, K.M. (1991). A cognitive neuropsychological model of limb praxis. *Cogn. Neuropsychol.* 8, 443.
20. Maeda, F., Kleiner-Fisman, G., and Pascual-Leone, A. (2002). Motor facilitation while observing hand actions: Specificity of the effect and role of observer's orientation. *J. Neurophysiol.* 87, 1329–1335.

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