

Motor cognition–motor semantics: Action perception theory of cognition and communication

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ABSTRACT

A new perspective on cognition views cortical cell assemblies linking together knowledge about actions and perceptions not only as the vehicles of integrated action and perception processing but, furthermore, as a brain basis for a wide range of higher cortical functions, including attention, meaning and concepts, sequences, goals and intentions, and even communicative social interaction. This article explains mechanisms relevant to mechanistic action perception theory, points to concrete neuronal circuits in brains along with artificial neuronal network simulations, and summarizes recent brain imaging and other experimental data documenting the role of action perception circuits in cognition, language and communication.

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1. Introduction

A respectable position views motor brain mechanisms as a slave system under the dictate of cognition. Accordingly, modality-specific sensory modules channel information to the central systems for attention, memory, language, concepts, decisions and perhaps even “the soul”, which, in turn, drive the motor output (for illustration, see Fig. 1, and see Fodor, 1983; Hubel, 1995). In this perspective, perception and action mechanisms work as functionally isolated (“encapsulated”) modules and their respective main purposes are to filter and preprocess sensory information for cognitive operations and to dress the cognitive operations into acts of motor movement.

A radically different position has been developed by Marc Jeannerod and his friends and colleagues (Boulenger et al., 2008; Braitenberg & Schüz, 1998; Fuster, 2003; Jacob & Jeannerod, 2005; Jeannerod, 1994, 2001, 2006; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Pulvermüller & Fadiga, 2010; Rizzolatti & Sinigaglia, 2010). In this view, cognition is built from action and perception, upon sensory and motor brain mechanisms. The action schema of GRASPING an object would thus not be a motor process only, but would connect with sensory information about small or large size (of the to-be-grasped object) and the integrated representation of

motor and sensory properties of the action would become the vehicle of active memory, attention-to-action, and action-related meaning or motor semantics (Fig. 2, see also Fuster, 2003, 2009). Action-supporting parts of the brain would thus change their role in corticofunctional interplay, from slave to master.

Eminent brain-theoretical arguments support the latter position, both structural and functional in nature. Anatomically, motor as well as sensory systems of the brain are not isolated modules. They are strongly connected reciprocally with both adjacent modality-preferential areas as well as more distant multimodal convergence and integration “hubs” on which other sensory and motor systems likewise converge (Braitenberg & Schüz, 1998; Sporns, 2013; Sporns, Tononi, & Kotter, 2005; Young, Scannell, & Burns, 1995). Physiologically, a major driving force of learning and plasticity in the brain is the correlation of the firing of nerve cells. Connected neurons that frequently fire together in synchrony are bound together more closely at a functional level, whereas neurons firing independently of each other, or in an antiphase manner, weaken their mutual links; even fine-grained temporal relationships in firing patterns can be mapped by spike-timing dependent plasticity (Bi & Wang, 2002; Tsumoto, 1992). When learning to GRASP an object, the correlation between perceived object size and the motor feature of grasp aperture can be mapped by the correlated activity of nerve cells encoding these parameters so that a circuit forms that spans frontocentral motor, premotor, parietal and occipital-visual cortex. The circuit links neurons in motor and sensory areas by way of nerve cells in

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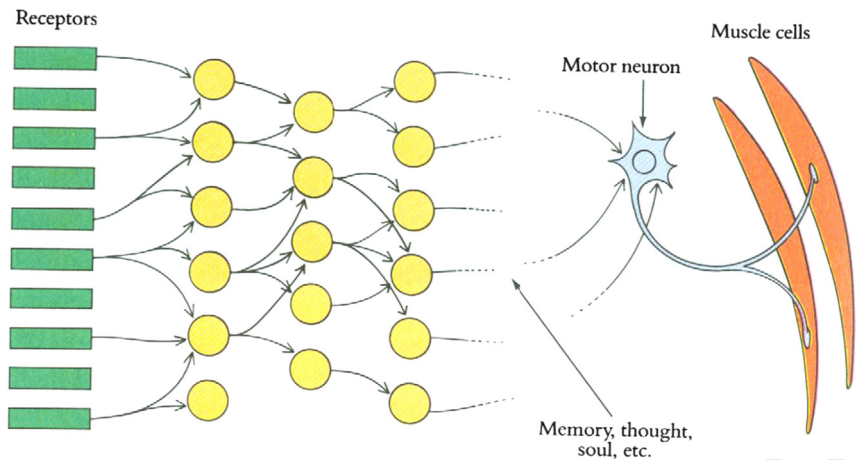


Fig. 1. Illustration of the organization of perception, action and central systems of the cortex as viewed in the modular tradition. Systems for perception, higher cognition and motor output are viewed as functionally segregated and linked in sequence. Adopted from Hübner (1995).

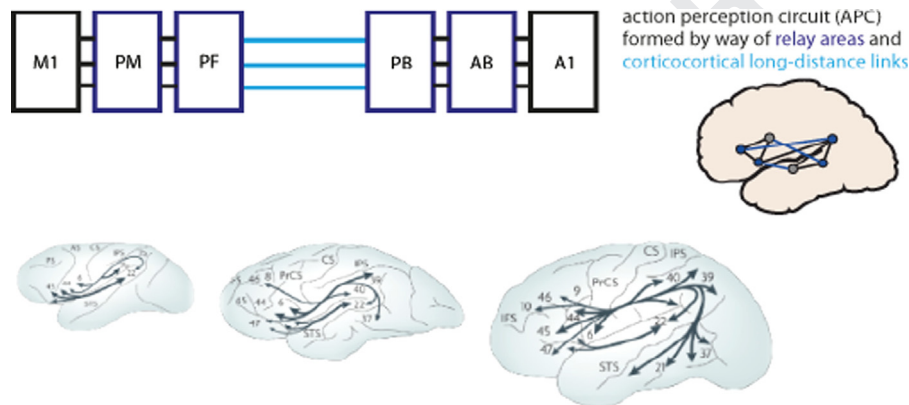


Fig. 2. Top panel: action perception circuits (APCs) that link motor and sensory information about actions. When learning to pronounce a syllable or word form, co-occurring activity in neurons in articulatory motor cortex (M1) and in primary auditory cortex (A1) will trigger correlated neuronal activity in areas connecting these sites, including premotor (PM), prefrontal (PF), auditory belt (AB) and parabelt (PB). Neuronal correlation and the available neuroanatomical connections lead to the formation of distributed neuronal assemblies for spoken word forms (Garagnani et al., 2007, 2008). The inset shows the approximate cortical distribution of such an articulatory-auditory APC, the putative correlate of a word form such as “grasp”. Bottom panel: Phylogenetic development of major long distance reciprocal cortico-cortical connections between inferior-frontal and temporal cortex in humans. Long distance bundles are shown from left to right for the macaque, chimpanzee and human brains (adopted from Rilling et al., 2008). Note the strong dorsal connection from inferior-frontal, precentral and central sulcus (IFS, PrCS, SC) regions to areas around the inferior-parietal and superior-temporal sulcus (IPS, STS) of the arcuate fascicle, which is only present in humans.

adjacent and convergence areas (including “hubs”) in the service of providing the machinery for an action schema, that is an ordered sequence of motor movements related to sensory-perceptual features, which can be adjusted to specific features of objects and contexts. Cortico-cortical links between the relevant motor, sensory and higher convergence areas (see Damasio, 1989) along with the correlated sensory and motor firing strongly argue for the existence of such action perception circuits, or APCs, as a basis of motor function (Jeannerod, 2006). If APCs carry action representations and link together sensory and motor information about actions, it appears straightforward to postulate that they should also be activated when actions, which the individual regularly performs, are being perceived (Jeannerod et al., 1995).

There is overwhelming evidence for the existence of APCs. The proof of mirror neurons active during execution of specific hand actions and likewise during visual perception of these same actions, along with their presence not only in one single area but in both premotor and inferior-parietal cortices, is strong support for the existence of action-specific links that integrate motor and sensory information about specific action schemas (Kohler et al., 2002; Rizzolatti & Sinigaglia, 2010). Action perception links exist not only for manual and mouth actions and their related visual

and acoustic perceptions, but equally in the case of human language, for linguistic-articulatory action schemas and their auditory counterparts (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Pulvermüller & Fadiga, 2010; Pulvermüller et al., 2006; Watkins, Strafella, & Paus, 2003; Yeung & Werker, in press). Further converging evidence comes from saccade-related sensorimotor neurons (Bruce & Goldberg, 1985) and from multimodal memory cells in prefrontal, premotor, anterior-temporal and parietal cortex, which provide additional support for the claim that the cortical representations of stimuli affording actions are organized by multimodal circuits spanning cortical areas (Fuster, 2003). In theory, it might be possible that single sensorimotor or mirror neurons bind action and perception information and cause these sensorimotor interaction effects, but, because the influence of single cortical cells on other cortical neurons is known to be weak and certainly could not change the metabolism of an entire area, it appears more realistic that these sensorimotor interaction effects are caused by neuronal assemblies of hundreds to thousands of neurons acting together as functional units (Abeles, 1991; Braitenberg & Schüz, 1998; Fuster, 2003).

Action perception circuits conceived as distributed neuronal assemblies establish a functional link between specific sets of

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