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Letter

Social affordances, mirror neurons, and how to understand the social brain

Beatrice de Gelder[1,2,*]

Gibson's notion of affordances refers to the opportunities for action that the environment offers, and that the organism can act upon. A good decade later, the discovery of mirror neurons (MNs) in rhesus macaques demonstrated that motor sequences are best viewed as actions (grasping) because they are organized by high-level goals (e.g., eating food) rather than by the physics of the effectors. The notion of affordance may resonate with MN researchers because it fits the idea that movements are organized as ensembles best defined by the agents' intention rather than by agent-independent physical properties. Recently, Bonini et al. [1] extended MN research on instrumental actions in the physical world to social interactions and linked MNs to a social affordance framework, placing the perception of conspecifics ('others') at the center. MNs and social affordance theory have been criticized for lack of clarity [2]: does combining them promise a step forward in understanding the social brain?

When launched by Lesley Brothers and David Perrett, the notion of a social brain focused on whether some circuits in the primate brain were dedicated to interactions with conspecifics. This social perception research program was subsequently narrowed down as social behavior was viewed primarily through the lens of mental state attributions. So far, neither MN nor affordance theory has clearly defined a social brain research program that explores neural processes specialized for social behavior that are not biased by folk psychological concepts. The core inspiration

of MNs was that sensorimotor processes implement social perception by sustaining direct other-to-self mappings. However, 30 years of discussion made it clear that this kind of direct mapping works only as long as sensorimotor intention descriptions of MNs rely on the interpretative machinery of folk psychology and its intuitive action categories. In other words, what defines the realm of the social is assumed rather than investigated. I briefly highlight three questions for making progress in social brain research. First, are there genuine social motor/action primitives? Second, how does the visual system perceive conspecifics, and do MNs play a core role? Third, how can a neural account be provided for prediction at the core of social interaction?

Are there genuine social action features?

MN and affordance theorists both use intuitive action categories, such that the social dimension is predefined by the researcher rather than from observation-based analysis. For example, what makes a threatening person a social affordance rather than a physical affordance like a falling rock? Both similarly trigger defensive behaviors (e.g., blink, duck, parry) [3]. Do social affordances trigger defensive behaviors that have different action/motor primitives than environmental affordances? There are currently few analytical and quantitative approaches to social perception that do not presuppose commonsense action descriptions assumed by the experimenter and/or rooted in natural language [4]. Using data-driven clustering of ethological recordings may reveal additional, possibly different action classes and different motor primitives and hierarchies than those provided by naïve observations (e.g., [5]).

How does the visual system perceive conspecifics, and do MNs play a core role?

Bonini et al. do not explore whether actions in response to social or physical affordances have different motor primitives

and hierarchies [1]. Instead, they propose that there is 'neural selectivity for information related to others' ([1], see p. 3). These other-selective neurons coexist with MNs and are found in areas intermingled with MNs. Furthermore, 'Neural selectivity for other related information [is found]…in areas in brain regions devoted to self-related processes' ([1], see p. 4). This spatial coexistence of other, mirror, and self neurons appears as the core mechanism of social perception. Is there independent evidence for 'other neurons' or do MNs play a direct role in conspecific perception? Human and non-human primate experiments have established that 'other' or conspecific perception is not sustained primarily by MNs but by a cortical network engaged in the visual analysis of bodies including ventral and dorsal areas as well as subcortical structures [6,7]. We do not currently understand how 'other' specific processes of visual analysis interface with MN activity but they are best viewed as distinct processes and networks.

How can a neural account be provided for prediction at the core of social interaction?

A behavior is not social simply because it involves people rather than objects, but because of the inherent reciprocity between agents' actions [8,9]. MN and social affordance approaches focus on shared coding and synchronization between agents but do not emphasize the predictive nature of social interaction. To prepare a defensive action, the victim will predict the expected reaction of the aggressor to the victim's intended defense reaction. The movement specifics of the observed threat behavior allow the victim to predict how the attacker will react to any defense behavior and optimize it. This is well illustrated in research on threat behavior. Pre-encounter, post-encounter, and actual strike situations are associated with a range of different behaviors, and each includes a different calculation of the future behavioral response of the aggressor

[8,10]. This dynamic reciprocity dimension seems to not be present in the notion of MNs/social affordances.

Concluding remarks

MN and affordance theory each on their own started from the important insight that organism–environment behavior and the underlying brain and neurobiology are not properly understood at just the physical level. However, combining both traditions does not, by itself, clarify what makes affordances social, nor does it clarify how MNs contribute to understanding affordances. Here I sketched three essential roads toward developing the intuitions and motivations for progress in social brain research.

¹Department of Cognitive Neuroscience, Faculty of Psychology and Neuroscience, Maastricht University, Maastricht, The Netherlands
²Department of Computer Science, University College London, London, UK

*Correspondence:
b.degelder@maastrichtuniversity.nl (B. de Gelder).

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