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**Beyond action-specific simulation:
Domain-general motor contributions to perception**

Clare Press¹ and Richard Cook^{2*}

¹Department of Psychological Sciences, Birkbeck, University of London,
Malet Street, London, UK

²Department of Psychology, City University London,
Whiskin Street, London, UK

*Corresponding author: Richard.Cook.1@city.ac.uk
Tel: +44 20 7040 8644, Fax: +44 20 7040 8877

Highlights

- Motor processes influence the visual perception of a wide range of events
- These mechanisms likely operate equivalently across social and non-social domains
- It is unclear whether action perception benefits from a special motor contribution

Abstract

Preoccupation with action-specific simulation theory, whereby covert imitation is thought to facilitate action interpretation, has overshadowed evidence that motor structures facilitate perception of numerous visual events extending far beyond others' actions. In light of these domain-general motor contributions to perception, the case for a special role of motor representation in human action perception may be far weaker than widely believed.

Key words:

Mirror neurons, action simulation, domain-specific, domain-general, motor theories

Action-specific simulation theory

Several authors have argued that internal action simulation, a process likened to covert imitation, contributes to the visual perception of others' actions. Modelling observed actions in this way is thought to help us make sense of these actions, allowing a better understanding of the actor's goal or motivation [e.g., 1]. For example, simulating a friend grasping a cup of coffee may help an observer infer that his partner intends to drink to satisfy her thirst. Importantly, it is hypothesized that action perception benefits from a unique kind of motor contribution, domain-specific processes recruited during the observation of human action (Box 1). Simulation theories of action perception have seen a remarkable renaissance following the discovery of mirror neurons, cells in the macaque premotor cortex that respond during passive action observation [2].

Although the discovery of mirror neurons stimulated interest in simulation theories, their field properties are not direct evidence of a causal motor contribution to perception. Their responses may be a consequence, not a cause, of action recognition [2, 3]. Nevertheless, studies examining the effects of motor interference indicate that motor processes do indeed make a causal contribution to action perception. For example, inducing a motor load through performance of a concurrent task modulates action perception [4]. Similarly, action recognition is impaired by neuropsychological lesions [3] and the application of disruptive transcranial magnetic stimulation [5] to premotor cortex (PMC).

These convergent results have been widely interpreted as evidence that action-specific simulation processes inform action perception. However, the effects described are also consistent with a domain-general framework, whereby the perception of actions and non-action events benefit from conceptually equivalent motor contributions. Consistent

with this suggestion, considerable evidence suggests that motor processes determine how, where and when we perceive numerous visual events unrelated to action.

Domain-general motor contributions to perception

Examination of the properties of the human motor system suggests that it has the capacity to influence perception of the physical environment. For example, neuronal populations in PMC and primary motor cortex encode simple parameters of planned and executed actions, including effector direction, position and velocity [2], attributes that describe events in both our physical and social environments. Cortical motor areas have been implicated in interval timing [6], contain populations of canonical neurons responsive to the sight of objects [2], and are intricately connected with oculomotor and attentional orienting mechanisms [7]. Given these properties, it is unsurprising that many findings implicate the motor system in the perception of physical events triggered by natural or mechanical forces [8]. The summary below is not exhaustive but illustrates how motor processes may contribute to the perception of visual events beyond action-specific simulation (see Figure 1).

Early visual processing. Several high-level visual areas have been implicated in action perception, notably the superior temporal sulcus [2]. However, recent evidence suggests that feedback from the motor system modulates neural responses throughout the visual system, most strikingly, in early visual areas responsible for processing simple stimulus features. For example, when head-fixed mice are placed on a spherical treadmill, self-motion is known to modulate the tuning of neural responses to stimulus orientation and size in V1 and the dorsolateral geniculate nucleus of the thalamus [9].

Temporal perception. Motor structures, including the PMC, cerebellum, basal ganglia and supplementary motor area (SMA), are thought to mediate interval timing [6, 8].

Neurons in medial motor areas of the macaque, in particular the SMA and pre-SMA, are recruited during interval timing tasks and neuroimaging studies suggest a similar role for these areas in humans. For example, judging the duration of arbitrary visual stimuli disproportionately recruits SMA relative to colour judgements about the same stimuli [6]. Patients with ventrolateral lesions of PMC also exhibit impaired learning of the temporal structure of sequences of arbitrary visual events [8].

Spatiotemporal integration and manipulation. Motor processes also inform spatiotemporal integration and manipulation in human observers. The rapid alternation of lights in a circular array gives rise to a bistable percept of apparent motion that can be perceived as either clockwise or counter-clockwise rotation. However, performing concurrent rotating movements biases perception in favour of the compatible direction [10]. The motor system also contributes to the representation of relative-phase, the degree to which stimulus elements move together. Hard-to-perform phase relationships are hard-to-perceive, and tapping performance interferes with visual phase matching [11]. Finally, motor processes aid the mental rotation of abstract forms. For example, performance on tasks that require participants to match mentally rotated shapes is improved when participants twist their bodies in the congruent direction, whereas incongruous twisting impairs matching [12].

Attentional selection. Findings with human observers suggest a close association between action preparation and domain-general mechanisms of attentional selection. For example, the preparation of movement on the left or right increases the magnitude of event related potentials, recorded using electroencephalography, to light-flashes in corresponding locations [7]. Similarly, tasks requiring observers to grasp a target shift attention toward action-relevant features (e.g., orientation) and away from action-irrelevant features (e.g., colour) during visual search [13].

Acquired sensorimotor prediction. Although the phylogenetic and ontogenetic origins of some mechanisms underlying motor contributions to perception remain uncertain, others clearly result from an individual's sensorimotor experience. For example, training studies with human observers indicate that action preparation can activate visual representations of arbitrary stimuli following periods of correlated 'doing and seeing'. Having been trained to expect differently oriented Gabor patches after right and left key-presses, participants are worse at detecting patches when they follow actions in a manner incongruous with training [14]. Additionally, having paired one key-press with faces and another with houses, these responses elicit greater activation in the fusiform face area and parahippocampal place area, respectively, in the absence of face or house stimuli [15].

Re-thinking the role of the motor system during action perception

The range of domain-general motor contributions to perception complicates interpretation of the effects of motor interference on action perception. Consider the recognition of point-light walkers, a popular paradigm in this literature. Extracting a coherent percept likely requires domain-general attentional processes, particularly when observers have to disregard noise dots. Inferring limb kinematics often necessitates perception of cycle duration and computation of local and global spatiotemporal change. Moreover, to recognise walking and running, actions defined by prominent relative-phase relationships, observers must identify that left and right limbs oscillate in anti-phase. Given the contribution of domain-general motor processes at each of these perceptual stages, impaired recognition of point-light walkers following motor interference [4] can be readily explained without appealing to action-specific simulation.

To demonstrate that action perception recruits a ‘special’ motor contribution, researchers must compare the effects of motor interference on closely matched action and non-action perceptual tasks; i.e., using non-action stimuli of comparable spatiotemporal complexity, to which it is equally easy to attend, and with which observers have equivalent sensorimotor experience. Under these conditions, disproportionate impairment of action recognition would suggest an action-specific motor contribution to perception. To date however, it is common for authors to examine the effects of motor manipulations on action perception only (e.g., [4]), or use non-action tasks that differ substantially in their ability to recruit domain-general mechanisms. For example, non-action stimuli are often simple in appearance (e.g., uniformly shaded geometric shapes) and animated with constant velocity motion (e.g., [5]). In contrast, action stimuli depict complex natural forms, animated with variable ‘minimum-jerk’ kinematics, whereby movements slow characteristically at turning points in the trajectory. Moreover, these action and non-action conditions differ in terms of correlated sensorimotor experience: Although our actions frequently predict features of observed actions, both our own and those of interactants, they rarely predict the onset or kinematics of geometric forms.

Is there a motor contribution recruited during the observation of human grasping that could not be recruited by the sight of a mechanical digger pivoting and scooping? This question captures the essence of our argument. When a passer-by observes the digger, motor feedback may influence early visual representations and further shape perception through mechanisms of interval timing, spatiotemporal integration, mental rotation and attentional selection. Moreover, when viewed by its operator, the digger’s movements may recruit acquired sensorimotor predictions: Unlike the passer-by, the operator has extensive sensorimotor experience whereby the movements of the digger’s scoop are exquisitely predicted by his actions in the cabin. These

contingencies may afford perceptual predictions conceptually equivalent to those acquired during sensorimotor training in the laboratory [14, 15]. Despite its mechanical form and kinematics, the digger may thus have the potential to recruit very similar motor contributions to perception to those recruited by the sight of grasping [5].

Concluding Remarks

Action-specific simulation theories, advocating a special role for the motor system in the interpretation of others' actions, have received considerable attention both from scientists and the popular media. However, many of the core assumptions of these models remain untested. We have highlighted how the motor system influences perception of visual events beyond the perception of others' actions. The breadth of these motor contributions underscores the pervasive role played by motor processes in visual perception and suggests that the case for a special motor contribution recruited by human action is far weaker than widely believed.

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Box 1: What makes a motor theory 'action-specific'?

Under a domain-general framework, action and non-action stimuli have the potential to recruit equivalent motor contributions to perception. By contrast, action-specific theories posit motor contributions to perception that exhibit tuning to observed action; i.e., mechanisms are recruited preferentially by stimuli exhibiting human form or kinematics, irrespective of correlated sensorimotor experience. Examination of the hypothesized neural substrate, cognitive mechanism and adaptive function of recent motor theories (e.g., [1]), indicates that they are action-specific; that non-action stimuli do not have the same potential to recruit the hypothesized motor contributions to perception as actions.

1) Neural substrate: It is proposed that the neural substrate mediating the hypothesized motor contributions is the mirror neuron system, and that this system always responds selectively to the observation of action (see [2] for a different perspective). Motor contributions mediated by such a substrate will therefore be preferentially recruited by actions.

2) Cognitive mechanism: Invoking action simulation, defined as covert imitation, as a mechanism, would be widely taken to imply action tuning. Close imitation, either covert or overt, requires an anatomical match between the mimic and the mimicked. For example, human actors can imitate the actions of other humans closely, can simulate a dog running only approximately, and have little or no capacity to simulate waves breaking on a shore [8]. The utility of motor contributions derived from simulation, thus defined, would therefore be greater when observing the actions of conspecifics than for physical events.

3) Adaptive function: Motor contributions that operate in order to yield insights about an actor's goal or intention will be tuned to the actions of living beings, insofar as motivational states are not attributed to inanimate objects: a Gabor-patch does not intend to change its orientation and oscillation is not the goal of a windshield wiper.

Figure

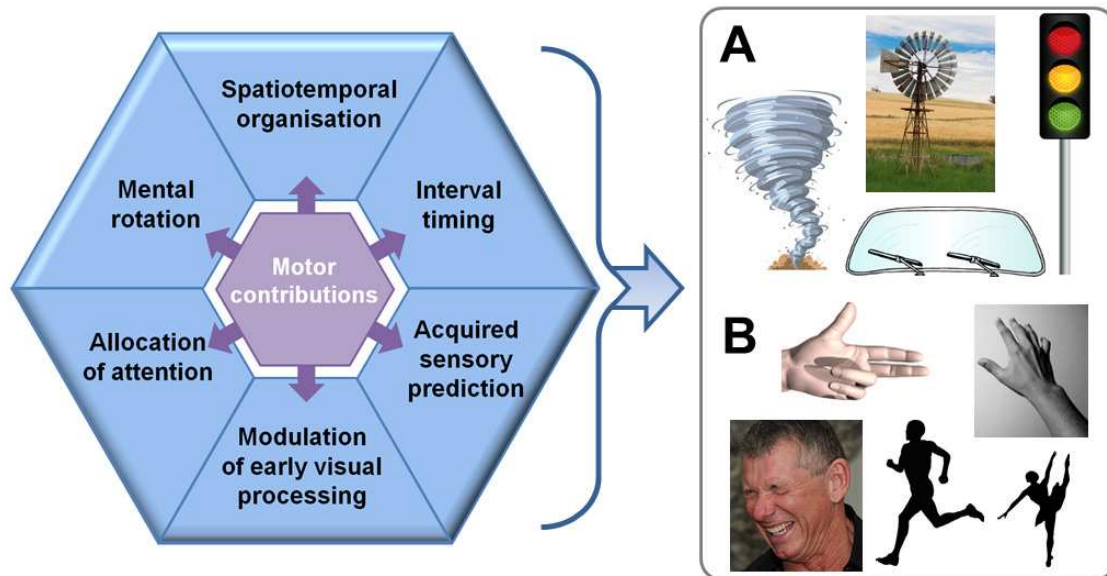


Figure 1: Domain-general motor contributions to perception

Considerable evidence suggests that the motor system contributes to the perception of visual events via a number of mechanisms, aiding perception of both our physical (A) and social (B) environments. Thus, motor-mediated effects on action perception may not reveal action-specific simulation processes, but rather motor effects on stimulus attributes reflected in early sensory processing, interval timing, spatiotemporal integration, mental rotation, attentional selection, or sensorimotor predictions acquired through experience.

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