

Perception as a Route for Motor Skill Learning: Perspectives from Neuroscience

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Abstract—Learning a motor skill requires physical practice that engages neural networks involved in movement. These networks have also been found to be engaged during perception of sensory signals associated with actions. Nonetheless, despite extensive evidence for the existence of such sensory-evoked neural activity in motor pathways, much less is known about their contribution to learning and actual changes in behavior. Primate studies usually involve an overlearned task while studies in humans have largely focused on characterizing activity of the action observation network (AON) in the context of action understanding, theory of mind, and social interactions. Relatively few studies examined neural plasticity induced by perception and its role in transfer of motor knowledge. Here, we review this body of literature and point to future directions for the development of alternative, physiologically grounded ways in which sensory signals could be harnessed to improve motor skills. © 2018 Published by Elsevier Ltd on behalf of IBRO.

Key words: motor skill learning, action perception, sensory feedback, human.

INTRODUCTION

In the process of learning, as the idiom states, ‘practice makes perfect’. However, performance gains can be attained through many different forms of practice, and what constitutes optimal practice is still an active field of scientific research pursued across multiple disciplines including psychology, education, neuroscience, sports, music, artificial intelligence, child development and also clinical fields of rehabilitation such as physical and occupational therapy. When acquiring new motor-skills, voluntary physical movement is considered most efficient for inducing short- and long-term changes in performance. Nonetheless, training that involves physical movement can be highly demanding and time consuming. It can take months or years for one to master highly complex motor skills such as those performed by professional athletes, or musicians. Moreover, this form of practice is extremely challenging in the context of rehabilitation following neurological insult, in which voluntary control of the affected limb is

very limited or absent altogether. Therefore, finding alternatives to voluntary physical movement as a means for improvement in motor skill performance is of great importance. Gaining a better understanding of the underlying biological processes that support the acquisition of motor skills is a necessary step in the development of such alternatives.

During the past two decades, a growing body of literature has demonstrated that sensory signals, especially those associated with actions, elicit significant neural activity in brain regions formerly considered as predominantly responsible for their overt execution (Rizzolatti and Sinigaglia, 2016). The fact that passive action perception and overt motor execution share neural representations raises the exciting possibility that sensory signals may be used as an alternative, or in addition to, physical practice, to modify and improve performance of motor skills. Although this potential is well recognized, and generally accepted, there is paucity of data to support it, and the underlying mechanism by which sensory signals affect motor performance and learning remains unclear.

In the current manuscript, we review existing behavioral and neural evidence showing that action perception not only evokes activity in motor pathways but also modifies behavior and facilitates learning. We begin by characterizing sensory-evoked neural activity in motor pathways, continue with how action perception implicitly modifies short-term behavior, and then

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Abbreviations: AON, action observation network; CP, Cerebral Palsy; FES, functional electric stimulation; IFG, inferior frontal gyrus; MEP, motor-evoked potentials; PD, Parkinson’s disease; rsfMRI, resting-state functional connectivity; SMA, supplementary motor area; SPL, superior parietal lobule; TMS, transcranial magnetic stimulation; TMS, transcranial magnetic stimulation; VR, virtual reality.

59 highlight the effects of perception on motor skill
60 acquisition. We conclude by pointing to future directions
61 for the development of alternative, physiologically
62 grounded ways in which sensory signals could be
63 harnessed to improve motor skills. Although imitation is
64 a highly efficient form of learning that relies heavily on
65 action perception, it entails concurrent voluntary
66 physical movement during the training (imitation) phase
67 and therefore beyond the scope of this review (Hurley
68 and Chater, 2005).

69 ACTION PERCEPTION ELICITS NEURAL 70 ACTIVITY IN MOTOR PATHWAYS

71 Perception and action have been traditionally considered
72 distinct and independent neural processes. Perceptual
73 mechanisms provide information about the external
74 world, while action-related mechanisms are involved in
75 selection, preparation and execution of goal-directed
76 behavior. However, the ideomotor principle, first
77 described by Lotze (1852) and James (1890), suggests
78 that these two functions share common representations
79 at the behavioral and physiological levels, and are there-
80 fore linked. This prominent idea has provided the basis for
81 the Common Coding approach (Prinz, 1997) and the The-
82 ory of Event Coding (Hommel, 2009; Shin et al., 2010).
83 These theories posit that the final stages of perception
84 and the early stages of action generation share common
85 features that allow a translation of information from one
86 system to another. For example, according to the Theory
87 of Event Coding, perceived events are represented in the
88 same format as planned actions. It is therefore plausible
89 that neural changes in sensory systems (e.g., visual,
90 auditory or tactile), lead to neural changes in the motor
91 system, and vice versa.

92 Evidence from animals

93 At the physiological level, substantial evidence has
94 accumulated over the last two decades for the notion of
95 sensory-evoked neural activity in motor pathways. The
96 most influential discovery was of a particular class of
97 visuo-motor cells that discharge not only when
98 executing an action but also when passively perceiving
99 similar actions performed by someone else (Rizzolatti
100 and Sinigaglia, 2016). These neurons, termed mirror neu-
101 rons, were originally discovered using single cell record-
102 ings in sector F5 of the ventral premotor cortex of
103 macaque monkeys (di Pellegrino et al., 1992; Gallese
104 et al., 1996; Rizzolatti et al., 1996). Following the original
105 discovery, the existence of mirror neurons has been
106 demonstrated in other regions of the monkey motor path-
107 way, including primary, premotor and parietal regions
108 (Fogassi et al., 2005; Tkach et al., 2007; Kraskov et al.,
109 2009; Dushanova and Donoghue, 2010; Vigneswaran
110 et al., 2013). Although extensively studied in the visual
111 domain, mirror neurons with audio-motor properties have
112 also been reported (Kohler et al., 2002; Keysers et al.,
113 2003). Today, neurons with mirroring properties have
114 been reported also in marmosets (Suzuki et al., 2015)
115 and song birds (Prather et al., 2008; Keller and

Hahnloser, 2009), demonstrating the pervasive nature of
such sensory-evoked neural activity in motor pathways
across the phylogenetic line.

Evidence from humans

In humans, the opportunities to directly record neural
activity are rare, and limited to specific clinical
situations. Nevertheless, one study with epileptic
patients provides direct evidence for the existence of
cells with mirroring properties in the supplementary
motor area (SMA), and also limbic areas such as the
Hippocampus, Para-Hippocampal Gyrus and Entorhinal
Cortex (Mukamel et al., 2010). Extensive indirect evi-
dence using non-invasive techniques (such as functional
magnetic resonance imaging; fMRI), suggests that the
anatomical distribution of regions with overlapping repre-
sentations of executed and perceived actions might con-
stitute a functional network (Buccino et al., 2001;
Gazzola and Keysers, 2009; Caspers et al., 2010;
Molenberghs et al., 2012). However, since the ability to
perform physical movement in an fMRI scanner is limited,
most studies rely on visual depictions of actions to delin-
eate an 'action-observation-network' (AON) (Cross
et al., 2009) which is responsive to visual perception of
actions performed by others. This network comprises
frontal and parietal regions typically considered as part
of the motor pathway (e.g., premotor, and supplementary
motor areas). Interestingly, some regions within the AON
respond to subliminally presented actions (i.e., in lack of
reported conscious perception) while other regions are
sensitive to the degree of visual awareness (Simon and
Mukamel, 2017). Evidence from other techniques such
as EEG (Muthukumaraswamy and Johnson, 2004;
Simon and Mukamel, 2016), MEG (Hari et al., 1998)
and transcranial magnetic stimulation (TMS) (Fadiga
et al., 1995) provide further support for sensory-evoked
responses in motor regions. Once again, although mainly
studied in the visual domain, there is ample evidence sup-
porting the existence of audio-motor mirroring properties
in humans as well (Hauelsen and Knosche, 2001; Lahav
et al., 2007; Margulis et al., 2009).

ACTION PERCEPTION INDUCES IMPLICIT CHANGES IN MOTOR PERFORMANCE

Action-related sensory input (such as observing someone
else perform an action) not only evokes neural activity in
motor pathways, but also implicitly affects motor
behavior. For example, during social interactions,
people tend to adopt the gestures and mannerisms of
interacting partners in an automatic, often unconscious
manner (Chartrand and Bargh, 1999; Kuhn et al., 2010).
Priming effects of observed actions have also been
reported – either facilitating or interfering with ongoing
actions even when the perceived actions do not directly
pertain to the task (Sturmer et al., 2000; Craighero
et al., 2002; Kilner et al., 2003; Ferguson and Bargh,
2004). Mere action observation has been shown to implic-
itly modulate various movement parameters such as grip
force (Salama et al., 2011), squeeze force (Obhi and

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