

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 IBRO. Published by Elsevier Ltd. All rights reserved.

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.

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

ACTION PERCEPTION ELICITS NEURAL ACTIVITY IN MOTOR PATHWAYS

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

Evidence from animals

At the physiological level, substantial evidence has accumulated over the last two decades for the notion of sensory-evoked neural activity in motor pathways. The most influential discovery was of a particular class of visuo-motor cells that discharge not only when executing an action but also when passively perceiving similar actions performed by someone else (Rizzolatti and Sinigaglia, 2016). These neurons, termed mirror neurons, were originally discovered using single cell recordings in sector F5 of the ventral premotor cortex of macaque monkeys (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). Following the original discovery, the existence of mirror neurons has been demonstrated in other regions of the monkey motor pathway, including primary, premotor and parietal regions (Fogassi et al., 2005; Tkach et al., 2007; Kraskov et al., 2009; Dushanova and Donoghue, 2010; Vigneswaran et al., 2013). Although extensively studied in the visual domain, mirror neurons with audio-motor properties have also been reported (Kohler et al., 2002; Keysers et al., 2003). Today, neurons with mirroring properties have been reported also in marmosets (Suzuki et al., 2015) 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 evidence using non-invasive techniques (such as functional magnetic resonance imaging; fMRI), suggests that the anatomical distribution of regions with overlapping representations of executed and perceived actions might constitute 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 delineate 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 supporting the existence of audio-motor mirroring properties in humans as well (Haueisen 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 implicitly modulate various movement parameters such as grip force (Salama et al., 2011), squeeze force (Obhi and

Hogeveen, 2010), movement trajectory (Hardwick and Edwards, 2011) and movement velocity (Bisio et al., 2010).

Moreover, implicit changes in performance have been reported in studies implementing force-field perturbations during reaching movements. A seminal study demonstrates that subjects implicitly learn the direction of the force-field in observational training. This is reflected by a reduced curvature of hand trajectory in post-observation test sessions (Mattar and Gribble, 2005). Furthermore, such learning seems to be invariant to the laterality of the observed hand – with similar levels of right-hand learning following observation of right or left hand during training (Williams and Gribble, 2012). Finally, studies investigating rhythmic movements report that spontaneous execution rate is implicitly biased by the rate of a previously observed action (Bove et al., 2009; Avanzino et al., 2015; Lagravinese et al., 2016).

Along with the behavioral findings, there is a relatively small body of literature that examined the link between neural activation during perception, and subsequent implicit changes in behavior. In a recent fMRI study, Aridan and Mukamel asked subjects to perform a serial finger tapping task at their own pace before and after observing a video of someone else performing the same task. Action observation resulted in an implicit change in self-paced tapping rate, which was absent when subjects did not observe the video. Importantly, the level of fMRI activity during observation in the left motor strip (contralateral to the observed hand), correlated with subsequent behavioral changes in the spontaneous tapping rate across subjects (Aridan and Mukamel, 2016). The involvement of primary motor cortex (M1) in behavioral changes due to action observation is further supported by several TMS studies reporting changes in motor-evoked potentials (MEP) that occur following a single 10-min observation session (Avanzino et al., 2015) and following several days of observational training (Stefan et al., 2005; Lagravinese et al., 2016). Conversely, inhibitory repetitive TMS (rTMS) applied to M1 following observational training disrupts behavioral effects of action observation (Brown et al., 2009). However, since TMS effects can propagate along the network connected to the stimulated region, the regional specificity of such findings is uncertain and might reflect changes in corticospinal excitability in other regions (such as premotor cortex; Valero-Cabré et al., 2017). Taken together, these studies provide substantial evidence that sensory-evoked neural activity in motor pathways plays a significant role in inducing implicit changes in motor performance following action perception.

Another line of research implicates the somatosensory cortex and cerebellum in observational learning. Using TMS, it has been shown that synchronizing peripheral nerve stimulation with the finger-closing phase during observation of a finger opposition task, enhances post-training MEPs (Bisio et al., 2015). In a study by McGregor and colleagues, subjects observed a model performing right hand reaching movements in the presence of a perturbing force-field (McGregor et al., 2016). Engagement of somatosensory

cortex during training (by applying concurrent electrical stimulation of the arm) disrupted observational learning effects when stimulation was applied to the right but not the left hand. Additionally, post-training modulations in somatosensory-evoked potentials (measured with EEG) corresponded with individual differences in learning. Imaging studies using the same force-field reaching task report that the levels of resting-state functional connectivity (rsfMRI) between left primary somatosensory cortex (S1) and a network of regions including bilateral PMd, bilateral M1, and left SPL, prior to observational training is a predictive marker of post-training performance scores (McGregor and Gribble, 2017). In another study, changes in rsfMRI between visual areas (V5/MT) and sensorimotor cortex (M1 and S1) and cerebellum following training corresponded with motor learning scores (McGregor and Gribble, 2015). It should be noted that the cerebellum is not typically reported in action observation studies (for large scale meta-analysis see (Caspers et al., 2010; Hardwick et al., 2017)). This suggests that cerebellar activation may be driven by an interaction between action observation and motor learning. Taken together, the behavioral and neural evidence suggest that observing actions performed by others evokes activity in primary motor and somatosensory cortex and can implicitly modulate behavior through the engagement of cerebellar and pre-motor regions. It should be noted that some of the tasks described above induce changes in behavior while other tasks induce learning (i.e., improvement in performance). For example, a change in spontaneous tapping rate from 2 to 3 Hz following observation is a change in behavior rather than learning (there is no element of improved performance). On the other hand, the tasks involving reaching in the presence of a perturbing force field do induce learning, since subjects exhibit improved performance relative to task instruction (e.g., perform an arm movement as straight as possible to reach the target). Regardless of change in behavior or learning, what is common to all tasks described above is that subjects were not explicitly instructed and are often not consciously aware of the manipulation. In what follows, we describe studies in which action perception is explicitly used for the purpose of learning.

ACTION PERCEPTION IMPROVES MOTOR SKILLS

During implicit transfer of motor behavior subjects are not instructed to observe the model for the purpose of improvement in task performance. Although stimuli are presented well above perception level, the perceptual manipulation is covert. Subjects are usually engaged in an orthogonal task or are unaware of the fact that their performance on the task will be subsequently re-evaluated. In some tasks (such as rhythmic finger tapping movements), it is impossible to ascribe changes in behavior to a learning process, since task instructions do not imply that any post-training tapping rate is better than the other. In the current section we discuss studies in which subjects attended sensory signals through

various modalities for the explicit intention of subsequent improvement on task performance (learning).

Sensory input in the visual modality

In humans, vision is a dominant sensory modality that induces learning. Using a ball rotation task, Nojima and colleagues showed improvements in performance following observation that were accompanied by increased MEPs, evoked by TMS over M1 (Nojima et al., 2015). In a study by Cross and colleagues, subjects learned to perform unique sequences of dance steps either through active training or through passively observing a video depicting someone else performing the sequence (Cross et al., 2009). Training sessions lasted five days and were accompanied by pre-, and post-training fMRI sessions. During fMRI sessions, subjects observed videos of dance sequences that they either learned by physical training or by observation. Activity in the left inferior parietal lobule (IPL) and the right inferior frontal gyrus (IFG) was stronger during observation of sequences that were trained relative to sequences that were not. Interestingly, this was true irrespective of training type (either physical or observation), suggesting an overlap between the two learning processes in these regions. In another study, Kirsch & Cross manipulated the sensory modality by which subjects were trained: audition (i.e., hearing the sound track accompanying a dance sequence; A), vision + audition (i.e., adding the video to the sound track; VA), or vision + audition + concomitant physical practice (PVA condition) (Kirsch and Cross, 2015). Following training, overlapping fMRI activity during observation of dance sequences trained in the VA and PVA condition was found in left pre-motor cortex, left intraparietal cortex, left superior frontal gyrus, and left posterior cingulate. Once again, these results suggest an overlap of training effects in these frontal-parietal circuits for physical and perceptual training.

Given the high degree of laterality in neural activity during execution, it was hypothesized that similar laterality would be obtained during action observation. Using a finger opposition task, Ossmy and Mukamel examined sensitivity of the neural networks subserving short-term observational learning, to the laterality (right/left) of the observed hand (Ossmy and Mukamel, 2016a). To this end, subjects learned sequences of finger movements inside the fMRI scanner by passively observing a right or left hand performing the task. In agreement with a previous behavioral study (Williams and Gribble, 2012), significant performance gains were obtained in both hands irrespective of observed hand laterality during training. However, across subjects, left hand observation resulted in positive correlation between left and right hand performance gains, while right hand observation resulted in negative correlation between hands (i.e., individuals exhibiting high performance gains in the right hand exhibited low gains in the left). Remarkably, this behavioral asymmetry is reflected by activity in superior parietal lobule (SPL) contralateral to the laterality of the observed hand. Thus during observational training, fMRI activity level in the SPL contralateral to the laterality of the

observed hand (right/left), predicted the subsequent performance gains in both hands.

While laterality of observed hand seems to influence learning, the size of observed hand does not (at least for short-term learning). In a behavioral study with adults, Ossmy and Mukamel, manipulated the size of observed virtual hands during separate sessions of physical training and training by observation (Ossmy and Mukamel, 2017a). Although larger virtual hand size during physical training resulted in increased performance gains, no such effect was found during training by observation – suggesting that despite the many overlaps in neural circuitry discussed above, there are still important differences between training by observation and physical training that deserve further exploration. An interesting open question is whether insensitivity to size during observation in adults also holds in young children. Children often learn by observing adult models, and performing the task requires a scaling transformation in order to map the visual input to the proportions of the child's smaller body. Therefore it will be interesting to see whether sensitivity to observed hand size will be found in children and whether it can explain individual differences in learning.

Sensory input in the proprioception modality

In addition to visual input, proprioceptive signals also play an important role in motor skill learning. Passive limb movement by an external source (e.g., robot or trainer), has been shown to introduce significant performance gains (Aman et al., 2014). At the behavioral level, passive movement has been shown to facilitate performance on various tasks such as drawing (Wong et al., 2012), reaching (Bernardi et al., 2015) and golf swinging (Kummel et al., 2014). Training by passive movement also facilitates learning of visuomotor rotation tasks (Cressman and Henriques, 2010; Sakamoto and Kondo, 2015). In some of the tasks described above the magnitude of learning effects were even similar for passive and active training. Interestingly, integrating learning by passive movement with learning by observation yields superior learning on a visuomotor rotation task relative to either form of training alone, but still inferior to actual physical training (Lei et al., 2016). Passive movement has been reported to have beneficial effects not only in unimanual but also in bimanual tasks (Beets et al., 2012). Thus, these studies suggest that although in most cases physical training is superior to training by passive movement, significant learning can still occur in the absence of voluntary drive and can be enhanced by combining various sensory modalities.

At the neural level, active and passive wrist flexion/extension or elbow movements have been shown to engage similar sensorimotor networks including parietal, motor, pre-motor and SMA regions contralateral to the moving limb (Szameitat et al., 2012; Estevez et al., 2014). With respect to plasticity, there is paucity of neural data and the literature is less consistent. In one study, one hour of passive cyclic wrist movement has been reported to facilitate motor-evoked potentials following TMS over contralateral motor cortex (Mace et al., 2008).

Conversely, another study reports that 30 min of training changes the direction of TMS-evoked thumb movement following active but not passive training (Kaelin-Lang et al., 2005). More consistent neuroimaging studies, show enhanced fMRI signal following passive training in regions such as primary motor cortex (M1), SMA and secondary somatosensory cortex (S2) (Carel et al., 2000; Lotze et al., 2003).

Thus training by passive movement introduces significant performance gains at the behavioral level and concomitant training-induced plastic changes in motor and somatosensory regions. Nonetheless, training by passive movement is not as effective as physical practice and engagement of volitional drive is still superior in terms of post-training performance gains. Elucidating the mechanisms by which volition drives motor-skill learning is an exciting topic for future research.

THE ROLE OF SENSORY FEEDBACK IN LEARNING

For the purpose of this manuscript we distinguish between two types of sensory signals. One type, which we term 'sensory input', is independent and not causally linked to the preceding actions of the perceiver. The second type – which we term 'sensory feedback', is a direct consequence of, and therefore causally linked to, the preceding motor acts of the perceiver. For example, when a guest presses a button to trigger the door-bell, we consider the evoked sound of the bell as auditory feedback with respect to the guest who pressed the button, but as auditory input with respect to the house residents. Thus a sensory signal with identical physical properties is treated differently depending on agentic point of reference (self or other). Sensory input has been mostly examined in the context of mirror neurons and the action-observation network (emphasizing sensory signals originating from *others*) – as discussed above. Sensory feedback has more often been examined in the context of motor control. Here we discuss the neural correlates of sensory feedback in the context of learning a motor skill.

As opposed to sensory input, sensory feedback is causally controlled by the training subject. In a recent neuroimaging study, subjects trained on a finger sequence task with their right hand either with or without visual feedback (Ossmy and Mukamel, 2016b). Visual feedback, when provided, was either congruent (i.e., subjects' real right hand finger movement controlled the movement of a right virtual hand), or incongruent (i.e., subjects' real right hand finger movement controlled left virtual hand movement). At the behavioral level, the addition of visual feedback during training modulated performance gains – such that congruent feedback increased and incongruent feedback decreased performance gains, relative to performance gains following training without visual feedback. At the neural level, fMRI activity levels in the SMA, and its functional connectivity with visual cortices predicted training induced changes in performance levels. In another recent study, subjects trained to perform hand grips at various force levels either with or

without visual feedback. Stronger trial-by-trial correlations were found between fMRI signal and task performance with (vs. without) visual feedback in bilateral PMd, IFG, posterior parietal cortex, V1, S2, and ACC (Mayhew et al., 2017). Ronsse and colleagues manipulated the sensory modality through which feedback was provided (visual or auditory) while subjects learned to perform a complex bimanual task (Ronsse et al., 2011). Although pre and post training performance levels were similar for the two sensory modalities, subjects who trained with visual feedback showed large performance decrements (i.e., reliance) when feedback was removed. At the neural level, the two training modalities resulted in changes within different neural pathways. Thus the existence of sensory feedback during training, and its modality, have important behavioral and neural consequences on the learning process.

Perturbations or manipulation of sensory input can also have important consequences on the learning process. One well-studied manipulation in the visual modality, is the use of mirrored visual feedback. TMS studies using mirrored visual feedback during training on a unimanual task report increased excitability in ipsilateral M1 (as measured by MEPs; Garry et al., 2005), and that such increased activity in M1 correlates with improvements in task performance with the non-trained ('mirrored') hand (Nojima et al., 2012). An fMRI study using mirror training reports training-induced changes in dorsal and ventral premotor cortex and supports the involvement of sensorimotor cortex ipsilateral to the non-trained hand in the learning process (Hamzei et al., 2012).

Rapid advances in the field of virtual reality (VR) allow sophisticated online manipulation of perceptual feedback in various sensory modalities such as visual (using 3D screens or head-mounted displays), auditory (using speakers or headphones), and tactile (robotic arms or vibrotactile actuators; for review see Sigrist et al., 2013). In a recent study, Ossmy and Mukamel developed a VR setup that allowed them to manipulate feedback in two sensory modalities – visual and proprioceptive (Ossmy and Mukamel, 2017b). Subjects learned to perform unique sequences of finger movements by physical training with their right hand, while receiving real-time movement-based visual feedback as if their immobile left hand was training. In agreement with previous studies, this visual manipulation resulted in significantly increased performance gains in the immobile hand following training. At the neural level, fMRI activation in left and right SPL and their degree of coupling with motor and visual cortex respectively, correlated with subsequent performance gains in the left, untrained hand (Ossmy and Mukamel, 2016b). Performance gains were further increased when left hand fingers were also passively moved by a device that yoked the left hand fingers to follow right hand voluntary finger movements during training. This supra-additive effect demonstrates that combining sensory modalities enhances learning and suggests that addition of other modalities (e.g., auditory) to existing manipulations might potentially further optimize learning.

In the context of bimanual tasks, a popular form for providing visual feedback that has been used is Lissajous plots. These plots provide a 2D representation of the relative phase of the two hands and have been shown to facilitate learning of complex bimanual phase relationships (Beets et al., 2012). At the neural level, training with such feedback has been reported to evoke significant training-induced changes in fMRI signal including both decreases and increases in motor related cortical and subcortical regions (Debaere et al., 2004).

Finally as mentioned earlier, size is yet another manipulation of visual feedback that can play a role in motor skill acquisition. In the context of pain, manipulating the size of visual feedback of a hand has been shown to modulate perceived pain in patients (Moseley et al., 2008; Ramachandran et al., 2009). In the context of learning motor skills, Ossmy and Mukamel manipulated the size of the visual feedback of virtual hands representing the subjects' real hands while physically training on a finger sequence task using their right hand (Ossmy and Mukamel, 2017a). Bigger virtual hand size feedback during physical training resulted in greater right hand performance gains – implying that compatibility between the size of the virtual hand and subject's real hand size facilitates learning (Ossmy and Mukamel, 2017a). Given the lack of such size effect during training by observation, the neural correlates of such size manipulations may provide important insight into the differences between perceptual and physical training.

Manipulation of sensory feedback during training has a strong behavioral impact on learning and task performance. Therefore elucidating the sensory features that need to be manipulated in order to induce improved learning is desirable. At the neural level, the addition and perturbation of sensory feedback modulates activity in sensorimotor networks. A better understanding of these networks may help guide neural perturbation studies (e.g., TMS) to target specific brain regions during the training process to facilitate learning.

ACTION PERCEPTION IN MOTOR REHABILITATION

The influence of action perception on motor performance is not limited to motor learning. It may also serve as an important scaffold for translational research. When training by voluntary movement is limited due to neurological deficits, the use of action perception as a substitute or training supplement in the rehabilitation process is appealing (Bassolino et al., 2015; Wenderoth, 2015). Indeed the powerful role of sensory input has been acknowledged and exploited in various clinical fields such as Parkinson's disease (PD), stroke, Cerebral Palsy (CP), and pain (Buccino, 2014). The methods by which sensory input or feedback are being used for therapeutic intervention include action observation, mirror therapy, and passive/assisted movements through the use of robot assistive devices or electrical stimulation.

The therapeutic benefits of visual input depicting actions have been examined by supplementing standard

rehabilitation procedures with sessions of passive action observation. For example, in a randomized trial with children suffering from CP, Sgnadurra and colleagues report that observation of videos depicting actions (rather than simply observing computer games), resulted in improved clinical scores that lasted up to 24 weeks post-training (Sgnadurra et al., 2013). In agreement with this behavioral result, using fMRI it has been shown in CP patients that passive observation of hand movements engages most of the nodes of the action-observation network identified in healthy participants (Dinomais et al., 2013). In PD patients, observation of repetitive finger tapping has been reported to increase self-paced tapping rate (Pelosin et al., 2013). Action observation sessions in stroke patients have also been shown to improve scores on the Box & Blocks test – improvements that lasted up to 4 months post-training (Franceschini et al., 2012). In a study with stroke patients, Ertlet and colleagues report significant improvement on various clinical scores lasting up to 8 weeks post training when action observation sessions (rather than observation of neutral visual stimuli) are interleaved with physical training (Ertlet et al., 2007). Furthermore, using fMRI, they show increased activity in visuomotor regions such as bilateral ventral premotor cortex, bilateral superior temporal gyrus, SMA and contralateral supramarginal gyrus in the experimental group. Finally, training by action observation has been also shown to prevent reductions in TMS evoked MEPs following arm immobilization using a cast (Bassolino et al., 2014).

Another form of intervention using visual signals is mirror therapy (Ramachandran and Altschuler, 2009). Through the use of mirror devices, visual input is manipulated such that active movement of one limb (typically the healthy one) is the source of visual input simulating movement of the opposite (clinically affected) limb. Thus, as opposed to passive action observation, in mirror therapy the subjects have direct causal influence over the visual input they receive. In stroke patients, Michielsen and colleagues show that mirror therapy improves clinical scores (Fugel-Meyer motor assessment) post-training relative to a control group (Michielsen et al., 2011). In addition, post training fMRI signals showed a shift in activation pattern toward the affected hemisphere.

Passive movement has also been shown to have beneficial therapeutic effects. In such training, the patient's limb is passively moved either by a robotic device or by a trained physiotherapist. Improved clinical scores have been shown in patients who suffered a cerebrovascular accident, following training using a robotic device to passively move their arm (Klamroth-Marganska et al., 2014). In another study with CP patients, combining passive movement (induced by the experimenter) with action observation, resulted in increased activity in contralesional pre-supplementary motor area, superior frontal gyrus (extending to premotor cortex), and superior and inferior parietal regions (Dinomais et al., 2013), suggesting that combining different sensory modalities (vision and passive movement) increases recruitment of motor regions and may have added beneficial therapeutic effects.

Finally, another form of assistive movement is functional electric stimulation (FES) which has been examined as a method to improve voluntary control of a limb following neurological insult (e.g., hemiparesis due to stroke). In this form of training, physical movement of the affected hand during training is induced by direct electrical stimulation of the muscles (for review see [Hayashibe 2016](#) and [Nussbaum et al. 2017](#)). The stimulation can be triggered by an external source (computer/clinician), or the patient himself. In the case of self-triggered stimulation, it could be either through use of the voluntarily-controlled non-affected hand, or by detection of partial initial movement of the affected hand. A meta-analysis suggests that volitional control of stimulation, is more effective than stimulation controlled by an external source (computer or physiotherapist) in terms of clinical outcome measures ([de Kroon et al. 2005](#)); see also [Shen et al. 2015](#)). Nonetheless, the effectiveness of FES relative to other methods is still debated given that some studies show improvement over conventional methods ([Sentandreu Mano et al., 2011](#), [Stein et al. 2015](#)) and others reporting no advantage ([McCabe et al. 2015](#)).

Thus an accumulating body of literature supports positive effects of action observation training and passive movement in various pathologies and rehabilitation contexts. However, it is important to note that these effects are modest and limited to specific outcome measures which do not always translate to actual improvement in patient's quality of life. Furthermore, group sample size in most studies is low. Given that performance gains following perceptual training are usually smaller than those obtained following actual physical training, it places a limitation on the expected performance gains following perceptual training. Nonetheless, since voluntary physical movement in some patient populations is severely impaired, these studies provide a promising avenue for future research in developing alternative forms of training to facilitate neuro-rehabilitation.

CONCLUDING REMARKS

There are many parallels between perception and overt execution of actions. Both have been shown to induce learning and both engage similar neural networks. In the current manuscript we reviewed three key topics with respect to perception of sensory signals and their role in motor skill learning: implicit changes in motor behavior, explicit learning from sensory signals produced by others and self, and the benefits of using sensory signals in rehabilitation. We examined this issue from both a behavioral and neural perspective. In reviewing these topics, we try to point to open questions and future directions of study.

At the neural level, sensory signals evoke activity in brain networks traditionally considered for their role in motor output. In some regions within the motor network, evoked activity does not seem to depend on subject's level of perception. At the behavioral level, perception is associated with priming effects and learning which can

also occur implicitly, in the absence of subject's conscious awareness. Despite these parallels, between sensory-driven changes in behavior and evoked neural activity in motor pathways, causal evidence linking the two phenomena is still missing, and the role of conscious awareness in the learning process remains to be further elucidated. Moreover, significant differences at the behavioral and neural levels exist between perceptual training (based on sensory signals) and physical training. For example, sensitivity to feedback size was only found during physical training and not observational training. Further exploration of such differences is needed and may provide important insights about the mechanisms of the two forms of learning.

Another open issue that deserves further attention concerns the dimensions of sensory signals that are important for learning. Issues of perspective (observing a hand from a first or third person perspective during training), laterality (learning from right hand observation or left hand observation), or size, are dimensions that have been only recently explored. Most of the current literature has focused on sensory signals in the visual and proprioceptive modalities. Since existing evidence suggests that the combination of vision and proprioception yields enhanced performance gains compared to each modality in isolation, adding other modalities (e.g., audition) holds promise for more effective training regimens that are based on perceptual input. Future research should continue to isolate the role of various perceptual parameters in the interplay between perception and motor skill learning. Cutting edge technologies such as virtual and augmented reality are quickly becoming accessible tools for researchers and can be used to manipulate perceptual parameters while performing experiments in more ecological, or restricted (e.g., fMRI scanner) environments. Such manipulations may provide important insight regarding the neural representation of sensory signals and their relevant dimensions that contribute to actual changes in behavior.

Future research along these lines may provide important insight for researchers in other fields such as artificial intelligence and robotics. These communities are interested in developing systems that learn motor skills. The evidence reviewed here suggest that learning models should incorporate sensory signals not only as external information recorded from sensory receptors to monitor consequences of actions, but also as functional knowledge used to refine parameters of the motor system. Reciprocally, psychologists and neuroscientists may benefit from building formal learning models that can be implemented in robots and use them as a fruitful avenue for testing theories about perception-based learning mechanisms that are often difficult to test experimentally.

Finally, it remains to be seen whether sensory signals can be used for refining real-world motor skills in various populations including children, musicians, professional sports players and clinical patients. Studies reviewed here remain narrow in focus, dealing mainly with simple

motor tasks and short-term training. Extension of these findings to complex movements, and multiple training sessions spanning longer time periods is needed. An intriguing line of future research is the use of neurofeedback (Marzbani et al., 2016). In such studies, subjects are provided with sensory feedback regarding their neural states and learn to modulate these states through volitional drive. An exciting recent primate study has demonstrated that training through neurofeedback (using a brain-machine-interface) generalized to yield consequent physical improvement on task performance (Vyas et al., 2018), thus providing proof-of-concept for another form of non-physical training as an alternative form of motor-skill learning. Ultimately, combining insights from basic motor behavior, neuroimaging techniques, cutting edge technologies, and well-known real-world practices will lead to a deeper understanding of the usefulness of sensory signals in motor learning and motor memory formation. This will not only provide a scientific basis for optimizing training strategies based on perception, but may also contribute to the development of new theoretical models of motor skill learning.

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