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The Effects of Sensory Manipulations on Motor Behavior: From Basic Science to Clinical Rehabilitation

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Abstract

Modifying sensory aspects of the learning environment can influence motor behavior. While the effects of sensory manipulations on motor behavior have been widely studied, there still remains a great deal of variability across the field in terms of how sensory information has been manipulated or applied. Here, we briefly review and integrate the literature from each sensory modality to gain a better understanding of how sensory manipulations can best be used to enhance motor behavior. Then, we discuss two emerging themes from this literature that are important for translating sensory manipulation research into effective interventions. Finally, we provide future research directions that may lead to enhanced efficacy of sensory manipulations for motor learning and rehabilitation.

Keywords

motor learning; contextual cue; sensory cue; context-dependent learning; rehabilitation

Modifying sensory aspects of a learning environment, such as by providing visual cues or auditory stimuli to be paired with a motor action, can affect motor performance and can modulate the effectiveness of the motor learning and rehabilitation (e.g., Azadi & Harwood, 2014; Lebold & Almeida, 2011; Thaut et al., 2007). Being able to robustly manipulate sensory information during motor tasks may therefore have important applications for improving motor learning in healthy individuals and motor rehabilitation in clinical populations.

Decades of research have shown that sensory manipulations can impact motor learning and rehabilitation. However, there is large variability across the field in terms of the experimental parameters employed (e.g., which types of sensory information were manipulated and which types of motor tasks were affected). Therefore, a primary focus of this review is to summarize a wide range of available literature across sensory modalities and highlight each

sensory modality's potential use in affecting motor learning and rehabilitation. Due to this broad focus, this review does not set out to provide a comprehensive examination into each sensory modality. Instead, it aims to provide a high-level understanding of how different sensory manipulations have been used to enhance motor performance, learning, and rehabilitation. We define sensory manipulations as changes in the sensory environment intended to affect one's behavior or performance on a task, including the addition (e.g., Ma, Trombly, Tickle-Degnen, & Wagenaar, 2004), removal (e.g., Bennett & Davids, 1995), and/or alteration (e.g., Ruitenberg et al., 2012) of sensory information. Our review is therefore different from an excellent recent review on multimodal augmented feedback for motor learning (Sigrist, Rauter, Riener, & Wolf, 2012) as we include sensory manipulations of both movement feedback (i.e., feedback) as well as sensory manipulations that precede movements to cue or prime upcoming movements. In addition, our review includes both studies that are concerned with effects of sensory manipulations during training (e.g., Roerdink et al., 2007) and with retention effects that persist after training during testing periods (e.g., Wright & Shea, 1991). While most of the time, sensory information is manipulated to provide a sensory cue during motor training (e.g., a metronome sound for gait training, as in Hausdorff et al., 2007), sometimes sensory manipulations involve changes in information that is incidental to a task (e.g., a change in display color that is not relevant to the motor task; Wright & Shea, 1991). While we primarily focus on the former type of sensory manipulation, we also discuss the latter type because such contextual manipulations are also known to affect motor performance (Wright & Shea, 1991). Finally, sometimes sensory information that provides a knowledge of results (e.g., visual feedback after a movement) is manipulated (e.g., Proteau, Marteniuk, & Lévesque, 1992). While this type of sensory manipulation is less common, we make this distinction when relevant.

To review the wide-ranging literature addressing sensory manipulations in motor learning, we first briefly summarize the literature from each sensory modality (i.e., auditory, visual, somatosensory, taste/olfactory, multimodal combinations) and highlight unique ways in which they are used to affect changes in motor behavior. We then discuss two emerging themes from this literature that are important for translating sensory manipulation research into practice. The first theme is what makes sensory manipulations effective. This is important since there are several factors that impact the effectiveness of a sensory manipulation, and some sensory manipulations have been found to be relatively ineffective (e.g., Deubel, 1995). The second is how the undesirable effects of sensory manipulations on motor learning can be reduced or eliminated. That is, while a sensory manipulation often enhances training outcomes, it can also make learning context-dependent and lead to poorer generalizability of a learned skill (e.g., poorer performance in untrained contexts compared to performance in the trained context; Lee, Winstein, & Fisher, 2016). This may have direct impacts for rehabilitation, as decreased generalizability may limit the transfer of skills learned in a clinic setting to a home setting. Finally, we suggest several future research directions that may lead to the enhanced efficacy of sensory manipulations for motor learning and rehabilitation.

Effects of Sensory Manipulations on Motor Learning and Rehabilitation

Auditory Manipulations

A significant portion of the literature on sensory manipulations, in both basic science and clinical research, focuses on auditory manipulations. Research studies combine a variety of motor tasks with auditory information to provide a specific sensory environment. These paradigms range from using a single tone (Ma et al., 2004), a repetitive sound (Hausdorff et al., 2007; McIntosh et al., 1997), and complex sounds such as piano pieces (Bangert & Altenmüller, 2003; Bangert et al., 2006; Haueisen & Knösche, 2001). These auditory manipulations are often paired with gait training (typically combined with rhythmic auditory cues in both healthy and patient populations, e.g., Hausdorff et al., 2007; Mendonça, Oliveira, Fontes, & Santos, 2014), and other motor tasks such as finger tapping (Thaut & Kenyon, 2003), reaching and writing (Ma et al. 2004), and even piano playing (e.g., Bangert & Altenmüller, 2003). While there are a variety of experimental paradigms, a common paradigm is the synchronization of repetitive auditory cues at different frequencies with movements such as walking and tapping (Hausdorff et al., 2007; McIntosh et al., 1997; Tecchio, Salustri, Thaut, Pasqualetti, & Rossini, 2000; Thaut & Kenyon, 2003). For example, people receive a repetitive auditory cue with a frequency slightly higher than their baseline/preferred frequency in gait training, and performance improvements in gait kinematics that align with the provided auditory cue, such as walking speed, are measured (Hausdorff et al., 2007). Another common paradigm involves learning associations between movements and auditory perception (e.g., associating pressing a specific piano key with a specific tone; Bangert & Altenmüller, 2003; Lahav, Saltzman, & Schlaug, 2007).

Behavioral and functional neuroimaging research suggests that auditory information is quickly and precisely integrated with motor behavior, which may account for why it has been extensively studied in research (Bangert & Altenmüller, 2003; Hausdorff et al., 2007; Lahav et al., 2007; Thaut & Kenyon, 2003; Thaut, Miller, Schauer, 1998). For example, non-musicians showed marked improvements in piano playing performance within only a few training sessions under 45 minutes or less (Lahav et al., 2007), and a change in cortical activation patterns was observed after just 20 minutes of piano training (Bangert & Altenmüller, 2003). In addition, the adjustment of motor behavior in response to auditory information is very sensitive, as people show immediate changes in their tapping interval to align their movements with the frequency of an external auditory cue (Tecchio et al., 2000; Thaut & Kenyon, 2003; Thaut, Miller, Schauer, 1998).

Supporting this strong relationship between auditory cues and motor behavior, neuroimaging studies demonstrate rich structural connectivity between auditory and motor regions of the brain, providing an explanation for why auditory information may affect motor behavior so effectively. Evidence suggests a number of brain regions are involved in controlling different aspects of movements required for combined auditory-motor activities (i.e., timing, sequencing), including the supplementary motor area (SMA), premotor cortex, supramarginal gyrus, prefrontal cortex, superior temporal gyrus, and cerebellum (Bangert et al., 2006; Chen, Penhune, & Zatorre, 2008; Thaut et al., 2009; Zatorre, Chen, & Penhune, 2007). In addition, there are direct and indirect connections between many of these regions.

Specifically, the auditory association areas have neural projections into and from the basal ganglia, and into the cerebellum (for a review, see Thaut & Abiru, 2009). Both the basal ganglia and cerebellum project onto the SMA (Akkal, Dum & Strick, 2007), and the striatum receives information from the inferior colliculus (part of the auditory pathway) and sends these converging projections to the SMA and premotor cortex for integration with motor movements (Koziol & Budding, 2009; Thaut & Abiru, 2009). Thus, this rich neural connectivity between auditory and motor regions may explain our natural tendency to integrate auditory information with movement.

Because of our predisposition to integrate auditory and motor information, providing auditory cues during motor rehabilitation is thought to be a viable way to enhance motor performance in individuals with Parkinson's disease (PD) and after stroke. For PD patients, converging evidence from experimental research, systematic reviews, and randomized crossover trials demonstrates improvements in gait performance when paired with auditory cues (Hausdorff et al., 2007; Lim et al., 2005; McIntosh, et al., 1997; Nieuwboer et al., 2007; Rochester, Baker, Nieuwboer, & Burn, 2011; Wittwer, Webster, & Hill, 2013). Several studies used rhythmic auditory stimulation as an auditory cue and demonstrated that it could improve a number of gait kinematics measured as performance, including speed, variability, step length, cadence, and stride strength (Hausdorff et al., 2007; McIntosh, et al., 1997; Nieuwboer et al., 2007; Rochester et al., 2011). In addition, the positive effects of auditory cueing, as measured by improved gait kinematics, occurred quickly, after only 100 meters (several minutes) of gait training with the cue (Hausdorff et al., 2007). Auditory cueing has also been shown to be effective in rehabilitation for post-stroke patients (e.g., Roerdink, Lamoth, Kwakkel, van Wieringen, & Beek, 2007; Thaut et al., 2007), and several review studies suggest that incorporating auditory cueing into post-stroke rehabilitation is a promising way to facilitate recovery of gait coordination (Hollands, Pelton, Tyson, Hollands, & van Vliet, 2012; Thaut & Abiru, 2009; Wittwer et al., 2013). Based on these findings, a post-stroke neurorehabilitation approach called music-supported therapy (MST) has emerged, which links music with rhythmic motor practice and has been shown to be clinically effective (Rodriguez-Fornells et al., 2012; Schneider, Münte, Rodriguez-Fornells, Sailer, & Altenmüller, 2010; Schneider, Schönle, Altenmüller, & Münte, 2007). MST is formulated on key principles emerging from research on brain plasticity and motor rehabilitation (Rodriguez-Fornells et al., 2012). While MST focuses on motor rehabilitation, it is similar to the more well-established neurologic music therapy (NMT), which has been widely used for motor, language and cognitive impairments (Thaut & McIntosh, 2014). In summary, research findings suggest that auditory information is readily integrated into human movement. Auditory-based manipulations may therefore be a potentially effective approach to enhance motor rehabilitation, especially to improve rhythmic motor actions, such as walking.

Visual Manipulations

Visual manipulations also comprise a large body of the basic and clinical research on sensory manipulations of motor performance and learning. Studies use and manipulate visual information, such as a target's appearance, color, or position (Azadi & Harwood, 2014; Osu, Hirai, Yoshioka, & Kawato, 2004; Wright & Shea, 1991), the brightness of the

environment (to show or limit visual information; Proteau et al., 1992; Moradi, Movahedi, & Salehi, 2014), and visual cues such as floor markers (Lebold & Almeida, 2011; Morris, Iansek, Matyas, & Summers, 1996; Suteerawattananon, Morris, Etnyre, Jankovic, & Protas, 2004). A range of different motor tasks have been used with these visual manipulations. The simplest visuomotor task is saccadic adaptation, in which people make rapid eye movements (saccades) from one location to a target while adapting to external perturbations (which is typically a small shift of the target as people move their eyes; e.g., Azadi & Harwood, 2014). However, more complex adaptation/skill tasks, such as reaching one's arm towards a target (Osu et al., 2004; Proteau et al., 1992), sequentially pressing keys with one's fingers (Wright & Shea, 1991), and even shooting a basketball, are also used (Moradi, Movahedi, & Salehi, 2014).

There are two common research questions in visual manipulation research. One is whether the manipulation of visual information affects performance (e.g., does a floor marker increase the step length of one's gait; Jiang & Norman, 2006), and the other is whether different visual cues can induce different motor responses (e.g., can people make different movements in response to different color cues of a target if they have been trained appropriately; Osu et al., 2004). While there are conflicting results in the literature (Azadi & Harwood, 2014; Woolley, Tresilian, Carson, & Riek, 2007), it does appear that visual cues, such as floor markers or specific target colors, can be used to both modify motor adaptation in experimental motor tasks and enhance motor performance in rehabilitation.

One key aspect of visual information compared to the other sensory modalities is that vision provides rich spatial information necessary for controlling our movements. More than a decade ago, Goodale (1998) pointed out the difficulty of disentangling visual and motor information, as visual processing plays an essential role in producing purposeful motor movements. Indeed, visual processing occurs along two pathways - a dorsal and ventral stream - which are generally believed to mediate spatial perception and recognition of objects, respectively (Goodale, 1998; Mishkin & Ungerleider, 1982). Goodale (1998) argued that both of the pathways play an integral role in producing purposive motor behavior. As a result, people may rely heavily on visual information, especially at an initial stage of motor learning, to improve on a task (Ruitenberg, Kleine, Van der Lubbe, Verwey, & Abrahamse, 2012). Due to this increased visual reliance, visual manipulation at an early stage of learning can deteriorate motor performance (Ruitenberg et al., 2012).

Building on this, evidence suggests that motor learning over time may actually be associated with reduced, rather than increased, dependence on visual perception (Bennett & Davids, 1995; Robertson et al., 1994). While inexperienced individuals initially show a strong reliance on visual information when they perform a motor task, this reliance on vision gradually decreases over training. For example, in a two-handed coordination task in which participants manipulate two handles to keep a tracker on target, people with high spatial sensitivity (e.g., better visual perception of spatial orientation) showed better performance at the early stage of training but not at the late stage, compared to those with low spatial sensitivity, indicating that visual information became less important over the course of motor learning (Fleishman & Rich, 1963). Consistent with this finding, other studies show that the removal of visual information hurts the performance of inexperienced individuals on a gross

motor task but does not affect the performance of skilled individuals, again suggesting a link between early learning and reliance on vision (Bennett & Davids, 1995; Robertson et al., 1994). We note, however, that motor learning does not always result in a reduction of dependence on visual perception (Proteau et al., 1992). While methodological differences (e.g., different motor tasks used) may account for the conflicting research evidence, further research is needed to clearly understand when and why reliance on vision will change through training.

Manipulations of visual information can also have implications for clinical practice, as individuals with PD and stroke show a strong dependence on visual information during motor tasks (Cooke, Brown, & Brooks, 1978; Vaugoyeau et al., 2007; Verschueren, Swinnen, Dom, & De Weerd, 1997). While some studies have shown that visual information can be helpful, such as floor markers cueing stride length for gait training (Jiang & Norman, 2006; Lewis, Byblow, & Walt, 2000; Lebold & Almeida, 2011; Sidaway, Anderson, Danielson, Martin, & Smith, 2006; Suteerawattananon et al., 2004), others suggest that removing visual information from training is more beneficial, for the reasons discussed above. For instance, balance rehabilitation for post-stroke patients was more effective when patients wore an eye mask during rehabilitation, removing visual feedback during training (Bonan et al., 2004). This may have forced patients to internalize the training and to not rely too much on visual markers, and may have reduced knowledge of performance based on visual input. Similarly, PD patients were found to be highly reliant on visual information during training, which limited generalizability to other environments (Verschueren et al., 1997). These patients performed worse on a motor task if the test environment lacked the augmented visual information they received in their training environment. Taken together, while providing visual information can help patients in some situations, it should be also noted that too much reliance on visual information can be maladaptive. In some conditions, motor training with visual manipulations should aim for a reduction of such visual dependence.

Proprioceptive Manipulations

Somatosensory information has not been as extensively studied as auditory and visual information in motor learning and rehabilitation, but there is research evidence suggesting that manipulating proprioceptive information can also affect motor performance and induce context-specific responses. While proprioception is a component of somatosensation that also includes touch and tactile information (Lundy-Ekman, 2007), here we focus on proprioception because relatively limited evidence has been found for how other types of somatosensory information may affect motor performance and learning (Burleigh-Jacob, Horak, Nutt, & Obeso, 1997; Dibble et al., 2004; Rochester et al., 2010). For proprioception, saccadic adaptation and arm reaching adaptation tasks are the most commonly used paradigms, and studies generally focus on whether specific proprioceptive cues can elicit different motor movements. In saccadic adaptation (described in the section on visual manipulations), it has been shown that different starting eye positions, which are considered a form of proprioception (Wang, Zhang, Cohen, & Goldberg, 2007), elicit context-specific responses (Alahyane & Pélisson, 2004; Shelhamer & Clendaniel, 2002). For example, two different initial eye positions (left and right) can be associated with a shift of a target in two

opposite directions, and people can show different motor responses depending on their initial eye positions to successfully adapt to the opposite shifts. Similarly, in an arm-reaching task, people can learn to adapt to perturbations such as a force that pushes their arm in a direction perpendicular to their movements or a rotation of visual feedback. Different proprioceptive cues, such as training participants to grasp a manipulandum with a specific grasp, and using different starting positions (which leads to slightly different arm postures), result in context-specific responses (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Ghahramani & Wolpert, 1997; Woolley et al., 2007). This suggests that proprioceptive cues can be used as a way to manipulate behavioral responses.

In spite of the fact that proprioceptive information is not as widely used as auditory/visual information in motor research, evidence suggests that its effects can be as robust as or perhaps even more robust than these other modalities (e.g., Gandolfo et al., 1996; Woolley et al., 2007). Proprioceptive cues are consistently found to be effective at inducing context-specific responses across studies, compared with other modalities, such as visual manipulations, which show variable success (Azadi & Harwood, 2014; Bahcall & Kowler, 2000; Deubel, 1995; Herman, Harwood, & Wallman., 2009; Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Woolley et al., 2007). This may not be surprising as proprioceptive feedback is a critical component of motor planning (Hocherman, 1993). In addition, as the somatosensory and motor cortices are located next to each other in the brain with many reciprocal connections between them, the connectivity between these cortices may contribute to the importance of somatosensory (proprioceptive) information in motor learning. Indeed, stimulation of the somatosensory cortex leads to long-term potentiation of cells in the motor cortex, suggesting a tight link between the two, and lesions of the somatosensory cortex can impair the learning of a new motor skill (Pavlidis, Miyashita, & Asanuma, 1993; Sakamoto, Porter, & Asanuma, 1987).

One key difference might account for why manipulating proprioceptive information is so effective in modulating motor performance compared to manipulating other sensory modalities. With proprioceptive cues, different patterns of muscle activations may be required to achieve the same goal (or movement). This is not typically true for other modalities. For example, when a manipulandum is grasped in two different ways, producing two proprioceptive cues (e.g., Gandolfo et al., 1996), two different sets of neural signals, which control different patterns of muscle activity, are reinforced in order to result in the arm moving towards the target. This means the proprioceptive information that cues the beginning of the task is not only highly relevant to the performance of the motor task, but it also strongly influences the very motor plan underlying that motor task. We will later discuss how the task-relevance of a sensory cue is a key factor in influencing the effectiveness of a sensory manipulation, but it appears that proprioceptive cueing can be a very effective manipulation due to how much it affects task performance. Thus, while proprioceptive cueing is relatively less well-studied than other modalities, a better understanding of proprioceptive manipulations may lead to novel effective sensory manipulations to improve motor rehabilitation.

Olfactory and Taste Manipulations

There is a body of research evidence suggesting that taste and olfactory information can be associated with memory and learning (e.g., Baker, Bezance, Zellaby, & Aggleton, 2004; Herz & Cupchik, 1995; Herz, Eliassen, Beland, & Souza, 2004; Herz, 1997; Rosas & Callejas-Aguilera, 2007; Schroers, Prigot, & Fagen, 2007; Smith, Standing, & de Man, 1992). However, most of the research using these sensory modalities employs non-motor tasks, such as explicit verbal memory tasks. While research regarding the effects of these modalities on motor performance and learning is lacking, a wealth of evidence suggests that these modalities have robust effects on explicit memory and can induce context-dependent behaviors (Baker et al., 2004; Herz & Cupchik, 1995; Herz, 1997; Rosas & Callejas-Aguilera, 2007; Schroers et al., 2007; Smith et al., 1992). As the purpose of this review is to examine the role of each sensory modality in motor learning, here we suggest that additional future research is needed to test the effects of taste and olfactory manipulations on motor performance and learning. However, we speculate that manipulation of olfactory information may be particularly interesting because it can be easily combined with motor tasks and because it induces relatively strong emotional responses (Herz & Cupchik, 1995; Herz, et al., 2004; Royet et al., 2000; Willander & Larsson, 2007). As internal states such as arousal and emotion (induced by non-olfactory stimuli) have also been linked with motor performance (Coombes, Janelle, & Duley, 2005; Hordacre, Immink, Ridding, & Hillier, 2016; Horslen & Carpenter, 2011; Movahedi, Sheikh, Bagherzadeh, Hemayattalab, & Ashayeri, 2007; Noteboom, Fleshner, & Enoka, 2001), one potential way that olfactory cues may also affect motor performance is by one's altering emotional state—although, this remains to be researched. Overall, we believe that the manipulation of olfactory/taste information during motor learning may represent a viable new area of exploration for affecting motor performance and enhancing motor learning and rehabilitation.

Combinations/Comparisons between Modalities

To date, relatively little evidence is available for how multimodal manipulations of sensory information affect motor performance and learning, as studies typically examine the effects of a specific, single modality instead of delving into interactions between modalities. Available research suggests that, similar to unimodal information, multimodal information such as audiovisual cues, can both induce context-specific responses in motor adaptation tasks and improve performance in rehabilitation tasks (Kennedy, Boyle, & Shea, 2013; Mak & Hui-Chan, 2008; Osu, Hirai, Yoshioka, & Kawato, 2004; Suteerawattananon, Morris, Etnyre, Jankovic & Protas, 2004). On the other hand, there is mixed evidence for whether combining different modalities will produce additional beneficial effects, as one of the studies provides evidence supporting such effects (Kennedy et al., 2013) while other does not (Suteerawattananon et al., 2004). More research on the efficacy of multimodal compared to unimodal information may also provide useful insights and implications for clinical practice, where multimodal cues may provide benefits for individuals who experience sensory processing deficits in single sensory modalities.

Emerging Themes

1. The effectiveness of a sensory manipulation is determined by task

relevance.—The first theme is what dictates the effectiveness of a sensory manipulation. As previously discussed, experimental sensory manipulations do not always affect motor performance or learning (e.g., Deubel, 1995). It seems reasonable that there should be a mechanism that selectively regulates attention to only useful sensory information. Perhaps not surprisingly, evidence suggests that sensory information is likely to influence motor performance when the manipulated information is relevant to the performance of the motor task. While arbitrary pairings of sensory inputs and movements may be learned, they are typically less successful (e.g., Azadi & Harwood, 2014; Gandolfo et al., 1996). For instance, we previously explained that during a saccadic adaptation task, people are capable of simultaneously adapting to two different perturbations (e.g., the shifting of the target in two opposite directions) linked with two different sensory inputs (e.g., initial eye positions; Shelhamer & Clendaniel, 2002). However, this only occurs when a sensory cue has key information to the task, such as target speed or starting eye position, but not when the cue contains task-irrelevant information, such as target color (Alahyane & Pélisson, 2004; Azadi & Harwood 2014; Bahcall & Kowler, 2000; Deubel, 1995; Herman et al., 2009; Shelhamer & Clendaniel, 2002). In addition, the relevance of a sensory manipulation may depend on the sensory modality and type of information it provides. For instance, visual feedback typically provides spatial information about a task, and auditory feedback provides temporal information. Consequently, in gait rehabilitation training, visual cues such as floor markers are shown to increase the stride length (a spatial aspect; Jiang & Norman, 2006; Lewis et al., 2000; Lebold & Almeida, 2011; Sidaway et al., 2006; Suteerawattananon et al., 2004), while auditory cues such as metronome sounds are generally shown to affect cadence performance (a temporal aspect; Ford, Malone, Nyikos, Yelisetty, & Bickel, 2010; Hurt, Rice, McIntosh, & Thaut, 1998; Roerdink et al., 2007; Suteerawattananon et al., 2004). We note that sometimes auditory cues are also found to affect stride length, perhaps because these gait kinematics are interrelated (that is, both cadence and stride length influence velocity, and therefore a change in one parameter may lead to changes in other parameters; Ford et al., 2010; Hurt et al., 1998).

Another piece of evidence for the link between task-relevance and effectiveness is that highly task-relevant sensory information seems to result in stronger context-dependent learning. For horizontal saccades (looking from left to right or right to left), horizontal initial eye positions (i.e., starting out looking at left or right) were found to result in more robust context-dependent responses than vertical initial eye positions (i.e., looking at up or down; Shelhamer & Clendaniel, 2002). Finally, in a sequence skill task in which people learned to execute a sequence of button presses, removing task-relevant stimuli (i.e., a sequence of key pressing) from a computer display was more detrimental to task performance than removing task-irrelevant stimuli (e.g., display color) after training with both types of information (Wright & Shea, 1991).

One reason why task-relevant sensory manipulations may be effective is due to their ability to help people direct their attention towards relevant information that will facilitate learning. In several polyrhythmic bimanual coordination studies in which people were required to

simultaneously move their upper limbs in asynchronous rhythmic patterns, learning was facilitated when people were provided with certain visual and/or auditory information representing the asynchronous movement patterns (Kennedy et al., 2013; Kovacs, Buchanan, & Shea, 2010a; Kovacs, Buchanan, & Shea, 2010b). Importantly, Kennedy et al. (2013) showed that when people were provided with auditory, visual, or auditory+visual information representing the goal pattern (e.g., the goal sequence either played as an audio recording, viewed as a sequence of visual lines, or both,) before actually moving, their movements became more accurate and stable compared to when they received a simple visual metronome cue during the task. They argued that the former type of sensory information helped people direct their attention from an internal to external focus of movement and allowed them to learn both the relative and absolute characteristics of the patterns, which is important for improving motor learning (Wulf, Shea, & Lewthwaite, 2010).

Taken together, these results suggest that clinicians can develop the most effective interventions if they identify and manipulate sensory information that is specifically relevant to the task. While task-relevant information will often be obvious, such as visual or auditory cues influencing gait length or movement velocity, in clinical settings, it may also be more subtle. For example, therapists may not pay attention to a slight tilt of a picture hung on the wall of a training room because it may be apparently irrelevant for balance rehabilitation. However, it may actually provide detrimental sensory information for post-stroke patients if they use it as a visual reference to help them maintain their balance (e.g., Slaboda, Barton, Maitin, & Keshner, 2009). Therefore, careful attention to the training environment and modification of even subtle task-relevant cues may provide a way to enhance motor rehabilitation.

2. Context-based learning increases context-dependence and decreases generalizability.—The bulk of this review has suggested that manipulating sensory information can improve motor performance and enhance rehabilitation. However, sensory manipulations are not always beneficial. Indeed, as discussed in the section on visual manipulations, increased reliance on visual information can decrease internalized learning and thus impair generalizability to contexts that lack that visual information. That is, motor learning with specific sensory manipulations may enhance performance in the trained environment (e.g., rehabilitation room), but training effects may be diminished in untrained environments (e.g., outside of the clinic). Thus, while it is important to understand how to use sensory manipulations effectively, it is also important to understand how undesired context-dependence can be reduced.

In motor learning, when a person makes an error, it is important to correctly identify a cause of the error because it dictates whether learning is linked to the body or to the learning environment (Berniker & Kording, 2008; Wolpert & Flanagan, 2010). This issue, known as credit assignment, becomes important because a person's belief about the source of errors can influence how they learn. That is, if they believe the source of error is internal (e.g., the person credits the error to themselves) versus external (e.g., the person credits the error to the environment), they may reduce their context-dependence and increase their internalization of the learning process, thus improving generalizability. To illustrate this

concept, when novice archers shoot an arrow and see it falling before reaching the target, their learning may depend on what they attributes their mistake to. If they believe that a hard blowing wind caused the error, they are likely to learn how to adjust their pulling force according to the wind. On the other hand, if they believe that they simply did not pull the bowstring hard enough, they are likely to update their internal motor plan to increase their pulling force. Learning in the latter case is likely to be transferred to different contexts because the locus of their adjustment will be internal, whereas learning in the former case may be manifested only when the wind is blowing in a certain way (i.e., context-dependent learning).

Research findings support a link between credit assignment and generalizability (Berniker & Kording, 2008) with suggestions that increased internal credit assignment leads to enhanced generalizability and vice-versa (Kluzik, Diedrichsen, Shadmehr, & Bastian, 2008; Torres-Oviedo & Bastian, 2010; Mukherjee et al. 2015). One way to influence an individual's credit assignment to themselves is to remove additional sensory information so that participants are more likely to assume that errors are internal. For example, in treadmill training, when people wear an eye mask that occludes their vision, their treadmill training transfers to overground walking more so than those trained without a mask (Torres-Oviedo & Bastian, 2010). This may be because visual input during treadmill training is contextually-specific to walking on a treadmill (e.g., visual information stays the same despite taking steps forward), and this is different from visual input during overground walking, in which visual information changes with each step. This specific visual information may provide some knowledge of performance that is linked to the training environment. As such, it may be perceived as a source of error, and therefore removing it increases one's internal credit assignment, leading to better generalizability. Similarly, improved transfer of gait training from a treadmill to overground walking was observed when people put vibrating tactors on their feet, which occluded the treadmill-specific somatosensory input during walking (Mukherjee et al. 2015). Credit assignment seems to play a key role in the degree of context-dependence, and learning can be less context-dependent when people believe that motor errors arise more from their own bodies. If a goal of rehabilitation is to enhance motor performance of patients in a variety of contexts (e.g., clinic, home, busy city street), then it is important to reduce dependence on certain sensory information that can potentially interfere with generalizing their motor performance to new environments. It may also be effective to use sensory information primarily early during a motor learning process, when reliance on visual information is high (as discussed in the section on visual manipulations). Once the skill is learned in the clinical context, then the clinician could have the patient practice in diverse contexts or without a specific sensory modality (e.g., wearing a eye mask to occlude vision) to then improve generalizability to other environments. Finally, simply encouraging patients to focus on internalizing their learning may also help lead to a better transfer of rehabilitation gains to real-world settings.

Discussion

In this review paper, we briefly summarized how manipulating different sensory information can affect motor performance and rehabilitation. Overall, studies across different modalities provide converging evidence that successful manipulation of sensory information can be

used to influence motor performance and enhance motor learning and rehabilitation. However, there are also considerable differences between sensory modalities, which may reflect the different types of information each modality contributes to motor performance as well as the different biological mechanisms connecting each sensory modality to the motor cortex. We also identified two emerging themes from the literature, which are that: 1) task-relevance is a key factor impacting the effectiveness of sensory manipulations and, 2) manipulating a sensory environment so that one assigns the source of errors to oneself may improve generalizability and transfer of learning to new contexts.

While research evidence supports the utility of sensory manipulations in motor learning and rehabilitation, there is a lack of research on several sensory modalities. Specifically, auditory and visual sensory information have received the most attention, but this trend may reflect the convenience, rather than effectiveness, of using these modalities compared to others. While manipulations of proprioceptive information also appear to be extremely effective in promoting the learning of different behaviors, additional research is needed in this area. In addition, future research may explore how other modalities, such as taste, olfaction, or multimodal combinations of sensations, impact motor learning in both healthy and clinical populations. In addition, this review was organized with a goal of comparing and contrasting sensory manipulations across the various sensory modalities. However, future work may find greater benefit in focusing in-depth on examining specific categories of sensory manipulations, such as the sensory cueing, sensory removal, or sensory expertise. Additional work could also examine the use of different sensory manipulations in directing attention through sensory information, resolving spatial and temporal characteristics of the task using sensory information, and simplifying task complexity using sensory information. Expanding this knowledge across these different directions may lead to the generation of new and effective ways to improve motor rehabilitation.

Another potential future direction for this area of research is the use of virtual reality (VR) and augmented reality (AR) environments, which have been shown to enhance motor rehabilitation (Brooks, Mcneil, Rose, Attree, & Leadbetter, 1999; Bryanton et al., 2006; Holden, 2005; Jaffe, Brown, Pierson-Carey, Buckley, & Lew, 2004; Rose, Attree, Brooks, Parslow, & Penn, 2000; Todorov, Shadmehr, & Bizzi, 1997; Webster et al., 2001). While VR is typically immersive (e.g., the person cannot see beyond the digital environment), AR provides a blend of digital and real environments (e.g., glasses that allow you to see digital information superimposed on the real world). VR and AR can be powerful tools to address the two primary themes found in this review. First, they can be used to manipulate sensory environments, to facilitate the use of and attention to task-relevant information. For example, patients have been shown to benefit from using a head-mounted VR device that produced virtual visual cues during gait rehabilitation (Baram & Miller, 2006). Unlike physical cues, such as floor makers, virtual cues using AR could also be applied in a variety of contexts (e.g., taken outside of the clinic to provide updated cues within a dynamic environment). In addition, VR and AR allows individuals to finely control and adjust sensory feedback,, allowing for the precise manipulation of both the temporal and spatial components of the sensory information presented. Research has shown advantages of using augmented environments, such as to provide only limited, easily processed perceptual feedback, in improving the acquisition of complex motor skills over real-world training (Todorov,

Shadmehr, & Bizzi, 1997). Secondly, VR and AR can be used to reduce context-specific sensory experiences that may lead to context-specific motor behavior and poor generalization. For example, when people wear a head-mounted display (HMD) and “walk” in a VR environment while they walk on a treadmill, their gait behavior becomes more similar to overground walking compared to walking on a treadmill without HMD (Sheik-Nainar & Kaber, 2007). VR and AR allow individuals to train in different virtual environments easily, thus potentially promoting greater generalization of training. Finally, studies suggest that people feel that game-based VR training is more enjoyable and interesting than similar training in a real environment, which may also contribute to improved therapeutic outcomes (Betker, Desai, Mett, Kapadia, & Szturm, 2007; Bryanton et al., 2006). While VR primarily manipulates visual information, these devices can be paired with auditory, proprioceptive, or other sensory manipulations to examine the effects of multimodal sensory cues or environments on learning. Thus, VR provides excellent opportunities to study many aspects of learning with context-specific sensory experiences and to engage patients in augmented environments for rehabilitation.

In summary, research suggests that effective manipulations of sensory information and learning contexts provide a viable way to improve motor performance, learning and rehabilitation. While different sensory modalities can be potentially used in practice, it should be noted that each modality has unique characteristics and may produce different effects on motor performance and learning. Task-relevance and credit assignment are two key factors to be considered in order to achieve desired rehabilitation goals. Future research may expand this field to examine manipulations of lesser-studied modalities, such as proprioception, olfaction, and taste. Finally, harnessing emerging technology, such as immersive virtual reality environments, may provide an engaging and portable way to implement effective sensory manipulations during motor training and rehabilitation.

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Box 1. Definitions of terms**Sensory manipulations:**

Changes in the sensory environment intended to affect behavior or performance on a task, including the addition (e.g., Ma et al., 2004), removal (Bennett & Davids, 1995), and/or alteration (e.g., Ruitenberg et al., 2012) of sensory information.

Context-dependent performance/learning:

Better performance in the trained context compared to performance in untrained contexts (Lee, Winstein, & Fisher, 2016).

Motor behavior: Measurable behaviors related to the control, development, and learning of movement (Keough, 2011; Spaulding, 2005; Whiting & Rugg, 2006).

Motor learning:

Changes to one's internal processes that affect how well a person is able to perform a motor skill (Schmidt & Wrisberg, 2008).

Motor performance:

How well a person performs a motor task at a given time, which can be observed and influenced by many factors, such as motivation and fatigue (Schmidt & Wrisberg, 2008).

Motor adaptation:

A type of motor learning in which a learner modifies motor behavior to optimize performance in a new task environment (Izawa, Rane, Donchin, & Shadmehr, 2008).