9 Building a dance in the human brain

Insights from expert and novice dancers

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As humans, we have an unparalleled ability to coordinate our bodies to perform an endless number of skilled actions. As dancers, this ability is even more impressive, as a dancer's motor repertoire comprises movements that are not only highly skilled, but also remarkably precise, complex, and coordinated. An intriguing feature of the human brain is how a network of seemingly disparate cortical regions and subcortical nuclei can give rise to dance movements, from the razor-sharp precision of 32 *fouettés en tournant* performed by Odile in *Swan Lake* to the contorted, convulsive, and seemingly out-of-control whole-body flings and gyrations that typify the choreographic vocabulary of Twyla Tharp's *Torelli*. Of particular interest to neuroscientists is the remarkable plasticity of the human brain to integrate different types of physical and perceptual experiences to learn new movements. Such abilities are quite pronounced in dancers, whose livelihood depends on rapid and adept movement production and reproduction. How does the brain accomplish this feat? Neuroscientists have recently observed that it is the extraordinary plasticity of seemingly disparate cortical regions and subcortical nuclei within the brain that gives rise to such movements. This network of brain regions works together when we observe someone else performing an action and then learn how to perform it ourselves.

Neuroscientists first found evidence of a neural system that matches action with perception in the brains of non-human primates (see also Chapter 8 by Calvo-Merino, this volume). Scientists stumbled on this finding almost by accident, when they were recording from single neurons within the ventral premotor cortex (area F5) of the monkey brain to determine how these neurons responded when monkeys grasped different items. These researchers observed, much to their surprise, that the same neurons that fired when monkeys performed a specific action (e.g., grasping a raisin) also fired when the monkey watched another monkey or a researcher execute the same action (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996a). Subsequent research revealed that these particular neurons do indeed respond preferentially to actions that are either observed or performed, which led researchers to name them "mirror" neurons. As such, mirror neurons appear to compose a cortical network that matches observation of actions with execution of those same actions (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996b). These specialized neurons have prompted researchers to propose that action perception and production processes form a bidirectional, interactive loop within the primate brain.

Since the discovery of mirror neurons in monkeys, many studies have investigated similar functional regions within the human brain, providing evidence for a human mirror neuron system (e.g., Rizzolatti & Craighero, 2004), or, more broadly, an *action observation network* (AON; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009b). For the purposes of this chapter, the term *action observation network* is used instead of *mirror neuron system*, since this term is more general and encompasses all of the brain regions involved in action observation processes, not simply the two main mirror neuron regions (inferior parietal and premotor cortices). As illustrated in Figure 9.1 (see also Box 9.1), the brain regions that compose the AON include the supplementary motor area (SMA), the ventral premotor cortex (vPM), the inferior parietal lobule (IPL), and posterior superior temporal sulcus/middle temporal gyrus (pSTS/pMTG; Binkofski et al., 2000; Decety, 1996; Grafton et al., 1996; Rizzolatti et al., 1996b; Stephan et al., 1995). Increasing evidence from behavioral, neuroimaging, and neurostimulation procedures suggests that action understanding might be explained by covert simulation of another's movements by an observer (Decety, 1996; Fadiga, Buccino, Craighero, Fogassi, Gallese, & Pavesi, 1999; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Jeannerod, 2001; Rizzolatti & Craighero, 2004).

The challenge for research on the relationship between action perception and action production is to determine the explanatory power and generalization of this network and its relationship to motor skill and new action learning. It is the hope of researchers in this field to eventually explore applications for the recovery of function after injury and improved learning and teaching practices. The focus of this chapter is on work my colleagues and I have performed on the neural and behavioral outcomes of humans learning to perform complex action sequences, specifically dance. First, I introduce work we have performed with expert dancers that probed questions of the neural representation of whole-body action expertise. Next I discuss findings from a study performed with novice dancers through which we addressed questions of observational learning and how learning is influenced by different action cues. I conclude with a brief discussion of the broader implications for this work and suggest several directions for future research.

My colleagues and I have turned to populations of expert and novice dancers to help us address such questions of action cognition for several reasons. Dance requires a great degree of coordination not only between the different limbs of the body, but also between perception and action, and time and space. As an example, most dancers can relate to the experience of

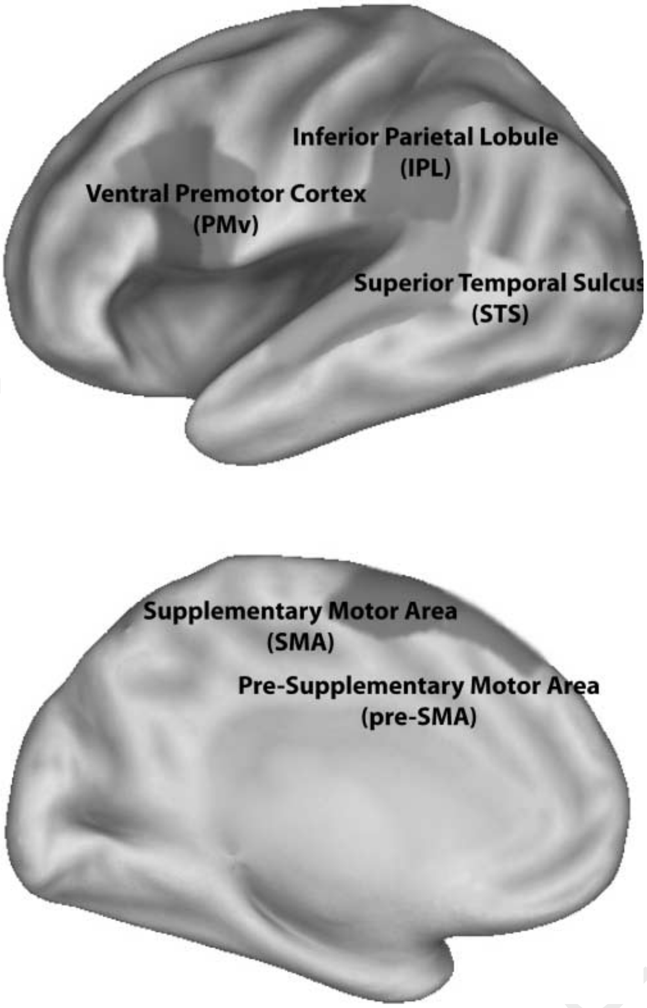

Figure 9.1 Cartoon representation of the action observation network (AON). The core regions that compose the AON are rendered here on partially inflated cortical surfaces using the PALS data set and Caret visualization tools (http://brainmap.wustl.edu/caret). The brain illustrations throughout this chapter appear different from the brains illustrated by Calvo-Merino (Chapter 8, this volume), because the Caret tools render brains to appear slightly inflated, which enables better visualization of activations deep within sulci and on the cortical surface. The AON is represented bilaterally, but for visualization purposes, the medial and lateral surfaces of the left hemisphere only are illustrated here. The AON includes the ventral premotor cortex (vPM), the inferior parietal lobule (IPL), the superior temporal sulcus (STS), and the supplementary and pre-supplementary motor areas (SMA and pre-SMA).

Box 9.1 **Brain areas involved in action observation processes**

SMA:	supplementary motor area
vPM:	ventral premotor cortex
dPM:	dorsal premotor cortex
IPL:	inferior parietal lobule
SPL:	superior parietal lobe
IPS:	intraparietal sulcus
pSTS:	posterior superior temporal sulcus
pMTG:	posterior middle temporal gyrus
ITG:	inferior temporal gyrus
pSTG:	posterior superior temporal gyrus

showing up to a technique class in a new studio, progressing with ease through the warm up or *barre* exercises, and then being expected to perfectly perform long and complex sequences of steps that have been rapidly demonstrated in the most cursory manner (see also Chapter 5 by Puttke, this volume). Dancers' ability to transform scant visual or verbal information into highly sophisticated movements has great potential value to scientists. Significant utility exists in examining both beginning and expert dancers to see how complex movements are learnt, remembered, and reproduced. Not only can scientists learn about the coordination and expression of complex actions by quantifying dancers' behavioral performance, but careful measurement of how such skilled actions are represented at the neural level can shed additional light on how the human body is capable of learning and performing such complex movements with limited information.

Placing the dancer's brain in a scientific context

In line with research from our laboratory, which has studied *de novo* dance learning in both expert and novice dancers, elegant work by several other laboratories has substantiated the feasibility of using dance learning and observation as a paradigm for investigating the properties of the AON (Brown, Martinez, & Parsons, 2006; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Calvo-Merino, Jola, Glaser, & Haggard, 2008; Calvo-Merino, Chapter 8, this volume; Jola, Chapter 10, this volume). The first such study investigated the specificity of the AON for observing one's own movement repertory compared to an unfamiliar and untrained movement repertory (Calvo-Merino et al., 2005; see also Chapter 8 by Calvo-Merino in the current volume). In this experiment, expert ballet dancers, capoeira dancers, and non-dancer control participants passively viewed ballet and capoeira dance clips while undergoing fMRI scanning (see Box 4.1 in Chapter 4 by Bläsing, this volume). The authors reported significantly greater activity within the AON, including bilateral vPM and IPL activity, right superior parietal lobe, and left STS, when dancers observed the movement style of their expertise. From this, the authors concluded that the AON is able to integrate one's own movement repertoire with observed actions of others, thus facilitating action understanding.

A second influential study by Calvo-Merino and colleagues (2006) examined the effects of visual compared to motor experience on AON activity during action observation. In order to parse visual familiarity from physical experience, expert men and women ballet dancers observed videos of movements learnt only by their sex, only by the opposite sex, or moves that are performed by all dancers (see Chapter 8 by Calvo-Merino, this volume). The motivation behind this procedure was to determine whether equally robust action resonance processes may be elicited by observation of movements that are equally visually familiar, because men and women dancers train together, but are unequal in terms of physical experience. The authors reported that when effects of visual familiarity are controlled for (i.e., when dancers watched moves from their own movement repertoire, compared to moves that they frequently saw, but never physically performed), evidence for action resonance based on pure motor experience was found in inferior parietal, premotor, and cerebellar cortices. The authors conclude that actual physical experience is a necessary prerequisite for robust activation in these areas of the AON. This study provides an excellent point of departure for one of the lines of research described below, wherein my colleagues and I were interested in measuring how purely observational experience is represented in the AON.

Together, the studies led by Calvo-Merino et al. (2005, 2006) and Brown et al. (2006) provide robust evidence for changes within the AON with the presence (or emergence) of execution competency. My colleagues and I have aimed to build on this foundation by addressing open questions regarding the establishment of motor and perceptual expertise, the sensitivity of this network to physical and observational learning, and how learning from another dancer's movements compared to just symbolic cues influences learning and neural activity. The studies discussed below address these three objectives through training experiments performed with expert and novice dancers. By tackling such questions about the function of the AON through use of both behavioral and neuroimaging measures in dancers, we aim to better characterize the processes that underlie the various ways people acquire new movements.

What expert dancers' brains can teach us

The first study our laboratory performed with dancers aimed to address three objectives (Cross, Hamilton, & Grafton, 2006). First, we sought to characterize how the human brain represents expertise for complex, whole-body actions (in this case, dance sequences). The second objective was to determine whether the neural signature for newly learnt complex dance sequences differs from kinematically similar sequences that are unlearnt. Finally, we wanted to determine if neural activity was related to individuals' perceived mastery of the dance movements that they learnt. We hoped that by tackling these questions, we might add a measure of clarity to a continuing debate in the study of action simulation concerning the relationship between the physical embodiment of actions (i.e., those actions that an individual can perform and has performed) and neural activity when observing such actions.

In this experiment, participants were asked to observe a dancer's movements and at the same time to imagine themselves performing those movements. In this situation, the visual stimulus guides and constrains the motor simulation. Because our task involved action observation as well, it is essential to consider how visual stimuli depicting human actions are able to drive motor regions of the brain. As mentioned previously, numerous neuroimaging studies implicate the motor and premotor areas that are classically associated with movement preparation as also being engaged when simply observing the actions of others (Buccino et al., 2001; Grafton et al., 1996; Grèzes & Decety, 2001; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Johnson-Frey, Maloof, Newman-Norlund, Farrer, Inati, & Grafton, 2003; Rizzolatti et al., 1996b). Behavioral studies have further demonstrated interactions between action perception and execution (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass, Bekkering, & Prinz, 2001; Hamilton, Wolpert, & Frith, 2004; Kilner, Paulignan, & Blakemore, 2003), and thus lend additional credence to the idea of overlapping neural processes for action observation and execution. A meta-analysis of 26 functional neuroimaging studies on action representations by Grèzes and Decety (2001) provides evidence that extensive overlap exists between brain regions active during action observation, simulation, and execution. Together, these findings suggest that a distinct set of brain regions compose the AON, and are active both when observing and when performing actions.

In our study, we recruited 10 expert modern dancers who were learning the movement vocabulary from Laura Dean's seminal modern dance work, *Skylight* (Dean, 1982). The dancers spent over 5 hours per week learning the *Skylight* vocabulary as part of their company's repertory. Importantly, this was a longitudinal study in which the dancers' brains were scanned once a week across 6 weeks of learning this new dance work. Such a method enabled us to effectively take snapshots of the expert dancers' brains as they progressed from unfamiliarity with the new movement vocabulary to an expert level of performance proficiency. During the weekly scanning sessions, the dancers watched 18 video clips of *Skylight* movements, and 18 videos of kinematically similar but unfamiliar and unrehearsed dance movements. The dancer in the video clips was filmed from behind as she moved in front of a mirror. This not only enabled our participants to see nearly 360° of visual information about the movements, but it also provided an ecologically valid viewing context, since dancers are accustomed to observing and practicing movements in front a mirror in a studio context. While the participants watched each video clip in the scanner, they were asked to imagine themselves performing each dance sequence. Following each video, a question appeared asking the dancers to rate their perceived performance ability for each sequence, at that particular point in time.

The behavioral and neuroimaging procedures yielded several exciting results about the representation of expertise in dancers' brains. Unsurprisingly, we found that the dancers rated their ability to perform the rehearsed *Skylight* movements as progressively greater across the 6 weeks of training, while their ratings of their ability to perform the control movements remained relatively unchanged (Cross et al., 2006). The neuroimaging results corroborated and extended previous work on expert dancers in several capacities. First, in line with what was reported by Calvo-Merino and colleagues (2005), we saw greater activation across a broadly defined AON, including parietal, premotor, supplementary motor, and superior temporal regions, when dancers watched dance movements compared to rest, and when they watched movements they had physically rehearsed compared to unrehearsed control movements (Figure 9.2, top two brains). The critical contribution of this study was that as the dancers' expertise with the rehearsed dance sequences increased, activity within vPM and IPL in the left hemisphere also increased with their perceived expertise (Figure 9.2, lower brain).

This study provided evidence for rapid and precise changes in AON responses within the brains of expert dancers learning a new dance. In just 6 weeks, dancers progressed from novices to experts with the *Skylight* choreography (as evidenced by their subjective evaluations of performance ability). While watching the movements they were most expert at performing, greater neural responses were observed in the left premotor cortex and the left inferior parietal lobule. These two regions have been found to contain mirror neurons in monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 1996a), and form the crux of the mirror neuron system in humans (Rizzolatti & Craighero, 2004). By studying dancers who were in the midst of intensive rehearsals to learn a new work, we were optimally poised to discover what goes on in the brain as individuals build movement expertise from the ground up. However, one major shortcoming of this study is that the dancers were not scanned prior to beginning rehearsals for *Skylight*. Thus, while we were able to take snapshots of their brains across the rehearsal process, we did not have a clear measure of how the AON responded to rehearsed movements before they were ever seen in the studio. With our next study, we attempted to overcome this issue, as well as the limitation of using subjective performance ratings, through investigation of novice dancers learning simple dance sequences.

What we can learn from the novice dancer's brain

While research with expert dancers has shed light on the neural correlates of highly skilled action embodiment (e.g., Calvo-Merino et al., 2005; Cross

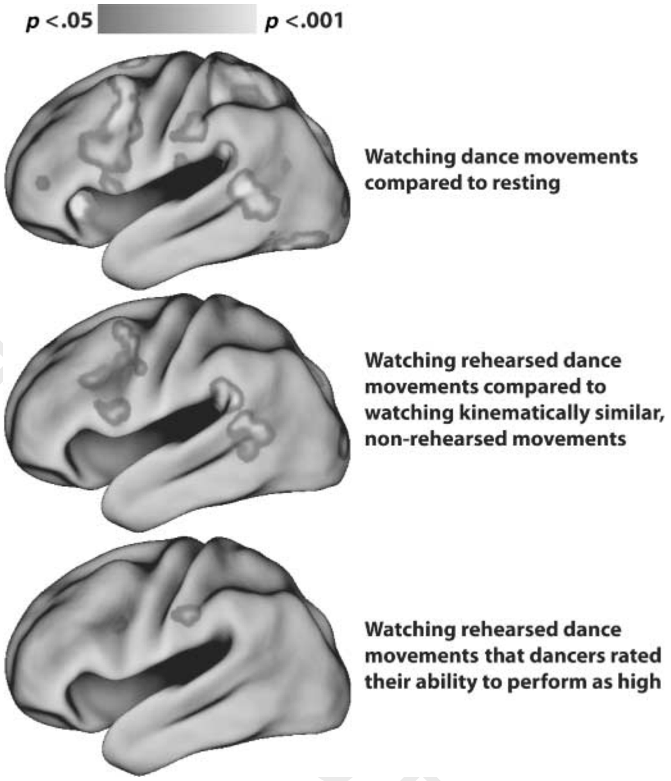

Figure 9.2 Results from functional imaging study with expert dancers. A selection of results (only the lateral surface of the left hemisphere) from three brain imaging contrasts from the Cross, Hamilton, and Grafton (2006) study on action expertise among expert dancers.

et al., 2006, Bläsing, Chapter 4, this volume), a look into the brains of novice dancers who are learning to integrate visual and auditory cues with coordinated whole-body movements can be equally instructive for our understanding of complex action learning. We know that many avenues exist for learning new dance movements. To return to the dance class example introduced earlier, if an instructor wants her students to perform a particular combination of steps, she could accomplish this in a number of different ways. She could verbally name or describe the sequence of individual steps, she could indicate or gesture the movements with her hands, she could show her students a string of symbols that denotes the combination in Laban movement notation (see Box 5.1 in Chapter 5 by Puttke, this volume), or she could perform the desired sequence herself.

To parse how different methods of learning might influence performance, this study focused on novice dancers. Here, we controlled how novice dancers learned new dance movements and examined resulting changes in each novice dancer's AON. We measured dance performance accuracy and neural activity within a group of participants who had no previous dance experience or training as they learnt simple dance sequences in an interactive video game context. In order to address our experimental objectives, we used a three-by-two factorial experimental design (Figure 9.3, panel A). We explored two separate, but related, avenues of new action learning in novice dancers: observational learning and learning from human versus symbolic action cues. This study was carried out over 8 consecutive days, as illustrated in Figure 9.3,

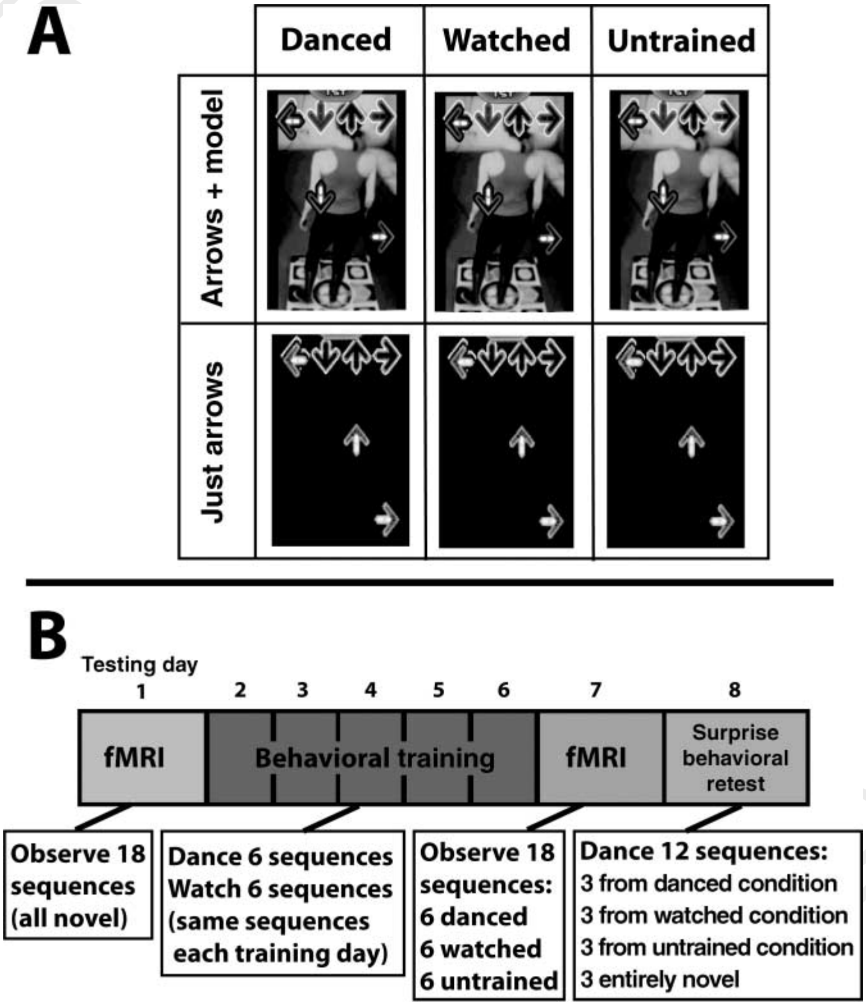

Figure 9.3 Experimental design and time course for experiments with novice dancers. Panel A represents the 3 (training experience: danced, watched, or untrained) by 2 (action cue: dancer with arrows or just arrows) study design. Panel B depicts the 4 phases of the study in chronological order.

panel B. Our first objective was to determine how observational learning, such as when one simply watches a dance instructor without imitating the movements, and then tries to reproduce the movements at a later point in time, is represented within the AON (Cross et al., 2009b). The second objective was to determine how movement training influences activity within the AON – both while observing an expert model accurately performing the actions (such as when one dances in step with a dance instructor while observing her movements) and when relying on purely symbolic cues (such as when one follows a diagram or symbolic notation of step patterns; Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009a). Even though both questions were investigated with a single study, for the sake of clarity, each objective is considered in turn.

Learning from observation

When we learn to walk, use a fork, or drive a car, we learn by first observing others do the task, and then practicing it ourselves. It is thus unsurprising that a wealth of behavioral research suggests that the quickest and most accurate learning results from observing and simultaneously reproducing another individual's movements (e.g., Badets, Blandin, & Shea, 2006; Bandura, 1977, 1986; Blandin, Lhuisset, & Proteau, 1999; Blandin & Proteau, 2000; Schmidt, 1975; Sheffield, 1961). This research has demonstrated that not only is observation helpful for learning (Blandin et al., 1999), but that physical practice is more beneficial than mere observation of new movements (Badets et al., 2006). One aim of our study with novice dancers was directed at further exploring the separate and combined contributions of these factors on acquiring novel movement sequences. Additionally, using functional neuroimaging, we aimed to characterize the neural underpinnings of observational learning with or without the added benefit of physical practice.

Early behavioral investigations by Sheffield (1961) led to the proposal that observation of a model provided a "perceptual blueprint", or a standard of reference for how the task to be learnt should be performed. Carroll and Bandura subsequently proposed that this perceptual blueprint improves learning by providing a means for the detection and correction of performance errors as well (Carroll & Bandura, 1987, 1990). Behavioral studies comparing observational and physical learning support the idea that observational learning in conjunction with physical practice can bolster learning over physical learning alone (Blandin & Proteau, 2000; Carroll & Bandura, 1990; Doody, Bird, & Ross, 1985; Lee, White, & Carnahan, 1990; Zelaznik & Spring, 1976; for a review, see Hodges, Williams, Hayes, & Breslin, 2007). In one such study, Blandin and Proteau (2000) asked participants to perform a task that involved performing a precise arm movement while avoiding obstacles. Participants physically rehearsed without observing a model perform the action, observed a novice performing the task before attempting to perform the task themselves, or observed an expert performing the task before attempting it themselves. Observation of either type of model enabled participants to develop error detection and correction skills as effectively as physical practice. This led Blandin and Proteau to conclude that individuals can develop error detection and correction as effectively from observational learning as they do from physical learning.

One of the primary theories why observational and physical learning have so much overlap is that they both engage similar cognitive processes (Barzouka, Bergeles, & Hatziharistos, 2007; Blandin et al., 1999; Bouquet, Gaurier, Shipley, Toussaint, & Blandin, 2007). For instance, a recent psychophysical and electromyographic (EMG; see Box 4.1 in Chapter 4 by Bläsing, this volume) study demonstrated that participants' learning of a novel, complex motor task is facilitated if they previously observed another individual learning to perform that same task, compared with watching another individual perform the task without learning, or learning to perform an unrelated task (Mattar & Gribble, 2005). However, as Blandin and colleagues note (1999), such findings do not mean that physical and observational learning are *identical* cognitive processes; particular features are unique to each kind of learning.

Such behavioral research establishes a solid foundation for exploring areas of overlap and divergence between observational and physical learning. However, it is difficult to determine with only behavioral experimentation the degree of correspondence of cognitive processes subserving these two types of learning. Behavioral and EMG studies alone cannot satisfactorily address the underlying neural mechanisms. Here we benefit from using functional neuroimaging, which can identify the neural mechanisms engaged during observational and physical learning. If both types of learning engage the same areas of the brain, then we can infer that both observational and physical learning engage comparable cognitive processes. Conversely, the emergence of different areas of neural activity based on learning would imply that distinct cognitive processes underlie these two types of learning.

We investigated observational learning by training novice dancers to perform complex dance movement sequences while manipulating training elements. Specifically, we sought to determine whether observational and physical learning result in quantitatively similar or different behavioral performance and patterns of neural activity. Because of the complexity and unfeasibility of having participants physically perform dance sequences in the scanner (but see Brown et al., 2006 for an innovative approach to this problem involving tango dancing in a PET scanner), we instead chose to train participants to perform the movement sequences with music videos outside the scanner, and then asked them to observe the training videos during the scanning sessions. The focus of this portion of the study was on differences between the three training conditions; danced, watched, and untrained (Figure 9.3A, B).

Seventeen young adult participants who had no dance training and no experience with playing dance video games first came into the laboratory to participate in an fMRI session while they watched and listened to 18 upbeat music videos. Half of these videos featured a person dancing along with arrows that scrolled upwards on the screen, and the other half had only the arrows scrolling on the screen. This first scanning session was followed by 5 consecutive days of dance training, where participants spent approximately 1 hour in the laboratory each day, practicing dancing six music videos (henceforth to be referred to as the "danced" condition), and resting while passively viewing, but not dancing, another set of six music videos (henceforth to be referred to as the "watched" condition).

We used StepMania software (www.stepmania.com), in conjunction with a dance pad connected via a USB to a desktop computer, to display the dance videos and record participants' dance performance. StepMania is a freeware version of the popular video game "Dance Dance Revolution" (Konami Digital Entertainment, Inc., Redwood City, CA). We chose to use an interactive video game in order to precisely quantify dance performance, instead of relying on subjective ratings, as we did in the Cross et al. (2006) study, while also maintaining participants' attention and interest across the lengthy training procedures.

Following 5 days of dance training, participants returned for a second fMRI session, where they observed the same 18 music videos from the first week of scanning. This time, however, six of those videos were highly familiar from having been physically practiced, another six videos were visually familiar from having been passively viewed during each training day, and the remaining videos had not been seen since the first week of scanning. In contrast to the instructions given to our expert dance participants in the study discussed above (Cross et al., 2006), participants in this study were instructed to simply observe the videos. Following the second scanning session, participants returned to the lab to perform a surprise dance re-test of a selection of the dance sequences they had practiced dancing, a selection of dance sequences they had passively observed, and a selection of untrained and entirely novel dance sequences.

Behavioral findings indicate that participants' performance of the sequences from the "danced" condition significantly improved across training days. Moreover, results from the surprise behavioral re-test show that participants were able to perform the dance sequences they passively observed during the week of training at an intermediate level between those sequences they danced and the untrained and novel sequences.

The imaging analyses were designed to accomplish three objectives. The first objective was to determine which brain regions were active when participants observed the dance music videos before ever stepping foot into the training room. This was achieved by identifying regions that showed a greater response while observing all music videos (task) compared to watching a static black screen with a white fixation cross in silence (baseline) from the pre-training scanning session. This contrast revealed broad activation within the action observation network. This pattern of activity was used as a mask for the next two imaging analyses from the post-training scanning session, in order to limit the search volume for the effects of interest. The next analysis identified neural regions that showed distinct response profiles when observing videos that were danced or watched. Here we found evidence that physical practice engages select components of the AON above and beyond passive observation. Specifically, participants recruited heightened activity in the right precentral gyrus when presented with videos they had danced, and did not recruit this same area when viewing videos they had only passively viewed during training. This pattern of findings is consistent with the notion that physical practice engages select components of the AON above and beyond passive observation (Aglioti, Cesari, Romani, & Urgesi, 2008; Calvo-Merino et al., 2006).

This is not to suggest that observational learning relies on an entirely different system than physical learning. Indeed, a conjunction analysis revealed that both physical and observational learning engaged activity in select areas of the AON (Figure 9.4). Further statistical analyses (detailed in Cross et al., 2009b) indicated that the neural responses within these two regions did not differentiate between videos that were danced or watched, but responded more strongly to videos that had been trained in either of these manners compared to videos that were untrained and observed only during scanning. When considered together, the imaging analyses from this study suggest that, at least among our sample of novice dancers, physical and observational learning share more commonalities than differences at a neural level.

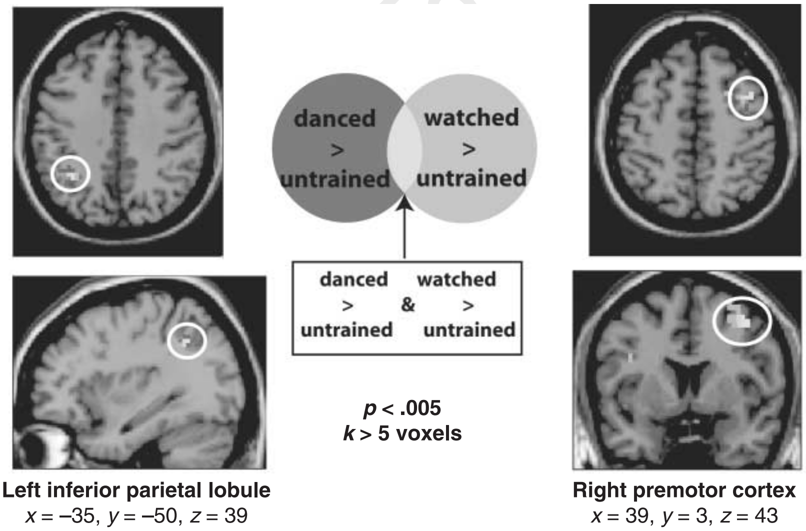

Figure 9.4 Brain regions that respond to physical and observational learning in novice dancers. Two regions of particular interest that demonstrated similar patterns of activity when novice dancers watched dance videos they had trained on throughout the week, or merely passively observed, are illustrated here on a rendered cortical surface of a standard brain from the Montreal Neurological Institute (MNI).

The converging evidence from our behavioral and neural measures serves to link the rich history of behavioral research on observational learning with the burgeoning field of neuroimaging inquiry into action cognition. We found it especially remarkable that such clear evidence emerged for observational learning in light of the fact that participants were never explicitly told to try to learn the sequences they watched each training day. Evidence from other studies suggests that the amount of observational learning we reported in this study could have been markedly increased if we had explicitly instructed participants to try to learn the sequences they watched during the training procedures (e.g., Hodges et al., 2007; Mattar & Gribble, 2005).

These results are generally in agreement with findings from the extant literature on dance representations in the brain (e.g., Cross et al., 2006; Calvo-Merino et al., 2005; Brown et al., 2006), which suggest that that AON, particularly parietal and premotor components of this network, is modulated by experience. The present investigation makes several novel contributions to this literature through inclusion of two critical control conditions, namely, the use of an "untrained" experimental condition in addition to the danced and watched conditions, and the inclusion of a pre-training scanning session. The inclusion of the pre-training scan is an especially valuable contribution, as it enabled us to quantify the effects of the dance training manipulation with greater precision than we were able to do in the Cross et al. (2006) study.

Of course, these findings are not without their limitations. The most serious limitation stems from our use of a within-subjects experimental design. A valid criticism of this design is that observational learning does not occur in a purely observational context, since all of our novice dance participants were also learning to dance particular sequences during the same sessions that they passively observed different sequences. However, we believe that our results are not invalidated by this criticism, as evidenced by dance performance scores and neural responses to stimuli from the untrained experimental condition. Put simply, if the skills participants were learning in the danced condition transferred uniformly to other conditions, then we would have expected a lot less differentiation between the watched and untrained conditions, which we did not see. Overall, what this portion of our study with novice dancers demonstrated is that several cortical regions of the AON respond in a similar manner to observational and physical learning. At present, a great need exists for future research to explore the different parameters that might influence observational learning at a brain and behavioral level, including motivation to learn, which part of the model provides the most information for learning a new skill, and how different kinds of instructions might influence observational learning.

Learning from other dancers versus learning from symbols

Another feature of action cognition that we examined with the same novice dancers was the specificity of the action observation network to learning from other humans, compared to learning from abstract symbols. In the past, several different functions have been proposed for the AON, including action prediction (Kilner, Friston, & Frith, 2007; Prinz, 1997, 2006; Schütz-Bosbach & Prinz, 2007), action understanding (Rizzolatti & Fadiga, 1998; Rizzolatti et al., 1996b; Rizzolatti, Fogassi, & Gallese, 2001), inferring the intention of others (Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005; Hamilton & Grafton, 2006; Kilner, Marchant, & Frith, 2006), and social cognition (Iacoboni & Dapretto, 2006). Previous imaging studies of this network have not directly compared these functions within the same experiments to determine whether different components of this network might serve specific, individual functions. One particularly unsettled issue is whether or not this network responds exclusively or even preferentially to observation of actions performed by other humans. For example, one could imagine that it is simpler to learn how to dance the *Macarena* from watching another person perform it than by following stick figure depictions or a computer simulation of the movements. One factor that can help determine whether the AON responds to the actions cued by other humans, per se, is whether it responds when actions are cued symbolically, or only to observation of another person performing the action. Moreover, if the AON has a specific role in action prediction and action understanding, then manipulating the degree to which an action can be easily understood should also affect the level of activity in the AON. One way this can be evaluated is by varying the amount of direct experience one has in performing an observed action. To accomplish this, we used the same novel dance training paradigm introduced above to determine whether activity within the AON is driven by action embodiment or by the form of the action stimuli.

If the AON is dedicated to action understanding, we might expect it to show a preference for biological motion stimuli, as some recent data suggest (e.g., Kessler et al., 2006; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004, Brass et al., 2000). Brass and colleagues (2000) were among the first to report that participants were measurably faster to imitate finger movements that were performed by another person compared to those that were cued by a spatial cue. Kessler et al. (2006) performed a follow-up study to Brass et al.'s (2000) to more fully investigate why this was the case. Using whole-head magnetoencephalography (MEG), Kessler and colleagues monitored participants' brain activity while they performed a finger tapping movement cued by a video of a finger tapping (biological movement condition) compared to a dot over the digit to move in a still photograph of a hand (non-biological movement condition). They report that left premotor and bilateral parietal and superior temporal cortices were more active during the biological than the non-biological movement condition. Further, they posited that these regions are probably working together (along with several other subcortical regions) to confer the behavioral advantage of faster reaction times when imitating biological movements compared to symbolically cued movements. Tai and colleagues report converging findings when individuals watched grasping performed by a human compared to grasping performed by a robot model controlled by an experimenter (Tai et al., 2004). They observed greater activity within the left premotor cortex when participants watched a human actor than when watching a robot model, which led them to conclude that the AON is specifically tuned to observation of biological movements.

The notion that the AON responds preferentially to human compared to non-biological action cues remains controversial. Several other studies have shown that this network will respond to non-biological stimuli in a similar way as to biological stimuli (Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Press, Bird, Flach, & Heyes, 2005). In one such study, Gazzola and colleagues monitored participants' neural activity with fMRI while they observed either a human hand or a robotic hand perform simple and complex actions (Gazzola et al., 2007). They observed robust activation across several regions of the AON, including dorsal and ventral components of the premotor cortex, superior parietal lobule, and the middle temporal gyrus when participants observed a human or robotic hand perform an action, compared to a static control image. Moreover, activation was greater when humans or robots were performing more complex, goal-oriented actions that were familiar to participants, such as grasping a cocktail glass, compared to simpler and possibly less relevant or familiar actions, like moving wooden blocks around. The authors interpret these findings as consistent with the notion that observation of familiar actions, or familiar action goals, will reliably and robustly activate the AON, regardless of the lack of correspondence between the acting agent and the observer (Gazzola et al., 2007).

The inferences that can be drawn from the study by Gazzola and colleagues (2007), and indeed, similar studies (e.g., Brass et al., 2000; Kessler et al., 2006; Press et al., 2005; Tai et al., 2004), are critically limited by participants' dissimilar amounts of experience or familiarity with the human and non-human action cues they observe within the task. For example, participants in these previous studies were most likely very familiar with observing hands grasping objects in every day life, but were probably less likely to come across robots grasping objects or abstract symbols cuing actions in their daily lives. With our study, we avoided confounding biological motion with familiarity through the use of intensive training procedures. Using this innovative approach, participants were taught to perform novel dance sequences with both biological and symbolic action cues (Figure 9.3A). Such a methodology enables a precise control of participants' familiarity and physical experience with the action stimuli they observe while being scanned. This permitted a measure of brain responses during action observation where biological motion could be studied independently from experience.

The objective of this portion of the study was to clarify the contributions of several key components of the AON to observation of action cues both with and without a human agent. Specifically, we tested whether the AON is driven by observation of other humans, or whether it is driven by observation of familiar or executable actions. We directly manipulated both the presence of a human dancer and participants' physical experience with the dance sequences. If the action observation network responds uniformly as a function of observing humans or experiencing, then we would expect stronger responses across all components of the AON when observing biological motion compared to non-biological motion (e.g., Kessler et al., 2006; Tai et al., 2004), and when observing trained compared to untrained sequences (e.g., Calvo-Merino et al., 2005; Cross et al., 2006). However, if it is the case that individual components of the AON are sensitive to different kinds of experience, we would predict that distinct components of this system should respond differently based on experience and the presence of a biological agent.

The experimental procedures were identical to those described above for the observational learning portion of the study. One critical feature of the training stimuli that merits restating is that for all categories of stimuli (danced, watched, and untrained), half of the videos featured an expert human model dancing the sequences along with the arrows, and half of the videos had only the arrows denoting the sequences without a human model. Interestingly, when we reanalyzed the behavioral performance data across the five days of dance training, a small but significant effect emerged of the presence of a human model. Participants' dance scores were marginally higher for sequences that included a human dancing along with the arrows (Cross et al., 2009a).

The imaging analyses for this objective pursued two aims: to determine the effects of the presence of a model on AON responses, and to determine the effects of training. The three-by-two factorial design (Figure 9.3A) was essentially distilled to a two-by-two factorial design for this portion of the study, with training (trained versus untrained) and presence of human (human present versus human absent) as the two factors of interest. Functional imaging data from the post-training scanning session revealed a strong activation within bilateral posterior temporal cortices when participants observed videos that had a human model present (Figure 9.5, top). A robust main effect of training was observed in the right ventral premotor cortex (Figure 9.5, bottom), suggesting that this area was sensitive to the effects of training regardless of the training stimulus. However, bilateral posterior temporal cortices were uniquely sensitive to training stimulus.

Taken together, this pattern of results indicates that some parts of the AON respond preferentially to physical experience (ventral premotor cortex) while other parts respond specifically to the presence of a human model (posterior temporal cortex). The finding that ventral premotor cortex (vPM) responds most strongly to cues for actions that have been physically experienced and not to the presence of a human model, advances our understanding of what this region contributes to action cognition. Since the discovery of mirror neurons in an analogous region of monkey premotor cortex (area F5) (Gallese et al., 1996; Rizzolatti et al., 1996a), several hypotheses have been

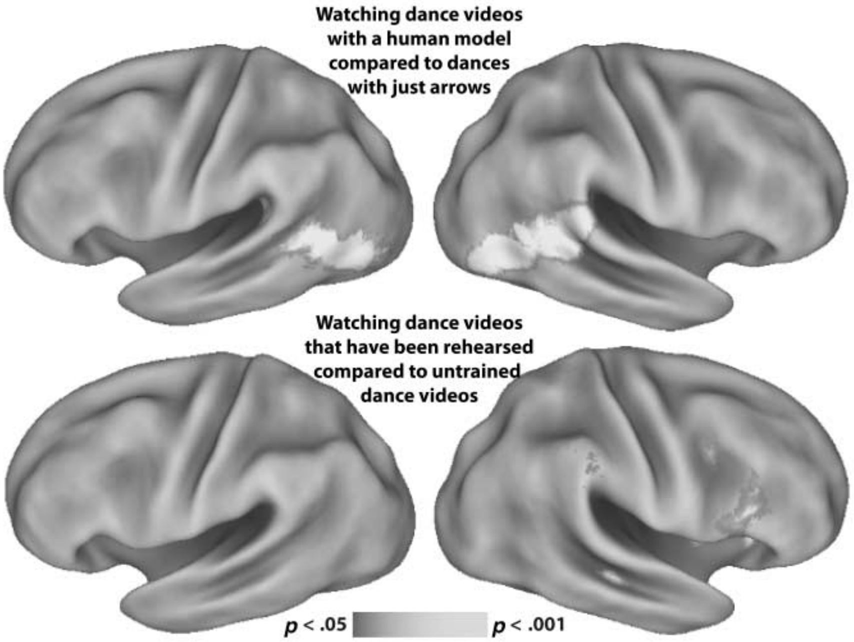

Figure 9.5 Brain regions that respond to training and the presence of a dancer in novice dancers. The top two brains illustrate brain regions that respond to the presence of a dancer on the screen, independent of novice dancer participants' training experience with the videos. The bottom two brains illustrate brain regions that respond to dance videos that the novice dancers have trained to dance, independent of the presence or absence of a dancer on the screen.

put forward for the role of premotor cortex in motor and social cognition, including predicting the ongoing actions of others (Kilner et al., 2007; Prinz, 1997, 2006; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005), inferring others' intentions (Fogassi et al., 2005; Hamilton & Grafton, 2006; Kilner et al., 2006), and social cognitive behaviors, including imitation and empathy (Iacoboni & Dapretto, 2006). A key question in distinguishing these hypotheses is the responsiveness of vPM to biological and non-biological stimuli. For example, if it were the case that vPM plays a specific role in social cognition, then we would expect it to show stronger responses to observation of human actors. Results from previous studies of this issue have been mixed (Brass et al., 2000; Gazzola et al., 2007; Kessler et al., 2006; Press et al., 2005; Tai et al., 2004). Symbolically represented actions are an ideal way to separate biological agency from action representation as the arrows do not resemble living agents but, following training, they are tied to specific motions. Thus, our data suggest that vPM does not respond specifically to human actions. Instead, vPM responses appear to be both flexible and dynamic, driven most strongly by action cues that are familiar from previous experience. This finding is in line with a theory recently advanced by Schubotz, who suggests that activity within the premotor cortex during action observation serves to predict ongoing, familiar events (Schubotz, 2007). The present findings are also compatible with the notion that vPM is involved in motor preparation, both implicit and explicit, for familiar actions (Grèzes & Decety, 2001; Harrington et al., 2000; Rizzolatti & Craighero, 2004).

In contrast, temporal regions, including posterior superior temporal sulcus (pSTS) and inferior temporal gyrus (ITG), demonstrate an almost opposite response profile to vPM with respect to prior experience and the presence of a human model. These temporal regions responded most robustly to the presence of a human model, regardless of prior physical experience. A well-established literature has demonstrated robust activity within posterior temporal regions (including pSTS, pSTG and ITG) during observation of biological motion (Allison, Puce, & McCarthy, 2000; Beauchamp, Lee, Haxby, & Martin, 2003; Grossman & Blake, 2002; Puce & Perrett, 2003).

One interpretation is that pSTS and pSTG (posterior superior temporal gyrus) are critically involved in the automatic identification of animate entities in the environment at a very early level of visual processing (Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005). Reliable activation of STS during tasks designed to explore properties of action resonance has resulted in the inclusion of STS as a component of the human mirror neuron system (Gazzola et al., 2007; Iacoboni & Dapretto, 2006; Keysers & Gazzola, 2007; Kilner et al., 2006). However, taking the present findings into account, it appears that STS's contribution to action resonance results from the observation of another human or biological form, not from action cues. This result is consistent with recent data that demonstrate that observing and imagining moving shapes activates premotor and parietal components of the AON, but only observation of moving entities that participants construe as animate leads to STS activation (Wheatley, Milleville, & Martin, 2007). We suggest that STS is involved in the visual analysis of socially relevant conspecifics' actions, and this processing subsequently feeds into premotor and parietal mirror neuron areas, but also to other brain regions for teleological processing (Csibra, 2007). Such an account of pSTS's involvement in person processing cognition is in accord with a recent meta-analysis performed on this region's functional profile (Hein & Knight, 2008). This means we should not just consider STS to be an input to the human mirror neuron system, but it instead has distinct functions of its own, especially with regards to social cognition.

It is important to consider how these new data relate to previous studies that have reported contradictory results regarding the AON's response to human and non-human action cues (Gazzola et al., 2007; Kessler et al., 2006; Tai et al., 2004). A persistent problem with many previous studies examining questions of action resonance is the issue of familiarity or experience with the action being observed or cued (de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Gazzola et al., 2007; Tai et al., 2004). Prior work performed with dancers has demonstrated that the more physically familiar an action is, the more the vPM responds when observing that action (Calvo-Merino et al., 2005, 2006; Cross et al., 2006, 2009b). It is thus likely that the discrepant results concerning vPM activation in response to observation of actions featuring human and non-human cues are a result of different degrees of experience with an action or action cue, and not the biological status of the agent, per se. In the present study, we have sidestepped this issue by training participants to perform complex sequences of dance movements that were entirely novel before the study began. Our findings that the premotor cortex responds more strongly to training than to the presence of a human model, and that posterior temporal areas respond to the presence of a human model but not to training, suggest that the AON comprises dissociable components involved in different aspects of action cognition. In particular, we suggest that activation of vPM does not necessarily reflect selective processing of human-related action stimuli. Instead, the present data emphasize the impact of motor familiarity on vPM responses and the presence of a human model on posterior temporal responses.

Implications and practical applications for dancers and beyond

At its essence, our laboratory's work with dancers is basic science research. However, findings from this basic research nonetheless have the potential to inform the way dancers and dance instructors approach their work. With both expert and novice dancers, we observed that participants showed stronger and more finely tuned neural responses within the motor areas of the brain when watching movements they had previously physically experienced. These results are corroborated by data recently reported by Aglioti and colleagues, who examined the corticospinal responses of professional basketball players and coaches observing a player making free shots (Aglioti et al., 2008). These authors report that, while the motor systems of elite athletes and expert observers are activated when watching actions belonging to their area of expertise, only the elite athletes demonstrated the ability to discriminate between accurate and erroneous performance, based on observation alone. Aglioti and colleagues conclude that only actual physical practice, which engenders embodied motor expertise, can transform an individual into a truly expert observer of skilled actions.

For teachers of dance, one suggestion might be to keep as active as possible in the instruction process, in terms of being able to perform all the desired movements at the most expert level possible. Although this suggestion might seem somewhat obvious and simple, it could facilitate an instructor's ability to more quickly and accurately diagnose and correct mistakes in dancers' movements. Intuitively, the research findings also suggests that dancers, particularly current dancers, as opposed to former dancers who have been out of the studio for years, might make the best dance instructors and evaluators, since their brains and bodies are highly and regularly practiced at matching action with perception (see also Chapters 1, 4, and 5 by Schack, Bläsing, and Puttke, this volume).

For dancers, the research findings that could have the most appeal and potential for studio applications are those concerning observational learning (Cross et al., 2009b). Although it is the case that actual physical practice is better than mere observation for constructing neural and behavioral representations of new actions (e.g., Aglioti et al., 2008; Calvo-Merino et al., 2006; Cross et al., 2009b; Frey & Gerry, 2006), it is nonetheless striking that simple observation can have significant effects on behavioral performance and activity within the AON. This suggests that dancers can continue the learning process even while waiting at the side of the studio for a turn to execute a combination, or, more importantly, when unable to rehearse because of physical injury (for impressive examples, see Chapter 5 by Puttke, this volume).

Indeed, Johnson-Frey presents a compelling case for speeded recovery from neurological injury (in this case, a cerebral vascular accident, or stroke) with the concomitant use of action observation and active action simulation, which is somewhat similar to the procedure we employed in our study with expert dancers (Johnson-Frey, 2004). Recent work with healthy older adults learning to encode new motor memories lends additional support to the idea that observation of actions, in concert with physical performance, can lead to more robust memory traces and motor learning (Celnik, Stefan, Hummel, Duque, Classen, & Cohen, 2006; see also Chapters 1 and 4 by Schack and Bläsing, this volume). Considered together, this research suggests that observing can help dancers to maintain choreography in their bodies, and observing while simultaneously imagining themselves performing might aid this process even more, as well as potentially facilitate recovery from physical (or neurological) injury.

Concluding remarks

As a final comment, it is important to note that "dance neuroscience" research did not necessarily stem from a desire to investigate how the experience of being a dancer influences the brain. Rather, neuroscientists have turned to dancers as a valuable human resource in possession of a rich skill set who can be studied to address broadly relevant issues of how the human brain coordinates perception with action. Neuroscientists' fascination with dancers will undoubtedly continue, as we seek to further characterize the sophisticated neural structure that underlies the complex choreography between action and perception.

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