Chapter 10
Motor Control in Action: Using Dance to Explore the Intricate Choreography Between Action Perception and Production in the Human Brain

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10.1 Introduction

Cue the crescendo: An audience watches as a ballerina takes center stage and precisely executes 32 *fouettés en tournant—en pointe*. Each revolution is performed with athletic deftness, spatial precision, and corporeal poise. Underlying the smooth delivery, the dancer's mind and body reach an apex: maintaining balance with arched feet, pointed toes, grounded core muscles, and postural stability. She generates impetus for the turns while coordinating her arms, shoulders, and hands, to appear light and effortless, with a smile on her face and perfect synchronization with the music. Complex coordination in a dance context extends well beyond the movement vocabulary of classical ballet dancers. It is cultivated among the many cultures of the world and their respective dance traditions. For the purposes of the present chapter, we define dance as bodily movements—whether choreographed or impromptu, rhythmic or asymmetric, with or without musical accompaniment—as a medium for artistic expression for individuals or groups. The ubiquity and purpose of dance have been examined in scientific contexts for over a century. First postulated by Darwin and corroborated by recent research, the origins of dance are speculated to be displays of courtship and mate selection, including indicators of symmetry, testosterone exposure in males, and synchrony with partner(s) (Fusani 2008; Shuster 2009).

Scientific investigation of dance can illuminate more than just its origins or the evolutionary function of coordinated movement, however. Of interest in the present chapter is how the behavioral and brain sciences are using dance paradigms in experimental contexts to better understand the neurophysiological substrates supporting

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links between the physical or affective experience of an observer and how the observer perceives a movement. We have chosen to focus on two particular points of convergence between dance and neuroscience, namely (1) how dance informs our understanding of action expertise, and (2) how dance advances our understanding of neuroaesthetics.

Nearly as many dance styles and traditions exist as there are human cultures: from the highly stylized, minimalist movements of Kabuki dancers in Japan to the rigorous, structured movement vocabulary of classical ballet, or the dramatized isolation of the eye muscles, neck, and knuckles in the Indian dance form of Kathakali, to the whole-body, poetic articulation of the dances of the Yoruba people in West Africa, humans all over the world create, perform, and watch dance. Only recently have scientists turned to this art form as a resource for research into motor control and aesthetics. In the first section of this chapter, we consider how early neurophysiological work with nonhuman primates gave rise to the notion of neural mechanisms that link action with perception, and how recent work with dancers has helped to refine our knowledge of how physical experience and expertise shape perception. In the second section, we delve into the realm of empirical aesthetics, specifically into the budding field of neuroaesthetics, to explore how this nascent field seeks to link subjective appraisals of stimuli with the neurobiological foundations that support such appraisals. Here as well, we highlight how research with dance and dancers is helping to move forward our understanding of the biological substrates of action perception and appreciation.

10.2 How Dance Informs Research Into Action Expertise

A question that has been of particular interest to philosophers for centuries, and to psychologists and neuroscientists ever since the advent of their fields, is how we are able to integrate physical and perceptual experiences to learn new movements. Such abilities are quite pronounced in professional dancers, whose livelihoods depend on rapid and adept movement, reproduction, and refinement. Before discussing how research with dancers advances our understanding of complex action learning and perception, it is first necessary to ground these questions within a broader, historical context. With the advent of cognitive psychology in the late nineteenth century, William James introduced the idea that action and perception processes likely converge or overlap in the human mind (James 1890). Neurophysiological investigation into the ability of the brain to use perceptual information to shape movement began in the mid-twentieth century, when information-processing explanations proposing complex transformations from perception to the organization and execution of action gathered momentum (Welford 1968; Sanders 1967, 1983; Mountcastle et al. 1975; Massaro and Friedman 1990). In the mid-1970s, Mountcastle and colleagues began the first investigations into putative neurophysiological mechanisms linking action with perception (Mountcastle 1975; Mountcastle et al. 1975; Yin and Mountcastle 1977). Through these seminal studies, Mountcastle and colleagues determined that neurons in parietal cortex respond to visual cues associated with specific actions.

Mountcastle and colleagues suggested that parietal cortex is a likely candidate for cross-modal convergence of action and perception, and established the foundation for the next several decades of further research into how these modalities interact (Andersen et al. 2004).

In the 1990s, research into the interface between action perception and production experienced an extraordinary surge in interest that was sparked by the discovery of so-called mirror neurons within the ventral premotor cortex of the macaque monkey. These neurons fired in a similar manner both when a monkey performed an action and when it observed another monkey or a human perform the same action (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996). A similar firing pattern when perceiving or performing actions was subsequently observed in the inferior parietal lobule (Fogassi et al. 2005), which suggested that perceiving others' actions engages a similar fronto-parietal circuit as executing actions.

One dominant explanation of these response profiles is tied to the notion of motor simulation (Jacob and Jeannerod 2005; Jeannerod 2001). The concept of motor simulation is consistent with other forms of mental simulation, which involve the reenactment of mental processes associated with previously experienced states (Barsalou 2008). Such states can be perceptual, motoric, or introspective. Hence, motor simulation is an instance of a more general concept of mental simulation (Jacob and Jeannerod 2005). Many researchers implicitly or explicitly hold that the mirror system is a key neural substrate for processes of motor simulation (e.g., Decety and Grezes 1999, 2006). In addition, motor simulation accounts of action comprehension have proposed that perceiving and understanding the action of another might involve the observer's brain simulating observed movements using their own motor system (Fadiga et al. 1995, 1999; Grafton et al. 1996; Rizzolatti et al. 2001). Thus, it is argued that through a process of motor simulation, action comprehension occurs by engaging specific parts of the motor system that would be used to perform the same action that is being observed (Rizzolatti et al. 2001).

Interest in mirror neurons has sparked hundreds of studies and an ongoing debate among researchers regarding the specific parameters, scope, and limitations of a possible action simulation system within the human brain (Gallese et al. 2011; Gallese and Sinigaglia 2011). While an exhaustive review of the past two decades of research performed in this domain is beyond the scope of this chapter (for reviews, see Grosbras et al. 2012; Molenberghs et al. 2012; Rizzolatti and Sinigaglia 2010), what a burgeoning corpus of research demonstrates is that neural tissue found within parietal and premotor cortices of the human brain is engaged when actions are performed and when they are observed. This work has given rise to the notion of a human mirror system, which consists of multiple cortical regions and shows evidence for behaving in a similar manner to individual mirror neurons found within nonhuman primate brains (Molenberghs, et al. 2012). A schematic representation of the human mirror system is depicted in Fig. 10.1.

The implications of a neural link between perception and action are broad-reaching and have been explored by scientists from disciplines and perspectives beyond neurophysiology and cognitive neuroscience, including the sport sciences, cognitive psychology, philosophy, and physical and occupational therapy (Johnson-Frey 2004;

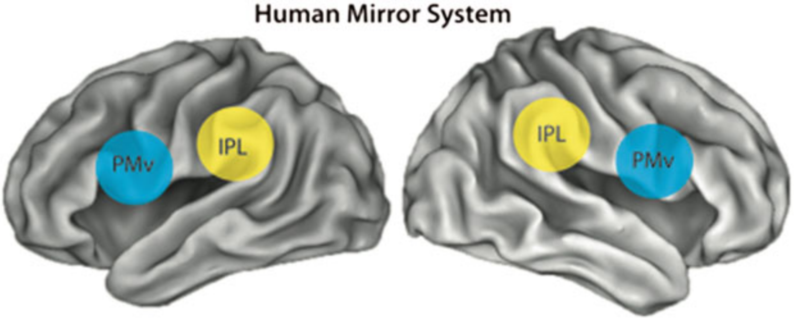

Fig. 10.1 Schematic representation of the human mirror system. The core nodes of the human mirror system are bilateral ventral premotor cortex (*PMC*) and inferior parietal lobule (*IPL*). While other regions within the human brain have been reported to show mirror-like properties, the strictest definition of the human mirror system includes only those brain regions where so-called mirror neurons, or cells that respond when performing an action or watching another perform an action, have been reported through neurophysiological investigations in the nonhuman primate brain

Braun et al. 2006; Jacob 2008; Goldman 2009; Yarrow et al. 2009; Guillot and Collet 2010; Moran et al. 2012). Moreover, some researchers have found that experimental paradigms that borrow from the arts, namely dance, offer an ideal means for advancing knowledge of how action and perception are linked (Bläsing et al. 2012). Paradigms incorporating dance training or the study of professional dancers have shed light on how motor expertise is manifest in the human brain, as evidenced by the two original studies to approach questions of action expertise using expert dancers as participants.

The first study to investigate how physical expertise with a particular dance style shapes neural activity when watching dance was conducted by Calvo-Merino et al. (2005). The authors studied a group of expert male capoeira dancers, expert male ballet dancers, and a group of age and sex-matched control participants. In this functional magnetic resonance imaging (fMRI) experiment, participants from all three groups watched 12 different 3-s videos depicting capoeira movements, and 12 different 3-s videos depicting ballet movements. The task was to indicate via a button press how tiring they thought each movement was. The authors found strong evidence in support of the idea that one's individual motor repertoire strongly shapes perception of others in action. Specifically, they found that when ballet dancers watched ballet or when capoeira dancers watched capoeira, they showed greater activity across brain regions associated with the mirror system, including left dorsal and ventral premotor cortices and posterior superior temporal sulci and bilateral intraparietal sulci. This finding is illustrated by the parameter estimates that quantify the relative amplitude of brain responses to watching the different kinds of dance videos among the three groups of participants. Crucially, no differentiation between the dance styles was seen in these regions within the brains of control participants. The authors concluded that long-held motor expertise markedly shapes perception, such that brain regions implicated in linking up performed with perceived actions are more active when an observer watches a particular movement he or she is physically familiar performing.

The study by Calvo-Merino et al. (2005) forged new territory in understanding how highly complex action and perception are linked in a number of ways. First, the data suggested that the mirror system codes complete action patterns, as opposed to individual movements. This was evidenced by the fact that movements from each dance style contained similar elements (such as swinging arms or jumping), yet the brains of capoeira and ballet dancers responded preferentially to their embodied movement style. The authors interpret this as evidence that neural architecture linking action with perception is sensitive to abstract levels of organization (such that two different dance styles can be distinguished). The findings are also important, in that they demonstrate the sensitivity of mirror system representations to *learned* movements, as opposed to innate action patterns that might be performed more or less by different groups of people.

A subsequent experiment more closely investigated this latter point in a longitudinal training study performed with a company of contemporary dancers (Cross et al. 2006). In this study, the authors scanned the brains of ten expert contemporary dancers once a week across 5 weeks of the rehearsal process as they learned a new piece of choreography that was rhythmically complex and lasted 25 min. The dancers rehearsed the new choreography for 4–5 days each week, and on each weekend, they underwent fMRI while watching 18 short-movement sequences from the work they were learning, or 18 kinematically similar control movements (all performed by the same dancer). While the dancers were in the scanner, their task was to watch each movement, imagine themselves performing it, and to evaluate how well they could perform each movement segment. At the end of each video clip, dancers reported on a 1–4 scale how well they thought they could physically perform the sequence they just watched.

The authors found that across the testing sessions, how the dancers rated their performance ability for the rehearsed movements significantly increased while their performance ability ratings for the (unrehearsed) control movements did not change. In terms of the neuroimaging findings, when the dancers watched movement that they had physically practiced compared to the kinematically similar control movement, more activity was seen within bilateral mirror system regions. This finding provided a clear replication and extension of what was reported by Calvo-Merino et al. (2005) with the ballet and capoeira dancers, demonstrating that de novo learning also results in marked differences in how similar movements with different experiential profiles are perceived. The most novel finding from this study, however, is what the authors found when they ran a parametric analysis querying brain regions whose activity increased with higher ratings of performance proficiency. This analysis revealed two small foci—left inferior parietal lobule and left ventral premotor cortex, which showed the strongest responses when dancers watched the movements that they were (individually) best at performing. What this finding suggests is that the better a dancer is at performing a movement he or she is watching, the more he or she simulates the observed action, and core mirror system regions within the left hemisphere are engaged by such processing.

These two highlighted studies using expert dancers to explore the neural signatures of physical expertise have been joined by a small but growing number of subsequent studies also using dancers to further knowledge on the impact of expertise on the brain (cf. Calvo-Merino et al. 2006; Orgs et al. 2008; Fink et al. 2009; Hänggi et al. 2009). Taken as a whole, these studies demonstrate how combining brain-imaging approaches with populations in possession of a highly specialized and skilled motor repertoire can advance our understanding of how action perception and performance are linked at behavioral and brain levels. However, the utility of dancers and dance paradigms for understanding how we perceive others is not limited to questions of motor expertise. In the following section, we explore how the dance domain can inform other aspects of the psychological and brain sciences, such as our affective appraisal of the movements of others.

10.3 How Dance informs Understanding of Aesthetics at Behavioral and Neural Levels

Another way in which research with dancers and the use of dance-based experimental paradigms has advanced understanding of how the brain perceives others in action is via empirical aesthetics. Classically, the study of aesthetics is associated with scholars in the humanities, such as philosophers, visual artists, and performing artists. For this reason, it is useful to define what, precisely, we mean by "aesthetics" when we discuss it in a scientific context. In consideration of the breadth of meanings and ambiguities the term "aesthetics" may carry, Brown and Dissanayake (2009) suggested that "aesthetics" has been used in two ways. In one sense, "the aesthetic" has been used to account for emotional responses that emerge when perceiving works of art, wherein art works (i.e., paintings, sculptures, sketches, dances, music) and the arts (i.e., corresponding activities or expressions) are fundamental to this usage. Another use of "aesthetics" is in reference to any system of valuation for the appreciation of beauty; the sensory preferences that humans and/or animals hold, with positive emotional responses towards objects resulting from selective attention (Orians 2001; Voland and Grammer 2003).

For this chapter, we will consider the term "aesthetics" as a heuristic for considering the experiences that result from the perception, appreciation, and/or creation of an artistic work. Aesthetics are studied and appreciated across myriad contexts including (but not limited to) faces, landscapes, music, dance, sculpture, food, paintings, mate selection, and machinery (Jacobsen 2006). For thousands of years, the only way in which aesthetic processing could be studied was to directly ask an individual about his or her experience with a stimulus, or observe their overt behavior toward a stimulus (Jacobsen et al. 2004, 2006). With the advent of cognitive neuroscience, new tools and techniques have enabled scholars from the psychological and brain sciences to explore the neurophysiological underpinnings of aesthetic perception. As such, neuroaesthetics offers another means of investigation into one's experience of the sublime. By simply being in the world, humans are in a constant state of aesthetic appraisal of ordinary objects, people, and experiences. The domain of neuroaesthetics aims to shed light on the nature of the aesthetic experience; that is, the relationship between the observer and the object, and the aesthetic processes that coalesce to create a rich relationship between stimulus and perceiver. As neuroaesthetics is a relatively new discipline, only a small number of empirical studies yet explored the affective relationship between an observer and a stimulus. Moreover, most of the work to date has focused on aesthetic responses to (static) visual artworks or music (cf. Cinzia and Gallese 2009; Blood and Zatorre 2001), with just a handful of studies that have explored the aesthetic responses in brain and behavior to dance. To place the dance neuroaesthetics research within a broader context, we first consider what we learn from the wider literature on empirical aesthetics and neuroaesthetics.

When a spectacle and its spectator meet, what the spectator beholds can vary from a fleeting sublimity to a sense of humdrum to a mere, neutral acknowledgment of an artwork. Each experience is, of course, personal to the beholder; one's personal preferences, expertise, and exposure, for example, may reflect in the evaluative judgments that follow, giving rise to inter-individual variability (Palmer et al. 2013). Underlying the aesthetic processing of a stimulus is an assortment of neural processing, including (but not limited to) activity within the medial orbitofrontal cortex (mOFC), a brain region associated with decision making, affective judgments, and expectation (Kawabata and Zeki 2004; Vartanian and Goel 2004; Kringelbach 2005). It thus appears that beauty is not so much in the eye, but instead the brain, of the beholder. In one recent study (Ishizu and Zeki 2011), volunteers drawn from a range of cultural/ethnic backgrounds were asked to rate a series of works—paintings or segments of music—as belonging to the categories of "beautiful", "neutral," or "ugly" while undergoing fMRI. The goal of the study was to determine where in the brain cortical activity correlated with experiences that participants rated as beautiful or ugly. The most striking finding from this study was that a portion of the mOFC was active when participants experienced a musically *or* visually beautiful stimulus. Of note, the intensity of activation within this region was correlated with ratings of the intensity of beauty. This region is thought to make rapid assessments as to the reinforcing properties of a stimulus, offering one possible pathway between reward, judgment and aesthetic pleasure upon perception. The authors concluded by offering a brain-based theory of beauty wherein the mOFC codes the aesthetic or rewarding value of a stimulus, regardless of its modality.

When further considering the relationship between the observed and the observer in an artistic context, a number of scholars have argued that understanding the role of empathy is crucial. Robert Vischer (1873; as referenced in Mallgrave and Ikonomou 1994) initially discussed empathy and its role in aesthetic experience as the notion of *Einfühlung,* which refers to the physical response when observing forms within art works (primarily paintings). This notion has subsequently been defined as "aesthetic empathy," and naturally applies to the dance domain as well, in what has been termed kinesthetic empathy (Hagendoorn 2004). In distinguishing from a passive mode of "seeing" and an active mode of "looking at," Vischer described how certain depicted forms, i.e., bodily postures or the function of muscles and limbs, could arouse certain

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feelings in response. Such nonpassive perceiving was proposed to involve a profound response of empathy. As a result, the body of the observer would resonate with the observed or depicted forms in the work. In turn, certain forms should evoke certain emotions. Hildebrand (1893) elucidated upon this idea, suggesting that in order to decipher a work, one has to implicitly grasp its creative process. Warburg proceeded to acknowledge this in his notion of *Pathosformel,* or form-evoking Pathos, wherein certain gestures, bodily forms, actions and expressions can be consistently detected throughout art history (Warburg 1999).

The array of dimensions involved in an aesthetic response of the observer is reflected by the body of research addressing the structure of this experience. One seminal theory that attempts to draw together notions of mirroring between the artist's work and the observer, grounded within contemporary neuroscientific understanding of the human mirror system, was proposed by Freedberg and Gallese (2007). In this account, termed the embodied simulation theory of aesthetics, the authors suggest that embodiment plays a significant role in appraising an artwork. Somewhat surprisingly, in many formal art criticism circles, empathy towards or bodily resonance with a work of art was previously dismissed as entirely intuitive subjective phenomena (Collingwood 1938). Due to accumulating research on the function and scope of the mirror system, however, this claim has been convincingly challenged. For example, when an observer watches a particular body part of someone else being touched, activation is seen within the brain of the observer as if the observer's own body were itself being touched (cf. Keysers et al. 2004). Freedberg and Gallese (2007) suggest that empathetic simulation is evoked by the representation of figures in an image, and a high degree of sensorimotor resonance with an agent depicted in an artwork is what leads to an aesthetically pleasing experience for the observer. The authors go on to propose that such resonance between an artwork and observer need not end at figural representations. Instead, an observer might experience some kind of somatic resonance with the artistic medium or technique used in the work. For example, an observer might be drawn in on a visceral level by the artistic gestures used to create a work, such as the brisk brushstrokes of Pollock, or the slashed cuts of a Lucio Fontana piece. This is what allows an observer to, as described by Freedberg and Gallese (2007), "[feel] the movement behind the mark" (p. 201).

Following on from the proposal that embodiment processes play a role in aesthetic appraisal, several research groups have turned to dance paradigms to further explore the role of kinesthetic empathy between the observer and artwork (in this case, the work of art is the movements performed by a dancer). The first study to do this was performed by Calvo-Merino et al. (2008) with a group of dance-naïve participants watching short-dance segments while undergoing fMRI. Several months after the fMRI experiment, the participants returned to the laboratory and rated the individual movements on a number of established aesthetic dimensions (after Berlyne 1974). In contrast to the mOFC findings that have been reported by experiments looking at aesthetic appraisal of static works of art and music (cf. Kawabata and Zeki 2004; Ishizu and Zeki 2011), the brain regions found to track with increasing aesthetic ratings of dance were located within bilateral occipital cortices and right premotor cortex. Thus, it appears that visual and sensorimotor cortices are more engaged when watching aesthetically pleasing dance, a finding that fits well with Freedberg and Gallese's (2007) embodied simulation account of aesthetics.

A subsequent study by Cross et al. (2011) sought to tie together the findings discussed in the previous section on embodiment and physical experience with what was reported by Calvo-Merino et al. (2008) concerning the involvement of sensorimotor brain regions in the aesthetic appraisal of dance. In this study, dance-naïve participants watched a range of ballet and contemporary dance movements performed by professional dancers while undergoing functional neuroimaging. Participants were asked to rate each movement on how well they could physically reproduce it (same question/scale used by Cross et al. 2006), and also how much they liked watching each movement. Behaviorally, the authors found a strong negative correlation between perceived physical ability and liking, such that participants most enjoyed watching those movements they rated as the most difficult to physically perform (Cross et al. 2011). To analyze the brain-imaging data, the authors ran parametric analyses to query brain regions that showed increasing responses based on increasing (or decreasing) ratings of physical ability or aesthetic value. The most interesting finding emerged from the interaction between parameters of perceived physical ability and aesthetic value. This analysis evaluated brain regions showing a stronger response when participants rated a movement as difficult to perform, but highly enjoyable to watch. The authors found that bilateral occipitotemporal cortices and right inferior parietal lobule showed increasing responses the more a participant liked watching a movement, and the less he or she could perform it.

When the findings of Calvo-Merino et al. (2008) and Cross et al. (2011) are considered together, they begin to build a compelling case in support of Freedberg and Gallese's embodied simulation account of aesthetics (2007). It appears that when watching dance, even dance-naïve observers engage sensorimotor brain regions associated with action perception and action performance to a larger degree when they find the movement aesthetically pleasing. One might conclude from these findings that embodied simulation of a dance piece is integral to aesthetic experience, although this hypothesis has not yet been tested directly. Along these lines, however, recent work from our laboratory is seeking to more fully characterize the role and impact of physical experience on aesthetic experience in dance contexts (Kirsch et al. 2013; Kirsch et al., in preparation). One of the patterns of findings most relevant to consider in light of Freedberg and Gallese's embodied simulation account of aesthetics concerns the relationship between the perception of one's ability to perform a movement, or the inherent complexity of a movement, and how much an observer enjoys watching the movement. Figure 10.2 illustrates findings from dance-naïve observers who watched a series of dance movements and were asked to rate their physical ability to perform the observed movements (panel A; Cross et al. 2011) or the perceived complexity of the movements (panel B; Kirsch et al. 2013), as well as how much they enjoyed watching them.

The plot in panel A and the first plot in panel B illustrate that dance-naïve observers enjoy watching most of those movements that they perceived as difficult or complex to perform. This pattern of findings might suggest that complex dance movements

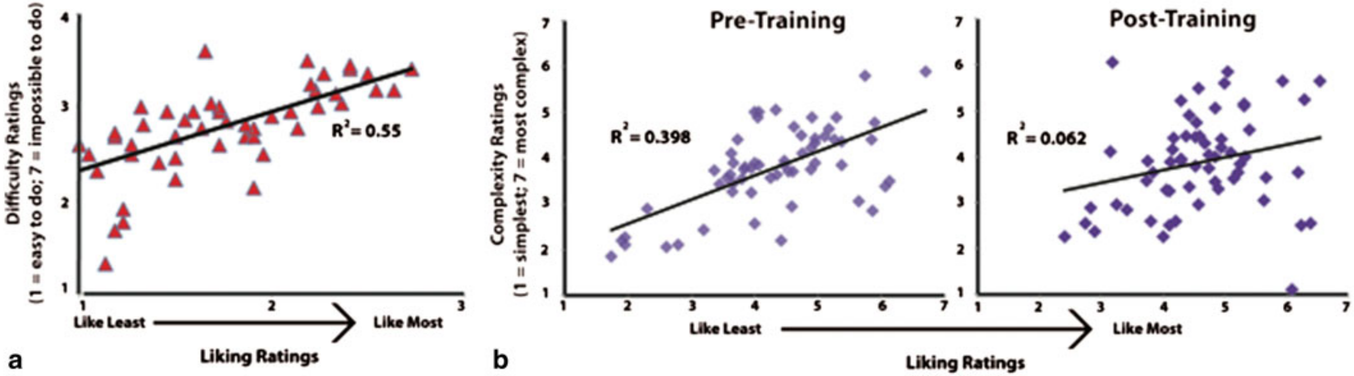

Fig. 10.2 Comparison of findings from Cross et al. (2011, panel A) and Kirsch et al. (2013, panel B) regarding the relationship between perceived ability to physically perform a movement or perceived complexity of a movement, and how enjoyable a movement is to watch. The relationship between perceived complexity/difficulty and liking is manifest as a positive correlation among dance-naïve observers, but once physical experience is gained, this relationship attenuates. (Figure adapted from Cross et al. 2011 and Kirsch et al. 2013)

engage observers more, perhaps by challenging them to embody the movement in a manner. However, the study illustrated in panel B (Kirsch et al. 2013) incorporated a training manipulation where participants learned to perform a subset of the movements they observed and rated before having any kind of dance training or experience. What the right plot in panel B illustrates is that after learning to physically embody a movement, the relationship between perceived complexity and enjoyment is no longer present. Of course, this finding raises more questions than answers, concerning how embodiment and aesthetic value are linked in the action perception and production domain. Ongoing work in our laboratory aims to further delineate the behavioral and neural consequences of the relationship between embodiment and affective processing of others' movement.

10.4 Conclusion

The aim of the present chapter was to illustrate the utility of dancers to scientists seeking to explore how action and perception are linked in learning, expertise, and aesthetics. We have attempted to place the action expertise and neuroaesthetics research with dance in a broader context that clarifies how and why scientists have worked with dance and dancers in their experiments. Neuroscientists initially turned to the domain of dance to use it as a means of addressing fundamental questions of action and perception, rather than to study its representation as an artistic medium in the human mind or body per se (Cross and Ticini 2012). With this being said, it is perhaps unsurprising that ever since the first neuroscience work with dancers started to emerge nearly a decade ago, many individuals in the dance community have been interested in what such research might reveal (or not) about the performance and perception of their art form. A number of cross-disciplinary forums and research projects are starting to emerge that attempt to find ways for artists and scientists to work together on research that mutually informs and benefits both the scientific and artistic domains (cf. Motion Bank (www.motionbank.org) and Watching Dance (www.watchingdance.org)). From a dance perspective, these endeavors have the possibility to illuminate factors that influence the performer–observer relationship, and to map the boundaries of an aesthetic experience. From a scientific perspective, such collaborations will undoubtedly reveal new ways of exploring fundamental aspects of human behavior and brain function with dance, both within and beyond the domains of action expertise and neuroaesthetics.

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