Pollick, F., Jola, C., Petrini, K., McKay, L., McAleer, P., Jang, S.H., MacLeod, C., and Simmons, D. (2013) *Experience and the perception of biological motion.* In: Johnson, K.L. and Shiffrar, M. (eds.) People Watching: Social, Perceptual, and Neuophysiological Studies of Body Perception. Series: Oxford series in visual cognition . Oxford University Press, New York, NY, USA, pp. 139-158. ISBN 9780195393705

http://eprints.gla.ac.uk/79171/

Deposited on: 08 December 2014

Experience and the Perception of Biological Motion

Frank E Pollick, Corinne Jola, Karin Petrini, Lawrie S McKay, Phil McAleer,
Seon Hee Jang*, Christine MacLeod, David R Simmons

Dept of Psychology, University of Glasgow, UK
*Dept of Dance, Sejong University, Republic of Korea

Many discussions of biological motion provide a standard list of human capabilities in the recognition of gender, emotion, action and identity from point light displays (PLDs) of human movement. While above-chance recognition of these stimuli is a great feat considering the limited information available in PLDs, what receives less attention is the low levels of performance and variability of response that sometimes occur. For example, a review and meta-analysis of gender recognition (Pollick, Kay, Heim & Stringer, 2005) showed that the average percentage correctly recognizing the gender of a walker was 66% from a side view and 71% from other viewpoints, and that there was a range of performance from 46% to 86% correct over all actions and viewpoints. An immediate thought would be that the quality of these displays and general experimental methods contributed to these differences. Another possibility would be that the important information for recognition is distributed across time and space and participants are intrinsically variable in their efficiency in accessing such information (Pollick, Lestou, Ryu, & Cho, 2002). Both these explanations suggest that the information available to observers to make their decisions varies, and thus so does performance (Loucks & Baldwin, 2009; Pollick & Paterson, 2008). However, another possible source of variability in recognizing biological motion could be the ability of the observer, and in this chapter we will explore this possibility. We propose that by studying the variability between how different groups perceive biological motion, we will not only inform more complete models of perception and the development of expertise, but also provide potentially important comparisons for particular conditions such as autism.

In the following introductory paragraphs we try to convince the reader of two views of biological motion perception that help to frame the variety of topics presented later in this chapter. The first is that understanding the variability among observers in biological motion perception is at least an interesting issue, if not a crucial one in developing a comprehensive theory of biological motion perception. The second is that, since the perception of biological motion is achieved via a distributed network of brain areas across the entire brain, there is ample opportunity for variability to arise as this brain network experiences new tasks and environments.

In any typical experiment in biological motion perception there is variability in responses of observers in achieving their task; if this is modest then it is typically

accounted for by a statistical distribution of responses, or if the variability is severe the results are likely never published. However, as the chapter by Kaiser & Shiffrar points out, variability of performance can sometimes be explained by taking properties of the observer into account. For example, the autism-like traits of observers go a long way towards explaining performance on a social task in biological motion perception. Other differences due to the experience of the participants might also influence how biological motion is processed for different tasks. Thus, it is possible that in the existing published data there are essential differences in mechanisms of biological motion processing that could explain the difference between the observer who performed the best and the one who performed the worst. Being able to explain such mechanisms would make our understanding of biological motion more complete. Similarly, to be able to interpret how autism impacts biological motion perception, it is useful to know whether autism is unique at impacting the perception of biological motion or whether effects found due to visual or visuomotor expertise might be similar in magnitude to those observed across the autism spectrum. Additionally, at the highest levels of movement appreciation, such as those associated with dance and athletic performance, we could ask whether there is any basis for the preferences shown by performers and audiences.

Recent years have witnessed a great increase in our understanding of the neural basis for human movement perception. An in-depth review of this topic would reveal controversies among models; we avoid this controversy by taking the perspective that each model is valid for at least some aspect of biological motion perception. Indeed, it is possible even that certain models might be more appropriate for particular populations. There are two essential dimensions that these neural models span: one dimension regards whether the form or the motion of the viewed action provides critical information; the second dimension regards whether recognition is mediated via visual processes alone or includes additional processes that incorporate knowledge of performing the actions. An umbrella term for this knowledge about how to perform an action is "simulation theory". The total span of these two conceptual dimensions includes a variety of brain areas that are shown schematically in Figure 1. What this schematic reveals are several areas distributed across the brain that are presumed to be relevant for different aspects of understanding viewed actions. A complex distributed network does not necessarily

guarantee that performance will vary between individuals or groups of individuals. However, such a complicated system is exposed to the risk that, due to disease, experience or differences in development of any one of its subcomponents, or connections among its subcomponents, it might perform in a manner that would negatively affect the perception of human movement. Thus, although it is speculative to say that variability in performance is a result of basic design principles of the brain in creating a system competent to cope with the challenges of recognizing actions, it certainly is plausible.
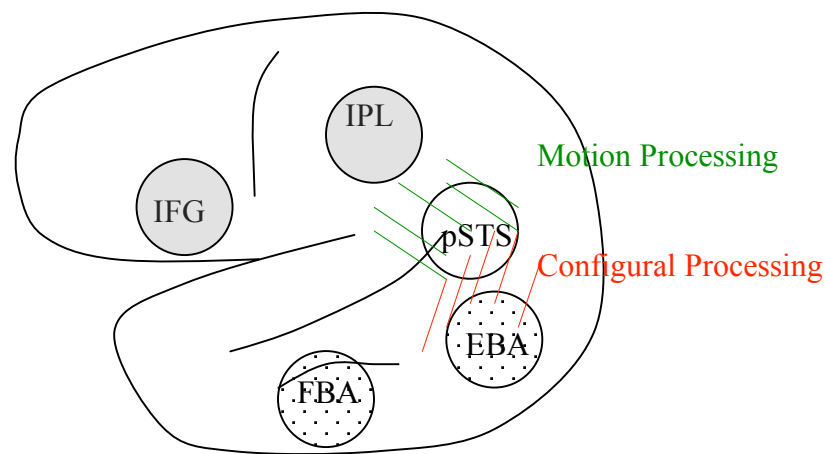

Figure 1. This diagram provides a simple schematic of some of the areas of the brain implicated in the processing of biological motion, and to illustrate that these regions are widely distributed. The posterior Superior Temporal Sulcus (pSTS) was one of the first regions identified for biological motion processing (Grossman & Blake, 2002), and has been shown to be divided into form and motion processing in the macaque (Vangeneugden, Pollick, & Vogels, 2009). Further processing of biological motion has been reported (Jastorff & Orban, 2009; Peelen, Wiggett, & Downing, 2006) to extend into form-selective areas which include the Extrastriate Body Area (EBA) (Downing, Jiang, Shuman, & Kanwisher, 2001) and the Fusiform Body Area (FBA) (Peelen & Downing, 2005). Finally, fronto-parietal circuits involving homologues of monkey mirror neurons that include the Inferior Frontal Gyrus (IFG) and the Inferior Parietal Lobule (IPL) have also been implicated in matching viewed actions to actions within one's own motor repertoire (Rizzolatti, Fogassi, & Gallese, 2001).

We have thus sketched out a case for the importance of understanding variability between observers in recognizing biological motion, and argued that the neural architecture for action recognition makes it plausible that such variability could exist. In

the subsequent sections we discuss how experience and development can influence the perception of human actions. For experience we consider visual, motor, multisensory and cognitive influences, while for development we consider the case of autism spectrum disorders (ASD). We primarily discuss results from the authors, and whenever possible consider data from functional brain imaging that could help to explain behavioural data. What we strive to achieve is a broad discussion of factors that contribute to performance in the perception of human actions.

<u>Visual and Visuomotor Experience in Action Observation</u>

As mentioned above, one of the primary dimensions discussed in human action recognition research is whether purely visual means are used or whether motoric encodings of how to achieve these actions are recruited. These two modes of recognition have been termed 'visual' and 'direct matching' respectively (Rizzolatti et al., 2001). The mechanisms of direct matching are provided by simulation theory, where watching human motion will automatically produce internal simulation in the viewer of the observed movements. Any recognition subsequent to this can involve a direct matching of the observed action to its internal representation of how it is achieved. However, the existence of direct matching mechanisms does not preclude that visual matching occurs alongside direct matching, and it seems likely that the interpretations supplied by both mechanisms are combined at some level. In addition, both our visual and motor systems are affected by experience and thus we can expect our recognition of biological motion to be a dynamic process shaped by experience. In the rest of this section we discuss evidence for both visual and motor experience modulating the recognition of biological motion.

One particularly appropriate example that demonstrates an effect of visual experience in recognizing human action is provided by Troscianko and colleagues, who studied how experience levels of video surveillance operators influenced their ability to judge hostile intent from short clips of video taken from actual surveillance cameras (Troscianko et al., 2004). In their study, experienced surveillance operators were compared to a novice group in their ability to predict whether a criminal activity was about to occur, indicating their prediction for 100 excerpts of video footage, each lasting

15 seconds and concluding prior to any criminal act. The data were analyzed using signal detection theory, with sensitivity (d') and bias calculated from observers' hits and false alarms. Results showed that while the two groups were indistinguishable in sensitivity, they did show a difference in bias. Experts showed no bias, while novices were biased to responding that displays were unlikely to result in incident. The case of expertise in viewing surveillance video provides a fascinating situation to explore how individuals can become skilled in judging the intent of others. We are currently starting to explore this topic using a combination of behavioural and brain imaging measures, and consider it a useful testbed for theories of action understanding in the real world. However, one concern is that the complexity of real-world scenarios makes visual analysis problematic and thus we are also examining other situations of complex movement that allow more control of events.

One such situation we are researching is watching dance. Dance is a fluid sequence of events which allows some control over the creation of the visual stimuli with which to explore expertise effects. In addition, watching dance supposedly involves action understanding, but predicting the intention of the dance movements or simply 'recognizing' them is not necessary when watching dance: a dance performance can also be enjoyed on emotional and sensory levels that may not require complete understanding of individual actions. The audience members experience a sense of motion and emotion through observing the performed movements, the performers' expressions, and from the narrative of the dance piece. Thus, dance enables us to study the transformation from perception of biological motion in a complex natural setting, without requiring processes primarily related to the various levels of action understanding (Hickok, 2008). The more basic sensations can be – and have been – described as kinesthetic empathy (Foster, 2008; Lipps, 1903 and 1906; MacFarlane, Kulka, & Pollick, 2004; Martin, 1939; Smyth, 1984). Following these concepts, the spectator should experience a kinesthetic sensation as if they themselves are executing the movements, possibly antecedent to action understanding. Previous research using dance as stimuli in execution (Brown, Martinez, & Parsons, 2006) and observation (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006) found enhanced brain activity in areas typically classified as mirror areas, including premotor and parietal cortices, and others

linked to biological motion perception such as STS. These and other studies indicate that dance spectators show sensorimotor brain activation that could be linked to the experience of a kinaesthetic sensation. Most authors have used dance to study whether there is an internal resonance while observing familiar movement, but with an emphasis on action understanding. For instance, Calvo-Merino et al. (2005) found that the intensity of spectators' brain activity is dependent on their motor experience; dancers showed higher brain activity when they were watching movements in the style they were trained in (i.e. ballet vs. capoeira). They concluded that motor familiarity enhances action simulation which, they suggest, serves action understanding. In a following study, which controlled for effects of visual familiarity with the observed movements, they showed stronger brain activity for movements with which the observers were motorically familiar, over and above any visual experience (Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006). These results showed that motor familiarity is an important factor in elaborating a state of embodiment that allows mentally generated sensations to occur when watching biological motion, whether action understanding is involved or not.

It is, however, quite difficult to disentangle visual from motor expertise in biological motion perception. An individual may be able to detect their own movements among the movements of other people using knowledge of their own motor repertoire (Loula, Prasad, Harber, & Shiffrar, 2005), but it is impossible to recognize oneself in a point-light display performing a movement not previously executed, and as such, a certain level of movement experience is always involved in these kinds of experiments (see also chapter by Calvo-Merino). Nevertheless, some of our recent experiments examining cortical excitability provide evidence for the idea that visual expertise alters the perception of dance movements in the observer. Motor-evoked potentials (MEP) created by single pulses of transcranial magnetic stimulation (TMS) have been used as a measure of cortical excitability: the bigger the average MEP, the higher the cortical excitability. It has been shown that the mere observation of an action enhances cortical excitability in a muscle-selective manner, as though the observed actions were executed (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). In a study on basketball shots, this distal muscle response was found to be selectively enhanced for actions in both motor and

visual expert groups, but the motor expertise of the athletes modulated their response in a time- and muscle-specific anticipatory manner (Aglioti, Cesari, Romani, & Urgesi, 2008). Beyond the framework of action understanding, we conducted a study to determine whether visual expertise in particular styles of dance could modulate corticospinal excitability in spectators with no motor experience in any type of dance. For this we compared corticospinal excitability of dance spectators who were experienced in watching ballet, to that of dance spectators who were experienced in watching a classical form of Indian dance known as Bharatanatyam. Our results showed that corticospinal excitability can be modulated by the spectator's visual experience in a muscle-specific manner (Jola, Grosbras, Kuppuswamy, & Pollick, submitted). Thus we know that visual experience alone is sufficient to modulate the motor response to watching dance. We are currently exploring this issue further using fMRI to compare responses to watching ballet between ballerinas, experienced ballet spectators and total novices to better understand how visual and motor experience influences perception.

Next, we discuss how mentally generated actions, or motor imagery, compares to the perception of movement. Research into simulation theory indicates how knowledge of movement can be used in a top-down fashion to influence visual perception. However, in this case we study how transforming symbolic representations of movement can be used to internally generate movement. To investigate this capability we examine the perception of motion based on Labanotation. Labanotation is an abstract symbol system for coding movements (see Figure 2), and is often used in dance to notate dance works of great value. The movement, however, has to be inferred by the reader. First, one has to translate the non-bodily symbols on the staff into a mental representation of the body. Second, once two consecutive postures – written from the bottom to the top – have been transformed into mental representations of body postures, the reader then has to find the most direct natural body movement between the two postures. A highly experienced Labanotationer is able instantly to translate the symbols from the notation into movements. In fact, Karen Hermes, a professional Labanotationer, claims to experience Labanotation herself as so realistic that instead of 'watching dance' in a theatre, she suggests that it is possible that one could enjoy it in the mind from simply reading the notation.

Figure 2: Example of Labanotation from the dance 'Flügel an Flügel' performed by dance company Hermesdance and choreographed and notated by Karin Hermes. The body positions seen in the image on the left are represented in the shaded region of Labanotation on the right. Labanotation is read from bottom to top, and the unshaded regions represent previous and subsequent postures respectively. The Labanotation includes components for each performer: the female dancer is represented in the left column of notation and the male dancer on the right. This example provides detailed notation, including aspects such as gaze direction and torso rotation, allowing exact reconstruction of the dance.

Evidence to support the plausibility of this claim by Karen Hermes for a direct embodiment of biological motion without the actual visual stimulation comes from the research of Mast, Berthoz, & Kosslyn (2001). They demonstrated that mentally generated motion, in this case visualizing a rotating configuration of dots, elicited similar effects (inducing a sense of motion) to actually viewing the dots. In a series of unpublished experiments, we thus investigated whether observers are able to instantiate mentally generated human movement percepts, as previously shown with induced motion percepts. The aim of these studies was to assess whether mentally generated movements engage the same movement observation mechanisms as do the perception of real stimuli. If mentally generated biological motion follows the same principle as visually perceived biological motion, we expect to find effects known from biological motion perception in visualized motion percepts. For this, we tested undergraduate students from Laban Trinity College in London who have been taught Labanotation for at least three terms by adapting two different research paradigms to Labanotation displays of movement. The

first paradigm examined the fact that body motion principles can be violated for alternating presentation of human body postures only under certain time constraints (Shiffrar & Freyd, 1990, 1993). The second paradigm examined the Stroop effect for evidence of automatic encoding processes (Stroop, 1935). For instance, previous studies have found evidence that individuals who were trained in reading music notation are able to automatically encode and embody the information gathered from notes (Stewart et al., 2003; Stewart, Walsh, & Frith, 2004). However, the results for both the alternating body postures task and the Stroop task failed to conclusively show evidence of similarity between mentally generated movements and observed movements. One possible explanation for this failure to find similarity is that mentally generated motion is represented in a different format from biological motion based on visual stimulation. This assumption is supported by a study showing that mentally transforming body postures using the Labanotation stimuli did not require additional mental rotation time, though pictures with real human bodies did (Jola & Haggard, 2006, see also Jola & Mast, 2005). The other possible explanation is that the participants of these studies simply did not have enough experience in reading the Labanotation. When students learn the notation in class, they have to transform the symbols into real body postures and usually need to execute the movements to be able to read the notation. Even once they are experienced enough to read the notation while sitting still (i.e. without motor execution) it remains a high-level cognitive task. Thus, the motor expertise of the dancers did not help them encode the notation into movements, and only once the reader is highly experienced are they able to embody the symbols directly to evoke a sensory experience. To conclude, the issue of what conditions are necessary and sufficient for the experience of movement notation to mirror the effects of visually experiencing movement remains an open question.

<u>Visual aesthetics and the enjoyment of watching dance</u>

One aspect of the visual experience of human movement, and of relevance to dance, is that certain types of dance seem generally more appealing to view than others, and that some people enjoy watching dance much more than others. This is particularly important for dance, where the movements are carefully crafted by a choreographer to

obtain an intended audience response to either the movement itself or the meaning it conveys. For example, viewing an action might result in transmission of a feeling primarily of kinesthesis, or it might result in transmission of emotion and narrative. It has been argued by Zeki (1999) that we can consider the artist to be a kind of neuroscientist who manipulates their art form to elicit particular brain responses. Thus by taking a scientific approach to reverse-engineer dance performance we can potentially illuminate fundamental aspects of biological motion perception.

In this section we consider some of the contributing factors that lead to aesthetic preferences when watching dance. A spectator can achieve visual expertise in certain types of biological motion, such as dance, by extensive exposure and engagement. However, this does not allow any conclusion to be drawn as to why people gain visual experience in the first place. It is not clear whether aesthetic preference is the driving force to watch particular types of dance or whether exposure itself is able to modify our aesthetic preferences. Daprati, Iosa and Haggard (2009), for example, found correlations between perceptual preferences and aesthetic changes in dance postures. Individuals had to rate the aesthetic value of abstract figures that symbolized the dance postures from the ballet *Sleeping Beauty* without being informed of their representational function. Those figures representing the most current modifications of the postures have been rated as more attractive than those representing postures from many decades ago. Thus, the authors concluded that changes in dance postures signified common aesthetic preferences. A number of publications have studied the neural mechanisms that are implicated in aesthetic preference, focusing on either individual differences or universal aesthetic principles (for a review see Nadal, Munar, Capo, Rossello, & Cela-Conde, 2008). However, it is only recently that the neuronal network of aesthetic appreciation in biological motion perception was investigated (Calvo-Merino, Jola, Glaser, & Haggard, 2008). This particular study, for example, showed that novices rated movements as aesthetically more pleasing when they involved certain biological motion parameters. In particular, vertical movements (e.g. jumps) were preferred to translational displacements (e.g. steps, on one level from the right to the left side). Correlations with brain data for the most liked versus most disliked movements showed a consensus network involving parietal and visual areas. These results are consistent with an fMRI study using a dancing

humanoid robot showed that the smoothness of motion is a critical parameter for motion- and body-sensitive visual areas (Miura et al., 2009). However, the authors also found that personal attitudes correlated strongly with the inter-participant variability in the parieto-frontal network, suggesting that action understanding is influenced by personal attitudes. In line with this, it was found that the aesthetic evaluation network partially overlaps with brain regions processing social and moral behaviour (Jacobsen, Schubotz, Hofel, & Von Cramon, 2006). As most types of dance involve a wide range of movements and movement qualities, we need further research not only on why certain movements are perceived as more aesthetically pleasing than others, but on why certain dance styles are preferred over others. It may be that these aesthetic preferences for certain types of biological motion are pre-dispositional.

Nevertheless, dance movements are aesthetic as well as emotionally expressive. Therefore, we hypothesized that empathic ability as a pre-dispositional personality factor may be related to individual preferences in watching dance, which may well be related to emotion processing. We studied dance because it has the advantage of invoking sensory sensations without requiring action understanding. However, it may be that action understanding affects which style of dance we prefer. We compared experienced spectators of ballet and the classical Indian dance form Bharatanatyam (which mainly consists of gestural actions and a clear narrative supported by the musical structure and prosody). We correlated the amplitude of TMS-evoked motor potentials measured during dance observation with the participants' individual self-rating in the inter-personal responsive index (IRI (Davis, 1980)) and the Autism Spectrum Quotient (AQ (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001)). We found that people with higher empathic abilities showed greater TMS motor-evoked potentials when viewing affective gestures. Thus, our data suggest that empathic abilities are relevant for the encoding of biological motion to kinesthetic and emotional information. To understand how observers become emotionally and cognitively engaged with a performance, or feel empathic towards the performers, may lead to a greater appreciation of how biological motion is processed. Our results suggest that, especially in classical dance forms such as ballet, both the motion and the properties of the spectator influence how a performance

impacts on the audience, and this leads to a more complete understanding of how biological motion is processed.

The sound of movement: Expertise affects multisensory representations

The previous sections describe how being expert with certain actions can change the way we perceive and process biological motion. Here we attempt to take this subject further and examine how expertise influences the way biological motion and its resulting sounds integrate. In general we find that human movement is accompanied with other sensory information, such as sound, and it is reasonable to assume that we usually need to integrate different sensory information to achieve a complete understanding of what another human agent is doing (Saygin, Driver, & de Sa, 2008). In watching dance, for instance, music is an important component of performance, framing the movement along with the stage setting, the costumes, and the level of literality of the actions. We have started exploring how the presence of music modifies the perception of dance, but this work is in the early stages and we do not yet have results to report. We have, however, already examined how experience influences the integration of music perception itself by using drumming actions with the corresponding acoustic information. We present these results below.

The combination of sight and sound requires a system able to integrate complicated sets of signals. These signals have different processing latencies due to dissimilarity in physical and neural transmission (Fain, 2003; King, 2005; King & Palmer, 1985; Spence & Squire, 2003). The human brain overcomes these differences by allowing the auditory and visual information to be processed as pertaining to the same event even when the signals are physically asynchronous (Dixon & Spitz, 1980). However, the neural tolerance for audiovisual temporal asynchrony is not unlimited, and the extent of this tolerance provides us with a measure known as the 'Temporal Integration Window' (TIW). The neural processes involved with integrating sight and sound might appear effortless for us, as do the processes underlying the spontaneous integration of individual point lights into a human form (Johansson, 1973); nevertheless, they are essential for our wellbeing.

An intuitive way to investigate the effect of expertise on multisensory integration of action is to measure changes in sensitivity to audiovisual asynchrony (Arrighi, Alais, & Burr, 2006; Hollier, Rimell, Hands, & Voelcker, 1999; Miner & Caudell, 1998; van Wassenhove, Grant, & Poeppel, 2007; Vatakis & Spence, 2006a, 2006b, 2007). By altering the degree of asynchrony between the visual and auditory stimuli, we obtain an indirect measure of the changes in the neural tolerance of audiovisual asynchrony, and can apply this measure to study expertise. To study expertise in multisensory processing, we need a domain where it is possible to differentiate between an expert and a novice population that do not share knowledge about certain multisensory actions. We chose music since it shares many characteristics not only with speech and dance, but also with object action (Vatakis & Spence, 2006a, 2006b) and is a very effective form of social communication. Furthermore, musicians possess knowledge about certain actions that is not shared with non-musicians, and this makes music events a perfect tool to study differences between experts and non-experts.

Drumming movements are very visually salient, in contrast to some other musical instruments, where asynchrony could be much harder to detect. For this reason we used drumming point light displays (Luck & Sloboda, 2007) in combination with a synthetic sound originating from a professional jazz drummer playing a swing groove (Figure 3), where "swing" denotes a jazz style (Waadeland, 2003, 2006). Point light displays (PLDs) allow us to isolate the effects of perceiving biological motion from contextual factors, and the specific rhythmic pattern of the swing groove makes a perfect simple stimulus to differentiate between novices and experts.
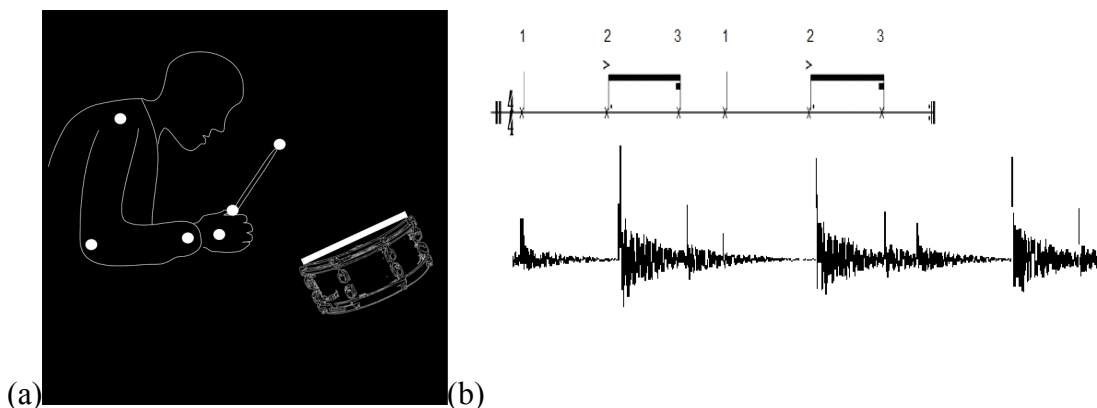
(a)   (b)

Figure 3. (a) Frame sample of the jazz drummer point light displays recreated from 3D data set (Waadeland, 2003; 2006); (b) waveform sample of the nine impacts sound selections, with relative three-beat cyclic pattern for accent on the second beat in the swing groove (see Waadeland (2006) for more details). The numbers 1, 2 and 3 at the top of the figure indicate respectively the first, second and third beats in the pattern, while > indicates the accented beat. *Note:* the drawing representing the drummer and/or the drum in displays (a) is shown only to describe the point light positions (white circles) and was not presented during the experiments. (With kind permission from Springer Science+Business Media: Experimental Brain Research, Multisensory integration of drumming actions: musical expertise affects perceived audiovisual asynchrony, volume 198, 2009, page 342, Petrini, et al., Figure 1.)

One of the questions that can potentially be answered using this kind of drumming action display is whether drummers, who are expert in the represented biological motion, are more sensitive to temporal asynchrony between the drummer's movement and the resulting sound than novices. Petrini, Dahl et al. (2009) showed that not only are drummers more sensitive to asynchrony (i.e. less tolerant of audiovisual asynchrony), but also that, unlike novices, their sensitivity depends less on the manipulation of other physical characteristics, such as drumming tempo (Arrighi et al., 2006; Petrini, Dahl et al., 2009) or audiovisual incongruency (Macdonald & McGurk, 1978; McGurk & Macdonald, 1976; van Wassenhove et al., 2007; Vatakis & Spence, 2007; Petrini, Dahl et al., 2009). Indeed, while novices are facilitated in detecting asynchrony for drumming displays with faster tempos (Arrighi et al., 2006; Petrini, Dahl et al., 2009; Petrini, Russell, & Pollick, 2009), and also for drumming displays where the covariation between

the sound and the drummer's movement has been eliminated (Petrini, Dahl et al., 2009; van Wassenhove et al., 2007; Vatakis & Spence, 2007), drummers are not. The evidence that musicians can tap at slower tempos than non-musicians (Drake, Jones, & Baruch, 2000) may explain why drummers are not affected by changes in drumming tempo when judging audiovisual simultaneity. Through practice, drummers acquire the ability to perform drumming actions at a wide range of tempos, which could be why changes in tempo do not affect the way drummers bind the familiar biological motion and its sound. These findings seem to indicate that, after a long period of musical practice, the binding of biological motion and its sound changes in such a way that additional factors are no longer used by our neural system to integrate the multisensory information. This is probably because the system reaches a very high and unbiased level of precision itself, and recent findings seem to further corroborate this conclusion. Petrini, Holt & Pollick (in press), for instance, found that only novices' simultaneity judgments were affected by the rotation of a drumming display (Figure 4a rotated at 90, 180 and 270 degree), while drummers' were not. That is, the tolerance to asynchrony of novices increased when viewing rotated audiovisual drumming displays, while that of the drummers remained relatively unchanged. This extends the findings of Saygin, Driver and De Sa (2008) to another kind of audiovisual biological motion event, and indicates that the gestalt of upright point light drumming enhances the detection of audiovisual asynchrony for musical novices but not for expert drummers. Hence, the nature of the visual stimulation can affect the perceived synchrony between the two sensory signals, but the extent of this effect is constrained by the level of experience with a particular multisensory event.

If drummers are better able to detect asynchrony because of their experience and familiarity with that certain biological motion and its resulting sound, then they should still be better than novices when only a part of the body information is presented in the drumming displays (Figure 4b).
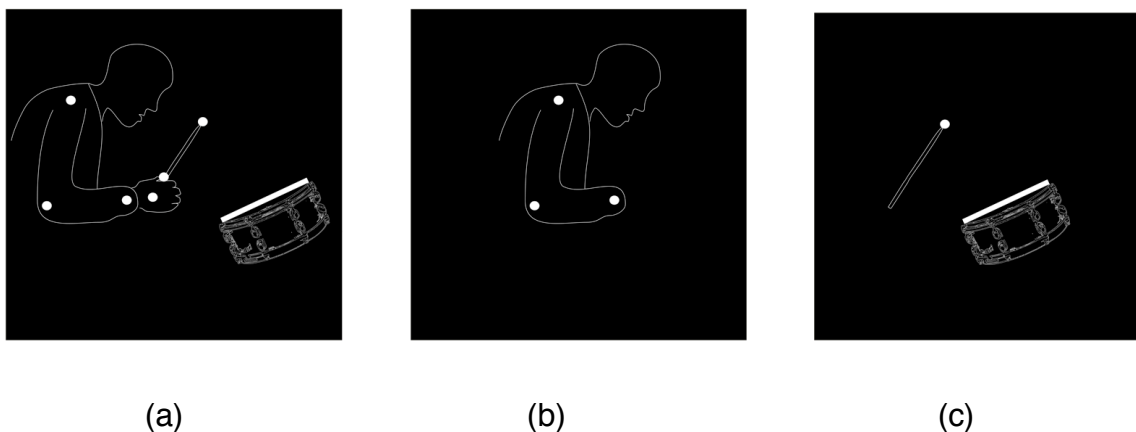
<div align="center">(a)   (b)   (c)</div>

Figure 4. (a) Display a: frame sample of the jazz drummer point light displays representing the shoulder, elbow, wrist, hand, grip, drumstick tip, and drumhead as a 25 degree rectangle. (b) Display b: frame sample of the jazz drummer point light displays representing the shoulder, elbow, and wrist. (c) Display c: frame sample of the jazz drummer point-light displays representing the drumstick tip, and the drumhead as a 25 rectangle. (Reprinted from Cognition, Volume 110, Petrini, Russell & Pollick, When knowing can replace seeing in audiovisual integration of actions, pages 432-439, 2009, with permission from Elsevier.)

In other words, while the drummers could have acquired, through practice, internal models specific to drumming biological motion that they can use to predict the sound occurrence when no impact point is presented, this should not be the case for the novices. In a further study (Petrini, Russell et al., 2009) we addressed this possibility and demonstrated that this is exactly what happens. Not only were drummers found to be better than novices at detecting asynchrony between the drummer's biological motion and the sound, but also they were the only group that could still bind the information from both sensory domains. Indeed it was found that novices were completely unable to discriminate between synchronous and asynchronous drumming displays when the impact point was eliminated (Figure 4b). However, when presented with either the intact drumming information (Figure 4a) or only the impact point (Figure 4c), drummers demonstrated a lack of difference in sensitivity to asynchrony, indicating that as long as the impact point is there they will use it as much as the novices, although maintaining a narrower audiovisual temporal integration window. Thus, while drummers can use both kinds of information, novices can only refer to the impact point when deciding whether or not the sound and the drummer's movement are part of the same action. These

findings suggest that expertise with a certain action enhances the ability to maintain a coherent representation of the multisensory aspects of biological motion. This assumption is strengthened by the finding that when drummers judged the simultaneity between the drumming biological motion and the sound of the aforementioned display from which the impact point information was eliminated (Figure 4b), their results were reminiscent of tapping tasks (Aschersleben & Prinz, 1995; Miyake, Onishi, & Pöppel, 2004), indicating that the acquired information for that specific action was used. In other words, when presented with only the point light arm information of the drumming display, drummers' points of subjective simultaneity occurred in some instances when the sound was leading the sight, showing the same anticipatory effect as that found in tapping tasks (Aschersleben & Prinz, 1995; Miyake, Onishi, & Pöppel, 2004). This interpretation suggests that drummers do not possess only a general enhanced ability to determine the co-occurrence of the auditory and visual information for any kind of multisensory event, but a more specific ability to use the representation of that action to bind sight and sound.

The idea that musical training with different instruments gives rise to specialisation is also supported by studies revealing differences in brain structures and functions when comparing different kinds of musicians (see Tervaniemi, 2009 for review). What we need to understand next is how these differences between experts and novices reflect different processes in the brain, in terms of recruitment in the integration of the multisensory aspects of biological motion. This is a fundamental question we tried to answer by using brain imaging techniques (Pollick et al., submitted). Specifically, we used functional Magnetic Resonance Imaging (fMRI) to measure the brain activity of a group of drummers and novices while watching synchronized or asynchronised drumming displays. The task was to determine whether the biological motion of the drummer and the sound matched or not (Petrini, Dahl et al., 2009; Petrini, Russell et al., 2009). The timings for the synchronous and asynchronous displays were determined for each participant immediately prior to entering the MRI scanner by a separate behavioral experiment (Petrini, Dahl et al., 2009). This predetermination of the optimal timings was necessary to exclude any difference in brain processes between drummers and novices that could be due to differences in task difficulty, rather than in the multisensory processing of biological motion. Behavioral results from subjects in the scanner

indicated that both groups were almost perfect in detecting when the drummer's movement and corresponding sound mismatched; yet despite this, the brain areas involved and their patterns of activation were different between novices and drummers. For example, the novices appeared to have greater activation in the middle frontal gyrus for both synchronous and asynchronous displays. Additionally, the parahippocampus and cerebellum revealed greater activation for asynchronous displays in the drummers and for synchronous displays in the novices. These results are complementary to those of Hodges, Hairston & Burdette (2005) who showed greater activity in audiovisual regions for experienced conductors when integrating sight and sound.

Taken together, it appears that the narrow tuning for audiovisual asynchrony exhibited by the drummers (Petrini, Russell & Pollick, 2009; Petrini, Dahl et al., 2009; Petrini, Holt & Pollick, in press) and potentially also the ability to fuse sight and sound from incomplete visual displays (Petrini, Dahl et al., 2009) results from both involvement of higher order (cognitive) processes for the novices in fusing together the audio and visual tracks as well as enhanced perceptual and simulation processes of the drummers in detecting asynchronous events. Further research is needed to examine how other kinds of extensive experience shape the processes of audiovisual integration. However, the current results allow us to conclude that drumming expertise enhances multisensory representations of biological motion and changes the brain areas involved.

Biological Motion Processing in Autism Spectrum Disorders

In this final section we will move from groups that show enhanced processing of biological motion, to a group that reputedly has difficulties in biological motion processing, specifically those who have a diagnosis of having an Autism Spectrum Disorder (ASD). The term 'Autism Spectrum Disorders' (ASDs) is used to refer to a range of disorders, usually autism and Asperger syndrome/disorder, that are typified by having, to a varying degree, impairments in three main areas known as the triad of impairments: social understanding, communication, and flexibility of thought (Frith, 2003). Recently, there has been increasing debate as to whether people with ASDs have a specific difficulty when it comes to processing biological motion. The relevance of this is that if biological motion processing is impaired in people with ASDs, then this could

either contribute to or be the cause of the social communication and relationship difficulties found in varying degrees among this population. Although there is an ever-expanding literature on this topic, researchers are divided as to the extent, or even the existence, of such impairments. Here we will discuss some of the most relevant literature in this area, with an emphasis on the possible differences in processing abilities that exist between people with ASDs and those without. This literature has also been recently considered by Kaiser & Shiffrar (2009).

The first study to examine biological motion processing in people with ASDs was carried out by Moore, Hobson and Lee (1997). Using point-light displays (PLDs), they compared biological motion processing in a group of 17 children and young adults with ASDs to a chronologically and verbally age-matched control group. As the ASD group had impaired language abilities the control group all had learning disabilities but were not diagnosed with an ASD. The stimuli were PLDs depicting either a person walking or an inanimate household object such as an opening and closing pair of scissors. The participants' task was to say what they thought the moving points were attached to. The stimuli were presented in increasing durations starting from 40ms and rising to 5000ms in varying increments. The participants in each group who could correctly identify the stimuli at each stimulus duration were then fitted with a psychometric function. Although there was a slight difference in the ASD group's ability to correctly identify PLDs of walkers when they consisted of only five points, Moore et al. (1997) concluded that there was no significant difference in performance overall between the two groups, though there were no details of the statistical tests used given in the paper.

Moore et al. (1997) did, however, find differences between the two groups in their ability to attribute the correct emotional state to PLDs containing depictions of different affects. Despite their ability to correctly describe the mechanics of the biological motion stimuli, they were poorer than the control group in their ability to correctly identify the affect of a point-light actor. Moore et al. (1997) concluded that there were no differences in the two groups' ability to process biological motion and that, instead, the ASD group's main difficulty was in the correct attribution of mental states to others.

More recently, and in support of the initial Moore et al. (1997) findings, Hubert, Wicker, Moore, Monfardini, Duverger & Da Fonseca (2007) found that an adult group of

people with ASDs were poorer in relation to controls when asked to subjectively describe emotions, but not when asked to categorize subjective states, actions, or to identify an object's motions. Furthermore, similar results were found using the same experiment in a group of children (Parron et al., 2008). It must be noted, however, that these were subjective reports of what the motions depicted and, as such, were deemed as correct or incorrect by the experimenter rather than with an objective measure. Furthermore, there was no mentioned attempt to control the motion energy of the stimuli across conditions, so it is perhaps the case that the ASD group found the object motion easiest and that the differences were due to the increasing complexity of the PLDs.

Some studies, however, have demonstrated that, in addition to difficulties in attributing emotions to PLDs, there are low-level biological motion processing deficits in people with ASDs. The first to demonstrate this were Blake, Turner, Smoski, Pozdol & Stone (2003), who used a technique that systematically manipulated the temporal phase relations between the points on a PLD, which substantially reduces the perception of the human form (Bertenthal & Pinto, 1994). Blake et al. (2003) showed one-second displays of unscrambled and temporally scrambled PLDs of various everyday actions to a group of children with ASDs and a group of typically developing children whose chronological ages matched the mental ages of the ASD group. The participants' task was simply to say whether the displays, which were presented in a random order, depicted a person or not. In contrast to Moore et al. (1997), Blake et al. (2003) showed a clear difference in discrimination of the stimuli between the control group and the ASD group, with d' scores being two and a half times higher in the former than in the latter, suggesting impaired biological motion processing in the ASD group. Furthermore, Blake et al. (2003) found negative correlations with performance on the task and the levels of severity of symptoms, as measured by the Autism Diagnosis and Observation Schedule, the Childhood Autism Rating Scale, and also, though only in the ASD group, mental age. It was also noted that of the 16 participants with ASDs, only 12 were actually able complete the task.

The contradictory nature of these studies poses an interesting question – if the participants in the Blake study had difficulty just stating whether the PLDs depicted a person, why were the participants in Moore et al. (1997), Hubert et al. (2007) and the

Parron et al. (2008) studies comparable to their respective control groups in all tasks except in the emotion categorization task? A key point to note is that the displays used by Blake et al. (2003) were far shorter than those of the other studies, being one second long compared with five seconds in the other studies. It is also possible that the difference may be due to the variation in ages of participants between the studies, with the participants in the Blake et al. (2003) study being considerably younger than those in the other studies. As such, it may be that people with ASDs can process the same information from biological motion as controls, but just take longer to do so.

To examine the issue of age, Annaz, Remington, Milne, Coleman, Campbell, Thomas & Swettenham (in press) used one-second PLDs to test the ability of children between the ages of 5 and 12 to discriminate intact from scrambled biological motion. They found that children with autism were impaired in the perception of biological motion and that their sensitivity to distinguishing between intact and scrambled PLDs did not improve with development. There are also reports of dysfunctional biological motion processing at even younger ages than those reported by Blake et al. (2003) and Annaz et al. (2009). In a recent study Klin, Lin, Gorrindo, Ramsay, & Jones (2009) showed that, unlike typically developed two-year-old children, children with autism failed to orientate to PLDs. In addition, when viewing displays of biological motion, the viewing behavior of children with ASDs was determined not by social cues, but by physical non-social contingencies that are disregarded by typically developed children. At this age it is likely that any problem with processing biological motion is present from birth, reflecting a lower level of a basic processing that is undeveloped, with a probable root in a dysfunctional neural system.

It must be noted, however, that there is some evidence that this deficit may be more deep-rooted than biological motion processing. A paper by Atkinson (2009) found that, in line with Moore et al. (1997), people with ASDs were impaired at attributing emotions and categorizing instrumental actions to both PLDs and full light displays. Atkinson attributed this not to a difficulty in processing biological motion, but to a difficulty in integrating low-level motion cues. This was based on regression analysis in which hit rates in predicting emotions were inversely related to log-scaled motion coherence thresholds. However, although motion coherence thresholds were significant

predictors of the number of correct responses in the affect categorization task, there was no significant difference between the two groups in terms of motion coherence thresholds. Additionally, Atkinson did not use a measure of biological motion processing per se, but instead moved straight from low level motion coherence thresholds to categorization of human actions and as such, despite the apparent link between motion coherence thresholds and categorization of human actions, the question of whether biological motion processing was intact in people with ASDs was not addressed.

A key point to note about the aforementioned behavioral studies is that typically there is a larger range of scores within the ASD group, regardless of whether there were significant task differences, suggesting more variability within the ASD population than the control populations. This is despite most studies exercising rigorous, usually paired, matching techniques between the various experimental and control groups on such items as age, gender and verbal and performance IQ, wherever possible. This may be due to the wide range of symptoms covered by diagnosis of ASDs and also the heterogeneity of symptoms seen within autism or Asperger syndrome when taken as distinct diagnoses. People with ASDs typically vary considerably in the extent to which they show difficulties within the triad of impairments. In addition, there are a number of sensory issues in ASDs that may or may not have an influence on biological motion processing, and the extent to which people experience these is also variable (for a full review see: Simmons, Robertson, McKay, Toal, McAleer, & Pollick, 2009). Given the variability on all these dimensions in people with ASDs, it is perhaps not unexpected that studies investigating biological motion processing will produce more conflicting than complementary results.

<u>Neural Correlates of Impaired Biological Motion Processing in ASDs</u>

A number of studies have looked for a potential neural correlate for the differences found in biological motion processing in people with ASDs. A recent study by Herrington et al. (2007) showed that several regions were less active in people with ASDs than in controls when contrasting an intact point light walker with fixation, such as the fusiform gyrus, middle temporal gyrus, superior temporal gyrus and the inferior

parietal lobule. Each of these regions has been implicated in motion and/or biological motion processing. Furthermore, Freitag et al. (2008) showed that although in an age- and IQ-matched control group, these regions, among many others, activated differentially to an intact versus a scrambled point light walker, none of these regions activated differentially in the ASD group. Additionally, the ASD group showed increased activation to intact versus scrambled point light walkers in regions that were not apparent in the control group, such as the hippocampus, thalamus, posterior cingulate gyrus and the precuneus. Recent work in our own lab suggests that even when biological motion processing appears intact in a group with ASDs, there are significant differences both in activation and patterns of effective connectivity to and from key regions between this group and age- and IQ-matched controls. More specifically, it appears that while the typically developed control group utilize a network comprising inferior-temporal and parietal connections, the ASD group seem to recruit a network comprising temporal regions, such as MT+ and the parts of the fusiform gyrus. This may be due to neural rewiring in some adults with ASDs that compensates for reduced connectivity between temporal and parietal regions or disrupted processing in specific temporal or parietal areas, and may reflect experiential strategies learned by this group to overcome difficulties experienced in childhood.

It seems therefore that there are many regions involved in the complex processing of information salient to biological motion, and that these might be differentially disrupted in subpopulations of individuals with ASD. A cause of this may be that, given an early neural disruption in people with ASDs, in some cases the brain has compensated by utilizing other regions, but has not done so in others. As such, it seems plausible that the extent to which the brain has adapted itself could reflect the degree to which people with ASDs have difficulties with biological motion processing, and that this may in part explain the high levels of variability reported for this population in processing ability.

We have seen that a number of studies have reported biological motion processing difficulties in people with ASDs. Some suggest that the main problem is attributing emotional states to PLDs (Hubert et al., 2007; Moore et al., 1997; Parron et al., 2008), while others claim that it may be a more deep seated problem with processing low level features of biological motion (Annaz et al., in press; Blake et al., 2003; Klin et al., 2009)

or even low level motion integration (Atkinson, 2009). One thing seems clear: the picture is complex and more investigation is needed to determine the specific difficulties people with ASDs have in processing biological motion, and also to determine whether these difficulties are uniform across the group or whether and how they vary across the autism spectrum.

General Discussion

In the introduction we proposed that the study of how different groups perceive biological motion would inform more complete models of expertise and the perception of biological motion, as well as provide important comparisons for conditions such as autism. In this final section we'd like to come back to this proposal, as well as highlight potential linkages between the topics presented.

We begin with a brief summary of the findings reported about watching dance, audiovisual integration in drumming and the perception of biological motion in autism. In watching dance we reviewed results suggesting that the empathic abilities and both the motor and visual experience of an observer influences their neurophysiological responses to observed movements. For audiovisual integration in drumming, we discussed how drummers' judgments of synchrony are unaffected by a wide range of factors that do influence the perception of novices. Moreover, the brain activity of drummers and novices showed marked differences when judging synchrony, even when both groups performed the task with high accuracy. Overall, these differences in brain activity were consistent with drummers using multisensory perceptual regions to perform asynchrony judgments, while novices recruited more frontal regions. For the perception of biological motion in autism, we reported that although there was little evidence to show that *adults* with ASD perform differently from matched controls on biological motion recognition tasks, there was evidence that the brain mechanisms used by this population are different. Namely we found that, for our ASD group, effective connectivity was restricted mainly to the temporal cortex when viewing biological motion, while for the matched controls effective connectivity included connections between parietal and temporal cortices.

This summary demonstrates that different groups do show systematic differences in their responses and ability to perform biological motion tasks. In addition the brain imaging data, although some of it preliminary, revealed differences in possible neural

mechanisms even when behavioral measures were equivalent between groups. Contrasting these results with the distributed network presented in the introduction reveals two possible ways in which experience shapes this network. The watching dance results suggest that experience enhances communication between distant aspects of this network, allowing visual and motoric representations to interact. The drumming data implicates a different mechanism, where enhanced multisensory representations in posterior regions of cortex appear to support the combination of sight and sound in the brains of drummers. These proposals of enhanced communication across distant brain regions and enhanced local representations provide a means to develop and test hypotheses of how experience shapes biological motion perception.

Both enhanced global communication and local representation can thus be characterized as properties of expertise and be applied to the case of biological motion perception in autism. The lack of effective connectivity between temporal and parietal regions in the ASD group would suggest a lack of expertise in processing biological motion. However, our behavioral data argues against this, as does the more extensive effective connectivity in the temporal lobe. This greater connectivity in temporal lobe is consistent with expertise mediated by more extensive local representations, similar to those that appear to exist in the multisensory brain regions of drummers. An interesting parallel between the drumming data and theories of ASD is found in the theory of Enhanced Perceptual Function (EPF) which states that individuals with ASD use more posterior regions in complex perceptual tasks and rely less on higher order perceptual processing (Mottron, Dawson, Soulieres, Hubert & Barack, 2006). Similar also to "Weak (Central) Coherence" (Happe & Frith, 2006) EPF results in perception where the context in which a stimulus is embedded has less influence on perception of the stimulus. Such descriptions are broadly consistent with the performance of our drummers in synchrony perception, where drummers show more posterior brain activations and a failure for higher order stimulus properties such as tempo and orientation to affect synchrony judgments of the drummers. While such a connection is speculative, and might not explain how drummers can judge synchrony when visual information is removed, it does lead to the hypothesis that the same principles that shape the development of

multisensory processing in drumming are at work in the development of biological motion in the temporal cortex of individuals with ASD.

Clearly, there is much work yet to be done to understand how we perceive biological motion. We believe that studying how experience and development shape biological motion processing in different groups is essential to understanding what are the *core* capabilities and mechanisms in biological motion perception. While an emphasis on variability and individual differences provides challenges to unite disparate data, the diversity of situations where specialized performance is obtained reveal that it is an essential aspect of behavior that needs to be understood.

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11(*9*), 1109-1116.

Annaz, D., Remington, A., Milne, E., Coleman, M., Campbell, R., Thomas, M., et al. (in press). Atypical development of motion processing trajectories in children 28with autism *Developmental Science*.

Arrighi, R., Alais, D., & Burr, D. (2006). Perceptual synchrony of audiovisual streams for natural and artificial motion sequences. *Journal of Vision, 6*(3), 260-268.

Atkinson, A. P. (2009). Impaired recognition of emotions from body movements is associated with elevated motion coherence thresholds in autism spectrum disorders. *Neuropsychologia, 47*(13), 3023-3029.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*(1), 5-17.

Bertenthal, B. I., & Pinto, J. (1994). Global Processing of Biological Motions. *Psychological Science, 5*(4), 221-225.

Blake, R., Turner, L. M., Smoski, M. J., Pozdol, S. L., & Stone, W. L. (2003). Visual recognition in biological motion is impaired in children with autism. *American Psychological Society, 14*(2), 151-157.

Brown, S., Martinez, M. J., & Parsons, L. M. (2006). The neural basis of human dance. *Cerebral Cortex, 16*(8), 1157-1167.

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243-1249.

Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905-1910.

Calvo-Merino, B., Jola, C., Glaser, D. E., & Haggard, P. (2008). Towards a sensorimotor aesthetics of performing art. *Consciousness and Cognition, 17*(3), 911-922.

Cross, E. S., Hamilton, A. F. D. C., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *Neuroimage, 31*(3), 1257-1267.

Daprati, E., Iosa, M., & Haggard, P. (2009). A dance to the music of time: aesthetically-relevant changes in body posture in performing art. *PLoS One, 4*(3).

Davis, M. H. (1980). Multidimensional Approach to Individual Differences in Empathy. *JSAS Catalog of Selected Documents in Psychology, 10*(85).

Dixon, N. F., & Spitz, L. (1980). The Detection of Auditory Visual Desynchrony. *Perception, 9*, 719-721.

Downing, P. E., Jiang, Y. H., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293*(5539), 2470-2473.

Drake, C., Jones, M. R., & Baruch, C. (2000). The development of rhythmic attending in auditory sequences: attunement, referent period, focal attending. *Cognition, 77*(3), 251-288.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during actiona observation: A magnetic stimulation study. *Journal of Neurophysiology, 73*(6), 2608-2611.

Fain, G. L. (2003). *Sensory Transduction*. Sunderland, MA: Sinauer Associates.

Foster, S. L. (2008). Movement's contagion: the kinesthetic impact of performance. In T. C. Davies (Ed.), *The Cambridge Companion to Performance Studies* (pp. 46-59). Cambridge: Cambridge University Press.

Freitag, C. M., Konrad, C., Häberlen, M., Kleser, C., von Gontard, A., Reith, W., et al. (2008). Perception of biological motion in autism spectrum disorders. *Neuropsychologia, 46*(5), 1480-1494.

Frith, U. (2003). *Autism: Explaining the enigma* (2nd ed.) Blackwell Science.

Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron, 35*(6), 1167-1175.

Happe', F. & Frith, U. (2006). The weak coherence account: Detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 37(1),* 5-25.

Herrington, J. D., Baron-Cohen, S., Wheelwright, S. J., Singh, K. D., Bullmore, E. I., Brammer, M., et al. (2007). The role of MT+/V5 during biological motion perception in Asperger Syndrome: An fMRI study. *Research in Autism Spectrum Disorders, 1*(1), 14-27.

Hickok, G. (2008). Eight problems for the mirror neuron theory of action understanding in Monkeys and humans. *Journal of Cognitive Neuroscience, 21*, 1229-1243.

Hodges, D. A., Hairston, W. D., & Burdette, J. H. (2005). Aspects of Multisensory Perception: The Integration of Visual and Auditory Information in Musical Experiences. *Annals of the New York Academy of Sciences, 1060*(The Neurosciences and Music II: From Perception to Performance), 175-185.

Hollier, M. P., Rimell, A. N., Hands, D. S., & Voelcker, R. M. (1999). Multi-modal Perception. *BT Technology Journal, 17*(1), 35-46.

Holt, S., Petrini, K., & Pollick, F. E. (in preparation). Expertise eliminates the effect of biological motion rotation on audiovisual asynchrony perception.

Hubert, B., Wicker, B., Moore, D. G., Monfardini, E., Duverger, H., Da Fonseca, D., et al. (2007). Brief Report: Recognition of emotional and non-emotional biological motion in individuals with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 37*, 1386-1392.

Jacobsen, T., Schubotz, R. I., Hofel, L., & Von Cramon, D. Y. (2006). Brain correlates of aesthetic judgment of beauty. *Neuroimage, 29*(1), 276-285.

Jastorff, J., & Orban, G. A. (2009). Human Functional Magnetic Resonance Imaging Reveals Separation and Integration of Shape and Motion Cues in Biological Motion Processing. *Journal of Neuroscience, 29*(22), 7315-7329.

Johansson, G. (1973). Visual-Perception of Biological Motion and a Model for Its Analysis. *Perception & Psychophysics, 14*(2), 201-211.

Jola, C., Grosbras, M.-H., Kuppuswamy, A., & Pollick, F. E. (In prep). Enhanced Cortical Excitability induced by watching dance.

Jola, C., & Haggard, P. (2006). Inbetween notation and dance. Cognitive processes in reading Labanotation. *Proceedings of the 24th Biennial Conference of the*

International Council on Kinetography and Labanotation (ICKL), Laban Centre Lon, UK, 2, 145-155.

Jola, C., & Mast, F. W. (2005). Mental object rotation and egocentric body transformation: Two dissociable processes? *Spatial Cognition and Computation, 5*, 217-237.

Kaiser, M.D. & Shiffrar, M. (2009). The visual perception of motion by observers with autism spectrum disorders: A review and synthesis. *Psychonomic Bulletin and Review, 16(5),* 761-777.

King, A. J. (2005). Multisensory integration: Strategies for synchronization. *Current Biology, 15*(9), R339-R341.

King, A. J., & Palmer, A. R. (1985). Integration of Visual and Auditory Information in Bimodal Neurons in the Guinea-Pig Superior Colliculus. *Experimental Brain Research, 60*(3), 492-500.

Klin, A., Lin, D. J., Gorrindo, P., Ramsay, G., & Jones, W. (2009). Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature, 459*(7244), 257-U142.

Lestou, V., Pollick, F. E., & Kourtzi, Z. (2008). Neural substrates for action understanding at different description levels in the human brain. *Journal of Cognitive Neuroscience, 20*(2), 324-341.

Lipps, T. (1903 and 1906). *Asthetik: Psychologie des Schönen und der Kunst.* Hamburg: Leopold Voss.

Loucks, J., & Baldwin, D. (2009). Sources of information for discriminating dynamic human actions. *Cognition, 111*(1), 84-97.

Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology-Human Perception and Performance, 31*(1), 210-220.

Luck, G., & Sloboda, J. A. (2007). An investigation of musicians' synchronization with traditional conducting beat patterns. *Music Performance Research, 1*, 26-46.

Macdonald, J., & Mcgurk, H. (1978). Visual Influences on Speech-Perception Processes. *Perception & Psychophysics, 24*(3), 253-257.

MacFarlane, L., Kulka, I., & Pollick, F. E. (2004). The representation of affect revealed by Butoh dance. *Psychologia, 47*(2), 96-103.

Martin, J. (1939). *Introduction to the Dance.* New York: Dance Horizons.

Mast, F. W., Berthoz, A., & Kosslyn, S. M. (2001). Mental imagery of visual motion modifies the perception of roll-vection stimulation. *Perception, 30*(8), 945-957.

Mcgurk, H., & Macdonald, J. (1976). Hearing Lips and Seeing Voices. *Nature, 264*(5588), 746-748.

Miner, N., & Caudell, T. (1998). Computational requirements and synchronization issues for virtual acoustic displays. *Presence-Teleoperators and Virtual Environments, 7*(4), 396-409.

Miura, N., Sugiura, M., Takahashi, M., Sassa, Y., Miyamoto, A., Sato, S., et al. (2009). Effect of motion smoothness on brain activity while observing a dance: An fMRI study using a humanoid robot. *Social Neuroscience*.

Moore, D. G., Hobson, R. P., & Lee, A. (1997). Components of person perception: An investigation with autistic, non-autistic retarded and typically developing children and adolescents. *British Journal of Developmental Psychology, 15*, 401-423.

Mottron, L., Dawson, M., Soulieres, I., Hubert B. & Burack, J. (2006). Enhanced perceptual functioning in autism: An update, and eight principles of autistic perception. *Journal of Autism and Developmental Disorders, 36(1),* 27-43.

Nadal, M., Munar, E., Capo, M. A., Rossello, J., & Cela-Conde, C. J. (2008). Towards a framework for the study of the neural correlates of aesthetic preference. *Spatial Vision, 21*(3-5), 379-+.

Parron, C., Da Fonseca, D., Santos, A., Moore, D. G., Monfardini, E., & Deruelle, C. (2008). Recognition of biological motion in children with autistic spectrum disorders. *Autism, 12*(3), 261-274.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology, 93*(1), 603-608.

Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron, 49*(6), 815-822.

Petrini, K., Dahl, S., Rocchesso, D., Waadeland, C. H., Avanzini, F., Puce, A., et al. (2009). Multisensory integration of drumming actions: musical expertise affects perceived audiovisual asynchrony. *Experimental Brain Research, 198*(2-3), 339-352.

Petrini, K., Russell, M., & Pollick, F. (2009). When knowing can replace seeing in audiovisual integration of actions. *Cognition, 110*(3), 432-439.

Pollick, F. E., Kay, J. W., Heim, K., & Stringer, R. (2005). Gender recognition from point-light walkers. *J Exp Psychol Hum Percept Perform, 31*(6), 1247-1265.

Pollick, F. E., Lestou, V., Ryu, J., & Cho, S. B. (2002). Estimating the efficiency of recognizing gender and affect from biological motion. *Vision Research, 42*(20), 2345-2355.

Pollick, F. E., & Paterson, H. M. (2008). Movement Style, Movement Features, and the Recognition of Affect from Human Movement. In T. F. Shipley & J. M. Zacks (Eds.), *Understanding Events: From Perception to Action* (pp. 286-307). Oxford: Oxford University Press.

Pollick , F. E., Petrini , K., Dahl , S., McAleer , P., McKay , L. S., Rocchesso , D., et al. (submitted). Fusing the sight and sound of swing-groove in the brains of drummers: Expertise alters audiovisual brain activation.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience, 2*(9), 661-670.

Saygin, A. P., Driver, J., & de Sa, V. R. (2008). In the footsteps of biological motion and multisensory perception: Judgments of audiovisual temporal relations are enhanced for upright walkers. *Psychological Science, 19*(5), 469-475.

Shiffrar, M., & Freyd, J. J. (1990). Apparent Motion of the Human-Body. *Psychological Science, 1*(4), 257-264.

Shiffrar, M., & Freyd, J. J. (1993). Timing and Apparent Motion Path Choice with Human-Body Photographs. *Psychological Science, 4*(6), 379-384.

Simmons, D. R., Robertson, A. E., McKay, L. S., Toal, E., McAleer, P., & Pollick, F. E. (2009). Vision in autism spectrum disorders. *Vision Research, 49*(22), 2705-2739.

Smyth, M. M. (1984). Kinesthetic Communication in Dance. *Dance Research Journal, 16*(2), 19-22.

Spence, C., & Squire, S. (2003). Multisensory integration: Maintaining the perception of synchrony. *Current Biology, 12*(13), R519-R521.

Stewart, L., Henson, R., Kampe, K., Walsh, V., Turner, R., & Frith, U. (2003). Brain changes after learning to read and play music. *Neuroimage, 20*(1), 71-83.

Stewart, L., Walsh, V., & Frith, U. (2004). Reading music modifies spatial mapping in pianists. *Perception & Psychophysics, 66*(2), 183-195.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology, 18*, 643-662.

Troscianko, T., Holmes, A., Stillman, J., Mirmehdi, M., Wright, D. B., & Wilson, A. (2004). What happens next? The predictability of natural behaviour viewed through CCTV cameras. *Perception, 33*(1), 87-101.

van Wassenhove, V., Grant, K. W., & Poeppel, D. (2007). Temporal window of integration in auditory-visual speech perception. *Neuropsychologia, 45*(3), 598-607.

Vangeneugden, J., Pollick, F., & Vogels, R. (2009). Functional Differentiation of Macaque Visual Temporal Cortical Neurons Using a Parametric Action Space. *Cerebral Cortex, 19*(3), 593-611.

Vatakis, A., & Spence, C. (2006a). Audiovisual synchrony perception for music, speech, and object actions. *Brain Research, 1111*, 134-142.

Vatakis, A., & Spence, C. (2006b). Audiovisual synchrony perception for speech and music assessed using a temporal order judgment task. *Neuroscience Letters, 393*(1), 40-44.

Vatakis, A., & Spence, C. (2007). Crossmodal binding: Evaluating the "unity assumption" using audiovisual speech stimuli. *Perception & Psychophysics, 69*(5), 744-756.

Waadeland, C. H. (2003). Analysis of jazz drummers' movements in performance of swing grooves-a preliminary report. In R. Bresin (Ed.), *Stockholm music acoustic conference* (Vol. 2, pp. 573-576). Stockholm.

Waadeland, C. H. (2006). Strategies in empirical studies of swing groove. *Studia Musicol Norvegica, 32*(169-191).

Zeki, S. (1999). *Inner Vision: An Exploration of Art and the Brain*. Oxford: Oxford University Press.