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The Role of Human Body Movements in Mate Selection

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Abstract: It is common scientific knowledge, that most of what we say within a conversation is not only expressed by the words' meaning alone, but also through our gestures, postures, and body movements. This non-verbal mode is possibly rooted firmly in our human evolutionary heritage, and as such, some scientists argue that it serves as a fundamental assessment and expression tool for our inner qualities. Studies of nonverbal communication have established that a universal, culture-free, non-verbal sign system exists, that is available to all individuals for negotiating social encounters. Thus, it is not only the kind of gestures and expressions humans use in social communication, but also the way these movements are performed, as this seems to convey key information about an individual's quality. Dance, for example, is a special form of movement, which can be observed in human courtship displays. Recent research suggests that people are sensitive to the variation in dance movements, and that dance performance provides information about an individual's mate quality in terms of health and strength. This article reviews the role of body movement in human non-verbal communication, and highlights its significance in human mate preferences in order to promote future work in this research area within the evolutionary psychology framework.

Keywords: nonverbal communication, body movement; motion; perception; mate choice

Introduction

In animal and human communication, visual, tactile, acoustic and verbal signals are transmitted from a sender to a receiver ("Lorenz-Tinbergen approach"; see Friedenberg and Silverman, 2006). Shanker and King (2002) described communication as a dynamic rather than a static process. This means that a signal is decoded by a receiver, who adds information to the signal, and then decodes its meaning. One particular process in communication is to send and receive wordless messages. This kind of information transmission is commonly referred to as "nonverbal communication" (NVC). Nonverbal signals include facial expressions, bodily orientation, movements, posture, vocal cues (other than words), eye gaze, physical appearance, interpersonal spacing, and touching (Bull, 2001; DePaulo, 1992). As such, they support and moderate speech, facilitate the expression of emotions, help communicating people's attitudes, convey information about personality, and thus negotiate interpersonal relationships, even in the form of rituals (Bull, 2001; Graham and Argyle, 1975).

In humans, many signals, such as facial expressions of emotion, are thought to be cultural universals (Ekman and Friesen, 1971; Ekman et al., 1987), although a closer look reveals that there is still variability in these signals (Grammer et al., 1988). Because nonverbal behavior conveys emotions, these cues are sometimes referred to as "nonverbal expressive behaviors" that can be used in self-presentation (DePaulo, 1992). NVC can also comprise a set of so called "honest" signals since it is rather difficult for an individual to suppress them, and make them more readily accessible to others (DePaulo, 1992). Thus, there seems to be some kernel of truth in the proverb that "actions speak louder than words" (Argyle, Salter, Nicholson, Williams, and Burgess, 1970; Argyle, Alkema and Gilmour, 1972; Bull, 2001). Most of the studies on human NVC research have investigated certain types of body movements such as gestures (Bull and Connelly, 1985; Goldin-Meadow, 1999; Graham and Argyle, 1975; Krauss, 1998), facial expressions (Ekman, 1972, 1993; Mehrabian and Ferris, 1967), gaze (Kleinke, 1986), and body posture (Bull, 1987), in order to better understand the complexity of human social encounters.

Some support on the significance of NVC in social life comes from studies that have investigated non-verbal cues in human courtship situations. In these studies, first encounters of opposite-sex strangers were covertly filmed in "unstaged interaction" to investigate flirting behavior (deWeerth and Kalma, 1995; Givens, 1978; Grammer, 1990; Grammer, Juette, Schmitt, and Honda, 1999; Grammer, Kruck, Juette, and Fink, 2000; Moore, 1985; Moore and Butler, 1989; Mühlenhard et al., 1986; Scheflen, 1965). When opposite sex strangers meet for the first time, they both face the risk of being deceived. Neither opponent is aware of the other's intention, thus both have to rely heavily on non-verbal cues. Grammer (1990) reported that, in such a situation, there is a remarkable consistency in the repertoire of female solicitation behaviors in the presence of a male stranger, including eye-contact, followed by looking away, special postures, ways of walking, and so on (see also Eibl-Eibesfeldt, 1971; Grammer, 1989; Moore and Butler, 1989). Interestingly, men were found to approach women who expressed high rates of signaling these behaviors more frequently. In later study, Grammer et al. (1999) found that some information about female interest is not only inherent in the number of certain non-verbal signals, but is also encoded in the quality of body movements, such as their amplitude and speed. For example, women moved more frequently, but also displayed smaller and slower movements when they were interested in a man. Men in turn reacted to the quality of these movements positively and judged the situation to be more pleasant.

Based on these findings, researchers have begun to emphasize that it is not only the type of gesture or posture that are important in courtship situations, but rather the ways in which such displays are carried out. More recent findings further support this by showing that the attractiveness perception of human dance correlates with aspects of an individual's mate quality (Brown et al., 2005; Hugill, Fink, Neave, and Seydel, 2009). However, there is still a dearth of research that highlights the relevance of body movement in human social perception compared to the large number of studies on static cues (i.e., studies on face and body morphology) that have been put forward primarily through the expanding field of evolutionary psychology. This is surprising, given that an inspection of the literature reveals a considerable number of studies that could be used to stimulate the academic discussion and research on the importance of body movement, also within the framework of sexual selection.

Thus, we consider it timely to review some of the key findings on the topic of human body movement and its relation to mate selection. Firstly, we summarize some consolidated findings on motion perception, in order to show which kinds of information humans can perceive out of body movement. Secondly, we outline knowledge about the biological relevance of such sources of information for human social life. Bearing in mind such information, we emphasize the importance of body movements in human mate choice and discuss recent attempts to define its signaling value. Finally, we present some conclusions and issues for further research.

Perception of human body movement

From the biological perspective it is of paramount importance for the survival of an organism to decode information based upon the perception of other organisms' movements (Johansson, von Hofsten and Jansson, 1980; Pavlova, Krägeloh-Mann, Birbaumer, and Sokolov, 2002; Pollick, Paterson, Bruderlin, and Sanford, 2001; Troje, 2003). In this regard, humans as highly social creatures are no exception, as they almost constantly gather information about peoples' gestures and expressions in order to derive information about their intentions (Blake and Shiffrar, 2007; Troje, 2003). Darwin (1872) already noted in his book *The Expression of Emotions in Man and Animal* that one can use dynamic rather than static cues when it comes to an understanding of what others are doing. Consider the variety of natural situations in which form cues are corrupted through dim lighting conditions or occlusions. In these situations, the ability to perceive useful visual information is based predominantly on the motion patterns of an organism (Grossmann and Blake, 1999; Pavlova et al., 2002). Similar scenarios apply to everyday situations. For example, the gait of a person has the advantage of primacy in impression formation, since it is often the first cue that is perceived when a stranger approaches, especially when from a distance (Montepare and Zebrowitz-McArthur, 1988). Humans focus on movement characteristics to collect socially relevant information about others, and it is a scientific challenge to understand the form and function of these cues (see also Blake and Shiffrar, 2007).

Point-light-displays and early work

One of the most prominent attempts to understand the signaling qualities of body movement is the work of Johansson (1973, 1976). He illustrated through the use of simple point light (PL) displays, that an observer receives a vivid impression of a person's movements from the placement of 10-12 lights placed on the major joints of the body (knees, ankles, elbows etc.). Such strong impressions are reported despite the lack of important morphological features, such as facial features, skin, or hair (e.g., Barclay, Cutting and Kozlowski, 1978; Bertenthal and Pinto, 1994), and within extremely short presentation times of fewer than 200 milliseconds (Johansson, 1976). When observers view the dot presentations in a static format then the set of elements is never interpreted as a human body and Johansson (1973, 1976) concluded that humans use motion cues for recognition. These early studies indicated that humans are sensitive to biological motion, even when confronted with limited information such as the PL's (Stevenage, Nixon and Vince, 1999).

Johansson's method appeared to be powerful in the assessment of human body movement and has stimulated other researchers (and still does). For example, Mather and West (1993) used the PL technique to demonstrate that humans could also identify animals, such as goats, baboons, camels, horses and other vertebrates on the basis of motion cues. Similar perception tasks have been conducted with cats, pigeons, chicks, and non-human primates as "perceivers", all of which could discriminate biological motion (Blake, 1993; Chang and Troje, 2008; Dittrich, Lea, Barrett, and Gurr, 1998; Omori and Watanabe, 1996; Regolin, Tommasi, and Vallortigara, 2000; Vallortigara, Regolin and Marconato, 2005; Oram and Perrett, 1994). Other studies showed that human infants are predisposed to selectively attend to biological motion (Fox and McDaniel, 1982; Moore, Goodwin, George, Axelsson, and Braddick, 2007; Norman, Payton, Long, and Hawkes, 2004; Pavlova, Krägeloh-Mann, Birbaumer, and Sokolov, 2001; Piotrowski, Jakobson and Troje, 2007). For example, Simion, Regolin and Bulf (2008) revealed that two-day old infants could discriminate between point-light animations depicting biological motion from those showing random motion patterns. The same infants selectively preferred to view displays containing biological motion, especially when depicted in a true (upright) form. Similarly, Kuhlmeier, Troje and Lee (in press) report that six-month old infants can even discriminate between leftward and rightward motion from point-light walkers.

Such findings demonstrate that the detection of biological motion is an innate capacity of the visual system, and is thus according to Simion et al. (2008) "…part of an evolutionarily ancient and non-species-specific system predisposing animals to preferentially attend to other animals".

Social perception of motion

Humans can quickly gather visual information from the gait of a counterpart. Such perceptions are adaptive in the sense that they allow people to successfully interact within their social environment (Zebrowitz-McArthur and Baron, 1983). Studies on the perception of PL displays revealed that humans derive a wide range of socially relevant characteristics from human gait patterns (e.g., Barclay, Cutting and Kozlowski, 1978; Cutting and Kozlowski, 1977; Kozlowski and Cutting, 1977). For example, observers were able to determine the action a person performs just on the basis of such highly degraded depictions such as PL displays (e.g., Dittrich, 1993; Norman et al., 2004; Johansson, 1976). Observers are also able to decode information about an individual's age (e.g., Montepare and Zebrowitz-McArthur, 1988), identity (e.g., Cutting and Kozlowski, 1977; Hill and Pollick, 2000; Loula, Prasad, Harber, and Shiffrar, 2005; Stevenage, Nixon and Vince, 1999; Troje, Westhoff, and Lavrov, 2005; Westhoff and Troje, 2007), sex (e.g., Kozlowski and Cutting, 1977, 1978; Mather and Murdoch, 1994; Sumi, 2000; Troje, 2002; Barclay et al., 1978), and sexual orientation (Ambady, Hallahan, and Conner, 1999) from PL displays alone. Moreover, observers could identify certain psychological properties from these gait stimuli, such as an individual's emotional condition (Atkinson, Dittrich, Gemmell, and Young, 2004; Brownlow, Dixon, Egbert, and Radcliff, 1997; Clarke, Bradshaw, Field, Hampson, and Rose, 2005; Dittrich et al., 1996; Pollick et al., 2001; Walk and Homan, 1984), the aim of an action (Barrett, Todd, Miller, and Blythe, 2005), the intent to deceive (Runeson and Frykholm, 1983), and existing alterations of gross motor activity, locomotion, and gait performance which indicate depression (Lemke, Wendorff, Mieth, Buhl, and Linnemann, 2000; Sloman, Berridge, Homatidis, Hunter, and Duck, 1982). In addition, it is possible to determine the body size of a walker (Jokisch and Troje, 2003; Troje, 2003), the weight of a box carried by a person (Runeson and Frykholm, 1983), and even the quality of an individual's dancing ability (Brown et al., 2005) based on motion cues alone. Individuals can also identify their own body movements with a fair degree of accuracy, and even detect their friends from PL displays (Loula et al., 2005).

While the previous paragraphs provide an impressive list of human perceptual processing from limited information, there is still much to discover about how the perceptual system actually extracts all of this information from motion cues alone (Todd, 1983). Some attempts to understand the nature of this task come from studies of gender recognition from gait. For example, Kozlowski and Cutting (1977) introduced a number of manipulations in computer animations of artificial women such as the amount of arm swing, walking speed, and occlusion of body parts. However, these authors found a significant effect only for speed of movement manipulations, such that faster walkers were categorized as females. In follow-up work, Cutting, Proffitt, and Kozlowski (1978) and Cutting (1981) showed that signals derived from the shoulder and hip region of a walker are of primary importance for gender discrimination. Results from lateral comparisons of male and female body movements conducted by Murray and colleagues (Murray, 1967; Murray, Drought, and Kory, 1964; Murray, Kory, and Sepic, 1970) revealed that lateral hip and shoulder rotations are comparable for both sexes and that the amount of upper body sway was greater in male subjects.

Cutting and colleagues suggested that gender identification might be achieved indirectly through the determination of a biomechanical invariant referred to as the "center of moment" (C_m) of a walker (Barclay, Cutting and Kozlowski, 1978; Cutting, Profitt and Kozlowski, 1978; Cutting, 1981). The C_m can be estimated from the widths of the shoulders and the hips. Thus, the C_m is higher in females than in males, since the shoulders of males are wider than the hips and vice versa in females (Cutting and Proffitt, 1981; Cutting, Proffitt and Kozlowski, 1978). While these studies emphasize the importance of movements of a walker's upper body (hips and shoulders) for gender recognition, other studies suggest that the motion of one's lower body (i.e., the legs) provides essential gender information (Todd, 1983; Yamasaki, Saki and Torii, 1991). According to Runeson and Frykholm (1983) geometrical and inertial differences are responsible for gender-specific kinematic patterns and may thus also facilitate gender recognition. In support, Mather and Murdoch (1994) found that naive observers could identify the gender of an actor very reliably when the display contained gender-specific lateral body sway. In their experiments, this motion cue dominates the structural cue based on torso shape (C_m).

More recently, Troje (2002) made a promising attempt to resolve the problem of gender recognition from motion displays. He decomposed motion capture data of men and women, and projected them into a mathematical space. In this space he applied established methods from linear statistics and pattern recognition to search for axes that best represent the differences between male and female walkers. As Troje (2003) argued, the results supported the well-known prototypes: an extreme male walker showed the gait of a hero in a classical western movie with a straddle-legged posture, the elbows are held away from the body, and the wide shoulders are performing a lateral body sway. In contrast, a feminine walker appears rather slim, the elbows are held close to the body and the upper body shows only little lateral motion, but there is a significant rotation of the hips. Moreover, it seems that these gender typical movement patterns are present already in infants and becomes more pronounced during adolescence (König, Schölmerich and Troje, 2008).

In summary, human movement patterns visually communicate social cues to which other humans are exquisitely sensitive and gender identification seems to be one of the most obvious signals that can be derived from movement. However, it is likely that there is more information encoded about an individual than just whether an individual is male or female. With reference to the quality of movement, it is likely that although there is variation on male and female body movement the differences between the sexes are probably greater than within sex, but opposite sex people might also be sensitive to the variation within individuals of one sex. It is this within-sex variation that interests evolutionary psychologists in terms of what they have recently been trying to link to an individual's mate quality.

Body movement in human attractiveness research

Evolutionary psychologists argue that in humans, like in other animals, sexually selected physical characteristics all pertain to health, thereby suggesting that humans have evolved to view certain features as attractive and preferable. In this view, human mate selection criteria have evolved through human evolutionary history and shape our perception of attractiveness and beauty (Buss, 1989; Gangestad and Scheyd 2005; Rhodes, Simmons and Peters, 2005). Human socio-sexual encounters are undoubtedly complex, but there is now a wealth of evidence to suggest that human mate preferences can be conceptualized within the sexual selection framework and that the principal mechanisms of mate selection are remarkably universal across cultures (Buss, 1985; Buss and Barnes, 1986; Buss and Schmitt, 1993; Feingold, 1992; Grammer, Fink, Møller, and Thornhill, 2003).

A key problem for assessing possible relationships between physical features and human mate preferences has been the ecological validity of the stimuli used. Typically, studies utilize static two-dimensional (2D) stimuli, i.e., facial and/or bodily photographs (see for review Grammer, Kiel, Striebel, Atzmüller, and Fink, 2003). In real-life mating situations it is likely that individuals are moving and base their mate preference assessment (at least initially) on multiple motion and behavioral cues (Rubenstein, 2005).

Viewpoint dependency and presentation mode

Perceiving physical attractiveness from static images of female or male forms seems to differ from those of moving bodies by changing viewpoint-dependant perceptions of shape. In a meta-analysis, Langlois et al. (2000) reported that studies in attractiveness research used different kinds of stimulus presentation modes (photographic images, video movies and *in situ* encounters), and these different modes might convey different types of information, which may subsequently lead to different attractiveness ratings. In support of this, some researchers also showed that moving stimuli were judged differently on attractiveness compared to static stimuli (Knappmeyer et al., 2002; Lander, Christie and Bruce, 1999; Riggio, Widaman, Tucker, and Salinas, 1991).

For example, men's preference for a woman's slim waistline (as indexed via the waist-to-hip ratio, WHR; Singh, 2002, 2006) was demonstrated only with still images. However, bodies in motion are dynamic sources of information, and this may have an effect also on the perception of cues such as the WHR. Doyle (2009) reported a peak shift effect in the attractiveness perception of WHR when women were moving. He argues that while walking, motion of the waist and hips results in continuously alternate left and right side WHR that are perceived as highly attractive. Modeling this in a female model with a WHR of 0.70 results in left and right side WHRs that are even smaller than 0.70, which are then perceived as "supernormal" (Doyle, 2009). Likewise, O´Toole, Edelman, and Bülthoff (1998) demonstrated the existence of a stimulus-specific effect in face recognition over viewpoint changes. Therefore, it could be that in human social encounters the dynamics of the face and body provide additional three-dimensional (3D) "representations" (Bloj, Kersten and Hurlbert, 1999; Knappmeyer et al., 2002), which affect their perception. In real life situations the face and the body of a person are almost constantly in motion, thus the perceptions of moving faces and/or bodies could differ from those of static representations (Grammer, Kiel, Striebel, Atzmüller, and Fink, 2003).

Comparative psychology of body movement

The late American modernist poet Charles Olson once stated that "*Men, everywhere, dance"*, and "*There are no human societies in which they do not"*, which leads evolutionary psychologists and anthropologists to the question about the origin of dance in humans, and the cultural universality of signals derived from biological motion. Darwin (1871) himself suggested that dance is a sexually selected courtship signal that is related to the quality of the dancer. This assertion can be regarded as one of Darwin's seminal insights into the evolutionary mechanisms of behavior in man and animals, given the evidence that dance is an important signal in mate choice in a variety of animals, including humans. Based on Darwin's observations of birds, Ellis (1976) provided an evolutionary explanation for primitive human dance and the "love dances" in many animals. He claimed that the origins of human dance date back even longer than the origins of modern man, and are thus firmly rooted in human evolutionary history. Hence, in search of an evolutionary origin of body movement as a courtship signal it seems worthwhile to consider comparative aspects with examples also from the animal kingdom.

Courtship dances are observed in many bird species, such as zebra finches (*Taeniopygia guttata*) (Williams, 2001), satin bowerbirds (*Ptilonorhynchus violaceus*)

(Coleman, Patricelli and Borgia, 2004; Patricelli, Uy and Borgia, 2003), duetting thrushes (*Cichladusa guttata*) (Todt and Fiebelkorn, 1980), and manikins (*Chiroxiphia linearis*) (Trainer and McDonald, 1993). These behavioral displays include movements of the body, the head, and the beak, but also find their expression in singing, specific postures, plumage erection and flight performances (Williams, 2001). They are part of a complex courtship display, which were ultimately designed to attract potential mates. Even female fruit flies (*Drosophila subobscura*) choose males on the basis of their ability to dance, which is interpreted as a signal of their neuromuscular condition (Maynard-Smith, 1956). Likewise, Rowland (1995) reported that female sticklebacks prefer males with high swimming speed. Many male spiders, especially the funnel-web spider (*Agelenopsis aperta*), and several jumping spiders (*Salticidae*), have developed elaborate courtship dances, e.g., lateral swaying of the abdomen and flexing the web, to entice females to mate (Clark and Morjan, 2001; Owens, 2003; Singer et al., 2000). Successful males in the funnel-web spider tend to sway their abdomens with a higher frequency, than unsuccessful males during courtship dance (Singer et al., 2000).

The evolutionary origin of dance in human courtship may be perhaps less well understood through the comparative account of similar patterns in birds or spiders. However, it is possible that it stems from the courtship displays of non-human primates, as our closest relatives in evolutionary genealogy (Sheets-Johnstone, 2005). Among primates, chimpanzees (*Pan troglodytes*) move their bodies or heads in courtship displays, aggressive and frustration behavior (Goodall, 1968). The "bipedal swagger" is a typical behavioral display in male chimpanzees, which occurs only rarely in females, and is an important part of courtship display (Goodall, 1968). During this display the male chimpanzee approaches the female, sits or stands, and extends his hands, lightly touching and then releasing his head, shoulder, back or knee. His body slowly moves forward and backward and from side to side (Kano, 1992). Kuroda (1984) observed that during courtship females often do not receive any visual sign other than the rocking gestures. These examples of motion as a courtship signal in our closest relatives can possibly give some information about the origin of dance in human male courtship rather than the examples about the "love-dances" of male spiders and birds. Sheets-Johnstone (2005) therefore assumes that dance in men has some evolutionary roots.

Human dance is unique in its style, and is likely related to bipedalism. Bipedalism facilitates a greater range of movement possibilities than is observed in quadrupeds. Thus, it seems to be essential for the creative dynamics that constitute the art of dance in humans, as the torso can twist and bend, the head can swivel, and the arms can swing in many directions (Sheets-Johnstone, 2005). To this day, few studies have been concerned with how humans use body movements such as dancing, for attracting mates. Early accounts were mainly based on ethnographic studies (Kurath, 1960). Later, Kaeppler (1978) provided an anthropological account of dance by emphasizing that dance is an activity dating back to prehistoric times that is displayed in rituals as a form of social communication, but also in courtship activity. Hanna (1987a) discussed the importance of dance in courtship rituals amongst humans in several societies, including the Acholi in Uganda (p´Bitek, 1966), a tribe on Mangaia, a southern Cook Island in central Polynesia, and the Medlpa in New Guinea (Hanna, 1995; Pitcairn and Schleidt, 1976). From the Acholi in Uganda, p´Bitek

(1966) reported that women discriminate between men on the basis of the vigor and endurance of their dance performance. In India and Morocco, Nevinson (1931) observed solitary dances that are performed to give pleasure to the opposite sex encounter. Furthermore, there are some European courtship dances such as the Basque “arresku”, the Norwegian “halling” and the Ukrainian “hopak”, in which men show off their physical prowess. In most societies, not only men dance to attract women, but also women express themselves through dance in order to receive attention from men.

With reference to evolutionary psychology, Hanna (1987b) points out that dance may be an adaptive behavioral pattern in sexual selection, as it is a medium, which displays beauty, health, strength, and thus sexual attractiveness. It is possible, that the disposition to dance facilitates human mate selection, though the variation in dance patterns and styles is certainly mediated by culture (Boas, 1944; Hanna, 1987a). However, this view is not uncontroversial, and some researchers have argued against the hypothesis that dance is sexually selected. For example, Hagen and Bryant (2003) suggest that dance has evolved as a coalition signaling system, which communicates coalition quality and thus signals cooperative behavior. However, these authors also admit that some mate qualities such as health, nutrition, proper development, endurance, and creativity are signaled via dance performances – and could facilitate the formation of coalitions with members of the opposite sex.

The quality of body movement

Most of the findings in studies on non-verbal behavior in human courtship were obtained with the “repertoire analysis method” (Grammer 1990; Grammer, Kruck, Juette, and Fink, 2000; Moore, 1985; Moore and Butler, 1989; Scheflen, 1965). However, this approach via pure observation on the basis of operationally defined behavior categories has several limitations. Categories are sometimes difficult to identify and the definition of some of them depend on the investigators (subjective) perception. Moreover, behavior categories can only give an approximation to how a receiver processes the information. Grammer, Fieder and Filova (1997) and Grammer et al. (1999) found that some information about a women’s courtship behavior is not only inherent in the frequencies of certain postures or gestures, but also encoded in the quality of body movements. They showed that women moved more frequently and displayed smaller and slower movements when they were interested in a man. Men in turn reacted to the quality of these movements positively, and judged the situation to be more pleasant. Consequently, the quality of body movement displays could be meaningful in courtship (Grammer, Fink and Renninger, 2002).

Aside from these studies, which give rise to the assertion that the quality of body movement is an important aspect of courtship behavior in humans, there have been only few attempts to actually quantify its signaling value. Some studies demonstrated that certain movements were perceived as being more attractive than others (Grammer, Kiel, Striebel, Atzmüller, and Fink, 2003; Fink, Seydel, Manning, and Kappeler, 2007; Knappmeyer et al., 2002; Morrison, Gralewski, Campbell, and Penton-Voak, 2007; Provost, Troje and Quinsey, 2008b; Sadr, Troje and Nakayana, 2006; Troje, 2003). Grammer, Kiel, Striebel, Atzmüller, and Fink (2003) found an association between motion quality and the attractiveness ratings of dance movements. Men and women demonstrating a bigger sweep in movements were judged as more attractive. In addition, men judged women as more attractive, the slower and less complex their body movements were. However, Grammer, Kiel, Striebel, Atzmüller, and Fink (2003) noted some limitation of their study in that they used movement descriptors which were based on motion history detection, and thus might not exactly capture the features people use when making judgments about the attractiveness of body movements.

Troje (2003) again used a PL stimuli approach to investigate the sex-typicality of an attractive gait. He found that women rated as being highly attractive by men, placed their feet almost on a straight line whilst walking, thus displaying the typical “cat walk”. Johnson and Tassinary (2005) displayed human walkers varying in terms of shoulder and hip sway. Observers focused their attention on the waist and hip regions of the body in order to identify the gender of the walker (i.e., masculine or feminine) and then the sex of the walker. Johnson, Gill, Reichman, and Tassinary, (2007) extended this research to demonstrate that observers identified the sexual orientation of computer-generated animations using assessments of body shape (primarily for women) and body shape and movement (for both males and females). Gender-atypical body movement had a strong effect on perceived sexual orientation and also influenced the accuracy of the judgments.

Using motion-capture-technology, Provost, Troje and Quinsey (2008) showed a contextually dependent shift in the female preference for sex-specific gait patterns in men. In these experiments, women rated “masculine” walking men as more attractive, especially when they were in the fertile phase of their menstrual cycle and more open to short-term mating opportunities. Further characteristics, which are inherently signaled via gait, are the age and height of a walker. Both measures are known to serve as initial criteria in human mate selection (e.g., Buss, 1989; Kenrick and Keefe, 1992) that could also be conveyed through body movement. While evolutionary psychologists argue that men have evolved preferences for youth in females, as this is linked to fertility and health, women place more emphasis on signs of male status. In this context, Schmitt and Atzwanger (1995) suggest a sex-specific association between pace and status in men. These authors found that men with higher status walked faster, whereas the pace of women was independent of their status. Furthermore these findings were not affected by proximate factors such as age, body height, next destination, and number of dates.

One central question in human attractiveness research is whether body movement signals information about an individual’s mate quality, and how strong such cues are in relation to those of the face and body. If dance, for example, is a sexually selected trait, it should reflect the genetic or phenotypic quality of the dancer.

Body movement and correlates of physical condition

Symmetry

The term “developmental stability” is used to refer to the capacity of the individual to develop a symmetrical phenotype, thus resisting developmental perturbations caused by “stress”, such as from disease, parasitism, or sex steroids (Livshits and Kobyliansky, 1991; Thornhill and Møller, 1997). These developmental challenges lead to small deviations in bilateral symmetry in morphological features and are usually referred to as fluctuating asymmetry (FA). There is some evidence for the assertion that movement reflects developmental stability (as measured via FA), from studies of both humans (Manning and Pickup, 1998) and animals (Garland and Freeman, 2005; Manning and Ockenden, 1994; Martin and López, 2001; Møller, Sanotra and Vestergaard, 1999; Swaddle, 1997). For example, Manning and Ockenden (1994) showed that FA in racehorses was a predictor of their performance. Manning and Pickup (1998) reported that male middle-distance runners with less body FA were ranked higher within their sport. More recently, Brown et al. (2005) found positive correlations between FA and the perception of dancing ability in a rural Jamaican sample of men and women. Similarly, Sadr, Troje, and Nakayama (2006) collected attractiveness ratings for motion-captured women, displayed as point-light walkers, and found that an increase of body symmetry was positively associated with perceived attractiveness of the walkers.

However, as Brown et al. (2005) noted, body symmetry is probably not the only correlate of variation in movement quality and may be moderated by a number of additional factors such as neuromuscular coordination, or health, including freedom from parasites. Moreover, they argued that attractive dances may be particularly difficult to perform, more rhythmic, more energetic, and more energy efficient (see also Grammer et al., 2003b; Mattes, Martin and Royer, 2000; Waters and Mulroy, 1999).

Sex steroids

One moderator between body symmetry and quality of movement could be gonadal sex steroids, such as testosterone (T) and estrogen (E). While asymmetries in movement may be readily observed as they are determined by skeletal and muscular structures, body movement may also indicate transient conditions of an individual, such as physiological states (Grammer, Kiel, Striebel, Atzmüller, and Fink, 2003). Since the 1950's, many top-class athletes in various sporting disciplines routinely used exogenous T to improve their performance (Fitch, 2008; Hartgens and Kuipers, 2004). Supra-physiological doses of T synthesize body protein, which results in an increase of muscle mass and physical strength, even without exercise (Bhasin et al., 1996; Hartgens and Kuipers, 2004). In some sports, athletes reported that their intake of anabolic androgenic steroids (AAS's) was also associated with a better recovery, a higher training load capacity and therefore an increase in physical and mental performances (Baume et al., 2006). Cardinale and Stone (2006) found a positive correlation between circulating T levels and vertical jump performance in men and women. However, Siegel et al. (2008), found no relationship between T levels and sequential movement performance in older and younger males.

Normal movements are partly dependent upon the inter-connected subcortical nuclei referred to as the "basal ganglia". The key structure is the striatum, and normal functioning within the basal ganglia is determined by the neurotransmitter dopamine (Albin, Young, and Penney, 1989). In animals and humans it has been demonstrated that the striatal dopaminergic system is modulated by estrogen. For example, fluctuations of estrogen during the estrous cycle in rats are associated with motor performance, with better performance being associated with estrogen peaks (Becker, Snyder, Miller, Westgate, and Jenuwine, 1987). Studies on women have showed systematic variations in motor performance throughout the menstrual cycle (Binkley, 1992; Chrisler and McCool, 1991;

Grammer, Fieder and Filova, 1997; Hampson and Kimura, 1988; Jennings, Janowsky, and Orwoll, 1998; Lebrun, 1993; Morris and Udry, 1970; Pierson and Lockhart, 1963; Saucier and Kimura, 1998; Stenn and Klinge, 1972), though the results from these studies are partly inconclusive.

Morris and Udry (1970) found that women were more active in walking or running activities at the times of peak fertility compared to other stages of their menstrual cycle. However, an earlier study by Pierson and Lockhart (1963) found no significant changes in reaction time and speed of arm movement across the menstrual cycle. More recently, Provost, Quinsey, and Troje (2008) recorded the kinematics of the walking patterns of young women at different cycle stages and found that men judged the walking performances of women in the luteal phase slightly higher on attractiveness than those of women in the follicular phase. These findings are puzzling in that they contrast previous reports on men's preferences for women's faces, which found that men rated women as more attractive at times of peak fertility (Roberts et al., 2004). Here is need for further investigation before drawing a conclusion on whether static and active cues of women across the menstrual cycle are perceived differently, or comprise a single ornament of mate quality that men are sensitive to.

Digit ratio

In addition to the effects of circulating T, studies have shown that in men and women a low digit ratio (i.e., the relative length of index to ring finger; 2D:4D) - a proxy of prenatal T - is correlated with physical fitness and high ability in sports, such as skiing (Manning, 2002), football (Manning and Taylor, 2001), sprinting speed in boys (Manning and Hill, 2009), athletics (Hönekopp, Manning and Müller, 2006; Pokrywda, Rachon, Suchecka-Rachon, and Bitel, 2005), and physical strength (Fink, Seydel, Manning, and Kappeler, 2006). Fink, Seydel, Manning, and Kappeler (2007) presented video clips of male dancers with low and high 2D:4D ratios to a sample of female judges, who rated them on perceived attractiveness, dominance, and masculinity. It was found that dances of men with low (masculine) 2D:4D ratios were rated higher on all three attributes than the dances of men with high (feminine) 2D:4D ratios. The authors concluded that even prenatal T has an influence on men's dancing abilities and women's perception of them.

Physical strength

Evolutionary psychologists argue that women have developed certain cognitive adaptations to visually assess physical fitness, athletic abilities and thus competitiveness in men, all of which are correlated with T, as mating with high quality males could increase their reproductive success. Studies on women's preferences for masculine male faces (Fink, Neave, and Seydel, 2007; Neave, Laing, Fink, and Manning, 2003; Swaddle and Reierson, 2002) and bodies (Sell et al., 2009) support this assertion by suggesting that women possess cognitive abilities to assess "formidability" (i.e., fighting ability and resource-holding potential) and physical strength from male face and body morphology. Recent research by Hugill et al. (2009) suggests that male physical strength is not only signaled via static representations of the face and body, but also via active displays such as dance. In their study women perceived dances of men, who were physically stronger (i.e., those with higher hand-grip strength), as more attractive and assertive. Thus, it was concluded that the association of physical strength with dancing ability could be moderated by an effect of T, whose production and metabolism mobilizes resources for the efforts of males to attract and compete for mates (Ellison, 2001). These findings are in line with studies, which have shown that as in most sports, dance fitness depends on the ability to develop high levels of muscle tension, i.e., muscle strength (Fitt, 1982; Koutedakis and Sharp, 1999), and that this together with agility, balance, and flexibility are positively associated with dance performance (Bushey, 1966).

Conclusion

Mate choice is arguably one of the most important decision-making task an individual has to master during its reproductive life, as via appropriate choice, an individual can ensure that its genes are passed on to offspring. By selecting a high-quality mate, the individual can also ensure that shared genes will end up in healthy and fertile offspring (Gangestad and Thornhill, 1997). Evolutionary psychology theories of mate choice thus focus on observable features (sexual cues) that are emitted by an individual, and which indicate valuable information about that individual's reproductive potential and quality. Although there is some consensus among evolutionary psychologists that evolutionary selection pressures have led to the development of certain physical characteristics and preferences for them, a number of open questions in attractiveness research remain. Most important, almost all studies on physical attraction have used static stimuli (images of faces and/or bodies). Little is known about the attractiveness of body movements, such as dance or gait, though both are presumably key signals in everyday life and social encounters. The apparent sex difference in human body movement leads to the question whether movement also signals aspects that are relevant for mate choice. Moreover, aside from the potential physical qualities that are signaled through human motion, could there be also personality characteristics encoded in the way we walk and/or dance that finally affect attractiveness assessments and mate preferences?

Studies indicate that humans use dynamic displays in courtship and make attractiveness decisions on the basis of cues they derive from body movement. Thus, it is possible, that evolution has shaped our brain in order to process body movement cues of other individuals in the context of mate selection, similar to evolved preferences for static morphological features of the face and body. Although the studies we have reviewed in this article lend some support to the notion that body movement signals information that is crucial for mate choice, as people are sensitive to the variation in movement styles and make attractiveness judgments based on them, the results should be regarded as preliminary. In order to support the hypothesis of an influence of human movement on mate preferences and actual mating decisions, further research is needed. Such research should make use of modern technology such as motion capturing, as this provides representations of real body movement (e.g., Brown et al., 2005; Knappmeyer et al. 2002; Provost, Quinsey and Troje, 2008; Provost, Troje and Quinsey, 2008; Troje 2002, 2003). The power of such methods is that they capture the whole range of people's body movement and, simultaneously, allow subsequent digital alterations and statistical analysis, based on objective motion descriptors. Here, reflecting trajectories can be used to robustly reconstruct joint angles of the 3D skeletal animation, and this information can be transformed onto a virtual human character. Thus, subsequent perception studies will be able to investigate possible associations of body movement, which is free from physical form, with numerous biological, physiological and personality characteristics. Such data will be useful to evolutionary psychologists, studying the signaling qualities of human body movements in relation to sexual selection, but also to other topics such as human computer interaction, smart surveillance, athletic performance enhancement and clinical studies.

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