

Ivar Hagendoorn

Some Speculative Hypotheses about the Nature and Perception of Dance and Choreography

I: Introduction

Ever since I first saw a dance performance I have wondered why it is that I am sometimes fascinated and touched by some people moving about on a stage, while at other times it leaves me completely indifferent. I will argue that an answer to this question has to be searched for in the way sensory stimuli are processed in the brain. After all, all our actions, perceptions and feelings are mediated and controlled by the brain. The thoughts and feelings evoked by a dance performance are no exception and thus they too have a neural substrate in the brain.

In music and the visual arts what has been called ‘neuroaesthetics’ (Zeki, 2001a) and ‘neuromusicology’ has already yielded some interesting insights. As one study showed, the aesthetic appeal of Mondrian’s paintings can be related to certain psychophysical properties of the visual system (Latto *et al.*, 2000). Earlier studies had found that the perception of oblique lines is slightly inferior to the perception of horizontal and vertical lines. Making clever use of the fact that some of Mondrian’s paintings have an oblique frame, the authors showed that people also *prefer* horizontal and vertical to oblique lines. Findings like this suggest that we have an aesthetic preference for those stimuli that are closely tuned to the respective sensory areas in the brain.

The present article draws an itinerary through various brain structures and shows how these may combine to ultimately give rise to the sensations we experience when watching a dance performance. Since watching dance is essentially a visual experience the present analysis concentrates on visual processing. This is not to deny that music is an integral part of most dance performances or that movements produce noise, which may influence visual processing and in the absence of a visual component elicit visual images. But, to state the obvious, if the stage lights go out the audience’s experience of the dancers’ movements will

Correspondence: Ivar Hagendoorn, Marnixstraat 18-A, 2518 PZ Den Haag, The Netherlands,
Email: ivar@ivarhagendoorn.com

Journal of Consciousness Studies, **11**, No. 3–4, 2004, pp. 79–110

be impaired. I should emphasize that the itinerary chosen here is only one of many routes that participate in the processing of dance, although I believe it to be a main route. At the start of this itinerary lies the observation that neural processing delays interfere with both perception and action. This problem is at once illustrated and brought to the fore in both the perception and practice of dance. Several authors have proposed in various forms that the brain compensates for these delays by creating predictions of forthcoming sensory and motor events (e.g. Berthoz, 2000; Kawato *et al.*, 1987; Wolpert & Flanagan, 2001; Engel *et al.*, 2001). Based on these considerations I will advance two hypotheses. I will argue that the deviation from and correspondence between the actual motion trajectory of a moving object and the trajectory as predicted by the brain of the observer, gives rise to two distinct emotional responses, analogous to the euphoria and frustration of catching or missing a ball. Through their sequential interplay these responses may reinforce each other to give rise to the feelings one can experience when watching dance. As a corollary I will argue that in forming a prediction of a moving object's motion trajectory the brain engages in a form of motor imagery which, through a different route, may contribute to a state of arousal.

Much of the present article is devoted to a discussion of the brain regions involved in the above processes (Figure 1). The unsuspecting reader should therefore be warned of some tough neuroscience ahead. (Some readers may wish to jump straight to section VIII where I present my two main hypotheses and then read back to how I got there). I will argue that mirror neurons, which become active both when a movement is perceived and performed, may constitute a neural bridge between action and perception. Interestingly, as I will show, one of the brain regions where mirror neurons have been found has also been associated with perceptual anticipation. I will then relate these findings to the literature on prediction and reward and argue that brain regions associated with prediction errors may also account for at least some of the emotions we experience when watching dance.

Different people will have a different understanding of the word 'dance', some may recall a ballet or a musical they once saw, while others may think of

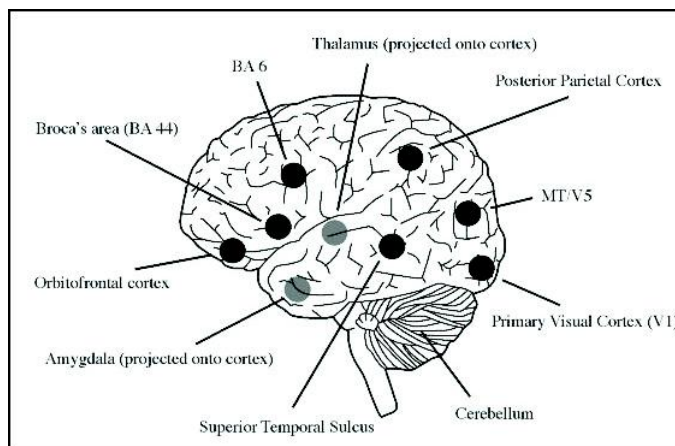


Figure 1.

Schematic representation of the main brain regions mentioned in the article and their approximate locations.

the movements they and others perform at a party. By dance or 'dance performance', I will here refer to a sequence of movements, not necessarily choreographed, of any length, from two seconds to two hours, whereby the goal of the movement is the movement itself. This is not so much a definition of dance, or dance as an art form, but an operational delimitation of the question I will be addressing here: why is it that it can be interesting to watch someone 'just dancing around' or, to avoid circular reasoning, going through a series of movements without any apparent goal, other than 'just' performing the movements? And what is it that choreographers *do* when they compose such a series of movements, with no other purpose than to be performed and seen? What goes on in their mind when they adjust a position or movement sequence? What are the neural processes that guide and constitute aesthetic judgment? My primary references here are works by choreographers such as George Balanchine, William Forsythe, Merce Cunningham and Jiri Kylián, often referred to as 'abstract' dance. However, movement sequences from martial arts when rehearsed 'as such' also fit the present description, so do Indian dances, Japanese *butoh* and various other dance traditions.

Having outlined how a movement sequence may bring about the feelings it does in certain dance performances, I will argue that choreographers like all other artists when creating a work, are implicitly led by the brain mechanisms underlying sensory experience and emotion. By making explicit some of these implicit considerations they may eventually be put to creative use, a proposition I will illustrate with some examples from my own choreographic work. I would like to emphasize from the outset that the ideas expressed here are tentative and not uncontroversial (e.g., Zeki, 2001b; Ione, 2001). However, it is only with their propagation and by inviting feedback from critics that they may be further developed.

II: From the Retina to the Brain

What we see is light and light reflected from surfaces. The difference between light hitting the eye or an arm, or a wall, is that inside the eye are light-sensitive receptors that transform the energy carried by the light into electrical signals. After some pre-processing these electrical signals are relayed along separate pathways to various specialized areas in the brain, where they are either used to form a visual representation of the stimulus or immediately translated into an action such as narrowing the pupil.

Of the various pathways emanating from the retina only two are directly involved in processing visual information for perception. One conveys information contributing primarily to the perception of movement, while the other is associated with the processing of colour and shape. Before reaching the visual areas of the brain, both pathways pass through the thalamus, the brain's central relay centre. From thereon the visual information is relayed to the primary visual cortex, where, after some intermediate processing, it is once more separated into different paths, each leading to a more specialized area. In all there are over 30 regions performing such tasks as determining colour, shape, solidity, size and motion of whatever hits the eye. It is currently believed that motion is processed



Figure 2.

Which limb belongs to which body? Jiri Kylian, *As if never been* (1992). Dancers: Nancy Euverink and Patrick Delcroix.

Photo:
© Dirk Buwalda.

in two areas, one of which, the middle temporal gyrus, often referred to as MT or V5, is involved in processing an object's speed and direction, while the other, the medial superior temporal area or MST, is specialized for detecting its dynamical properties, like rotation and tilting.

It seems likely that all connections between these higher visual processing areas are reciprocal. What's more, information may re-enter a given area after it has been processed in any number of other areas (Martin, 2002). It is difficult to see how the different attributes of a scene that are analysed in specialized areas would otherwise be integrated into a visual image, a feature of the visual system often referred to as the 'binding problem', a 'problem' since its workings are still largely unknown (Robertson, 2003). With respect to motion perception the binding (or maybe we should say 'unbinding') problem, comes down to determining what is moving and what is stationary, and distinguishing between the motion of different parts of a single object and the motion of different objects, something choreographers like to play with (Figure 2). Already we catch a glimpse of how aspects of the visual system can be employed artistically. By keeping the background and some attributes of an object constant, a choreographer can create a setting which, in terms of brain processing, leaves more resources available for processing one salient feature — movement, for instance.

Not all visual information passes from the thalamus to the primary visual cortex. One pathway leads straight to MT, one of the areas specialized in visual motion processing. This may be why some people with damage to the primary visual cortex are nevertheless able to perceive movement, a condition called blindsight (e.g., Schoenfeld *et al.*, 2002). Another pathway projects from the thalamus to the amygdala, a brain structure associated with emotional behaviour, in particular in relation to danger (LeDoux, 1996). The direct pathway from the thalamus to the amygdala ensures that the brain can already begin to respond before an object has been identified, for instance by modulating the processing in the visual cortex, with which it is reciprocally connected, or by initiating

withdrawal. Even though theatres tend to be relatively safe environments, by emulating the perceptual characteristics of potentially dangerous events, the brain will respond in much the same way as in the case of a real threat, as every movie director knows. A possible explanation for this is that from an evolutionary point of view it is better to retreat ten times too often than once too few. A related explanation is that in these circumstances the emotional system overrules cognition. We are carried away even though we know 'it's only a movie'. The opposite, by the way, may also occur: we may cognitively value something we don't enjoy, for instance an avant-garde dance performance with little or no movement.

Interestingly, the amygdala also appears to play a role in attributing emotions to movements. When watching animation movies featuring simple geometric figures like circles, squares and triangles, people tend to attribute emotions such as joy, anger and frustration to the figures based on the nature of their movements (Heider & Simmel, 1944). Patients with damage to the amygdala, however, fail to assign emotions to the movements of such figures (Heberlein *et al.*, 1998). It would therefore be interesting to investigate how these patients respond to dance, especially if the dancers were to wear single-coloured costumes and masks or hoods covering both head and face so as to create a purely graphic display.

III: Motion Anticipation and Smooth Pursuit

Having hit the retina it takes between 50 and 100 milliseconds before the information carried by a light particle reaches the visual cortex. Some simple arithmetic shows that a car driving at 100 km/h will have covered an additional 2 to 3 metres by the time the light activates the appropriate regions in the brain. To make up for this delay it has been conjectured that the brain somehow forms a prediction of the path of a moving object (Nijhawan, 1994). According to this view the brain forms an internal simulation of the trajectory covered so far, on the basis of which the object's movement is extrapolated into the future. Such an extrapolation would ensure that its perceived position coincides with its actual position.

Perceptual anticipation and prediction are likely to involve both low- and high-level brain processes. It has been proposed that a rudimentary prediction in the form of a forward shift of the image occurs as early as the retina (Nijhawan, 1997; Berry *et al.*, 1999; for a review, see Nijhawan, 2002). At the level of object representations, learned characteristics of the behaviour of target objects (e.g., the bouncing of a ball) bias the processing of its speed and direction of motion (the second bounce is lower than the first). Getting to the roots of this phenomenon, an intriguing study, which compared the performance of astronauts catching a ball on earth and under zero gravity, recently suggested that the brain uses an internal model of gravity-induced acceleration when predicting the trajectory of a falling ball (McIntyre *et al.*, 2001).

Various other experimental findings support the hypothesis that motion perception is predictive. It has been found that, if a moving target suddenly

disappears, its last position is remembered as being slightly ahead of its actual final position, a phenomenon technically known as representational momentum, which suggests that the percept is shifted forward (Freyd & Finke, 1984). What's more, even still images of an object in motion, such as that of a falling glass, exhibit 'representational momentum', in that they convey information about the motion implied in the picture (Freyd, 1983). This, of course, is nothing new to dance audiences. While many dance photos could also have been posed, some 'capture' the dance (see Figure 3, as well as Figures 6 and 9). They extend the movement frozen by the camera forward in time. Interestingly it has been demonstrated that watching still photographs with implied motion yields increased neural activity in MT/MST, the part of the visual cortex involved in the processing of visual motion (Senior *et al.*, 2000; Kourtzi & Kanwisher, 2000).

Perhaps some of the most compelling evidence for the predictive nature of motion perception has come from the study of fast ball sports like tennis, baseball and cricket. In baseball, outfielders run to where they expect to be able to catch a fly ball, which implies that the brain forms a prediction of the ball's trajectory (McBeath *et al.*, 1996; McLeod *et al.*, 2001). Land and McLeod (2000) recorded the eye movements of batsmen in cricket as they prepared to hit an approaching ball. They found that the batsmen's eyes monitored the ball shortly after its release, then made a predictive saccade to where they expected it to hit the ground, waited for it to bounce and then tracked its trajectory for 100–200 ms afterward. As the authors argue 'information provided by these fixations may allow precise prediction of the ball's timing and placement'. If this is true for moving balls, why wouldn't it also be the case for human movements such as dance?

The study by Land and McLeod (2000) demonstrates that the central nervous system employs two types of eye movements to track a moving target: saccades



Figure 3. Implied motion. A good dance photo 'captures' the dance. The movement appears to continue in the direction of motion. Indeed, photos such as these yield increased activity in MT/MST, the part of the visual cortex involved in the processing of visual motion (Senior *et al.*, 2000; Kourtzi & Kanwisher, 2000). William Forsythe, *As a Garden in this Setting* (1992). Dancer: Regina van Berkel (l), Tony Rizzi (r). Photo: © Dominik Mentzos.

and smooth pursuit. Saccades direct the fovea, the high-acuity region at the centre of the retina, towards a target in discrete jumps. Smooth pursuit eye movements stabilize the image of the object on the retina by smoothly rotating the eyes in congruence with the motion of the target. Sometimes, however, moving the eyes alone is not enough and the head, and if necessary other parts of the body, are integrated into the smooth pursuit movement. In tennis, the heads of the umpire and the public can often be seen to move from side to side as they track the ball. What's more, when tracking an object with binoculars or a camera, the eyes are fixed and the body adjusts to keep the object within view. I would therefore like to suggest that the mechanisms for tracking a moving target — eyes, head or attention — form a continuum and as such share a common neural network, which predicts the trajectory of the moving target.

While many studies have investigated the properties of neurons in visual motion area MT and the neural mechanisms of smooth pursuit eye movements and saccades, surprisingly few have analysed the functional neuroanatomy of visual motion anticipation. Ando (2002) recently reported the results of a functional neuroimaging experiment using fMRI, in which participants had to predict the motion trajectory of a virtual three-dimensional object. The data revealed activity in the intraparietal sulcus, the inferior and superior parietal lobules (BA 40 and BA 7), the dorsal premotor cortex (BA 6), the inferior frontal gyrus (BA 44, Broca's area) and the lateral cerebellum. These findings are in congruence with recent experiments by Schubotz and Von Cramon (2001; 2002a; 2002b). They found increased activity in the right ventrolateral premotor cortex (BA 6) and the right intraparietal sulcus, as subjects predicted the last in a series of 12 sequentially displayed circles of different size, which created the illusion of regularly pulsing motion (Schubotz & Von Cramon, 2002b). What is perhaps most interesting about these results is the activation of premotor regions, as in all experiments the task was purely perceptual.

Catching a ball, hitting a moving object or tracking a target with a camera, all require a form of sensorimotor integration. Visual information about the object's motion trajectory has to be instantaneously transformed into movement of the body, whether the eye, finger, hand or arm. The results by Ando (2002) and Schubotz and Von Cramon (2002b) indicate that even in the absence of a motor task, attending to and predicting the trajectory of a moving target activates premotor regions. On a speculative note Schubotz and Von Cramon suggest that

when we try to predict how a target will move, the motor system generates a 'blueprint' of the observed motion that allows potential sensorimotor integration. In the absence of any motor requirement, this blueprint appears to be not a by-product of motor planning, but rather the basis for target motion prediction (Schubotz and Von Cramon, 2002b).

What's more, since the lateral premotor cortex is also activated when predicting a colour or pattern transition or a change in auditory pitch, Schubotz and Von Cramon (2002a) suggest that the lateral premotor cortex is involved in the prediction of any kind of sequential event, with human movement as a special case.

Additional evidence for the involvement of motor areas in perceptual anticipation comes from the study of handwriting movements. It has been shown that when writing an 'l' followed by another 'l', the first 'l' is written down faster than when it is followed by an 'n' (Orliaguet *et al.*, 1997). Further experiments demonstrated that, when watching a dot as it traces the curve of an 'l', observers are able to use information about its kinematics to predict the upcoming letter, 'l' or 'n' (Kandel *et al.*, 2000a; 2000b). Chaminade *et al.* (2001) used positron emission tomography (PET) to measure brain activity as observers predicted the continuation of the motion trajectory of a dot produced by mechanical, pointing and writing movements. All three conditions were associated with a common neural network comprising the orbitofrontal and right frontal cortex. However, unlike Schubotz and Von Cramon (2002b), activation of the premotor cortex and the right intraparietal sulcus was found only when the trajectory had been produced by a pointing movement. The authors also report increased activity in the superior parietal lobule and Broca's area (BA 44) during the anticipation of writing movements, two of the areas that were also activated in the fMRI study by Ando (2002). Some caution in interpreting the findings by Chaminade *et al.* (2001) is warranted though, since the baseline condition required subjects to indicate whether they expected the dot to move up or down. This, however, is itself a prediction task and can therefore not be properly used to test for perceptual anticipation. In summary, while the results are not unequivocal they do partially reinforce each other, suggesting that (pre-)motor areas are involved in predicting visual motion, which obviously would include the movements of a dancer or group of dancers.

IV: Apparent Motion

It frequently happens that a moving object is temporarily occluded from view, an arm which briefly moves behind the body, a car entering a tunnel or a dancer who disappears behind one of the other dancers. In principle almost anything can happen while we are unable to see the object, but in practice most objects continue along their track and we are able to accurately predict where and when it will reappear.¹ Indeed, we tend to be surprised if the object does not reappear or at a different location. Conversely, once the object has reappeared the brain is able to infer the motion trajectory between the points where it vanished and resurfaced. The latter is a specific example of what is known as 'apparent motion', since we did not really see the object move, we merely saw it dis- and reappear.

The term apparent motion is commonly used to refer to the illusory perception of motion from the rapid sequential display of static images as in a film or 'motion picture'. Consider a prototypical film consisting of two frames, one with two vertically aligned dots on the left, the other with two vertically aligned dots on the right. If the two frames are rapidly interchanged, the dots are perceived as

[1] A choreographer aware of this phenomenon could manipulate dancers, movements and stage props such that part of the audience sees what is occluded from the rest of the audience as in William Forsythe's *Enemy in the Figure* (1987), which features a wavy-shaped wooden panel positioned diagonally on the middle of the stage.



Figure 4. Apparent motion of the human body. When alternately shown two body positions the brain chooses a biomechanically feasible path to connect them. The example used in most experimental studies shows a hand behind and in front of a knee, the idea being that the hand cannot move through the leg. If the hypothesis is correct in the above example the brain will simulate a movement of the head underneath the arm, a movement most people are unlikely to have previously performed. Dancer: Ester Natzijs. Photo: © Ivar Hagendoorn.

jumping from left to right and back. However, this is only one of several *logical* possibilities, the upper and lower dots could in principle have swapped positions. This classic example illustrates that given a point A and B, the visual system selects the shortest path to connect both points, that is, to describe the movement needed to go from A to B (e.g., Dawson & Pylyshyn, 1988). However, as shown by Shiffrar and Freyd (1990; 1993), if A and B are *body* positions, perception follows an anatomically feasible path, even though a physically impossible route may be shorter (Figure 4).

A recent PET study in which subjects were briefly presented with two body positions and subsequently had to choose between a direct impossible and an indirect possible connecting movement, yielded selective activation of regions in the primary motor and superior parietal cortex, but only if the connecting movement was biomechanically possible (Stevens *et al.*, 2000). On the basis of these findings the authors suggest that

we might expect an absence of motor executive activations during the visual perception of actions that an observer interprets as beyond his/her motor capabilities, e.g., *a technically challenging ballet movement*. In such cases, the impossibility of completing the action is determined within the context of the observer's own motor experience rather than in terms of the general movement limitations of the human body [emphasis mine].

This hypothesis could be tested empirically by first showing two positions unlikely to be the beginning and end of a continuous movement and subsequently the movement that connects them.

Stevens *et al.* (2000) suggest that, when connecting two body positions, the brain engages in a form of motor imagery to create the motion percept. Motor imagery refers to the mental performance of a movement, or, more formally 'a dynamic state during which the representation of a given motor act is internally rehearsed within working memory without any overt motor output' (Decety & Grèzes, 1999). It is the experience of seeing and feeling oneself executing a

movement, a kinaesthetic feeling of speed, effort and changing body configuration. As Jeannerod (1994) explains ‘visual images are experienced by the self in the same way as a spectator who watches a scene, motor images are experienced from within as the result of a first-person process where the self feels like an actor rather than a spectator’. Thus, according to this view, if within a movement sequence part of the body is temporarily occluded, the brain will either extrapolate the movement from the last visible position or interpolate between the positions before and after the occlusion, by covertly performing the movement itself.

V: Biological Motion

Most of the experimental studies discussed so far dealt with the movement of abstract stimuli like dots or virtual balls. If we want to learn more about dance we will have to consider movements of the (whole) human body. As it turns out there is a large body of evidence which shows that humans have a special ability for recognizing what has become known as biological motion, the visual motion patterns of humans and animals. In the early 1970s Gunnar Johansson developed a now classic technique whereby an actor was filmed as he moved through a darkened room with small light bulbs attached to the head and key joints such as the shoulders, elbows, wrists, hips, knees and ankles. When the actor was sitting in a chair people watching the film reported seeing nothing but a random collection of lights. But as soon as the actor started moving they instantly identified the pattern as that of a moving person. In a second experiment a dancing couple was filmed under the same conditions and again observers had no difficulty in identifying the moving pattern of lights as that of a dancing couple (Johansson, 1973).

This technique has since been replicated in a variety of experimental settings.² The lights, or their more contemporary motion capture equivalents, were placed on other parts of the body, actors were instructed to perform a range of activities, from hammering to greeting to climbing a staircase, and the display as a whole has been turned upside-down or masked with a cloud of random noise (for a review, see Pinto & Shiffrar, 1999). One experiment demonstrated that people are able to recognize acquaintances and even themselves from a point-light display of their movements. In fact in this particular experiment the probability of correct self-recognition was even higher than all other probabilities (Beardworth & Bukner, 1981). The latter is particularly striking since apart from dancers, most people don’t often see themselves moving. Not only does this rule out the possibility that recognition was due to perceptual learning, as might be suspected if the phenomenon only showed up in the perception of other persons, it also suggests once more a possible link between motor and perceptual processes. Another experiment showed that people are able to extract an emotional state from motion characteristics alone (Dittrich *et al.*, 1996). For this experiment the

[2] Given the number of experimental studies, it may surprise that only recently, some 25 years after the original experiments, the potential of this technique has been explored in a ballet (video projected on a scrim covering the full stage height as part of the set design), Merce Cunningham, *Biped* (1999), in collaboration with multimedia artists Paul Kaiser and Shelley Eshkar.

researchers asked two dancers to portray fear, anger, grief, joy, surprise and disgust. The movements were recorded as such and using a point-light display. Participants in the study then had to judge which emotion was being portrayed. Interestingly they got 88% right from the full display and 63% from the point-light display.

In recent years various neuroimaging studies have examined the brain regions associated with the recognition of biological motion from point-light displays (Bonda *et al.*, 1996; Grossman *et al.*, 2000; 2002; Vaina *et al.*, 2001; Grezès *et al.*, 2001; Servos *et al.*, 2002). A common area found in all studies is a region on the (posterior) superior temporal sulcus (STS). In addition, perhaps not unexpectedly, Grossman *et al.* (2000), Vaina *et al.* (2001) and Grezès *et al.* (2001) report activity in MT/MST. Other areas that were found to be significantly activated were the cerebellum (Grossman *et al.*, 2000; Vaina *et al.*, 2001), the lingual gyrus (Servos *et al.*, 2002), the ventral premotor cortex (Grezès *et al.*, 2001) and the amygdala (Bonda *et al.*, 1996). The activation in STS is consistent with neurophysiological studies in monkeys (Oram & Perrett, 1994). Using single cell recordings it was shown that some neurons in the superior temporal cortex are selectively activated by arm movements and the direction of walking. The posterior STS therefore appears to be a key area for the recognition of biological motion.

Neurological case studies provide further evidence for this hypothesis. Howard *et al.* (1996) and Vaina *et al.* (1990) report patients who, because of a lesion in the visual motion processing areas MT/MST, are practically motion blind, but are still able to perceive biological motion. This led Beintema and Lappe (2002) to re-examine the stimuli used in point-light studies. They observed that the standard point-light displays exhibit what they call 'local image motion': each individual dot, for instance the dot tied to the right elbow or the left ankle, traces a stationary trajectory through space and thus not only contains motion information but also information about its location on the (implied) body. They therefore developed an alternative technique in which the location of the light points changes from frame to frame and position and motion information are dissociated (e.g., the point that was on the elbow in the first frame moves somewhere between elbow and shoulder in the second frame, then changes again in the third frame, etc.). Even though Beintema and Lappe's 'sequential position walker' as they call it, is somewhat more difficult to recognize, observers' performance is comparable with standard point-light displays. Based on these findings they suggest that the perception of biological motion relies on the sequential analysis of body postures.

Point-light displays were originally intended to show how little information is needed for the human brain to recognize human motion. There is a danger that explaining this phenomenon, which is essentially a laboratory condition, becomes an end in itself. Real-life motion stimuli are often imperfect, due to differential lighting conditions and partial occlusion, but as the study by Beintema and Lappe (2002) shows, standard point-light displays may be 'perfect in their imperfection'. It may surprise that only few neuroimaging studies have been

performed using real human movements as stimuli, rather than point-light displays. Decety *et al.* (1997) and Grèzes *et al.* (1998) conducted a PET study using video filmed pantomimes of opening a bottle, hammering a nail, sewing a button or turning the pages of a book as stimuli, as well as movements from American Sign Language. Participants were instructed to memorize the movements so that they could either imitate or recognize them after the scanning session or to just watch the movements. Since the subjects were unfamiliar with American Sign Language the authors were able to make a distinction between the observation of meaningful and meaningless movements. In the absence of a goal, observation of both meaningful and meaningless movements activated the occipital–temporal junction, which corresponds to MT/V5, the superior occipital gyrus, the middle temporal gyrus and the inferior parietal lobe. Meaningful movements also activated the dorsal precentral gyrus (BA 6), the inferior frontal gyrus (BA 44/45) and the fusiform gyrus, whereas meaningless movements resulted in stronger activation in the inferior parietal lobe, the superior parietal lobule and the cerebellum. If the goal was to imitate, both meaningful and meaningless movements led to activation in the cerebellum and the occipital–parietal (‘dorsal’) pathway extending to the premotor cortex, while meaningful movements additionally activated the supplementary motor area (SMA) and orbitofrontal cortex.

The differences in activated areas between observing point-light figures and the experiments by Decety *et al.* (1997) and Grèzes *et al.* (1998) may be due to the fact that the former represented full body motion, whereas the latter were confined to movements of the hand and arm. It would therefore be interesting to replicate the study by Decety *et al.* (1997) with the higher spatial resolution that can be obtained with today’s fMRI and using full body movements rather than movements of the arm and hand alone. In combination with a point-light version of the same movements, it could then be tested whether real human movements and their point-light representation do indeed rely on the same neural mechanisms.

Of course it would go too far to straightforwardly extrapolate any of these findings to the perception of dance. The motion stimuli in the study by Decety *et al.* (1997) were very short, lasting for as little as 4 seconds and were restricted to movements of the hand and arm, with only the upper limbs and trunk being shown on a computer display. What is perhaps most interesting about these two studies is that differences between the observation of meaningful and meaningless movements on the one hand and cognitive strategy on the other can actually be detected at the level of neural processing. Translated to dance one may therefore speculate about a difference in neural processing already at the level of perception between watching the abstract ballets of for instance George Balanchine and the expressionist more gestural based dance theatre of Pina Bausch.

VI: Mirror Neurons

Above I have briefly outlined some of the brain regions involved in (biological) motion perception and perceptual anticipation. Although the evidence is as yet inconclusive, it appears that motor regions contribute to action perception. What

is missing is a possible mechanism or a common computational framework linking these scattered reports.

Some years ago neuroscientists discovered a population of neurons in the premotor cortex of a monkey that discharge both when the monkey performs a movement and when it observes the same action performed by someone else (Rizzolatti *et al.*, 1996; Gallese *et al.*, 1996). These so-called ‘mirror neurons’ could therefore provide a neurophysiological bridge between perception and action. At first sight mirror neurons appear to respond in much the same way as the neurons in the superior temporal cortex that respond to the sight of a moving hand, face or body (Oram & Perrett, 1994). What is striking about mirror neurons, though, is that they also fire when the monkey *performs* a movement. Therefore they cannot be exclusively visual. A recent study showed that mirror neurons in the premotor cortex also respond to auditory stimuli, making them not just bi- but multimodal (Kohler *et al.*, 2002).

At present there is much speculation about the role of mirror neurons in perception and behaviour. Rizzolatti *et al.* (1996) have suggested a role in the understanding of motor events. The brain has an implicit knowledge of the immediate consequences of its own actions, that is, of the movements it generates, both in terms of its changing relation to the external world, as in terms of a change in body state and body configuration. This knowledge is the result of an association between the representation of a movement and its consequences, in other words,

the movement has a meaning (e.g., ‘grasp’) and this meaning is represented by a specific cortical activation pattern. Mirror neurons show that this movement knowledge can be attributed to actions made by others. When an external stimulus evokes a neural activity similar to that which, when internally generated, represents a certain action, the meaning of the observed action is recognized because of the similarity between the two representations, the one internally generated during action and that evoked by the stimulus (Rizzolatti *et al.*, 1996).

This account, if correct, might explain why people understand not only mime, but also non-imitative movements in dance, which have a more abstract ‘meaning’. The back of the hand is more vulnerable than the palm, so leaning on the back rather than the palm of the hand may exude a sense of ‘vulnerability’. It may also explain why a dancer balancing in a virtuoso position may inspire awe and be

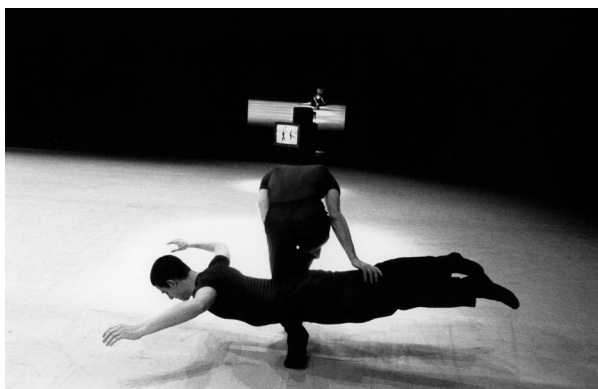


Figure 5.

Is he actually? To understand what is going on the brain virtually performs the movement and body configuration. Jirí Kylián, *Click–Pause–Silence* (2001). Dancers: Patrick Marin and Stefan Zeromski.

Photo: © Joris-Jan Bos.

literally breathtaking: we hold our breath as we internally simulate the movement (see Figures 5, 6 and 8).

Jeannerod (1994; 1997) has suggested a role for mirror neurons in the learning of new motor skills. There is now a growing body of literature linking mirror neurons to imitation learning (Meltzoff & Prinz, 2002; Hurley & Chater, 2004), which of course is the basis of not only dance education but also much choreography. Jeannerod (1994) gives the example of a pupil learning a motor skill such as playing a musical instrument, but we could also think of a choreographer demonstrating a new movement sequence to a dancer. Although the dancer remains immobile during the demonstration, he or she must somehow internalise the movement, that is, he or she must form an image of the movement sequence as it unfolds. The choreographer in turn will compare the movements of the dancer with what he himself had in mind and in the words of Jeannerod '[will] experience a strong feeling of what should be done and how'. As Jeannerod continues,

Similar feelings may be experienced by sports addicts watching a football game on television. They mentally perform the appropriate action to catch the ball (and indeed, they express frustration when the ball has been missed by the player). The vividness of the imagined action can induce in the watchers changes in heart and respiration rates related to the degree of their mental effort (Jeannerod, 1994; 1997).

Although mirror neurons have only been directly demonstrated in monkeys, there is accumulating evidence that similar cells or a similar *mirror system* exist in humans. As one experiment showed, the observation of human movement facilitates the same muscle groups and motor circuits as when the movements are executed (Fadiga *et al.*, 1995). Neuroimaging studies also suggest the existence of a human mirror system. Iacoboni *et al.* (1999) performed an fMRI experiment in which participants were instructed to imitate a finger movement, lift a finger in response to a spatial cue or to just watch either the finger movement or the spatial cue. Activation in the left inferior frontal cortex (BA 44, Broca's area), the right anterior parietal cortex and the right parietal operculum was significantly higher during imitation than in the other tasks. Of particular interest is the activation in Broca's area, since this area has been proposed to be the human homologue of area F5 in the monkey premotor cortex (Rizzolatti & Arbib, 1998), where mirror neurons were first discovered. To directly test the involvement of Broca's area in imitation Heiser *et al.* (2003) used transcranial magnetic stimulation (TMS) to temporarily disrupt processing in the left inferior frontal cortex as subjects imitated a finger movement or alternatively, performed a finger movement in response to a visual cue. It was found that while simple key presses were unaffected, imitation was significantly impaired during the application of TMS, thus providing evidence for the involvement of Broca's area, or at least the region comprising Broca's area, in imitation. However, Manthey *et al.* (2003) recently reported that the ventrolateral part of the premotor cortex (BA 6) and *not* Broca's area (BA 44) was predominantly activated when subjects observed 36 short movies of simple goal-directed actions. This is in congruence with findings by Decety *et al.* (1997) for the observation of meaningful movements, but at odds with the observation-only condition in, for instance, Iacoboni

et al. (1999). If Broca's area is associated with imitation one would expect it to be activated during all instances of action observation, as indeed in the observation only task in an experiment similar to Iacoboni *et al.* (1999) by Carr *et al.* (2003), which used facial expressions instead of finger movements. It may therefore be too early to draw firm conclusions about the precise role of Broca's area in the perception of action or about the location of a brain region subserving the function of matching action observation and execution.

Subsequent experiments by Iacoboni *et al.* (2001) also revealed increased activity in the superior temporal sulcus (STS). While this is consistent with findings that report activation during the perception of point-light displays of human motion (see references above), interestingly and somewhat unexpectedly activation was greater during the imitation task. This could of course be due to increased attention, but Iacoboni (2003) offers an intriguing alternative explanation, suggesting that

the increased STS activity may be due to efferent copies of motor commands originating from fronto-parietal mirror areas. These efferent copies would allow a prediction of the sensory consequences of the planned imitative action that would be compared with the description of the observed action provided by STS.

Although Iacoboni *et al.* (2001) provide some evidence in favour of the latter hypothesis it may be difficult to show that this is indeed what is happening.

Gallese (2002) also interprets mirror activity in premotor regions in terms of efference copies of motor commands, but places premotor mirror neurons at the receiving rather than the sending end, suggesting that they perform a simulation of the planned movement, allowing for the prediction of its sensory consequences. Interestingly this hypothesis is in line with findings reported above, that suggest a role for the lateral premotor cortex (BA 6/44) in predicting perceptual events (Schubotz & Von Cramon, 2002a; b). This raises the question whether the same neural mechanism underlies *either* perceptual anticipation and imitation *or* the computations of the lateral premotor cortex.

VII: A Common Representational Framework

Neural processing delays interfere not only with the sensory system, but also with motor control. As various computational studies have shown, sensorimotor loops are too slow to allow feedback control of fast coordinated movements (e.g., Kawato, 1987). To overcome this problem it has been proposed within the motor control literature that the brain uses what are known as internal models to calculate a feed-forward motor command from the desired motion trajectory (for a review, see Kawato, 1999). An internal model in general is a system that mimics the behaviour of a natural process. Internal models come in two types. An *inverse* model provides the motor commands necessary to perform a movement. A *forward* model captures the forward or causal relationship between the input to a system and its output, by predicting the next state of the system, given its current state. Thus the *forward* model predicts how the pointer will move if the mouse is moved. The *inverse* model estimates how the mouse should be moved

so that the pointer moves in the desired direction. In the context of motor control, forward models could compensate for delays in sensory feedback, anticipate and cancel out the sensory effects of self-produced movements or transform the errors between the desired and actual outcome of a movement into the corresponding errors in the motor command (Wolpert, 1997; Wolpert *et al.*, 1995). It seems reasonable to suppose that, when tracking a rapidly moving target with a cursor, as controlled by a mouse or joystick — think of a computer game — the brain also forms a forward model of its motion trajectory. From here it is only a small step to the hypothesis that the brain forms a forward model of a target's motion trajectory regardless of whether it tracks the target with a mouse, the eyes, a camera or attention, and whether the target is a dot on a screen, a ball, a limb or a dancer. Indeed the term forward model is just a technical notion for the predictive function referred to in previous sections.

There is accumulating evidence that the brain does indeed employ internal models. Above we already encountered one instance in the form of catching a ball on earth and in outer space (McIntyre *et al.*, 2001). Of relevance to the present context is a recent study by Mehta and Schaal (2002). Comparing the output of various computational models with actual performance of a visuomotor task requiring subjects to balance a pole on a finger, a task which depends crucially on visual feedback, they conclude that the data are best described by a forward model at the sensory processing stage. Given the nature of this task, it seems reasonable to extend these results to the visual tracking of a moving target, whether with the eyes or head.

In recent years various authors have proposed a role for internal models, more in particular forward models, in the perception of action and the understanding of behaviour (Blakemore & Decety, 2001; Jeannerod, 2001; Gallagher & Jeannerod, 2002; Gallese, 2002; Rizzolatti *et al.*, 2001; Iacoboni, 2003; Wolpert *et al.*, 2001; 2003). In its most intriguing and also most speculative form, it is hypothesized that, when watching human movement, the predictions of a forward model are compared, not with sensory feedback from the own body, but with the next movement of the person performing the movement (Wolpert *et al.*, 2003). This extends the computational logic of internal models far into the realm of understanding intentions (Blakemore & Decety, 2001) and social cognition (Gallese, 2002; Iacoboni, 2003; Wolpert *et al.*, 2003).

To illustrate this hypothesis it may be instructive to go back to the example of a choreographer demonstrating a movement sequence to a dancer and interpret it in the context of forward and inverse models. When the choreographer performs the movement, along with the motor commands that innervate the musculoskeletal system, efference copies of the motor commands are fed into a corresponding forward model, which simulates the sensory consequences of the movement. These predictions can be compared with visual and proprioceptive feedback and used to update the movement in real-time or to improve its future performance. The possible role of forward models in perception becomes most apparent when we consider what happens the moment the choreographer watches the dancer imitate the movement sequence. The relevant inverse models

are now run ‘off-line’, without acting on the musculoskeletal system, and their output is sent directly as input to the corresponding forward models. The output of the forward models is now compared with the movements of the dancer and in case of an error give rise to the ‘feeling of what should be done and how’ referred to by Jeannerod (1994; 1997).

It should be emphasized that, while attractive for reasons of its theoretical appeal, this framework is speculative. For instance, the present scenario does not specify how and where visual information is transformed into a format that can be used as input to a forward model. Iacoboni (2003) speculates that, when imitating a movement, the STS forms an inverse model of the movement to be imitated. It then sends a visual description of the movement to the mirror areas in the parietal and premotor cortex, which generate the motor commands necessary to perform the movement, a copy of which is sent back to the STS as input to a forward model, which predicts the sensory consequences of the planned movement. However, there is no experimental evidence that the computations of the STS do indeed constitute an internal model, whether inverse or forward model or both. What’s more, whereas Gallese (2002) suggests that mirror neurons in premotor cortex act as a forward model, an interpretation recently put forth by Schubotz and Von Cramon for ventral lateral premotor cortex as a whole³, Blakemore and Decety (2001) propose the cerebellum as a possible repository of internal models. This need not be contradictory though, since internal models may be located in all brain regions having synaptic plasticity, as pointed out by Kawato (1999).

VIII: Two Hypotheses

I would now like to propose two hypotheses. First of all I would like to speculate that, when watching dance, the brain is submerged in motor imagery. If this hypothesis is correct when watching dance the observer is in a sense virtually dancing along. Above I have reviewed some lines of evidence in support of a role for motor areas in the perception of human movement. Using magnetoencephalography (MEG) it has recently been demonstrated that, when listening to piano music, pianists exhibit involuntary motor activity in the unilateral primary motor cortex (Haueisen & Knösche, 2001). Since this requires auditory information to be mapped onto motor areas it is not improbable to assume that watching dance also activates motor areas.

It is also *plausible* that watching dance involves a form of motor imagery. To state the obvious, with the exception of some avant-garde performances that question the assumptions of other performances, dance has a high movement density. Movements are at once fast and slow and often intertwine without any clear beginning or end. Even within a solo the next movement may already have started before a motion percept of the previous movement has been formed. It also frequently happens that some limbs are temporarily occluded from view or that a dancer briefly disappears behind another dancer. As argued above the brain will complement the movement by interpolating between the *positions* it

[3] Poster presented at the CNS meeting in New York, March 2003.

did perceive, which in case of body positions means choosing a biomechanically feasible path. Stevens *et al.* (2001) have provided tentative evidence that this task involves motor areas. In dance the brain has to work overtime in this respect, as it is confronted not only with a flood of movement, but also with movements not part of the brain's own movement repertoire. And just as actual movement when exercised to excess produces a state of arousal, so may virtual movement.

It would be interesting to directly test the hypothesis put forth here, for instance by recording the brain activity of someone watching a short dance sequence. Since this is likely to activate a variety of brain areas the results may be difficult to interpret. However, in principle the stimuli would not be very different from those used in biological motion studies or the experiments of Decety and Grèzes (1997) or Manthey *et al.* (2003).

In the example adapted from Jeannerod (1994; 1997) it was said that a choreographer watching a dancer imitate a movement 'experiences a strong feeling of what should be done and how', yet it was not explained how and where this *feeling* arises. Jeannerod also remarked that spectators who see a player miss a ball will experience a sense of frustration. This however depends which side they are on. The same event, hitting a target, whether in soccer, basket ball, golf or combat, can be a reward for one person and a punishment for another. Rewards and punishments are the technical notions for the positive respectively negative value ascribed to a stimulus. Rewards, like all sensory stimuli, can be both anticipated and unanticipated. At the level of neural processing single cell recordings from monkeys indicate that dopamine neurons respond to the delivery of an unexpected reward. What's more, if the monkey learned that a certain stimulus always preceded delivery of the reward, dopamine neurons would respond to the predictive stimulus rather than the reward itself. The output of dopamine neurons therefore appears to encode reward expectation. Another way of saying this is that dopamine neurons code for an error in the prediction of reward, the discrepancy between the occurrence of reward and the *predicted* occurrence of reward (Schultz, 2000).

Dopamine neurons are not the only neurons that respond to prediction errors. Neurons in the orbitofrontal cortex, a brain region that has been implicated in the processing of emotion (Rolls, 1999), have also been found to be activated when stimuli deviate from their expected value. Nobre *et al.* (1999) asked subjects to respond as quickly as possible to visual targets appearing at peripheral locations in the visual field. Immediately preceding the target a visual cue was presented that either correctly or incorrectly predicted the location of the upcoming target. This experiment is particularly interesting since the network of activation in the latter condition comprised regions associated with sensory prediction (the lateral premotor cortex, BA 6), attention (the posterior parietal cortex) and emotion (the orbitofrontal cortex). Janata and co-workers (2002) recently reported significant activity in the orbitofrontal cortex as eight musically experienced listeners performed a perceptual discrimination task requiring them to respond whenever they heard a note played by a flute instead of a clarinet, or when a note violated local tonality. Similar results had previously been reported in a task whereby

participants were asked to respond to the degree of dissonance or consonance in the chords accompanying a melody (Blood *et al.*, 1999). Goel and Dolan (2001) finally found the orbitofrontal cortex (BA 10/11) to be associated with the appreciation of humour in the form of semantic and phonological jokes of the kind ‘Why did the golfer wear two sets of pants?... He got a hole in one,’ which are based on the juxtaposition of expectation and its resolution.

The function of the orbitofrontal cortex may therefore be to evaluate the reward value of environmental stimuli and to attach an emotional ‘tag’ to a prediction error. In support of this hypothesis in a fascinating fMRI study Anderson *et al.* (2003) recently showed that, with respect to olfaction, stimulus intensity was associated with activation in the amygdala, regardless of whether the odour was pleasant or unpleasant. Activity in the right medial orbitofrontal cortex by contrast correlated with pleasantness, but not intensity, while a region in the left lateral orbitofrontal cortex responded to both unpleasantness and intensity. Even though these results cannot be straightforwardly extended to other than olfactory stimuli, the fact that the same event, a goal in sports, as noted above, almost instantly brings about two opposite responses, suggests that a similar dissociation may underlie visual processing.

I would now like to propose the following scenario. When watching dance, to keep track of the movement, which may require a visuomotor transformation in order to move the eyes or head, the brain makes an internal prediction of its motion trajectory and dynamics. As argued in the previous section this task is described by the computational logic of forward models. A deviation from the expected path results in a prediction error. If the same movement sequence were to be repeated, the prediction error would be used to adjust the next prediction so that the visual representation of the motion trajectory and dynamics would be learned and the prediction error would converge to zero.⁴ Since in dance the following movements are usually different, the brain will put a premium on increasing the likelihood of getting the next movement right. It does so by focussing attention on processing the motion stimuli. Interestingly dopamine neurons have also been proposed to play a role in the regulation of attention (Nieoullon, 2002) and could control a ‘nonselective form of attention or arousal, which is dependent on uncertainty and designed to aid the learning of predictive stimuli and actions’ (Fiorillo *et al.*, 2003). Furthermore, if within a sequence of movements the predicted path of a given section *corresponds* to the actual path, the orbitofrontal cortex awards a positive tag, if it *deviates* it awards a negative tag. The almost instant sigh an audience gives out if in a ballet a dancer suddenly falls, a radical deviation from the expected continuation of the movement, may be regarded as the physical manifestation of such a negative tag.

[4] The activity of dopamine neurons has been shown to resemble a class of reinforcement learning algorithms known as temporal difference models, in which prediction errors are used to adjust the model’s parameters (Schultz *et al.*, 1997). What is most interesting in the present context is that the standard temporal difference model can be extended to incorporate internal models, whereby dopamine neurons code for the difference between the actual reward and the reward predicted by a forward model (Suri, 2001). This could, with the emphasis on could, bring the observed activity of dopamine neurons in line with the computational logic of forward models.

Thus in dance there is a double route to pleasure, one operates through the increased allocation of attention and by promoting a general state of arousal if a movement deviates from its predicted path, the other by rewarding the correct prediction of the motion trajectory. It follows that *without* the interplay of correct and incorrect predictions the brain may as it were ‘lose interest’⁵: if the movements are too predictable attention wanes and we feel bored; if they are too erratic and unpredictable there is no positive reinforcement, which ultimately leads the brain to focus attention on something else. Anecdotal evidence for this hypothesis can be gathered both from audience responses and dance reviews.

Now dopamine neurons respond to errors in the prediction of reward, so the question is, where is the reward in watching dance? And how does the above scenario lead to the conscious experience of pleasure? It could be that the mechanisms that evolved to facilitate avoiding and catching moving objects are also activated in the absence of immediate threats or rewards. When pursuing a goal the final reward may only occur after considerable effort and so the brain may have evolved a motivational mechanism, which signals to the person whether he is on or off track, analogous to the childhood pastime whereby the distance from a hidden object is indicated by ‘cold’, ‘warm’ and ‘hot’. There may also be an evolutionary advantage in correctly predicting the motion trajectory of a moving target (think of trying to hit it or having to avoid it). Even though this, of course, is only speculative, it means that correctly predicting the unfolding of a movement is by its very nature rewarding: after all, how could doing something *wrong* be rewarding?⁶

Everyday experience tells us that there is an asymmetry between positive and negative tags: we are not thrilled every time our perceptual expectations are met, even though we tend to be surprised if they aren’t. On the other hand, we can ascribe a goal to almost any movement, for example which of two cars will reach the traffic lights first, and rejoice if our prediction is correct. Thus it appears that the emotional tag, when juxtaposed to a goal, gives rise to a feeling of pleasure or frustration, which is consistent with the distinction between emotions and feelings put forth by Damasio (1994; 2001). An emotion according to Damasio is ‘a patterned collection of chemical and neural responses that is produced by the brain when it detects the presence of an emotionally competent stimulus’ whereas feelings are ‘the mental representation of the physiological changes that characterize emotions’ in juxtaposition to the mental images that caused them (Damasio, 1994; 2001). This may also explain why we can be puzzled by our own emotions, for instance, when for the first time in our life, we attend a dance performance. The act of going to a theatre to watch someone perform a series of movements may be enough to establish the sort of goal that is a necessary but not sufficient condition for deriving pleasure from watching movement. Indeed, as I myself have witnessed, the same people who will cheer if a dancer performs on

[5] Properly speaking it is the person who loses interest.

[6] I would like to thank Ricarda Schubotz for drawing my attention to this possible explanation.

stage, will ignore her if she performs on the street in front of the theatre, an artistic and behavioural experiment I one day hope to formalize.

The idea that the elicitation, undermining and fulfilment of expectations underlie our affective response to dynamic stimuli is well established in music theory (e.g., Meyer, 1956; Tramo, 2001) and has also been proposed as a possible explanation for humour (Deacon, 1997; Goel & Dolan, 2001). Interestingly a recent fMRI study investigating the neural correlates of listening to Western tonal music showed a similar network of activation as has been hypothesized here, comprising the precentral gyrus (BA 6), inferior frontal gyrus (BA 44), the cerebellum, all three of which may be associated with perceptual prediction, and the orbitofrontal cortex (BA 11), in addition to regions associated with auditory processing (Janata *et al.*, 2002). A PET study whereby neural activity was measured as subjects listened to pre-selected music which elicited an intense emotional response, often referred to as 'chills' or 'shivers-down-the-spine', yielded increased activity in the ventral striatum and midbrain, both sources of dopaminergic signals, the orbitofrontal cortex, the medial supplementary motor area (BA 6), the insula and the cerebellum (Blood & Zatorre, 2001). These studies therefore not only add to the hypothesis put forth here, they also suggest that one reason music and dance go together so well is that both stimuli share the same neural mechanisms.

With respect to humour, Marc Jeannerod recently gave an interesting interpretation in terms of internal models of why we laugh when we see a clown pretending to make a huge effort to lift a seemingly heavy object, fall on his back. 'We laugh', according to Jeannerod, 'because we have created in ourselves an expectation by simulating the effort of the clown, and we see something that is very different from the expectation. The effect we see is at discrepancy with respect to our internal model, and this is the source of comedy' (Gallagher & Jeannerod, 2002).

IX: The Beautiful and the Sublime

The second hypothesis has a remarkable resemblance with the aesthetic theory of the German philosopher Immanuel Kant (1724–1804). In his analysis of aesthetic judgment Kant draws a distinction between the beautiful and the sublime. Beauty, according to Kant, is the feeling we experience and subsequently endow upon the object of our experience, when we discover a harmonious order, whether in art or in nature, that appeals to the mind's own drive towards creating order. The sublime also refers to a feeling, or perhaps better, a state of mind, but differs quite markedly from the beautiful in that it is characterized by disorder and internal conflict. Faced with an immense object, a skyscraper or a Boeing 747, or a powerful phenomenon like a hurricane, the faculty of imagination, in Kantian terms, is overwhelmed, unable to form an adequate representation of the phenomenon at hand. This in itself would not be much of a problem if it were not for the faculty of reason, which demands that every object be captured in its totality. It is at this moment of conflict that, again in Kantian terms, the subject realizes that even though it cannot represent this grand object, it can conceive of it as such. That is, the subject



Figure 6. Before the brain has figured out what it sees, the dancers have already moved into a different body configuration. What remains is the memory of something seemingly impossible, here captured on a photo. Notice also the symmetry and extension of lines in the body. This is what, in combination with the fluidity and effortlessness with which the movements are performed, creates a sense of beauty, the virtuosity of the positions and movements fills us with awe and keeps our attention span at peak level. At the back of the stage a mirror doubled the image of the dancers. Jiri Kylián, *Click–Pause–Silence* (2001). Dancers: Stefan Zeromski and Elke Schepers. Photo: © Joris-Jan Bos.

becomes aware of the ‘presence’ of something that exceeds ‘representation’. The sublime is the feeling which accompanies the resolution of this conflict. In a more contemporary terminology we could say that the sublime refers to a moment of intense awareness, following an initial moment of disorientation, during which attention peaks and the self is filled with awe.

It is this feeling or state of mind that can be said to characterize the thrill of watching dance. It is triggered by the failure of the brain to correctly predict the unfolding of a movement sequence and maintained by its effort, through increased attention, to keep up with the movement.⁷

Following the same logic we can also account for beauty, which may be defined as the feeling that arises when the movement trajectory as simulated by the brain, and the actual perceived movement as it unfolds in front of our eyes, coincide. In the event of human motion, this feeling is intensified if the perceived movement is performed seemingly without effort (Figure 6).

It follows that slow and fluid movements are more likely to be considered beautiful than fast, jerky movements. This prediction appears to agree

[7] Surprisingly it is not only neural processing delays that pose a challenge to the perception of (fast) moving objects, the human brain also takes a long time to respond to *slow* visual target motion (Kawakami *et al.*, 2002), possibly because it requires increased attention.

remarkably well with audience responses and dance reviews, although of course familiarity with a particular style or movement aesthetic influences the ability to predict the unfolding of movements, as can be concluded from the above. Here is, for instance, what one dance critic wrote when *Firsttext*, a ballet by William Forsythe, was first performed in London at the Royal Ballet in 1995.

[the dancers] have come up with astonishing ways of coordinating their limbs and timing their interconnections — but they are no match for Sylvie Guillem. She has the reactions of a racing driver, the hyper-agility of a computer-generated figure: hardly a pretty sight, but we're not here to watch pretty (Parry, 1995; my emphasis).

Within a proper conceptual framework the feelings experienced when watching dance can thus be called 'aesthetic'. It should be emphasized though that the distinction between the beautiful and the sublime made here is purely conceptual, and that actual experience is a mixture of a variety of feelings. The beautiful and the sublime are best seen as two moments of an otherwise indeterminate feeling or experience. Just how indeterminate and conflicting aesthetic experience can be is exemplified by the many words we use to describe our feelings, or indeed our struggle to find the words that carry exactly the right subtleties. This does not attest to the inadequacy of language, but rather to the complexity of the feelings involved.

XI: From Perception to Principles of Aesthetic Experience

Movement proper is only one aspect of dance and for a complete picture we will also have to look into other features of the visual system than motion processing. In their seminal paper, *The science of art: A neurological theory of aesthetic experience*, Ramachandran and Hirstein (1999) introduced eight, as they claim universal, laws of aesthetic experience. In short these laws are: enhancement of features that deviate from average; grouping of related features; isolation of a particular visual clue; contrasting of segregated features; a dislike of unnatural perspectives; perceptual problem solving, which refers to the pleasure the brain takes in deciphering ambiguous scenes; metaphor; and symmetry. The elicitation and resolution of expectations can be considered a principle specific to dance, music and cinema. Ramachandran and Hirstein continue where Rudolf Arnheim, in *Art and Visual Perception. A Psychology of the Creative Eye*, first published in 1954, had stopped, providing it with the neurobiological foundations made possible by recent advances in cognitive neuroscience.

The main law or aesthetic principle, according to Ramachandran and Hirstein, is what they call a peak-shift effect. By accentuating traits that are otherwise considered to be distinctive, perception can be intensified. What are characteristic features of women? Breasts, hips and waists. And thus, from Indian art to cartoons, manga and computer games such as Tomb Raider, we find women with large breasts, tight waists and pronounced hips. The visual system immediately recognizes these features as belonging to a woman and, because of the exaggeration, gives off a quicker and stronger than usual response. One problem with the peak-shift effect as defined by Ramachandran and Hirstein is that

it may be difficult to apply to landscapes and still lives or the work of artists like Rogier van der Weyden. Another problem is that, as Wittgenstein (1953) showed in his *Philosophical Investigations*, it is at least doubtful whether there is such a thing as an essence or an essential feature. Rather than saying that an artist emphasizes essential features, I would therefore like to suggest that he emphasizes *some* features. Whether they are essential or not is irrelevant, they *become* essential in his work. Art is leaving out and emphasizing what remains, hoping that what is left is essential and says something definite, albeit fleetingly. Following this line of thought, dance can be seen as a reverse-engineered peak-shift effect in human movement perception.

The second principle suggested by Ramachandran and Hirstein concerns the grouping of related features. The brain constantly searches for patterns, structures and other regularities in the environment. Since patterns tend to signal an object or an underlying regularity that the brain can use to its advantage, it pays to be apt at recognizing patterns, even if from time to time it means being lured into seeing things that aren't there. It follows that by adding structure and pattern an artist can please the viewer or audience. The frame acceleration in the movie *Koyaanisqatsi* (1983), for instance, revealed the implicit patterns in traffic. In dance synchronizing the movements of limbs belonging to different bodies teases the brain into seeing a kind of moving hyperbody. Having patterns evolve in time creates tension and suspense, both synonymous with anticipation. Consequently it may not be necessary to perfectly organize everything in a ballet, since the brain of the observer will do part of the job all by itself. However, as in *La Bayadère* or Balanchine's *Symphony in Three Movements*, razor-sharp and perfectly synchronized lines create a peak-shift effect in pattern perception, at which Ramachandran and Hirstein (1999) and Ramachandran (2001) also hint.⁸

As to the other principles introduced by Ramachandran and Hirstein, symmetry of course is a principle that is very popular, both in classical ballet and



Figure 7.

Grouping and contrast. Count with me: group vs. individual, sitting vs. standing, front vs. back stage, hat vs. bare head. The scene and its subsequent unfolding are perfectly composed. Pina Bausch, *Viktor* (1986).

Photo: © Jochen Viehoff.

[8] I disagree with Ramachandran (2001) that introducing a postural peak-shift in a point-light display would create a stronger response than real movement and be more pleasing to watch. As argued above, point-light displays show how little information is needed to recognize biological motion. Enhancing the outcome of this process of subtraction is not necessarily a postural peak-shift. Distorting the point-light display may even make the movements more difficult to observe.

modern dance, whereas contrast can be achieved by the opposition of a group and an individual, male and female, left and right, front and back, global movements involving the whole body and local movements confined to one limb, etc. It should be noted that none of these principles specify how they are to be applied. Apart from that, the application of one principle may coincidentally



Figure 8.

Symmetry and perceptual problem solving. How do they do it? Notice also how arms and legs align and extend into space. Jirí Kylián, *Dreamtime* (1983). Dancers: Gaby Baars, Elke Schepers and Johan Inger.

Photo: © Dirk Buwalda.

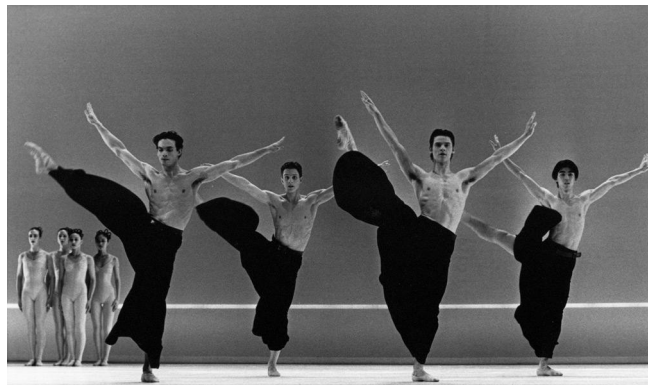


Figure 9.

Grouping, symmetry, contrast. Hans van Manen, *Große Fuge* (1971). Dancers: Netherlands Dance Theatre 2.

Photo: © Joris-Jan Bos.

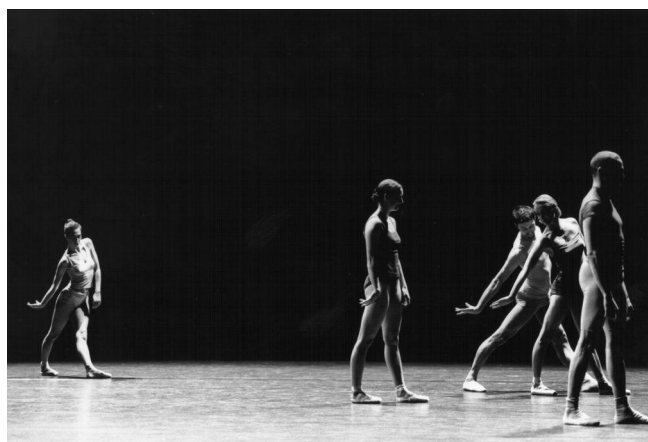


Figure 10.

Grouping in combination with isolation of a particular visual clue. The photographer clicked at the right moment, but the fact that he could make the photo means that the moment was already implicated by the choreographer. William Forsythe, *Workwithinwork* (1998). Dancers: Ballett Frankfurt.

Photo: © Dieter Schwer.

implicate another, which is why even a formal analysis like this remains ambiguous as to what produces which effect to what extent (Figures 7–10).

XII: Conclusion. The Nature of Dance and Choreography?

The feelings we experience when watching dance are the product of a myriad of sensory, cognitive and emotional brain processes. As such they are not accidental but depend on the properties of the brain processes involved in the analysis of sensory stimuli and on the interaction of expectations, associations and personal preferences as laid down in the brain. The present analysis has been limited to only one aspect, that of sensory processing, which itself has been largely narrowed down to one feature. Nothing was said about the functional organization of visual motion processing areas MT and MST in relation to dance, which many will no doubt see as a grave omission. However, I would be happy if as a result of the present article others will be encouraged to correct my errors and omissions.

In so far as sensory processing is concerned there is no difference between an audience watching the finished work and a choreographer watching a work in progress. A choreographer will continue adjusting a piece until every aspect has been fine-tuned to its desired perceptual and emotional effect. The feelings experienced by the audience are therefore in part prefigured by the choreographer. From this it follows that the feelings embedded in a choreography can be regarded as a function of the properties of the brain mechanisms that give rise to these feelings. I would therefore like to suggest that what is composed in a choreography is at once the material — movement — and the sensation it entails, first and foremost a sensation of movement, but extending to other feelings, events and contingencies.⁹ Choreography could thus be defined as the two-way merger of movement and sensation, whereby movement passes into sensation and vice versa. When creating or rehearsing a ballet both choreographer and dancers are as much spectator as they are author and composer. It may be said that what are exercised during rehearsals are movements, but they are exercised to learn the moves as much as to craft the sensations they entail. The art of dancing is as much ‘moving’ as it is knowing the effect a movement sequence has on the

[9] The philosophically inclined reader may see in this hypothesis the resonance of what French philosophers Gilles Deleuze (1925–1995) and Félix Guattari (1930–1992) in *What is Philosophy?* argue is the aim of art, ‘by means of the material, to wrest the percept from perceptions of objects and the states of a perceiving subject, to wrest the affect from affections as the transition from one state to another: to extract a bloc of sensations, a pure being of sensations.’ (Deleuze & Guattari, 1994). Their notion of percept is somewhat idiosyncratic and differs from its common usage in cognitive neuroscience. For Deleuze and Guattari, percepts are no longer perceptions, any more than affects are feelings or affections. ‘They are independent of a state of those who experience them’ (Deleuze & Guattari, 1994), they have an existence of and in themselves. What Deleuze and Guattari are trying to say is that the artist has enveloped into the work of art the perceptual and emotional effect it has on the observer. Why are we moved, thrilled or delighted by a ballet, a novel or a movie? We are because what is caught and preserved in a work of art is not only an act or a situation, but also the emotional affect it entails. The interested reader is also referred to *Les Muses* (1994) by the French philosopher Jean-Luc Nancy who argues that a work of art opens up a realm of perceptual qualities beyond the traditional definition of the senses. For instance music is more than ‘sound’ and encompasses such qualities as melody, rhythm, timbre, tonality, consonance, dissonance and chroma.

observer. It is knowing where to put an accent, which phrase to emphasize, when to accelerate or when to release. Most of this knowledge is implicit and dancers like to refer to it as 'the body's knowledge', but this is just metaphor, it all resides in the brain. It encompasses the principles of perception and motor control and what is summed up by experience, the product of years of training, itself shaped by tradition, that is, the choices and aesthetic preferences of past generations.

In this article I have attempted to make explicit some of the implicit principles that govern the perception of dance and thereby its creation. Perception, of course, is only the springboard leading up to the judgement involved in creating a work of dance. Nonetheless a better understanding of the brain mechanisms involved in perceiving dance may help dancers and choreographers in fine-tuning their material to its perceptual effect, after all, this is what they already do, implicitly.

What is true for dance may also hold for cognitive neuroscience. As cognitive neuroscientists probe deeper into the neural mechanisms for recognizing human movement, they devise ever more complex and subtler motion stimuli. Effectively this means *choreographing* appropriate movement sequences. A meeting of cognitive neuroscience and choreography could therefore tell us more about both perception and dance.

In my own work I try to translate what I have here referred to as 'principles of perception' into techniques dancers can use when they are improvising (Hagendoorn, 2003). One such technique is based on the principles of a mechanism not discussed here: attention. Movements can be distinguished into *global* movements involving the whole body or an arm or leg and *local* movements involving a hand, shoulder or finger. Now whatever is global or local depends to a large extent on the preceding and subsequent movements. By switching between global and local movements a dancer can bring structure into her dancing and 'expand' or 'contract' the attention of the audience into space or onto a focal point. Indeed one could say that this is what choreographers do: they compose movements such that they draw and maintain attention. Several other of my improvisation techniques address the tendency of the brain to extrapolate a movement. Knowing this tendency a dancer can consciously play with it by either continuing a movement into its 'natural' or 'most likely' direction or by what one of my dancers once called 'going against the logic of the movement'. A simple example is to undo a body configuration not by withdrawing or re-moving the limb that gave rise to it, but by moving another limb. If this sounds complicated just stick your right arm between your legs and instead of removing your arm move your right leg around your arm.¹⁰ Practice these techniques and surprise your friends and colleagues at the next party you attend.

The real test for any theory is whether it explains existing and predicts new experimental findings. In the present case these 'experimental findings' take the shape of ballets and dance performances. The problem with 'explaining' why something is 'good', or is generally considered as such, even when concentrating

[10] Examples can be found on my website, <http://www.ivarhagendoorn.com>.



Figure 11

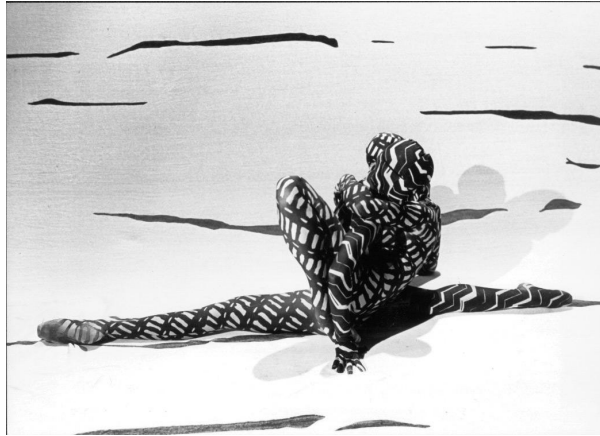


Figure 12

Figures 11 and 12. Find the dancer(s). Great photos, but on stage costumes of dancers and background merge, as they do in these stills, making it difficult to discern the movement. This, of course, was the original concept, but it worked much better than intended. Ed Wubbe, *Perfect skin*. (1993). Dancers: Charlotte Baines, Mariëlle de Jong and Rinus Sprong (l). Mariëlle de Jong and Rinus Sprong (r). Photo: © Hans Gerritsen.

on perceptual effects, is that there may be several competing and equally valid explanations. This follows from the fact that the aesthetic principles mentioned above can only be isolated in theory, in practice some or all combine and reinforce each other, as the illustrations show. An interesting aspect of the present account is that it also explains why some things *don't* work (e.g., Figures 11 and 12).

But, as I once heard a voice say in *The Vile Parody of Address*, a ballet by William Forsythe, 'Despite what I keep saying it doesn't have to be this way'.

Acknowledgements

I would like to thank William Forsythe, Michael Arbib and Ricarda Schubotz for many thought-provoking discussions about dance, the brain and aesthetic experience, and Sarah-Jayne Blakemore and the anonymous referees for their comments on an earlier version of this article. I would also like to thank the dancers of the Frankfurt Ballet, both past and present, for their friendship and hospitality as well as the dancers I myself have had the pleasure of working with, especially Andrea Mitschke, Raphaëlle Delaunay and Ester Natzijl.

References

- Anderson, A.K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D.G., Glover, G. *et al.* (2003), 'Dissociated neural representations of intensity and valence in human olfaction', *Nature Neuroscience* **6**, pp. 196–202.
- Ando, H. (2002), 'Human Brain Regions Involved in Visual Motion Prediction', *NeuroImage* S20054.

- Arnheim, R. (1974), *Art and Visual Perception. A Psychology of the Creative Eye. The new version* (Berkeley, CA: University of California Press).
- Beardworth, T., Bukner, T. (1981), 'The ability to recognize oneself from a video recording of one's movement without seeing one's body', *Bulletin of the Psychonomic Society* **18**, pp. 19–22.
- Beintema, J.A., Lappe, M. (2002), 'Perception of biological motion without local image motion', *Proceedings of the National Academy of Science USA* **99**, pp. 5661–3.
- Berry, M.J., Brivanlou, I.H., Jordan, Th.A., Meister, M. (1999), 'Anticipation of moving stimuli by the retina', *Nature* **398**, pp. 334–38.
- Berthoz, A. (2000), *The brain's sense of movement* (Cambridge, MA: Harvard University Press).
- Blakemore, S.-J., Decety, J. (2001), 'From the perception of action to the understanding of intention', *Nature Reviews Neuroscience* **2**, pp. 561–7.
- Blood, A.J., Zatorre, R.J., Bermudez, P., Evans, A.C. (1999), 'Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions', *Nature Neuroscience* **2**, pp. 382–7.
- Blood, A., Zatorre, R.J. (2001), 'Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion', *Proceedings of the National Academy of Sciences* **98**, pp. 11818–23.
- Bonda, E., Petrides, M., Ostry, D., Evans, A. (1996), 'Specific involvement of human parietal systems and the amygdala in the perception of biological motion', *The Journal of Neuroscience* **16**, pp. 3737–44.
- Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J.C., Lenzi, G.L. (2003), 'Neural mechanisms for empathy in humans: A relay from neural systems for imitation to limbic areas', *Proceedings of the National Academy of Sciences USA*, early edition.
- Chaminade, Th., Meary, D., Orliaguet, J.-P., Decety, J. (2001), 'Is perceptual anticipation motor simulation? A PET study', *NeuroReport* **12**, pp. 3669–74.
- Damasio, A. (1994), *Descartes' Error. Emotion, Reason and the Human Brain* (New York: Avon).
- Damasio, A. (2001), 'Fundamental feelings', *Nature* **413**, p. 781.
- Dawson, M.R.W., Pylyshyn, Z.W. (1988), 'Natural constraints on apparent motion', in: Pylyshyn, Z.W. (Ed.), *Computational processes in human vision* (Norwood, NJ: Ablex), pp. 99–120.
- Deacon, T. (1997), *The symbolic species. The co-evolution of language and the human brain* (London: Penguin).
- Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E. *et al.* (1997), 'Brain activity during observation of actions. Influence of action content and subject's strategy', *Brain* **120**, pp. 1763–77.
- Decety, J., Grèzes, J. (1999), 'Neural mechanisms subserving the perception of human actions', *Trends in Cognitive Sciences* **3**, pp. 172–8.
- De Duve, Th. (1996), *Kant after Duchamp* (Cambridge MA: MIT Press).
- Deleuze, G., Guattari, F. (1994), *What is Philosophy?* [transl. H. Tomlinson and G. Burchell] (New York: Columbia University Press).
- Dittrich, W.H., Troscianko T., Lea, S.E., Morgan, D. (1996), 'Perception of emotion from dynamic point-light displays represented in dance', *Perception* **25**, pp. 727–38.
- Engel, A.K., Fries, P., Singer, W. (2001), 'Dynamic predictions: oscillations and synchrony in top-down processing', *Nature Reviews Neuroscience* **2**, pp. 704–16.
- Fadiga, L., Fogassi, L., Pavesi, G., Rizzolatti, G. (1995), 'Motor facilitation during action observation: a magnetic stimulation study', *Journal of Neurophysiology* **73**, pp. 2608–11.
- Fiorillo, C.D., Tobler, P.N., Schultz, W. (2003), 'Discrete coding of reward probability and uncertainty by dopamine neurons', *Science* **299**, pp. 1898–902.
- Freyd, J. (1983), 'The mental representation of movement when static stimuli are viewed', *Perception and Psychophysics* **33**, pp. 575–81.
- Gallagher, S., Jeannerod, M. (2002), 'From action to interaction', *Journal of Consciousness Studies* **9**, pp. *****.
- Gallese, V. (2002), 'The Shared Manifold Hypothesis', *Journal of Consciousness Studies* **8**, pp. 33–50.
- Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G. (1996), 'Action recognition in the premotor cortex', *Brain* **119**, pp. 593–609.
- Goel V., Dolan R.J. (2001), 'The functional anatomy of humor: segregating cognitive and affective components', *Nature Neuroscience* **4**, pp. 237–8.
- Grèzes, J., Costes, N., Decety, J. (1998), 'Top-down effect of strategy on the perception of human biological motion: a PET investigation', *Cognitive Neuropsychology* **15**, pp. 553–82.
- Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, Ch., Segebarth, Ch., Decety, J. (2001), 'Does perception of motion rely on specific brain regions?', *NeuroImage* **13**, pp. 775–85.
- Grossman, E.D., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G. *et al.* (2000), 'Brain areas involved in perception of biological motion', *Journal of Cognitive Neuroscience* **12**, pp. 711–20.
- Grossman, E.D., Blake, R. (2002), 'Brain areas active during visual perception of biological motion', *Neuron* **35**, pp. 1167–75.

- Hagendoorn, I.G. (2003), 'Cognitive dance improvisation. How study of the motor system can inspire dance (and vice versa)', *Leonardo* **36**, pp. 221–7.
- Haueisen, J., Knosche, T.R. (2001), 'Involuntary motor activity in pianists evoked by music perception', *Journal of Cognitive Neuroscience* **13**, pp. 786–92.
- Heberlein, A.S., Adolphs, R., Tranel, D., Kemmerer, D., Anderson, S., Damasio, A. (1998), 'Impaired attribution of social meanings to abstract dynamic visual patterns following damage to the amygdala', *Society for Neuroscience Abstracts* **24**, p. 1176.
- Heider, F., Simmel, M. (1944), 'An experimental study of apparent behavior', *American Journal of Psychology* **57**, pp. 243–9.
- Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., Mazziotta, J.C. (2003), 'The essential role of Broca's area in imitation', *European Journal of Neuroscience* **17**, pp. 1123–8.
- Howard, R.J., Brammer, M., Wright, I., Woodruff, P.W., Bullmore, E.T., Zeki, S. (1996), 'A direct demonstration of functional specialization within motion-related visual and auditory cortex of the human brain', *Current Biology* **6**, pp. 1015–19.
- Huetzel, S.A., Mack, P.B., McCarthy, G. (2002), 'Perceiving patterns in random series: dynamic processing of sequence in prefrontal cortex', *Nature Neuroscience* **5** (5), pp. 485–90.
- Hurley, S., Chater, N. (2004), *Perspectives on Imitation: From Cognitive Neuroscience to Social Science* (Cambridge, MA: MIT Press).
- Iacoboni, M., (2003), 'Understanding others: Imitation, language, empathy', in *Perspectives on Imitation: From Cognitive Neuroscience to Social Science*, ed. Hurley, S., Chater, N. (Cambridge, MA: MIT Press).
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G. (1999), 'Cortical mechanisms of human imitation', *Science*, **286**, pp. 2526–8.
- Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M-C. *et al.* (2001), 'Reafferent copies of imitated actions in the right superior temporal cortex', *Proceedings of the National Academy of Sciences USA*, **98** (24), pp. 13995–9.
- Ione, A. (2001), 'Innovation in art and science. Reply to Semir Zeki', *Trends in Cognitive Sciences* **5**, p. 140.
- Janata, P., Birk, J.L., Van Horn, J.D., Leman, M., Tillmann, B., Bharucha, J.J. (2002), 'The cortical topography of tonal structure underlying Western Music', *Science* **298**, pp. 2167–70.
- Jeannerod, M. (1994), 'The representing brain: Neural correlates of motor intention and imagery', *Behavioral and Brain Sciences* **17**, pp. 187–245.
- Jeannerod, M. (1997), *The Cognitive Neuroscience of Action* (Cambridge, MA: Blackwell).
- Jeannerod, M. (2001), 'Neural simulation of action: A unifying mechanism for motor cognition', *NeuroImage* **14**, pp. S103–9.
- Johansson, G. (1973), 'Visual perception of biological motion and a model for its analysis', *Perception and Psychophysics* **14**, pp. 202–11.
- Kandel, S., Orliaguet J.P., Viviani, P. (2000), 'Perceptual anticipation in handwriting: the role of implicit motor competence', *Perception and Psychophysics* **62**, pp. 706–16.
- Kant, I. (1987), *Critique of Judgment* [transl. W.S. Pluhar] (Indianapolis: Hackett).
- Kawakami, O., Kaneoke, Y., Maruyama, K., Kakigi, R., Okada, T., Sadato, N. *et al.* (2002), 'Visual detection of motion speed in humans: spatiotemporal analysis by fMRI and MEG', *Human Brain Mapping* **16**, pp. 104–18.
- Kawato, M. (1999), 'Internal models for motor control and trajectory planning', *Current Opinion in Neurobiology* **9**, pp. 718–27.
- Kawato, M., Furukawa, K., Suzuki, R. (1987), 'A hierarchical neural-network model for control and learning of voluntary movement', *Biological Cybernetics* **57**, pp. 169–85.
- Kohler E., Keysers C., Umiltà M.A., Fogassi L., Gallese V., Rizzolatti G., (2002) 'Hearing sounds, understanding actions: action representation in mirror neurons', *Science* **297**, pp. 846–8.
- Kourtzi, Z., Kanwisher, N. (2000), 'Activation in human MT/MST by static images with implied motion', *Journal of Cognitive Neuroscience* **12**, pp. 48–55.
- Land, M.F., McLeod, P. (2000), 'From eye movements to actions: how batsmen hit the ball', *Nature Neuroscience* **3**, pp. 1340–5.
- Latto, R., Brain, D., Kelly, B. (2000), 'An oblique effect in aesthetics: Homage to Mondrian', *Perception* **29**, pp. 981–7.
- LeDoux, J. (1996), *The emotional brain. The mysterious underpinnings of emotional life* (New York, Simon & Schuster).
- Manthey, S., Schubotz, R.I., von Cramon, D.Y. (2003), 'Premotor cortex in observing erroneous action: an fMRI study', *Cognitive Brain Research* **15**, pp. 296–307.
- Martin, K.A.C., (2002), 'Microcircuits in visual cortex', *Current Opinion in Neurobiology* **12**, pp. 418–25.
- McBeath, M.K., Shaffer, D.M., Kaiser, M.K. (1995), 'How baseball outfielders determine where to run to catch fly balls', *Science* **268**, pp. 569–73.
- McIntyre, J., Zago, M., Berthoz, A., Lacquaniti, F. (2001), 'Does the brain model Newton's laws?', *Nature Neuroscience* **4**, pp. 693–4.

- McLeod, P., Reed, N., Dienes, Z. (2001), 'What we do not know about how people run to catch a ball', *Journal of Experimental Psychology: Human Perception and Performance* **27**, pp. 1347–55.
- Mehta, B., Schaal, S. (2002), 'Forward models in visuomotor control', *Journal of Neurophysiology* **88**, pp. 942–53.
- Meltzoff, A.N., Prinz, W. (2002), *The imitative mind: Development, evolution and brain bases*. (Cambridge: Cambridge University Press).
- Meyer, L.B. (1956), *Emotion and meaning in music* (Chicago: University of Chicago Press).
- Nancy, J.-L. (1994), *Les muses* (Paris: Galilée).
- Nieoullon, A. (2002), 'Dopamine and the regulation of cognition and attention', *Progress in Neurobiology* **67**, pp. 53–83.
- Nijhawan, R. (1994), 'Motion extrapolation in catching', *Nature* **386**, pp. 256–7.
- Nijhawan, R. (1997), 'Visual decomposition of color through motion extrapolation', *Nature* **386**, pp. 66–9.
- Nijhawan, R. (2002), 'Neural delays, visual motion and the flash-lag effect', *Trends in Cognitive Sciences* **6**, pp. 387–93.
- Nobre, A.C., Coull, J.T., Frith, C.D., Mesulam, M.M. (1999), 'Orbitofrontal cortex is activated during breaches of expectation in tasks of visual attention', *Nature Neuroscience* **2**, pp. 11–12.
- Oram, M.W., Perrett, D.I. (1994), 'Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli', *Journal of Cognitive Neuroscience* **6**, pp. 99–116.
- Orliaguet, J.P., Kandel, S., Boe, L.J. (1997), 'Visual perception of motor anticipation in cursive handwriting: influence of spatial and movement information on the prediction of forthcoming letters', *Perception* **26**, pp. 905–12.
- Parry, J. (1995), 'Out on a limb', *The Observer*, 30 April 1995.
- Pinto, J., Shiffrar, M. (1999), 'Subconfigurations of the human form in the perception of biological motion displays', *Acta Psychologica* **102**, pp. 293–318.
- Ramachandran, V.S. (2001), 'Sharpening up "The Science of Art". An interview with Anthony Freeman', *Journal of Consciousness Studies* **8**, pp. 9–29.
- Ramachandran, V.S., Hirstein, W. (1999), 'The science of art: A neurological theory of aesthetic experience', *Journal of Consciousness Studies* **6**, pp. 15–51.
- Rizzolatti, G., Arbib, M.A. (1998), 'Language within our grasp', *Trends in Neurosciences* **21**, pp. 188–94.
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L. (1996), 'Premotor cortex and the recognition of motor actions', *Cognitive Brain Research* **3**, pp. 131–41.
- Rizzolatti, G., Fogassi, L., Gallese, V. (2001), 'Neurophysiological mechanisms underlying the understanding and imitation of action', *Nature Reviews Neuroscience* **2**, pp. 661–70.
- Robertson, L.C. (2003), 'Binding, spatial attention and perceptual awareness', *Nature Reviews Neuroscience* **4**, pp. 93–102.
- Rolls, E.T. (1999), *The Brain and Emotion* (Oxford: Oxford University Press).
- Schoenfeld, M.A., Noesselt, T., Poggel, D., Tempelmann, C., Hopf, J.M., Woldorff, M.G. et al. (2002), 'Analysis of pathways mediating preserved vision after striate cortex lesions', *Annals of Neurology* **52**, pp. 814–24.
- Schubotz, R.I., von Cramon, D.Y. (2001), 'Functional organization of the lateral premotor cortex: fMRI reveals different regions activated by anticipation of object properties, location and speed', *Cognitive Brain Research* **11**, pp. 97–112.
- Schubotz, R.I., von Cramon, D.Y. (2002a), 'Predicting perceptual events activates corresponding motor schemes in lateral premotor cortex: an fMRI study', *NeuroImage* **15**, pp. 787–96.
- Schubotz, R.I., von Cramon, D.Y. (2002b), 'A blueprint for target motion: fMRI reveals perceived sequential complexity to modulate premotor cortex', *NeuroImage* **16**, pp. 920–35.
- Schultz, W. (2000), 'Multiple reward signals in the brain', *Nature Reviews Neuroscience* **1**, pp. 199–207.
- Schultz, W., Dayan, P., Read Montague, P. (1997), 'A neural substrate of prediction and reward', *Science* **275**, pp. 1593–9.
- Senior, C., Barnes, J., Giampietro, V., Simmons, A., Bullmore, E.T., Brammer, M. et al. (2000), 'The functional neuroanatomy of implicit-motion perception or representational momentum', *Current Biology* **10**, pp. 16–22.
- Servos, Ph., Osu, R., Santi, A., Kawato, M. (2002), 'The neural substrates of biological motion perception: an fMRI study', *Cerebral Cortex* **12**, pp. 772–82.
- Shiffrar, M., Freyd, J.J. (1990), 'Apparent motion of the human body', *Psychological Science* **1**, pp. 257–64.
- Shiffrar, M., Freyd, J.J. (1993), 'Timing and apparent motion path choice with human body photographs', *Psychological Science* **4**, pp. 379–84.
- Suri, R.E. (2001), 'Anticipatory responses of dopamine neurons and cortical neurons reproduced by internal model', *Experimental Brain Research* **140**, pp. 234–40.
- Stevens, J.A., Fonlupt, P., Shiffrar, M., Decety, J. (2000), 'New aspects of motion perception: selective neural coding of apparent human movements', *NeuroReport* **11**, pp. 109–15.
- Tramo, M.J. (2001), 'Music of the hemispheres', *Science* **291**, pp. 54–6.

- Vaina, L.M., Lemay, M., Bienfang, D.C., Choi, A.Y., Nakayama, K. (1990), 'Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: a case study', *Vision Neuroscience* **5**, pp. 353–69.
- Vaina, L.M., Solomon, J., Chowdhury, S., Sinha, P., Belliveau, J.W. (2001), 'Functional neuroanatomy of biological motion perception in humans', *Proceedings of the National Academy of Sciences* **98**, pp. 11656–61.
- Wittgenstein, L. (1953/19993), *Philosophical Investigations* [transl. G.E.M. Anscombe], (New York: Prentice Hall).
- Wolpert, D.M. (1997), 'Computational approaches to motor control', *Trends in Cognitive Sciences* **1**, pp. 209–16.
- Wolpert, D.M., Flanagan, J.R. (2001), 'Motor prediction', *Current Biology* **11**, pp. R729–32.
- Wolpert, D.M., Ghahramani, Z., Jordan, M.I. (1995), 'An internal model for sensorimotor integration', *Science* **269**, pp. 1880–2.
- Wolpert, D.M., Ghahramani, Z., Flanagan, J.R. (2001), 'Perspectives and problems in motor learning', *Trends in Cognitive Sciences* **5**, pp. 487–94.
- Wolpert, D.M., Doya, K., Kawato, M. (2003), 'A unifying computational framework for motor control and social interaction', *Philosophical Transactions of the Royal Society London B* **358**, pp. 593–602.
- Zeki, S. (2001a), 'Artistic Creativity and the Brain', *Science* **293**, pp. 51–2.
- Zeki, S. (2001b), 'Closet reductionists', *Trends in Cognitive Sciences* **5**, pp. 45–6.