THE PERCEPTION OF

BIOLOGICAL MOTION

- UNDER SPECIAL CONSIDERATION

OF THE

TWO VISUAL SYSTEMS FRAMEWORK -

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1 Introduction

The perception of biological motion is – as will be pointed out in this paper – a fascinating instance of the form-from-motion-effect (FFM), as well as part of social cognition. Moreover, perception of biological motion is a paradigmatical case for many other issues in cognitive psychology: It emphasises the reconstructive nature of the visual system, it shows the power of top-down processing and could be of primary importance for the two visual systems framework, which has become widely accepted in cognitive neuroscience in recent years. Furthermore, biological motions are very ecologically valid stimuli and in many respects, the perception of biological motion is quite similar to face perception: Both are stimuli that are physically complex, yet psychologically very important; computational complex, but done with ease and even by young infants suggesting a specially devoted neural machinery for both. The striking similarities and important differences between face perception and perception of biological motion will be addressed later in this paper.

Curiously enough, the scientific research of the perception of biological motion hasn´t received the attention it deserved: The whole field was started relatively late – in 1973 by Johansson and since then, only around 60-70 relevant papers adressing issues relevant to biological motion have been published in total. Also, most major textbooks of psychology and even perception neglect the phenomenon altogether. Considering the potential importance of the study of the perception of biological motion for many fields of psychology, this neglect is most surprising, it´s reasons open to speculation.

This paper serves the purpose of reviewing the most important findings in the field so far and discussing it´s implications in the light of the two visual systems framework. In order to do this, I will give a brief outline of relevant parts of the two visual framework in the next section, before going into details of biological motion perception.

As the study of social cognition is generally on the rise on cognitive neuroscience, I expect that the study of the perception of biological motion becomes far more prominent in the future.
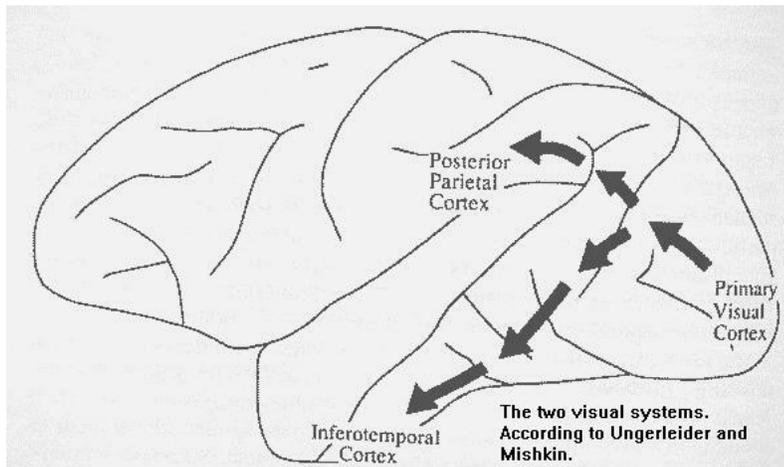
2 The two visual system framework

It would be far beyond the scope of this paper to address all the issues and topics that surround the two visual systems framework in a manner that would be really appropriate and differentiated enough. For our purposes, we have to be content in outlining some of the main milestones in the development of the approach and emphasising the decisive characteristics of these framework while trying to avoid the construction of straw-men positions. After all, the main purpose of this section is be an advanced organizer for the discussion of the issues that follow later. It´s important to keep this limitation in mind when reading the following sections; for a more detailed account, see Goodale & Milner (1995) or Norman (in press).

2.1. Evolution and history of the approach

The initial notion of two separate processing streams in the visual system was brought up by Schneider (Schneider 1967) who studied the visual system of hamsters. He differentiated between object and spatial vision, which he localized in geniculostriate vs. tectofugal systems, emphasising the subcortical systems involved in the perception of hamsters. This initial neuroanatomical findings did not receive too much attention in psychology; the field was essentially still dormant for more than another decade in this respect. This state of affairs changed not until 1982, when Ungerleider & Mishkin (Ungerleider & Mishkin, 1982) summarized their work in the extrastriate visual system of the macaque. This publication had a major impact on psychology, sparked much subsequent research and shaped our basic view of higher visual processing. Their findings about specific and replicable deficits following selective lesions in the temporal and parietal cortex support the notion of a functional division between spatial and object perception in the visual system. The main difference compared to Schneider is, that they localise the functional distinction in late ("high") cortical regions, beginning only after V1 without reference to subcortical distinctions. They also assign a functional role to this anatomically distinct

systems, claiming that the dorsal processing stream (V1 à MT à MST à PPC) subserves spatial perception and object location (the "where"-system), whereas the ventral processing stream (V1 à V4

The two visual systems. According to Ungerleider and Mishkin.

à IT) underlies object perception and recognition (the "what"-system).

The next major breakthrough in the development of the two visual systems approach (after the notions of Ungerleider & Mishkin became widely accepted in psychology) was achieved by Goodale & Milner (Milner & Goodale, 1995). They basically confirm the anatomical distinction between the dorsal and the ventral processing streams of higher visual processing in human and nonhuman primates but re-interpret this distinction in respect to the functional role in vision.

Goodale & Milner review many findings to support their claim, but the main evidence for their re-interpreation derives from neuropsychological findings, carefully analysing the deficits and disorders following selective lesions, especially visual form agnosia, in humans. They suggest that the two systems use in principle the same information, but use it in different ways for different computational goals, the dorsal system (now termed the "how" system) using the visual information to guide on-line action while the ventral system (still termed the "what" system) presumably uses the information for conscious perception and object recognition.

These findings about the anatomical and physiological structure of higher visual processing in humans are now widely accepted and known in psychology. We now have reached a point, where this evidence is used to alter and develop theoretical notions about perception and action, as well as information processing in a more general way. An excellent example of this trend is illustrated by Norman (in press), who tries to resolve old-standing conflicts between notions of ecological and constructivist psychological viewpoints, by mapping them to the workings of these distinct processing streams.

2.2. Evidence supporting the two notion of visual processing streams

The claims by Ungerleider & Mishkin and Goodale & Milner set off much research to test these ideas and look for confirming evidence, as well as their implications.

The distinction between the two visual systems is mainly a separation of functions of the visual system in order to meet the computational needs of different adaptive perceptual goals. The main goals recognised by the two visual system approach deal with object perception (object discrimination, object categorization and object recognition) and interaction with objects in space (for example, reaching, locomotion and grasping). Therefore, according to notions held by most proponents of the two visual systems framework, characteristics commonly suggested to be associated with the dorsal processing stream ("the action system") that facilitate the interactions with objects are:

- An egocentric frame of reference (Body-centered coordinates)

- A high speed of processing (subserved by fast projections, M-fibers)

- Unawareness of the processing (often, conscious awareness even interferes)

- A prospective, anticipatory time-frame (subserving real time online-processing, avoiding lags in actions)

- A generally high temporal sensitivity, vs. low spatial sensitivity (many receptive fields of dorsal areas are restricted to peripheral vision)

- No memory or representations of the actions involved (as the online-processing-demands for actions change rapidly, due to the interaction with the world, generation of representations of object properties is not necessary.)

- The ultimate goal of the processing is the guidance of body movements. ("Action")

Conversely, the computational characteristics attributed to the ventral stream are:

- An allocentric frame of reference (world-centered metrics, facilitating object identification)

- A comparatively low speed of processing (subserved by slower P-fibers).

- Conscious awareness of the processing.

- A retrospective time-frame (taking past experience with the objects into account)

- A generally high spatial vs. a low temporal sensitivity (The receptive fields of neurons in the ventral stream always share a foveal part).

- The existence of stable representations and the involvement of long term memory (Object recognition, Identification and categorisation crucially depends on stable stored memories of object properties and features).

- The ultimate goal of the processing is the recognition of objects. ("Perception")

Obviously, the two processing streams can be essentially described as possessing complementary computational processing characteristics, the respective characteristics are suitable to serve the different goals. These rather sever differences supporting a strong interpretation of the two visual system framework: A view that asserts a two essentially separated visual systems that divide the processing demands for perception and action between them.

In the literature, there is a huge body of neuropsychological and psychophysical evidence as well evidence from neuroimaging studies that confirms the validity of the attributions of the characteristics to the two visual streams as laid out above. Unfortunately, I´m seriously lacking the space to review this evidence in the appropriate systematic manner that I planned to do. Therefore, I restrict myself to the citation of exemplar evidence for the validity of these attributions. Fortunately, the body of evidence in the literature is largely coherent, rendering the citation of multiple evidence mostly redundant.

Evidence for a difference in processing speed between the systems can be found in many visual areas; for example, Cusick (1997) describes the lag of ventral system projections behind projections of the dorsal system to be typically in the range of around 40 ms.

The reality of the **anatomical** distinctions between the systems and the characteristics of their receptive field as well as their projections have been replicated and mapped over and over again (Ungerleider & Haxby, 1994; Milner & Goodale, 1995).

There is an abundance of **neuropsychological** literature on the topic. For example, the phenomena of blindsight, which is the ability to perform some actions like locomotion and tracking better than chance without any conscious awareness of this ability has been interpreted as confirming the distinction between an unconscious action system and a conscious perception system, basically by existence-proof. The classic studies by Milner & Goodale (1995) suggest a double-dissociation between the object-recognition and object-related action. One of their patients (D.F.) had lesions in the ventral stream (temporal lobe) and suffered from visual form agnosia – the patient was drastically impaired in object recognition and tasks of perceptual orientation matching, whereas he was still able to see the object and appropriately interact with it (for example in goal-directed movements like the orientation posting task). Another patient (R.V.) with lesions in the dorsal stream (in the parietal lobe) was able to see objects and to recognise them, but showed just the opposite pattern of impairments in neuropsychological tasks than D.F.

Even **developmental** evidence can be cited in support of the validity of the distinction between two visual systems. Decalages between the performance in perceptual tasks and action performance of young infants was interpreted as reflecting the relative independence of the two visual systems even in development (for a review, see Bertenthal 1996).

Finally, **psychophysical** evidence also largely supports the notion of functional dissociation. Studies observing the exact path and trajectory of goal-directed actions like reaching and grasping show the anticipatory nature of the aperture of the fingers. Similarly, there is a dissociation in the impact of

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common visual illusion like the Titchener circles or the Müller-Lyer-illusion on perceptual, vs. on action performance (for example, see Wraga et. al. 200). As Wraga et. al. point out, even if the effect is not totally dissociated in perception vs. action, the magnitude of the illusions is in general by far larger in perceptual judgements of the stimuli than in measures of action performance, like the aperture of fingers trying to estimate the width of objects (like models of Titchener circles).

These studies are troubled by tricky methodological problems, suggesting alternative explanations for some of them, but in total there is overwhelming evidence in support of the validity of this dissociation (Wraga, et. al. 2000).

2.3. Controversial issues

Of course, matters are rarely so clear-cut in science as suggested by Goodale & Milner (1995) or Ungerleider & Mishkin (1982). It´s not totally clear, if proponents of the two-visual-system approach accurately reviewed the known literature or if the selectively neglected some of the existing evidence for a more complicated state of affairs, in order to achieve progress in the advancement of coherent theories and frameworks. For example, the fate of projections by K-cells to the V1 (Casagrande, 1994) is not entirely clear. Most likely, they terminate in V1 and their signals contribute to both processing streams or modulate the activity in V1. But maybe they don´t and constitute another (minor?) parallel processing system, dealing with different kinds of visual information. The relevance of this finding for the two visual system theory is not easily determined, but it illustrates the point that matters are likely to be more complicated as pointed out by Milner & Goodale (1995). Moreover, even proponents of the two visual systems framework don´t share a common set of beliefs about the nature and functional role of the two visual processing streams. In fact, the two visual systems framework is rather to be thought of as a family of approaches. In most cases, the consensus already ends with the notion that there are two different processing streams. All other issues like the functional role are still highly debated. For

example, Ungerleider & Haxby (1994) reject the functional interpretation by Goodale & Milner and rigorously defend their views about the functions of the different visual systems. The complex nature of processing in the visual system provides opportunity for further differentiation even within the visual streams; as (for example) Jeannerod makes plausible, the dorsal system is far from being a coherent system, but consists of many distinct sub-streams providing special functions. The interpretation of the decalages in infant development as evidence for the two visual systems distinction has also been challenged. For example, Diamond (1991) attributes these to problems in the control of goal-directed action due to an immature prefrontal cortex. Not surprisingly, it´s also contested if the different processing streams are really independent and distinct systems or if the differential role in processing is more a matter of degree, which is more likely. In addition, the discussion about the degree of interactions between the two systems, the amount of crosstalk that is going on at different levels of processing and the question if there is a re-integration of the information provided by the system has been very intense lately – remaining unresolved.

This discussion was further encouraged by major findings in psychology relevant to this issue:

With the discovery of "mirror neurons" in the premotor cortex of the macaque, Rizzolatti (1996) supported previous claims about the importance of **social cognition** for primates, presumably relying on information from both processing streams. Also recently, Bradley et. al. (1998) discovered the neurological basis for the **structure-from-motion**-effect (SFM), the ability to recognize objects on the basis of their motion patterns. Bradley et. al. localize this function in MT, an area of the dorsal processing stream which is therefore obviously involved in object perception - conflicting with claims and predictions made by proponents of the two visual systems hypothesis (see above). The rest of this paper is devoted to the discussion of a fascinating instance of both social cognition and structure from motion at the same time: **The perception of biological motion**. The remarkable ability of the human brain to perceive biological motion is potentially of the highest relevance for the two visual systems hypothesis.

3 The perception of biological motion

This chapter is the heart and core of the entire paper and deals with various aspects of biological motion perception.

3.1. The establishment of the biological motion phenomenon

The first thing in order to show that it is sound to study the perception of biological motion as a separate category is, that biological motion actually constitutes a phenomenon on it's own right – with unique properties that are interesting enough to be worthwhile to take the effort and pain to study them. On first sight, the distinction between the perception of biological motion and the perception of other objects and motions seems to be face-valid, but face-validity is not enough, it won't be convincing to sceptical scientists trying to keep the arsenal of concepts as simple and thrifty as possible or those trying to subsume the perception of biological motion under the framework of other kinds of motion perception. A priori, it is quite possible that the obvious distinction is drawn on superficial grounds, merely reflecting the scientist's tendency for arbitrary classification. Therefore, this section reviews converging evidence that the perception of biological motion actually is a valid conceptual category in it's own right – with connections to other concepts.

3.1.1. The classical Johansson study

Johansson (1973) literally established the study of the perception of biological motion in psychology, as well as coined the term "biological" motion for motion patterns of animal and men. So it makes sense to discuss his classical article first.

According to Johansson (1973), biological motion is characterised by a high degree of complexity in spatiotemporal movement patterns, distinguishing it from other, less complex types of motion. As the perception of forms (contours) and motion are inherently confound in everyday scenes of biological
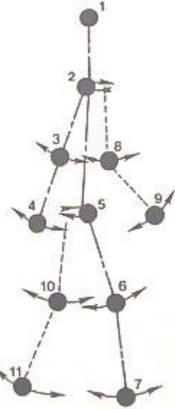
The point-light walker stimulus
(only the dots, no numbers or lines)

motion, Johansson invented his ingenious paradigm to disentangle these components and to study the motion part of "biological motion", which was used in almost all subsequent studies concerned biological motion. In his paradigmatic study, he used stimuli that were generated by attaching lights at the major joints and head of an actor and filming him in a dark room, while he is performing various actions, most prominently walking, which created to the most-widely used stimuli in this field: "The point-light walker", consisting of 11-13 moving dots of light. The motion trajectories of these lights are pendulum-like relative to the joint, establishing the distinctive, non-rigid nature of this motion. Strikingly, if subjects are presented with stimuli like the point-light walker, even this -

Point-light walker and trajectories of individual point-lights
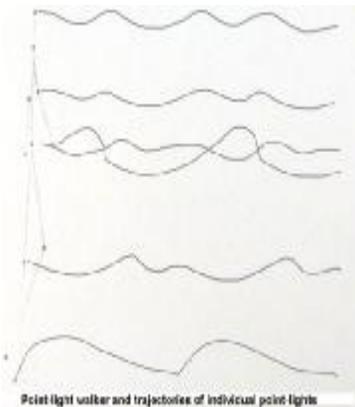
seemingly - impoverished stimulation almost immediately leads to a vivid and compelling experience of the percept of a walking person in the perceiver. Obviously, the information conveyed in the moving dot-pattern was enough and extractable by the visual system to reconstruct, identify and recognise the depicted biological objects. The information seems to be really carried by the motion signal – single frames taken from the motion

stream are totally unidentifiable and meaningless to the observer, linking this phenomenon closely to motion perception. The ability of perceivers to reconstruct the depicted objects without effort reminds
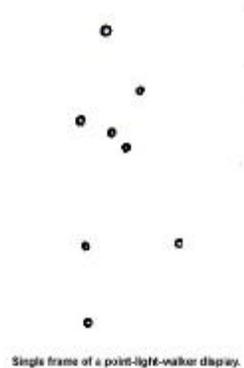
Single frame of a point-light-walker display.

of the classical gestalt principles, where observers are able to recognise simple objects that are defined by very sparse information, suggesting the notion that the brain has an inclination to organise the stimulus-patterns in a certain way. The tendency to perceive animate objects from biological motion can´t be accounted for by the classical principles known to gestalt psychologists,

extending number of known obvious organisational tendencies used by the brain. The ease of the perception of biological motion despite complex stimulus structure raises the question if there is a

specialised neural machinery, providing this ability. The existence of such specialised brain areas would be strong evidence to actually consider biological motion a genuine motion category, therefore, much of the rest of this section is dedicated to the identification of this machinery.

3.1.2. Neuropsychological evidence

In many other cases, the search for brain structures underlying a specific behaviour started with a close look at neuropsychological deficits after lesions. If psychologists can show a double-dissociation of functions accompanying certain distinct lesions, this hints to the existence of different brain structures or pathways generating this behaviour. Despite all the shortcomings of lesion studies like their anecdotical and correlational nature (mostly discussing case studies), it still is a valid approach with the potential to serve as a guidance for more sophisticated methods of analysis like neuroimaging or electrophysiological studies.

The findings in the literature on this topic are no too abundant, but probably enough to consist a case of double-dissociation between the perception of biological motion and the perception of other motions.

A first intriguing finding is reported by Vainy et. al. (1990). Their patient A.F. had lesions in posterior parietal pathways and underwent extensive psychophysical tasks. The performance of the patient was severely impaired in many tasks like the perception of coherent motion in random noise. Yet, the patient was perfectly able to identify objects defined by biological motion and other structure from motion (SFM) effects like a 3-D cylinder by moving dots. Conversely, there is evidence (Cowey & Vaina, 2000) about a patient (AL) with intact form perception and intact motion perception without the ability to recognise biological motion. Unlike motion-blind patients with damage in MT, he still can see the motion, but not what it represents – similar to prosopagnosia. The patient was also impaired in other form-from motion tasks, still seeing the motion but unable to use the visual motion information for recognition. The authors term this disorder "visual motion agnosia" and it is obviously caused by large lesions in the rostral ventral temporal cortex.

This suggests the notion that the reconstruction of structure from motion is not just a serial computational act from early to late dorsal areas (MT, MST, etc.) but could take place in parallel. Maybe other areas are able to extract the information from this dot-patterns in motion.

These general findings are supported by other studies, using point-light-walkers and other stimuli to point out that damage to human MT/V5 (Schenk & Zihl, 1997a) leads to general deficits in perception of coherent motion in the contralesional half-field, while leaving the rest of vision performance intact (featuring the patient LM), whereas damage to the superior parietal cortex and the superior temporal sulcus (STS) leads to impaired FFM and perception of biological motion performance (Schenk & Zihl, 1997b).

These studies suggest that biological motion indeed is an instance of FFM and that it is dissociable from the perception of coherent motion. Still, these studies don´t allow a localisation of the areas involved in biological motion perception – the patients in these studies usually had very large lesions that don´t even allow to narrow the possibilities down to a single lobe.

Research done by McLeod et. al. (1996) doesn´t help to resolve the puzzle: Patients with damage confined to MT were unable to judge movement velocity of single dots, but could still interpret biological motion, yet were unable to detect biological motion in a mask of random dots and were impaired in their performance of FFM-effects for rigid objects. This complex patterns of results suggests that MT is important in the segmentation of the scene, necessary if many objects are present, but that a parallel system surpasses MT to provide FFM and biological motion effects.

Another stream of evidence useful for interpreting the issue at hand is the analysis of neuropsychological disorders in general. Especially autism and Williams Syndrome seem to be relevant This perspective assumes that biological motion perception is not only an instance of FFM, but also places it in the theoretical context of social cognition. Presumably, social cognition abilities are largely independent of other cognitive abilities and it is possible to show a dissociation between autism and Williams Syndrome in the use of information in this theoretical context.

Williams Syndrome is a rare genetic disease that results from certain deletions on chromosome 7. Symptoms are a general moderate mental retardation with an especially strong deficit in spatial tasks, where patients with Williams Syndrome usually score within the 1st percentile. They also suffer from an impaired perception of coherent motion and impaired performance in visually guided action, whereas low level vision and language comprehension are still intact. This pattern of deficits would be consistent with a selectively affected dorsal stream and an intact ventral stream. Interestingly enough, these patients show an excellent performance in the interpretation of biological motion (Jordan, et. al., unpublished), specifically they were perfectly able to perceive the direction of a point-light walker in a noise-mask of random static dots, random dots in motion and yoked motion. They also show no impairment in their social life.

Conversely, autistic subjects suffer from disrupted social functioning, are unable to understand the concept of attitudes and the guiding role of beliefs in other people while the rest of their cognitive functions can be normal or above normal. Also, while their perception of the direction of the gaze of someone else is intact, they are incapable of using this information to attribute intentions and mental mental states in general to this people (Allison et. al., 2000).

The dissociation's shown above emphasise the fascinating nature of the perception of biological motion and suggest distinctive neural machinery underlying this performance. Efforts undertaken to uncover this neural system are discussed in the next section.
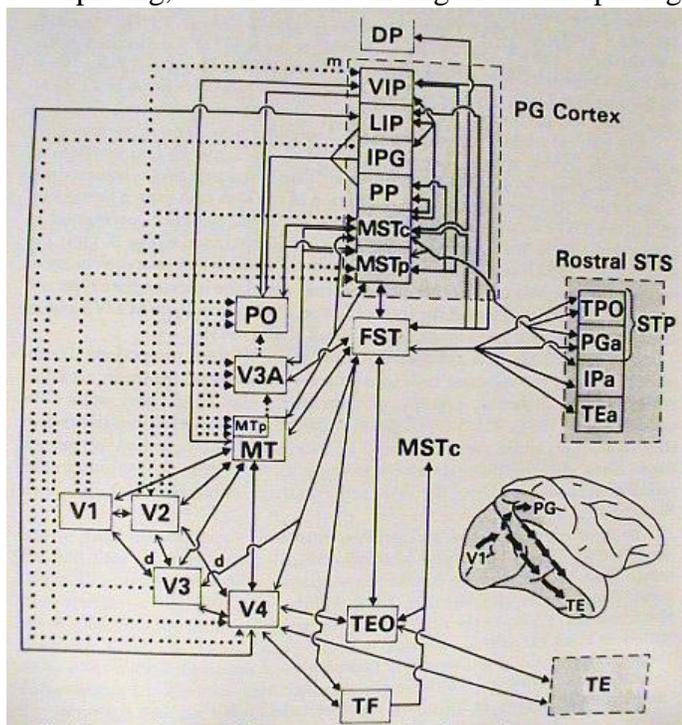

3.1.3. Evidence from neuroimaging studies

Compared to neuropsychological methods, neuroimaging studies using PET or fMRI allow for a more systematic approach and promise a finer-grained analysis of the phenomena, potentially leading to the localisation of the brain areas used in biological motion perception. Generally, it is beneficial to be cautious in interpreting the findings of neuroimaging studies – contemporary studies almost always use the subtractive methods, which doesn´t show absolute activation of areas per se, but differences in

activation between in different conditions. It´s important to keep this in mind – it´s tempting to dichotomise results that are more graded and not so clear-cut in reality, potentially biasing our notions. With this in mind, a quick review of the studies on the phenomena to date reveals one result that is generally agreed upon:

Perception of biological motion in one or another way is always accompanied by activity in the STS (Allison et. al. 2000). Depending on the respective study, the studied motion (whole-body motion as opposed to movement of body parts, etc.) and the respective control conditions – which are extremely important when using the subtractive method – the increased activity varies within STS. This is not surprising, as our understanding of the morphologically complex STS-region in humans or macaque is


premature at best. According to Cusick (1997), this area would be ideally situated anatomically to carry out that kind of analysis and specific structure from motion-effect. It receives projections from both dorsal and ventral processing streams and presumably integrates this information. (see picture). This region in general, but the STP (superior temporal polysensory cortex) in particular was considered as an integrative "association" since a long time. It´s

The famous diagram of the connection of visual areas in macaque cortex

located lateral anterior to MT and anterior to KO and anterior and superior to V5.

It seems that activation in seeing whole-body movement biological motion is especially increased in the posterior STS, as well as the left intraparietal sulcus (Grèzes et. al., 2001). This study used especially careful and differentiated between relatively many different stimulus conditions. For example, activation in the perception of rigid-object motion was usually located posterior to the activation of non-rigid biological motion.

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Moreover, some other studies like Grossman, et. al. (2000) also report – besides the activation in the STS – there was also increased activity in the medial cerebellum. This finding is very intriguing, as the cerebellum is usually associated with the function of timing and coordination of complex movement sequences in the planning of own motor acts. The study also revealed that the implicit contours that are defined by motion in point-light walkers can't fully account for the biological-motion effect. Motion-defined contours activated region KO, but not region STS. Also, the MT/MST-complex is not differentially active during the perception of biological motion, even though the absolute activity in MT is elevated.

Interestingly, perception of whole body movement as well as movement of body parts both activate STS (Allison et. al. 2000). Also, a study conducted by Bonda et. al. (1996) places the perception of biological motion in STS in a broader context: It´s part of an extended system with projections to the amygdala, the orbitofrontal cortex and the prefrontal/premotor cortex (Rizzolatti et. al. 1996). In this PET-study, both reaching for an object and whole-body motion activated the STS, but only the

Location of STS-region in relation to other systems in human cortex
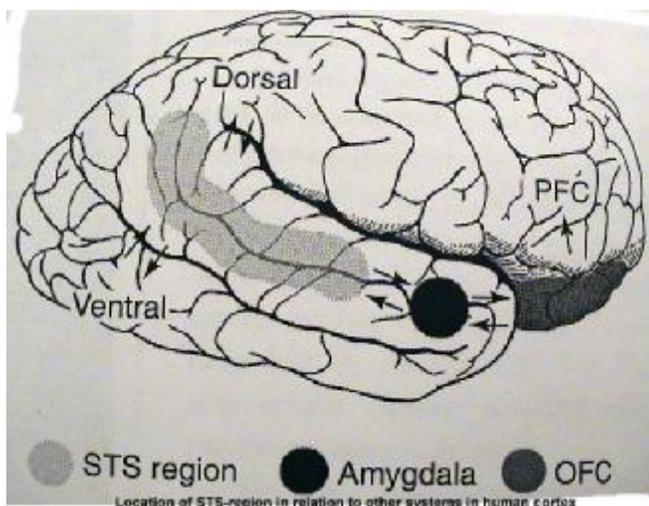
perception of the whole-body motion resulted in an increased activity in the (right) amygdala, while the perception of goal directed hand motion like the reach for an object differentially resulted in increased activity in the left intraparietal sulcus. This hints to the significance and functional role of this system for social interactions or the engagement of the fight/flight-mode as discussed in paragraph 3.1.5. and 3.2. The activation in the amygdala presumably reflects the emotional evaluation of the perceived stimuli with an optional engagement of the limbic system.

It´s also encouraging, that known psychophysical facts about the perception of biological motion (see paragraph 3.2.), like the problems identifying an inverted point-light walker are reflected in the

activation patterns of neuroimaging studies (Grossman, et. al. 2001). The authors found, that the activity in posterior STS is graded: Perception of a canonical point-light walker activates posterior STS more than an inverted point-light walker, which in turn activates the area more than nonbiological motion or patterns of random-dot noise. They also showed that the activity in posterior STS can be increased by imagery of biological motion.

In conclusion, all these findings point to the existence of a specialised machinery which provides the analysis of the kinematics that define biological motion. Most likely, this specialised regions are located in the STS, especially the posterior STS. This adds to the large proportion of neural tissue in the cortex that was already known earlier to be devoted to the analysis of motion information (like MT, MST and KO) in general – reflecting the importance of motion information for the organism.

3.1.4. Evidence from electrophysiological studies

Converging evidence for the role of the STS comes from studies of the STPa in macaques. The results are clear-cut and confirm the neuroimaging findings.

Most of our knowledge about the electrophysiological properties of neurons in STPa in respect to biological motion stimuli derive from studies conducted by Oram & Perrett (Oram & Perrett 1994, Oram & Perrett 1996).

As Oram & Perret emphasise, STPa in the macaque has afferences from both dorsal (from MST) and ventral (from inferior IT) streams and the area as such has a very complex cytoarchitecture (Cusick, 1997). Therefore, it is not surprising, that this molar characteristics are reflected in the tuning properties of individual cells in these areas. What they find is basically, that there are multiple populations of cells intermixed in STPa, some of them sensitive to forms (especially faces and other body parts), some of them tuned for motion direction. Some are tuned for specific combinations of form and direction, for example some cells fire maximally, if presented with the profile of a face facing left and if the direction of motion of this stimulis is in accordance with that (going left). Large numbers of cells (up to 30%) in

STPa were found to have these conjoint response characteristics. In total, over 50% of the neurons in STPa were tuned for some kind of form from motion effect resulting from biological motion perception, differing in preference for body view, body part, direction of motion and type of body motion. It was also shown that the cells in STPa have very large receptive fields like the cells in IT.

The findings of Oram & Perret are very encouraging, suggesting that an integration of form and motion information really takes place on a neural level and that the site is in fact potentially useful for the perception of social and biologically significant actions. Their work is basically an existence proof. The next step ahead in terms of electrophysiology would be to elicit and test the specific algorithm of neural coding that underlies the perception of biological motion. Through the works of Oram & Perret, we know that these cells are potentially capable of doing that. We don´t know yet, how. In order to do that, we also would need to have specific hypothesis about the nature of these algorithms (see paragraph 4).

3.1.5. Embedding biological motion in a larger theoretical framework.

The findings discussed in previous sections of this paper leave little room for reasonable doubt that the perception of biological motion exists as a valid psychological category in terms of brain activation as well as perceptual experience. Even if our understanding of specific questions about the perception of biological motion is still premature, the convergence of findings resulting from many studies using various different methodologies is very encouraging. In this particular section, we turn our attention to the functional role of biological motion perception and the potential relations to larger cognitive systems. Unfortunately, this section will contain much educated speculation – which reflects the current status of research in this field.

Actually, most scientist in the field currently suggest that the perception of biological motion is an instance of social perception, which is the first part of a larger social cognition network like Adolphs (1999, 2001) or Allison et. al. (2000).

By reviewing neuropsychological cases like the classical Phineas Gage, who lost his orbitofrontal cortex in an accident, resulting in disrupted social behavior, while leaving other cognitive functions intact, Adolphs (1999) makes plausible, that social cognition could be a rather modular cognitive system in it´s own right, largely independent of processing of physical stimuli and analysing the complex social environment which is the immediate living space for most human and non-human primate species. This leads to the notion that this system represents living objects quite differently than nonliving objects and that the STS-region is an analogue of the fusiform face area which is dedicated to face processing.

This perspective has the potential of reconciling many psychological findings with evidence provided by cognitive neuroscience. For instance, mirror neurons could underlie the ability for observational learning described by Bandura (Adolphs 2001).

As Adolphs points out, there is a network involving the STS and the fusiform face area(social cognition), the amygdala, orbitofrontal cortex and cingulate cortex (social cognition), leading to social action via the hypothalamus and mirror neurons (Rizzolatti et. al. 1996), carrying out the computational demands of social interactions.

These concepts are supported by Grèzes et. al. (1998) and Decety et. al. (1999) who point out that in order to understand intentions of other organisms and to be able to perform imitational behaviour and observational learning (as primates do), perception and action must be somehow commensurate, sharing coding principles. For Grèzes et. al. (1998), the perception of biological motion is the first step of imitation and imitation is the link between perception and action. Decety et. al. (1999) explicitly states that the perception of biological motion most probably serves communicational purposes, that observers understand the actions of other individuals in terms of the same neural code that they use to produce the same action themselves.

Frith & Frith (1999) put the emphasis on the role of the STS region in mentalizing. They discuss the function of the STS region and the prefrontal cortex in mentalizing activity, tested with paradigms of

imitation and false beliefs. They argue for a brain system that represents mental states analogues to spatial locations and trace these abilities to the macaque, where the neural anatomy is better understood. The upper STS seems to be more sensitive to movements of hands and faces, while the lower STS is specialised for movements as goal-directed actions (e.g. firing only if reaching for an object, not reaching alone).

The most elaborate review of findings in this theoretical context was done by Allison et. al. (2000). The STS is not only active in the analysis of whole-body point-light-walker motion, but also activated by gaze direction (which is an important social cue in most animals, staring is a strong threat signal in macaques), movement of mouth, hands and other limbs, as well as static images of implied goal-directed actions (like reaching for an object vs. reaching alone). Therefore Allison et. al. (2000) claim, that the STS is not only devoted to the analysis of biological motion, but also to all kinds of stimuli that signal attention and allow to understand the own behaviour in the context of the behaviour of others and vice versa which allows to build the complex social hierarchies as done by humans and non-human primates.

In total, these theoretical works suggest two functions for the perception of biological motion: One is rather communicative, allowing the interpretation of the variety of signals that other animals emit, the other is rather mental, allowing the representation of mental states of other animals, taking into account their intentions and beliefs in interpreting and predicting their behaviour.

Both of these functions have a high adaptive value in evolutionary terms and it´s certainly very important for the individual to be able to have this functions. Yet, it´s impossible to decide which of these functions are actually carried out by the neurons in STS. Maybe the one, maybe the other, maybe both.

Actually, the theoretical problems are even worse. The positions that are outlined above don´t take some of the findings about the perception of biological motion into account: For instance, not only social animals like primates perceive biological motion. As Blake (1993) points out, cat´s are perfectly

able to recognise point-light walking cat´s. This seriously challenges all high-level social explanations, as cat´s live most of their lives as solitaires, possibly reducing the social explanation to a just-so story. The findings of Blake can´t be disputed on methodological grounds, in a series of carefully designed experiments, Blake effectively showed that cat´s are indeed sensitive for the kinematic information contained in point-light biological motion display.

Moreover, humans can easily identify a wide variety of animals from point-light displays that are attached to the animals major joints. The fact that humans can reliably recognise point-light-animals as exotic as camels and goats (as shown by Mather & West, 1993) casts serious doubts on the communicative function of the perception of whole-body biological motion.

These findings can be integrated in an hypothesis alternative to the social interpretations (communication and mentalizing), namely fight/flight. For predator or prey, it is crucially important to quickly and reliably detect the presence and identity of other animals, often under circumstances of bad lighting, distracting background textures and occluders (like in the jungle). Therefore, it is presumably very adaptive to be able to use information carried on another channel that distinguishes the living object from the background, using motion as a segmentation and segregation cue, regardless of the special intentions of these animals. Interestingly, many prey animals have adopted strategies to deprive the predator from this crucial information: If approached, they freeze, destroying the structure from motion effect, effectively causing the predator to lose track of the prey in many cases. Also, most predators use this to their advantage when hunting prey: Cat´s directly approach their prey, holding tail and head straight without moving them and are generally moving in a very cautious manner; often, this works out, they are obviously perceived as part of the background by the prey animal and don´t get detected until they are very close. In this view, motion serves as a very powerful segmentation cue used in object recognition and biological motion is just one instance of this more general principle. As pointed out by Andersen & Bradley (1998) and Bradley et. al. (1998) using electrophysiological

methods, even MT is involved in this structure-from-motion effect and definitely serves segmentation purposes, which also has undeniable adaptive value for the organism.

This contrasting hypothesis regarding the adaptive function of the perception of biological movement for the individual is equally valid and can´t be refuted on the basis of currently existing data.

Further studies will have to be made to resolve this question. Preliminarily, I suggest that these hypotheses don´t have to be logically exclusive. Obviously, biological motion consists of several different subclasses, allowing all three functions equally, all of them are processed by the STS, while the interpretation of these processing is done by different subsequent systems (like the prefrontal cortex or the amygdala) in parallel. If this notion is valid, it makes sense to assume that the global whole-body motion is important for detection and identification of other animals, a subset of these (limb-movements) are used in the analysis of actions used for mentalizing and a specific subset of these are further processed for their communicative and signalling content to interpret and convey messages.

3.2. Properties of biological motion perception

This section deals with a rather detailed review of the characteristics of biological motion perception on different levels of analysis as far as they are known to date.

3.2.1. Basic properties and characteristics of biological motion perception

There are some characteristics of biological motion perception that are generally agreed upon, replicable and uncontroversial. I will refer to them as "basic properties" and review them briefly, because there is no room for a broad review in this context, but want to mention them to illustrate some of the amazing and unique features of this fascinating phenomenon. Cited for the respective characteristics are exemplary authors that contributed to this questions, not all that contributed to it.

Defining characteristics (Johansson 1973, Ahlström et. al. 1997): Observers are in general perfectly capable of detecting the presence of a living organism defined by 11 point-lights attached to major joints if in motion. This amazing ability immediately disappears, if observers are presented with single frame displays of the same dot-patterns.

Temporal characteristics (Neri et. al. 1998, Hill & Pollick 2000): The perception of biological motion has interesting temporal characteristics. Most subjects are able to accurately judge the presence of a living object defined by point-light-walker display 200 ms after stimulus onset. If the walker is presented in a mask of random dot-motion noise, identification performance of subjects gets far better with increased presentation time of the stimulus, levelling off only after 3 seconds, indicating a very long temporal integration interval. Other evidence also emphasises the importance of the temporal characteristics in defining biological motion (compared to spatial characteristics): The detection of point-light-walker displays as biological motion strongly deteriorates, if the individual dot-light trajectories are phase-distorted (temporally perturbed). Also, subjects were better able to identify specific persons that they saw depicted as point-light walkers before, if certain sequences of their actions were temporally exaggerated, enhancing the distinctive signal carried in this temporally coded information.

Spatial characteristics (Ahlström et. al.1997, Thornton et. al. 1998): Compared to the temporal characteristics, the spatial information's contained in the display don´t seem to be too crucial. Subjects performance in recognising point-light walkers (even in noise) doesn´t drop much, if the dot-lights are displaced and moved from the major joints to interjoint positions. Changing the spatial frequency of the dots or texturing the dots in a textured background didn´t influence the perception performance. Moreover, in some displays of point-light walkers (those that are derived from filming actors), there are occluders present, defining an implicit contour – potentially causing the effect. Yet, there are possibilities to algorithmically construe point-light walker displays without occluders which seems not to be crucial for the performance of subjects under most viewing conditions.

Action, Sex and Familiarity (Dittrich 1993, Koslowski & Cutting 1978): Subjects aren´t just able to detect the presence of a living object defined by biological motion or judge their direction of movement, they are also capable of recognising specific actions that are depicted by point-light walkers, recognising the sex of the depicted walker and even recognise friends by their gait – emphasising the extreme sensitivity of subjects to biological motion perception and the richness of information that they can reliably extract from these seemingly deprived point-light displays.

Masking-studies (Thornton et. al. 1998, Ahlström et. al. 1997, Bertenthal & Pinto 1994):

Not only can people derive very differentiated information from impoverished point-light walker displays, this perceptual performance is also very robust, suggesting that several different mechanisms might underlie the observed behaviour. Observers judgements of biological motion remained accurate, despite adding static points, adding up to1000 randomly moving dots or adding moving dots that moved in the same direction as the point-light walker. Most disturbing was the introduction of motion noise that consisted of triads of dots, resembling "artifical limbs" and moving in a biological-motion fashion. Subjects were also easily able to perceptually separate several different superimposed point-light walkers at the same-time, canonical or scrambled. The deletion of single dots from the pattern also doesn´t change the vividness of the perception – up to a point: Single dot trajectories taken from a point-light walker display don't give a vivid impression of biological motion. The sensitivity to biological motion increases exponentially with the number of illuminated joints, the detection-slope is far steeper than for the detection of other types of motion.

The apparent robustness of biological motion perception could reflect it´s evolutionary importance; most likely, several different redundant systems contribute to this perception, ensuring proper functioning under adverse perceptual conditions.

Orientation-selectivity (Sumi 1984, Pavlova & Sokolov 2000): As indicated by the masking studies, local motion noise doesn't hamper the vividness of the percept much, decreasing the probability and role of local processing in biological motion perception. This notion is supported by another striking

feature of biological motion perception: Like face-perception, the perception of biological motion is strictly orientation-selective and severely impaired when presented with inverted point-light walkers. As suggested in the research on face-perception, this could reflect the fact that top-down, holistical global processing is taking place (instead of a bottom-up feature analysis).

Luminance (Grossman & Blake, 1999): The apparent effects of luminance on perceptual performance emphasise the affinity of biological motion perception to general structure from motion effects compared to the perception of coherent motion. Under dim-light conditions, the perception of coherent motion is unaffected, while the perception of biological motion and the perception of structure from motion are severely impaired. The reduction of luminance sacrifices spatial resolution for sensitivity in the visual system. As coherent motion involves the integration of motion signals over space and time, whereas SFM and biological motion require spatial and temporal differentiation, this differential effect of reduced luminance on perceptual performances can be expected. This effect also demonstrates, that spatial information is non totally unimportant in biological motion and FFM-effects, as suggested by the findings above.

3.2.2. The role of experience

The perception of biological motion can also be understood as an example of the workings of one of the inherent organisational principles used by the brain in object recognition to make sense of impoverished information. Most of these binding principles were already laid out by the gestalt psychologists. Analogous to those, the tendency to reconstruct point-light displays as moving living organisms can be seen as reflecting this inclination of the brain. This suggests a template-like, innate representation of biological motion properties in specific brain structures justified by the psychological importance of detecting living objects by their movement characteristics, reflecting a biological preparedness for this kind of stimuli. An alternative explanation is that the phenomenon of biological motion perception is just a common structure from motion effect, and the superior detection

capabilities of biological motion over point-light-display of rigid, nonliving objects (Shiffrar, et. al. 1997) can be explained by the excessive experience of the observer with the motion properties of living organisms, a hypothesis Bradley et. al. (1998) would tend to. Again, similar things have been proposed for face perception and object recognition

A resolution of this conflicting explanations over the status of biological motion and the role of experience with the stimulus material would require extensive training studies, where observers are familiarised with point-light displays of non-living objects over a long period of time before testing them. Unfortunately, no such studies have been done so far to specifically decide between this hypotheses in a strict and appropriate way. Fortunately, we can rely on the results of studies on biological motion perception in infants and children to get an idea of the relevance of experience in the perception of biological motion.

These studies suggest that not too much experience is needed to differentially perceive biological motion. As Fox & McDaniel (1982) point out, infants at the age of 2 months are unable to perceive to show a differential sensitivity to biological motion stimuli, while infants at the age of 4 months already are. Capabilities shown at this age are very likely to be largely intrinsic, available to the infant well before the infant is able to locomote. Using habituation paradigms, Bertenthal et. al. (1987) could even find discriminatory effects for biological motion in infants that were only 3 months and ruled out alternative explanations like the total amount of motion present in the stimuli. These results show that the ability to organise moving dots in ways of biological motion isn´t slowly acquired through experience. Still, it remains unclear, why there is a delay of 2 months and   why neonates don´t show perception of biological motion effects – even if some interpret early imitation behavior of the neonate as a reflection of their biological motion perception performance (Meltzoff & Moore, 1983).

It´s also unclear if the infant actually experiences the three-dimensional form that is defined by this motion. Moreover, the performance of these infants in the discrimination of biological motion displays is far from perfect and take a long time to build. The perceptional abilities of children reaches that of

adults only at age 5 (Pavlova et. al., 2001), reflecting the effects of experience with the stimuli or more innate brain-maturing effects. Interestingly, Pavlova et. al. (2001) also emphasise, that 3 year old children weren´t best at the perception of canonical point-light-walker displays – their performance peaked in the perception of point-light displays of dogs. Adults perception of point-light-walkers is far better than that of dogs. This could actually reflect an experience effect, as the canonical walker is not so canonical for small children, as the canonical dogs better fit their own height.

Indisputable, some kind of training is necessary to explain the superior capabilities to detect biological motion. The remaining question is, if the kind of required training is phylogenetic (provided by evolution) or ontogenetic (provided by learning), most probably both – an interaction of prepared structures that provide the innate capability, enriched with specific content acquired through learning.

It´s important to address this issue here, but it would be premature to draw a definite conclusion on the basis of the existing studies until research comes up with more decisive evidence, most likely to be derived from training studies. One studies that used training (of cat´s) shows the explanatory potential of this kind of studies (Blake, 1993): Cat´s were trained to perceive point-light walkers of cat´s. The training had a positive transfer effect on the perception of human point-light walkers, showing that the learning effect isn´t solely based on a particular set of familiar stimuli. Moreover, it was impossible to train the cat´s to differentially respond to patterns of point-light cat´s that moved in an unnatural way, suggesting that this effect doesn´t rely on arbitrary trained stimuli but that the system is prepared to process some types of stimuli more than others – yet clearly, more research is needed on this issue.

3.2.3. Computational considerations of biological motion processing

A basic characteristic of biological motion stimuli is their complex nature: Individual points and their motion trajectories don´t carry information about the shape or the action of the object, neither does the static dot pattern – whereas the dynamic pattern of motion vectors does – requiring the neural integration of these motion vectors in space-time. As illustrated by the masking studies discussed

above, the introduction of masking noise on a local level doesn´t effectively disturb the perceived pattern. Therefore, the neural machinery underlying this ability must be capable of achieving this integration – the neurons that are involved must have large receptive fields like neurons in MT (Bradley et. al., 1998) or STS (Cusick, 1997) and have tuning curves for motion in space-time.

We don´t really know yet, if biological motion is just an instance of the general structure from motion-effect that is presumably carried out by MT (Andersen & Bradley 1998) or if there is more to it, justifying a distinction between biological motion perception and other SFM-effects, with biological motion perception additionally engaging STS. The evidence reviewed in section 3.1. favors the latter interpretation. This distinction could map on the different computational requirements of the processing of rigid vs. nonrigid (biological) structure from motion effects, which are in fact not identical (Pollick, 1997). Moreover, there are other genuine hints that support the notion of the uniqueness of biological motion as pointed out by Shiffrar (1994) and Shiffrar et. al. (1997): The analysis of motion is either local or global. Most motion is undoubtedly perceived and analysed local, therefore subject to the so-called "aperture problem": Local motion behind an aperture is ambiguous, this reflects the situation of neurons with small receptive fields, like in V1. This individual motion-patterns need to be bottom-up
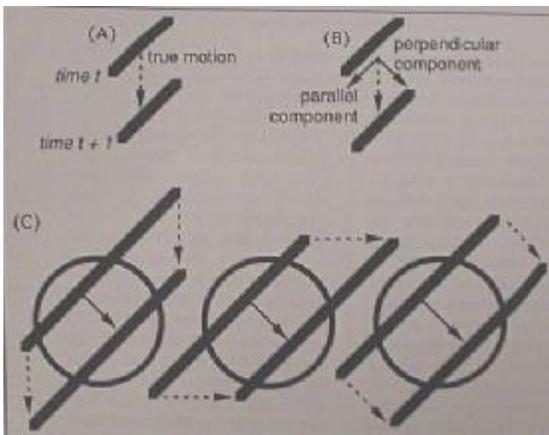
The aperture problem - local motion is inherently ambiguous.

integrated in higher cortical areas like MT. Shiffrar presented subjects with point-light-displays of rigid and non-rigid objects behind apertures (therefore revealing only distinct parts of the stimulus). The results are striking: Only the point-light-walkers were still accurately recognised, all other objects like cars or scissors weren´t recognised behind the apertures, supporting the claim that biological motion perception is processed globally, avoiding the aperture problem, whereas other Form-from-motion processes are obviously subject to the aperture problem.

In addition to that, apparent motion paradigms (Shiffrar, 1994) show that if subjects are presented with consecutive frames, generally they most likely "see" movement along the shortest of all possible paths. This wasn´t the case in depictions of moving people or moving limbs: Subjects perceived movements consistent with biological motion paths, violating the shortest path principle.

These arguments encourage the belief in the unique nature of the biological motion phenomena – but the questions remains: If this is a specific computational task, which information in the spatio-temporal motion pattern can be used by the brain to reconstruct the object from the motion?

Bertenthal & Pinto (1993) specifically address this issue: In general, biological motions are repetitive and well-organized in space-time. The movement of the dots is highly systematic: The dots are moving in a fixed distance, while rotating in a specific depth plane, they move in a pendular fashion attached to hierarchically nested limbs along a vertical axis. The walker also abides to the law of gravity: To optimise the maintenance of a stable centre of gravity, the walker uses dynamic symmetry while walking – the limbs move in alteration and so do the dots that depict that limb.

Still, the complex trajectories of the single dots could be grouped very differently, the relationship between the dots is not unambigious especially in introduced motion noise; Bertenthal & Pinto suggest that the brain uses temporally defined invariants and the constraints that arise from them to disambiguate and reconstruct the connectivity pattern. Specifically, they suggest three constraints:

Frequency entrainment: Two or more oscillators of the same object share the same frequency or period. All limbs of a walker are connected to each other, so the frequencies of all oscillators belonging to the object are synchronised.

Phase locking: Two or more oscillators of the same object remain stable relative to each other in the phase of a motion cycle. Most common are phase relations of 0° and 180°, reflecting the structure of alternating limbs.

Periodic attractors: The motion can be represented as a circle in a phase-plane diagram. Velocity and position repeatedly assume the same values as the movement continues.

Taken together, the information provided by a point-light walker is highly structured in space-time and the brain could use the suggested temporal constraints to disambiguate the stimulus. Indeed, it is not unlikely, that the brain actually uses the dynamic principles by Bertenthal & Pinto to organise the percept. Therefore, this paragraph could inspire and guide future research on these computational issues – we still have no understanding which neural mechanisms actually underlie the perception of biological motion; even if interpreted in the context of the structure from motion effect, which is yet also poorly understood (Andersen & Bradley 1998).

3.3. Implications for the theory of two visual systems

The findings presented by the research on the perception of biological motion pose a serious challenge for the classical model of the two visual systems framework, especially in regard to potential interactions between the two processing streams. The resolution of this challenge could provide enlightening insight in the nature of the visual system and modify as well as qualify the rather coarse two visual systems approach in important respects. Most likely, the processing streams are re-integrated again in the STS-region; the systems are interacting to resolve specific computational problems occurring in social cognition in general and most strikingly in the perception of biological motion in particular. With the rather sparse literature on the perception of biological motion on hand, we have barely established fundamental characteristics of this phenomenon. Therefore, it would be clearly premature to attempt to draw a definitive conclusions about the implications for the two visual systems hypothesis on the basis of available evidence. It seems to be evident that the phenomenon actually exists and provides a worthwhile and useful paradigmatic case for further investigation because of it´s potential implications for our models of perceptual systems in general, as well as our ideas about the relationship of the dorsal and ventral processing streams and the notions about the role of social cognition in the brain in particular.

Even if it´s too early to draw conclusions about the two visual systems framework in general, based on research on biological motion, it´s appropriate to emphasise some more concrete modifications that are suggested by the data on hand.

Most likely, our ideas about representations have to be reframed in light of the evidence about structure from motion and biological motion. Our understanding of stable representations is not very good in the first place, with a high degree of fuzziness and coarse use of language terms in most theories. It´s not unreasonable to claim that the term "representation" is among the most widely (ab)used in all cognitive psychology. Obviously, the dorsal system also seems to be involved in information-representation:

I hereby suggest the notion that the posterior STS (STPa) constitutes a complementary area to IT and the gyrus fusiformis. Like neurons in these areas, neurons in the posterior STS are tuned for the recognition (!) of specific, physically complex, but psychologically relevant stimuli. Obviously, the representations in IT and the gyrus fusiformis are defined in spatial terms, namely form and spatial frequency (texture). Conversely, representations in the posterior STS seem to be defined in terms of spatio-temporal patterns (complex trajectories of motion vectors). This information is most likely to be sufficiently provided by projections from the dorsal system (MT and MST) alone. Maybe these representations are reinforced by projections from the ventral system to other parts of the complex and large STS region, and integrated into more abstract meta-representations of objects. This double-coding could constitute a social-property-space (which would make sense). In any case, some of the representations in STS seem to be defined in terms of space-time, which is probably enough information for most purposes. The orientation-specific performance of the perception of biological motion further supports the similarity between face perception and the perception of biological motion, suggesting the existence of spatiotemporal templates that are matched with the incoming perceptual information. Further research has to determine if this notion is valid by rigorously testing the implications and predictions that arise from it. The fact that these notion arose from the study of biological motion exemplifies the potential relevance of this field for psychological research.

In general, it´s not yet clear if the dorsal system also gives rise to representations, or if the ventral system also processes motion information. Both notions are possible to resolve the structure from motion findings as shown in biological motion perception paradigms and both would imply major modifications of the two visual systems framework, even though were not able to decide between these possibilities yet.

4 Discussion, Summary and Questions for further research

The two visual systems approach has been extremely useful in recent years as a guiding heuristic that sparked much insightful research and organised a lot of empirical findings in an elegant and economical framework. However, the growing interest in phenomena like social cognition in general and biological motion perception in particular suggests that the strong claims made within this framework could be invalid or at least lead to some major revisions and qualifying modifications of the existing models. We can expect these modifications to take place accompanying our growing understanding of this intriguing phenomenon. Hopefully, as more scientists in the field can appreciate the validity and relevance of biological motion perception, this will spark a large number of new studies in the field, rapidly extending and deepening our understanding of the issues at stake.

It is still surprising, that this field has not already gotten more attention in research: Obviously, it´s a separate category of perceptual stimuli, there is localised neuronal machinery devoted to it´s analysis and the computational problems to be solved are unique. Moreover, most details like coding of the phenomena on a neural level are still unknown – Oram & Perrett (1994, 1996) did a mere existence-proof. In addition, this particular field has an amazing integrative potential for many psychological fields such as developmental psychology, social psychology, cognitive psychology, cognitive neuroscience and even the psychology of language.

Furthermore, a better understanding of the perception of biological motion could also facilitate our understanding of the production of biological motion, which is doubtless very important in itself. Some emphasise that these are in fact most likely to be complementary processes (Bertenthal & Pinto 1993). As could be seen in many parts of this review, more research is needed to resolve many of the still debated and fundamental questions that are surrounding this exciting phenomenon. I think, it would be worthwhile to devote much more time and effort to the intriguing study of biological motion perception and therefore, I want to suggest some of the most promising questions that are awaiting to be answered. To obtain new insights and answer old questions, we need future studies that are carefully designed to address them:

It is still unclear, if the perception of biological motion is more an instance of social cognition or more a particular effect of the structure from motion-effect for more adaptive predator/prey interactions. Also, the relationship between social cognition and form-from-motion perception remains unclear.

First findings are encouraging: Interestingly, biological motion perception processed mainly in right STS, an area that can also be activated by the presentation of merely social stimuli (like facial expression) without necessarily involving moving stimuli, suggesting its role in the representation and analysis of social stimuli (Narumoto et. al, 2001).

It´s also unclear, if the STS is an area that ultimately re-integrates information from the dorsal and ventral streams again, or if the STS just happens to be another late parallel system that uses ventral and dorsal information for the special computational demands that arise if an organism interacts in a social space. Related to this, we don´t know much about the role of ventral information in the processing and interpretation of biological motions. It´s possible that the point-light walker methodology underestimates the importance of information of the ventral system by relying solely on motion information. In other words, the effects that were found could be results of methodological artifacts. If we want to know, if this is indeed the case, we need to invent alternative paradigms to assess the perception of biological motion without the sole use of point-light displays. If this would lead to

converging evidence; we would have further compelling evidence about the reality of social representations and would be able to get a more accurate and more general picture of the processes involved in the perception of goal-related biological motion. First findings are encouraging. Depictions of implied actions can obviously lead to motion perception (or motion imagery?)

In a similar fashion, it is not yet totally clear, if perception of whole-body motion and the perception of the motion of body-parts involved in the perception of (implied) action performance is subserved by the same computational processes. Most likely, this is not the case (see above) which again begs the question, what the real difference in the underlying neural architecture involved in the respective processes is.

Many things remain unclear: The always fuzzy neuropsychological evidence should best be reinforced by complementary TMS-studies. The question of innate or learned processing templates in biological motion perception needs to be resolved by extensive training studies. Claims by some theorists that we understand the motion of others in terms of our own motion could be strictly tested by presenting biological motion stimuli that depict impossible motion patterns (like flying humans) and assessing the impact on dependent variables like performance measures or neural firing rates. Similar to this, it would be very interesting to know if the perception of structure from motion by point-light display is far worse for inanimate rigid objects compared to biological motion stimuli. If the performance for biological motion stimuli is far better and independent from training effects, this would suggest the involvement of an additional, more specially devoted neural machinery. No study to date addresses this question in a systematic way.

Finally, most research of the role of STS in social cognition has been done in non-human primates and the mapping of homologue areas in humans are not very advanced yet. Also, one should keep in mind, that the STS is an extremely complex and inhomogeneous area in many ways. It´s unclear, how many different functions are embedded there; narrowing down the function to social cognition or biological motion perception would be premature, given our knowledge to date.

In terms of concrete studies that could and should be done, I suggest that it would be one of the most fascinating studies possible to train a monkey in the perception of biological motion and other displays and to test the specific neural firing patterns of neurons in STPa in response to that. Most likely, these neurons extract the informations that are conveyed in the biological motion pattern that is structured by the constraints pointed out by Bertenthal & Pinto (1993) in a way that makes use of these constraints. Findings like that would be a fascinating major breakthrough in our understanding of the computational capabilities of the human brain.

What should I say more? I think it´s pretty evident that there is much more that we need to know about the perception of biological motion. The field virtually begs for further research. Let´s go for it!

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