Understanding Biological Motion

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Abstract

The ultimate goal of biological motion perception is to be able to *understand* actions so as to provide an answer to the question, "Who did what to whom and why?" This inference capacity enables humans to go beyond the surface appearance of behavior in order to successfully interact with others and with the environment. In addition to its functional importance, understanding biological motion bridges several major fields, including perception, reasoning, and social cognition. However, despite its paramount role in human perception and cognition, only limited progress has so far been made in understanding biological motion. After reviewing the relevant literature, this essay argues that future research needs to identify the contributions of three basic processes involved in understanding biological motion: perception of animacy, causality, and intention. The involvement of these basic processes needs to be investigated both in the typical healthy population as well as in populations with mental disorders, such as autism spectrum disorders and schizophrenia. We also suggest that a productive research approach should focus on more interactive actions of the sort often observed in the natural social environment, rather than solely using the single-actor displays that have been typical in previous work. It is further emphasized that there is a need for a theoretical and computational framework within which these different types of processing can be united. We propose that the predictive coding framework provides a good candidate.

INTRODUCTION

In 1872, in his seminal work demonstrating parallels in the way humans and animals express emotions, Darwin noted that "actions speak louder than pictures when it comes to understanding what others are doing and feeling" (Darwin, 1872). Darwin's claim is supported by the fact that many animal species are sensitive to motion patterns generated by other living organisms, presumably due to the ecological importance of *biological motion*. Superior perception for biological motion manifests itself in two pervasive behavioral characteristics: the robustness of recognizing actions, and sophisticated inference in understanding them, that is, grasping the intentions of actors. In support of the first characteristic, numerous psychophysical studies have

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demonstrated that human observers show an exquisite ability to accurately identify attributes of an actor, such as identity (Cutting & Kozlowski, 1977), emotional state (Dittrich, Troscianko, Lea, & Morgan, 1996), and gender (Kozlowski & Cutting, 1977), even when the stimulus lacks a detailed human body form (e.g., a point-light display consisting of only a few discrete dots representing joint movements). The remarkably rapid, accurate, and robust perception of biological motion has inspired a great deal of research directed at understanding how the visual system achieves this perceptual feat in recognizing actions.

However, the second characteristic—sophisticated inference in understanding biological motion—is arguably more essential for human perception and cognition. In order to successfully interact with others and with the environment, the human mind is equipped with the ability to make inferences that go beyond the surface appearance of behavior. For example, with a brief glance at the crowd in Times Square in New York, you can not only recognize which pedestrians are walking in relaxation and which are running in a hurry but also readily identify people who are interacting with others (e.g., walking together while having a conversation; shaking hands). Furthermore, you can predict other people's actions in the near future (e.g., expecting someone to extend a hand to wave goodbye to a friend). The ultimate goal of biological motion perception, it seems, is to understand and predict actions in which multiple individuals interact, and to make inferences about other individuals' intentions and goals by evaluating their actions.

For several reasons, systematic research on biological motion understanding needs to be pursued with greater vigor. First, the inference capacity of the human visual system exceeds that of the most advanced machine vision. For example, in the investigation of the Boston Marathon bombing case in 2013, extensive video from surveillance camera systems was available, but it was the trained human eye that led to arrests. Hence, understanding how humans make inferences and predictions about actions will doubtlessly play an important role in guiding the development of more advanced machine vision systems.

Second, within the human population, the ability to understand biological motion varies among individuals. Within the first days of life, human newborns show selective preference for biological motion (Simion, Regolin, & Bulf, 2008), supporting the hypothesis that detection of biological motion is an intrinsic capability of the human visual system. However, this evolutionarily basic ability is impaired for people with disorders such as autism (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Klin, Lin, Gorrindo, Ramsay, & Jones, 2009). One of the core symptoms distinguishing autism from other disorders is lack of ability to infer the meaning of observed actions, which makes it difficult to carry on effective interactions with others. This

impairment is generally believed to contribute to the severe cognitive and social consequences of autism in later life (Kaiser & Shiffrar, 2009). Hence, investigation of the key mechanisms underlying action understanding may potentially guide the development of behavioral interventions to help individuals with autism to adopt compensatory strategies.

Third, understanding biological motion plays an essential role in bridging several important fields, including perception, reasoning, and social cognition. A precursor of biological motion processing is the extraction of motion information using general motion detectors; hence, biological motion perception offers a window to study the interactions between high-level visual processing and low-level motion processing. The outcome of biological motion perception must feed into a reasoning system that infers the intentions and goals of other individuals, yielding social understanding. Currently, relatively little research has addressed the connections between perception and reasoning, and even less has investigated the further connection to social cognition. Hence, theoretical investigations and empirical tests are both needed to advance understanding of the perceptual and cognitive architecture that supports the social human mind.

In the past decades, the vast majority of studies of biological motion have focused on simple and stereotyped actions, such as walking and running, which involve *a single agent*. Little progress has been made in quantifying what visual information is used in predicting other people's (inter)actions, determining how action representations are utilized in these inferential tasks, and assessing how perception and reasoning operate synergistically to infer hidden goals and intentions. This essay will focus on how biological motion enables human agents to effectively interact with objects and other agents in the environment. We will first review classical and recent work relevant to understanding biological motion. We then propose a unified computational framework, and point to future research directions for work on this fundamental issue in perception and cognition.

BUILDING BLOCKS FOR UNDERSTANDING BIOLOGICAL MOTION

In order to carry out effective social interactions, human minds need to address the fundamental question of "who did what to whom and why?" by identifying causal relationships between individuals' actions and inferring the intentions of individuals. For example, when we observe an interaction between an individual and an object (e.g., a person throws a ball), what we really see is a *living* actor that *causes* a change in the states of an object (e.g., positions, moving directions of the ball), in order to *achieve* certain subjective goals (e.g., to hit a basketball net). Although the brain performs this complex analysis with little effort, the process is sophisticated, involving

three distinct, but related, types of analyses: animacy (i.e., perceiving the moving agent as a living being, and the moving ball as not), causality (i.e., inferring that the person is the cause that makes the ball fly), and intention (i.e., understanding what the actor wants to achieve by his or her action).

ANIMACY AND CAUSAL PERCEPTION

A classical investigation into animacy judgments was performed in the context of the perception of causality (Michotte, 1946/1963). Michotte showed that moving geometric shapes give rise to a vivid perception of animacy, and even of meaningful interactions between an animate object and an inanimate object. Around the same time, Heider and Simmel (1944) showed that such simple stimuli even yield perceived intentions (e.g., one shape would seem to "want to catch" another shape). These pioneering studies highlight human sensitivity to animacy, causality, and intentions, even in stimuli devoid of regular social cues (such as body movements and facial expressions).

The work by Michotte, and others (Scholl & Tremoulet, 2000), has provided evidence that animacy can be directly perceived in a stimulus, rather than inferred from associations between stimulus elements. Specifically, the perception of animacy is fairly fast, automatic, irresistible, and highly stimulus-driven (Scholl & Tremoulet, 2000). For example, small changes in the speed of a moving shape, which are unlikely to change humans' high-level cognitive inferences about the movement, can nonetheless induce or abolish a perception of animacy (Michotte, 1946/1963). Accordingly, Michotte (1946/1963) proposed that some special and automatic mechanisms for analyzing perceptual input are responsible for giving rise to a "genuine causal impression." This hypothesis is supported by evidence showing that processing of such causal interactions is not influenced by attention (Blakemore *et al.*, 2003).

Hence, two of the building blocks for the understanding of biological motion—animacy and causal perception—depend on perceptual quantities. Any change in the stimulus, or in the mechanisms with which the brain processes these stimuli (e.g., due to brain diseases), could affect the understanding of intentions, and hence the social understanding of the actions.

The Inference of Intention

The third building block of understanding biological motion is to infer other people's intentions, which requires making a connection between the observed behavior (e.g., body movements) and the inferred mental states (including intentions) of the actor. This process involves taking what has been called an *intentional stance* (Dennett, 1987), and requires the observer to have extensive knowledge of how actions may arise from a combinations of internal factors. Such a mentalizing process (Frith & Frith, 2006), also termed *theory of mind* (Premack & Woodruff, 1978), is largely built on conscious and unconscious cognitive inferences about intentions of the perceived actor.

Different types of inferential processes are involved in understanding intentions from biological motion. Recently, it has been suggested that intentions can be divided into goal-directed intentions, and those that require multistep movements, with an orthogonal dimension of social to nonsocial intentions (Chambon *et al.*, 2011). It is possible that simple goal-directed intentions (e.g., grabbing a mug to drink something) may be directly perceivable or may be retrieved by internal motor simulation (Brass, Schmitt, Spengler, & Gergely, 2007), without the need for explicit inferences. However, interpretation of more complex intentions—those that are essential in social contexts—most likely depends on cognitive inferences (Keysers & Gazzola, 2007; de Lange, Spronk, Willems, Toni, & Bekkering, 2008). These latter, more complex, inferential processes are classically thought to be at the root of some of the disorders affecting social cognition, such as autism.

In order to make correct inferences about intentions, humans need to combine directly perceivable information, such as body movements, as well as animacy and even causality, with prior knowledge about intentions underlying similar dynamic instances observed previously in social contexts. According to Marr's three levels of analysis in vision (Marr, 1982), we need to examine biological motion understanding at computation, representation and neural implementation levels. To achieve the balance between incoming "sensory-driven" information and prior knowledge, Bayesian inference provides a mathematical framework at the computational level to understand the function and purposes of biological motion (Knill & Richards, 1996). The predictive coding framework provides a testable theory at the representation and implementation levels to make connections to neuroscience and behavioral studies (Friston, 2010), which will be discussed in detail as one of the emerging trends.

PREDICTIVE CODING FRAMEWORK FOR UNDERSTANDING BIOLOGICAL MOTION

In a predictive coding framework, the brain aims to explain incoming sensory data by making inferences about the potential causes of the sensory data. These predictions (in computational terms, "empirical priors") are sent down to a processing level primarily driven by sensory information, where they are subtracted from the incoming information. If the prediction is inaccurate, a large residual of the sensory data (i.e., the prediction error) remains unexplained. This information about the discrepancy between prediction and observation is sent back to the higher (less sensory) levels in order to adjust the prediction. If the prediction is reasonably accurate, and only a small error signal (prediction error) remains, the system can conclude that the predicted (i.e., inferred) causes were indeed present. Such loops are present in both early sensory levels and high-level brain areas, where intentions are processed. Therefore, depending on the stage within the visual system, inferred causes consist of intentions at higher levels of hierarchical processes; while at lower levels, they are more mechanical causes (e.g., a ball hitting another ball), or simply the presence of a stimulus. Therefore, within the predictive coding framework, there is no major difference between perceptual and cognitive inferences. The "perception" of the presence of a stimulus relies on an identical computational schema as the "inference" of the presence of an intention.

Biological motion understanding involves a hierarchical system involving different stages from low-level processing to higher level processing, that is, local motion processing, biological motion processing, animacy and causal perception, and intention inference. When a problem occurs at higher level processing, this could lead to difficulties in inferring intentions (Kilner, Friston, & Frith, 2007), which in turn may cause an incorrect prediction of what the observed actor may do in the future. These wrong predictions will differ greatly from the input and create a large prediction error, which requires additional processing at this lower level to resolve the disagreement between predictions and observations. Hence, malfunction at a higher level could therefore cause an increased demand of attention to lower level element (i.e., details), which could account for some behavioral atypicalities observed in autism (van Boxtel & Lu, 2013b; Friston, Lawson, & Frith, 2013; Van de Cruys, de-Wit, Evers, Boets, & Wagemans, 2013). Similarly, when lower level processors do not function in a typical way, this could cause inaccurate perception of animacy, which could in turn affect how well an observer can infer the intentions of the observed actor.

FUTURE DIRECTIONS

In this section, we identify three main themes that may guide future research investigating how humans achieve deep understanding of biological motion for effective social interactions.

Relationship between Perceptual and Cognitive Inferential Processes

To achieve deep understanding via biological motion, the human mind relies on a sophisticated interplay between three tight interrelated basic processes: perception of animacy, causality, and inference of intention. In future studies, it will therefore be important to separate different contributions of these individual processes to biological motion understanding. This type of work is important, both for determining the constraints on the inference of intentions and for quantifying the contributions of each process in accounting for individual differences. Without recognizing the distinction between these three basic processes, it would be difficult to understand the origins and determinants of certain psychological disorders that involve problems in social cognition and develop principled intervention programs.

Isolating these distinct factors is not easy. For example, in certain experimental paradigms, a stimulus manipulation intended to change the intention inference process may instead change the perception of animacy, resulting (indirectly) in a change in inferred intentions. This potential confound was recently addressed by Gao and colleagues (Gao, Scholl, & McCarthy, 2012) in a psychophysical study in which moving geometric shapes were perceived to be animate and intentional. By manipulating the stimulus carefully, the researchers were able to maintain the same level of perceived animacy, while varying the perceived intentions of the shape elements. They showed that some areas [such as the posterior superior temporal sulcus (pSTS)], which were previously thought to be involved in the perception of animacy, are actually more related to the detection of intentionality. Their study demonstrates the promise of developing visual stimuli to discriminate inferential processes of intention from perceptual processes involving animacy and causality. We consider studies that demarcate the influence of animacy, causality, and intention to represent an important future research direction.

Meanwhile, realistic action stimuli will also be important because natural social stimuli are more complex than the combined movements of simple geometric shapes. For example, several studies demonstrated that the perception of animacy depends on the correct relationship between internal and external movements (Michotte, 1946/1963; Thurman & Lu, 2013), for example, an actor will look less animate when he/she moves too fast in relation to how fast its extremities move. Such complex interactions between internal and external cues in biological motion stimuli will need to be researched more thoroughly.

Finally, there is an emerging trend to investigate how social scenarios are perceived using controlled biological motion stimuli. Although inferences about intentions are especially important in social/interactive contexts, research on this topic is challenging due to the complexity of this inferential task. Identifying interactions between actors is obviously more complicated than perceiving the action of a single individual, and recent imaging work has indeed shown that additional brain structures (including the STS, and more frontal areas) are recruited when an interactive scene is analyzed (Backasch et al., 2013; Iacoboni et al., 2004). Systematic investigations on intention inference are needed to deepen our understanding on this important problem in human perception and cognition. Indeed, it is one of the stated goals of the Human Brain Project (2012, p. 34), a major scientific research project sponsored by the European Union. The initial research forays in this direction have yielded interesting data. For example, psychophysical experiments provided evidence to show top-down influences of interactive information at very early levels of processing in the visual system. In case of the detection of a point-light actor in a noisy background, it was found that detection was easier when individuals with physical interactions (i.e., dancing and boxing partners) (Neri, Luu, & Levi, 2006). A similar finding is reported (Manera, Del Giudice, Bara, Verfaillie, & Becchio, 2011) for communicative interactions (e.g., hand gestures). Therefore, interactive information is able to impact perception at very early stages within the visual hierarchy. In addition, more research is needed to examine human predictability of future actions in complex social environment. In the literature, researchers employed predictive tasks to address this question using single actor stimuli (Graf et al., 2007). Future research will likely focus on systematically examining the ability of humans to predict biological motion in social/interactive scenes involving more than one actor.

Investigating the Predictive Coding Framework

The previous section focused on experimental investigations into perceptual and inferential processes involved in understanding biological motion. However, to arrive at a complete understanding of human action understanding, these separate influences need to be integrated within a unifying computational framework (van Boxtel & Lu, 2013b). The predictive coding framework has recently garnered a lot of attention, because it provides a parsimonious explanation of various problems in autism, including both altered social perception and visual perception (van Boxtel & Lu, 2013b; Friston *et al.*, 2013; Van de Cruys *et al.*, 2013). This explanation focuses on two important elements in the predictive coding framework. The first is that there is an imbalance between bottom-up "sensory" inputs and top-down prediction-driven priors. Different theories point to different causes of the imbalance, emphasizing either increased/altered sensory processing or decreased high-level (prior) information, but it should be emphasized that these theories are not mutually exclusive. In fact, different types of autism may depend on different causes.

The second element in the predictive coding framework is its circular architecture, where a change in low-level processes is forwarded to a high-level process, which then produces a different prediction (empirical prior), followed by subsequent alteration of low-level processing. The predictive coding framework, because of its circular architecture, is more complicated compared to previous models that attempt to explain perceptual deficiencies to either low-level or high-level processing; however, the predictive coding framework has the advantage of being consistent with known brain architecture (Mumford, 1992), thus yielding interpretations of empirical findings that may more closely link social cognition to its neural substrate. Future work will need to investigate how prior knowledge is updated with experience, and how it is applied by the brain depending on the expected precision of their inferred causes (Feldman & Friston, 2010)

There have been recent efforts to explain autism within the framework of predictive coding (van Boxtel & Lu, 2013b; Friston *et al.*, 2013; Van de Cruys *et al.*, 2013). These largely theoretical advances need to be put to empirical tests, and future research should be aimed at providing evidence for the influence of predictive coding mechanisms in autism. Importantly, the predictive coding framework can be used to guide research in new directions, leading to potential insights regarding how the balance between priors driven by predictions and likelihoods driven by sensory information affects perception, and perhaps social cognition in general, in mental disease, and in the general population (e.g., van Boxtel & Lu, 2013a; Rhodes, Jeffery, Taylor, & Ewing, 2013).

Thus, the predictive coding framework (especially when developed into a computational model) will allow to test very specific predictions and may allow future research to determine which parts of the framework are related to perceptual and cognitive deficits, and how such deficits may be counteracted. Experimental and computational work directed at both the perceptual and inferential levels, as well as their interaction, will be a very fruitful future endeavor.

Connection to Mental Disorders

Apart from the focus on the theoretical predictive coding framework, we expect more research at the interface between perception and cognition in the context of mental disorders that affect cognition, especially research that dissociates the problems related to animacy, causal perception, and intention inference. As noted earlier, deficits in social perception may result from a problem in any of these three (or other) mechanisms. Although the emphasis of the field has been on social deficits in autism, there is evidence that social cognition in general is very much based on the interplay between all three processes. For example, the pSTS is involved in the perception of biological motion (Grossman *et al.*, 2000), while at the same time being an important hub in the understanding of intention (Frith & Frith, 2003; Gao *et al.*, 2012).

It is also sensitive to other social cues, such as where someone is looking (Pelphrey, Morris, & McCarthy, 2004).

In fact, the STS may be at the crossroads of perception and the inference of intention and social cognition (Allison, Puce, & McCarthy, 2000; Castelli, Happe, Frith, & Frith, 2000; Frith & Frith, 2003; Gao et al., 2012), being hypoactive in autism (Zilbovicius et al., 2006) and hyperactive in schizophrenia (Backasch et al., 2013). Perhaps, the pSTS is important in connecting the inferred intentions to a certain stimulus in the visual array. Problems in the attribution of intention are potentially central to the understanding of autism and schizophrenia. For example, hallucinations in schizophrenia can be viewed as an "over-attribution" of causation/intentionality. Patients attribute a cause to a certain percept, or an intention to a certain action, that did not actually exist (see, e.g., Backasch et al., 2013). Contradistinctively, people with autism may suffer from a weaker attribution of intentions. For example, children with autism spectrum disorder (ASD) show deficits in understanding social intentions in biological motion displays relative to typically developing children (Centelles, Assaiante, Etchegoyhen, Bouvard, & Schmitz, 2013). However, they may not necessarily have a deficit in identifying the observed action (e.g., Saygin, Cook, & Blakemore, 2010).

This type of research, at the crossroads of perception and intention inference, will be a fruitful contribution. With these future directions in mind, we can look forward to an increased understanding of what separate processes are essential to the understanding of biological motion stimuli, and how they work together, based on detailed computational models.

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REFERENCES

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267–278.
- Backasch, B., Straube, B., Pyka, M., Klohn-Saghatolislam, F., Muller, M. J., Kircher, T. T., & Leube, D. T. (2013). Hyperintentionality during automatic perception of naturalistic cooperative behavior in patients with schizophrenia. *Social Neuroscience*, 8(5), 489–504.
- Blake, R., Turner, L. M., Smoski, M. J., Pozdol, S. L., & Stone, W. L. (2003). Visual recognition of biological motion is impaired in children with autism. *Psychological Science*, 14(2), 151–157.
- Blakemore, S. J., Boyer, P., Pachot-Clouard, M., Meltzoff, A., Segebarth, C., & Decety, J. (2003). The detection of contingency and animacy from simple animations in the human brain. *Cerebral Cortex*, 13(8), 837–844.

- van Boxtel, J. J. A., & Lu, H. (2013a). Impaired global, and compensatory local, biological motion processing in people with high levels of autistic traits. *Frontiers in Psychology*, 4(209), 1–10.
- van Boxtel, J. J. A., & Lu, H. (2013b). A predictive coding perspective on autism spectrum disorders. *Frontiers in Psychology*, 4(19), 1–3.
- Brass, M., Schmitt, R. M., Spengler, S., & Gergely, G. (2007). Investigating action understanding: Inferential processes versus action simulation. *Current Biology*, 17(24), 2117–2121.
- Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage*, *12*(3), 314–325.
- Centelles, L., Assaiante, C., Etchegoyhen, K., Bouvard, M., & Schmitz, C. (2013). From action to interaction: Exploring the contribution of body motion cues to social understanding in typical development and in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 43(5), 1140–1150.
- Chambon, V., Domenech, P., Pacherie, E., Koechlin, E., Baraduc, P., & Farrer, C. (2011). What are they up to? The role of sensory evidence and prior knowledge in action understanding. *PLoS ONE*, 6(2), e17133.
- Cutting, J. E., & Kozlowski, L. (1977). Recognizing friends by their walk: Gait perception without familiarity cues. *Bulletin of the Psychonomic Society*, *9*, 353–356.
- Darwin, C. (1872). *The expression of the emotions in man and animals*. London, England: John Murray.
- Dennett, D. C. (1987). The intentional stance. Cambridge, MA: MIT 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(6), 727–738.
- Feldman, H., & Friston, K. J. (2010). Attention, uncertainty, and free-energy. *Frontiers in Human Neuroscience*, *4*, 215.
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, *11*(2), 127–138.
- Friston, K. J., Lawson, R., & Frith, C. D. (2013). On hyperpriors and hypopriors: Comment on Pellicano and Burr. *Trends in Cognitive Sciences*, 17(1), 1.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalising. *Philosophical Transactions of the Royal Society B*, 358, 685–694.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. Neuron, 50(4), 531–534.
- Gao, T., Scholl, B. J., & McCarthy, G. (2012). Dissociating the detection of intentionality from animacy in the right posterior superior temporal sulcus. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 32(41), 14276–14280.
- Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., & Prinz, W. (2007). Predicting point-light actions in real-time. *NeuroImage*, *36*(Suppl 2), T22–T32.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, 12(5), 711–720.

- Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *The American Journal of Psychology*, 57, 243–249.
- Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., & Fiske, A. P. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *NeuroImage*, 21(3), 1167–1173.
- Kaiser, M. D., & Shiffrar, M. (2009). The visual perception of motion by observers with autism spectrum disorders: A review and synthesis. *Psychonomic Bulletin & Review*, 16(5), 761–777.
- Keysers, C., & Gazzola, V. (2007). Integrating simulation and theory of mind: From self to social cognition. *Trends in Cognitive Sciences*, *11*(5), 194–196.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, 8(3), 159–166.
- Klin, A., Lin, D. J., Gorrindo, P., Ramsay, G., & Jones, W. (2009). Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature*, 459(7244), 257–261.
- Knill, D. C., & Richards, W. (1996). *Perception as Bayesian inference*. Cambridge, England: Cambridge University Press.
- Kozlowski, L., & Cutting, J. E. (1977). Recognizing the sex of a walker from a dynamic point-light display. *Perception & Psychophysics*, 21(6), 575–580.
- de Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology: CB*, *18*(6), 454–457.
- Manera, V., Del Giudice, M., Bara, B. G., Verfaillie, K., & Becchio, C. (2011). The second-agent effect: Communicative gestures increase the likelihood of perceiving a second agent. *PLoS ONE*, *6*(7), e22650.
- Marr, D. (1982). Vision: A computational approach. San Francisco, CA: Freeman & Co..
- Michotte, A. (1946/1963). *The perception of causality* (Miles T.R., Miles E. Trans.). New York, NY: Basic Books (Original work published 1946).
- Mumford, D. (1992). On the computational architecture of the neocortex II. The role of cortico-cortical loops. *Biological Cybernetics*, *66*(3), 241–251.
- Neri, P., Luu, J. Y., & Levi, D. M. (2006). Meaningful interactions can enhance visual discrimination of human agents. *Nature Neuroscience*, 9(9), 1186–1192.
- Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience*, *16*(10), 1706–1716.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1(4), 515–526.
- Rhodes, G., Jeffery, L., Taylor, L., & Ewing, L. (2013). Autistic traits are linked to reduced adaptive coding of face identity and selectively poorer face recognition in men but not women. *Neuropsychologia*, 51(13), 2702–2708.
- Saygin, A. P., Cook, J., & Blakemore, S. J. (2010). Unaffected perceptual thresholds for biological and non-biological form-from-motion perception in autism spectrum conditions. *PLoS ONE*, 5(10), e13491.

- Scholl, B. J., & Tremoulet, P. D. (2000). Perceptual causality and animacy. Trends in Cognitive Sciences, 4(8), 299–309.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States* of America, 105(2), 809–813.
- The_HBP-PS_Consortium (2012). The human brain project. A Report to the European Commission. Lausanne, Switzerland.
- Thurman, S. M., & Lu, H. (2013). Physical and biological constraints govern perceived animacy of scrambled human forms. *Psychological Science*, 24(7), 1133–1141.
- Van de Cruys, S., de-Wit, L., Evers, K., Boets, B., & Wagemans, J. (2013). Weak priors versus overfitting of predictions in autism: Reply to Pellicano and Burr (TICS, 2012). *i-Perception*, 4(2), 95–97.
- Zilbovicius, M., Meresse, I., Chabane, N., Brunelle, F., Samson, Y., & Boddaert, N. (2006). Autism, the superior temporal sulcus and social perception. *Trends in Neurosciences*, 29(7), 359–366.

FURTHER READING

- Blake, R., & Shiffrar, M. (2007). Perception of human motion. Annual Review of Psychology, 58, 47–73.
- Feldman, H., & Friston, K. J. (2010). Attention, uncertainty, and free-energy. *Frontiers in Human Neuroscience*, *4*, 215.

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, *50*(4), 531–534. Michotte, A. (1946/1963). *The perception of causality*.

Scholl, B. J., & Tremoulet, P. D. (2000). Perceptual causality and animacy. Trends in Cognitive Sciences, 4(8), 299–309.

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