Universidade do Minho
Escola de Psicologia

Maria Isabel Almeida da Costa Pinto Lisboa

Infants' Perception of Biological Motion Configuration

janeiro de 2021

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Statement of Integrity

I hereby declare having conducted this academic work with integrity. I confirm that I have not used plagiarism or any form of undue use of information or falsification of results along the process leading to its elaboration.

I further declare that I have fully acknowledged the Code of Ethical Conduct of the University of Minho.

University of Minho, February 26th

Maria Isabel Almeida da Costa Pinto Lisboa

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A Percepção da Configuração do Movimento Biológico em Bebés

Resumo

Para compreender os outros, interpretar as suas ações, emoções ou intenções, é necessário aprender a descodificar o movimento dos nossos parceiros sociais. Para isso, primeiro, precisamos de ser capazes de orientar a nossa atenção para o movimento das outras pessoas; em seguida, necessitámos de integrar o movimento das diferentes partes do corpo (por exemplo, dos membros) na configuração coerente e global de um corpo humano em movimento—a isto designamos de processamento configural; só então é que finalmente somos capazes de interpretar o objetivo e o significado de uma ação. O processamento configural do movimento biológico é um processo básico, mas altamente relevante na interpretação do significado de uma ação e, consequentemente, crucial para a interação social e para a cognição social humana.

A investigação acerca do desenvolvimento da percepção do movimento biológico indica que o processamento configural surge durante o primeiro ano de vida (Bertenthal, 1993), associado à maturação cortical dos bebés e ao seu desenvolvimento sociocognitivo (Pavlova, 2012).

A presente dissertação pretende investigar o desenvolvimento do processamento configural na percepção do movimento biológico durante a primeira metade do primeiro ano de vida dos bebés. Para isso, combinamos duas técnicas de investigação da Psicologia do Desenvolvimento, distintas mas complementares: o functional near-infrared spectroscopy (fNIRS) e o procedimento de atenção preferencial (preferential looking). Nesta dissertação são então apresentados os resultados de quatro estudos experimentais, dois de fNIRS e dois comportamentais, realizados em bebés com idades compreendidas entre os três e os sete meses de idade.

No Capítulo 1 é apresentada uma extensa revisão da literatura sobre o papel do processamento configural na percepção do movimento biológico, ou seja, sobre como esta competência perceptual é relevante para a cognição-social humana e, em particular, para o desenvolvimento sociocognitivo dos bebés.

No Capítulo 2 e 3 são apresentados e discutidos dois estudos de fNIRS realizados com bebés de sete meses. Estes foram os primeiros estudos realizados na infância, que mediram a resposta hemodinâmica do cérebro ao movimento humano utilizando displays de pontos de luz (*point-light walkers)* como estímulos. Estes estudos visaram investigar se a percepção do movimento biológico é sustentada, na infância tal como nos adultos, pelo funcionamento do sulco temporal superior direito (STS direito). O STS é uma área central do córtex humano para o processamento de estímulos sociais, e o processamento da configuração do movimento biológico parece também ocorrer neste local em adultos (Deen, Koldewyn, Kanwisher, & Saxe, 2015).

No Capítulo 4, são apresentados dois estudos de atenção preferencial, um longitudinal e outro transversal. Os dois estudos pretendem perceber quando é que os bebés preferem uma configuração coerente do movimento humano. Especificamente, procuram descobrir quando, na infância, surge uma preferência pela configuração coerente e global humana de uma pessoa a andar em relação a um estímulo cujas posições dos pontos de luz foram randomizadas. Bebés de três e cinco meses foram testados num estudo transversal, e bebés de três, cinco e sete meses de idade, longitudinalmente.

Finalmente, no Capítulo 5, discutimos e concluímos acerca as implicações das nossas descobertas. Encontramos importantes mudanças de desenvolvimento na percepção da configuração do movimento biológico durante os primeiros meses de vida—os nossos resultados contribuem para uma compreensão mais completa da percepção do movimento biológico em bebés e das origens e desenvolvimento da cognição social humana.

Palavras-chave: fNIRS, infância, movimento biológico, olhar preferencial, relações configurais

Infants’ Perception of Biological Motion Configuration

Abstract

To understand others, interpret their actions, emotions or intentions, we have to learn how to decode human motion. For that, first, we need to start by paying attention to the motion of others; afterward, we have to be able to integrate the individual and local motion of moving body parts (such as limbs) into the coherent and motion configuration of a whole human body acting—this is called configural processing; only then we are finally able to predict, interpret, and understand the goal and meaning of an action. Configural processing is a basic but highly relevant process in biological motion perception with implications on action understanding, social interaction and in human social cognition.

Developmental research on biological motion perception indicates that configural processing emerges during our first year of life (Bertenthal, 1993), associated to important cortical specializations, and to infants’ social-cognitive development (Pavlova, 2012).

The present dissertation investigated the development of configural processing in biological motion during the first half of infants’ first year of life. For that, two distinct but complementary techniques from developmental research were combined: functional near-infrared spectroscopy (fNIRS) and the preferential looking procedure. This dissertation presents and discusses the outcomes of two neuroimaging and two behavioral experiments conducted with infants, aged from three to seven months of age, on the perception of biological motion configuration.

Chapter 1 begins with an extensive literature revision on the role of configural processing in biological motion perception, namely, on how this basic perceptual skill is relevant for human social abilities and, in particular, for infants’ social-cognitive development.

In Chapter 2 and 3, two fNIRS experiments conducted with seven months old infants are presented and discussed. These were the first fNIRS studies conducted in infancy, using point-light walkers as stimuli. They intended to investigate whether the perception of biological motion is underpinned, in infants as in adults, by the right superior temporal sulcus (right STS) functioning. The right STS is a cornerstone for human social-cognition, and biological motion configural processing occurs in this site in the adults brain (Deen, Koldewyn, Kanwisher, & Saxe, 2015).

In Chapter 4, two preferential looking experiments, one longitudinal and another cross-sectional, are presented. These two studies intended to find when, in infancy, emerges a preference for biological motion configuration. Specifically, when, in infants aged three to seven months, emerges a preference for the coherent motion configuration of a person walking in relation to scrambled display.

Finally, in Chapter 5, we discuss and conclude about the implications of our findings. We found important developmental changes in the perception of biological motion configuration during the first few months of life—our results contribute to a broader understanding of biological motion perception in infancy thus to the origins of human social-cognition.

Keywords: biological motion, configural relations, fNIRS, infancy, preferential looking.

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BM – Biological Motion

PLW – Point-light Walker

PLD – Point-light Display

STS – Superior Temporal Sulcus

pSTS – posterior Superior Temporal Sulcus

rpSTS – right posterior Superior Temporal Sulcus

FBA – Fusiform Body Area

EBA – Extrastriate Body Area

IFG – Inferior Frontal Gyrus

fNIRS – Functional Near-Infrared Spectroscopy

HbO_2 – Oxy-hemoglobin

HbR – Deoxy-hemoglobin

HbT – Total-hemoglobin

EEG – Electroencephalography

ERP – Event Related Potentials

fMRI – Functional Magnetic Resonance Imaging

BOLD – Blood Oxygen-Level-Dependent Imaging

ROI – Region of Interest

ASD – Autism Spectrum Disorder

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Chapter 1. General Introduction

How is it that infants learn to decode the meaning of a pointing gesture or to predict that an approaching person intends to interact?

One of the most extraordinary humans abilities is to understand someone's behavior by looking at their movements. Maybe because of that, human infants devote a great deal of time looking at moving people around them.

Infants begin to prefer or to look at some motions more than others, and not long after, they begin to understand the meaning of human actions. By adulthood, we are so skilled at interpreting and predicting the motion of others that we do so constantly in our everyday life in the time of a glimpse. Albeit, these assessments involve the coordination of multiple processes, such as: selective attention to the motion of others; configural processing, i.e. integration of the movement of isolated body parts (such as limbs), into the global form of a person in action; perception (and prediction) of the actions of others not as mere movement but as intentional and goal-oriented.

Perception of human motion plays a fundamental role in identifying, interpreting and predicting the actions of others (Blakemore & Decety, 2001) as numerous information is extracted solely from the coherent dynamic outline of a human body in motion (Pavlova, 2012).

Johansson's (1973) early work demonstrated that illuminating the joints of a walking person is sufficient for a human observer to experience an immediate and compelling impression of a person walking—nonetheless this stimulus collapses into a meaningless percept if the initial positions of the illuminated dots are randomized (or scrambled), showing that the configural relations between the dots are important – see Figure 1.

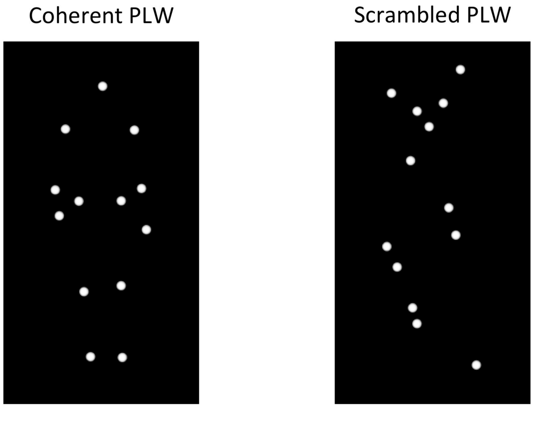

Figure 1. A single frame of a coherent point-light walker (left) and of a scrambled point-light walker (right).

There is a unique spatial-temporal relation between the dots that compose a point-light display—or the parts of an acting person—in making biological motion, a special class of social stimulus for humans. These relations are termed configural relations.

Perceiving configural relations in biological motion is one of the first steps into understanding human actions: only through perceiving motion configural relations, we can then identify a human, an action, the goal of an action or even its intention or emotion (A. P. Atkinson, Dittrich, Gemmell, & Young, 2004; Dittrich, 1993; Johansson, 1973, 1976; Jokisch, Daum, & Troje, 2004; Moore, Brownell, & Slaughter, 2012; Runeson & Frykholm, 1983). There are a number of processes operating at different levels in biological motion perception that are likely not independent (Hoehl & Bertenthal, 2021; Moore et al., 2012; Thornton, 2018). Perceiving configural relations in biological motion are one of the first processes thus a central mechanism for a wider understanding of human social cognition/perception (Blakemore & Decety, 2001; Johansson, 1973, 1976; Moore et al., 2012; Thornton, 2018; Troje, 2013). Despite this, it is still unclear how do we perceive or what are the mechanisms behind biological motion configural processing.

Several psychological and computational models have attempted to explain configural processing in biological motion. In particular, the mechanisms by which we organize the individual constituents of a point-light walker into a meaningful, unique and coherent global configuration of a person walking (Cutting, 1981; Giese & Poggio, 2003; Johansson, 1976; Lange & Lappe, 2006; Troje, 2008; Troje & Chang, 2013; Troje & Westhoff, 2006). These models are, however, incomplete.

The major limitation, common to all of these models, is that none accounted for the ability of perceiving configural relations during early stages of development — see Masahiro Hirai & Senju (2020) for a very recent exception. This is a critical gap because the perception of biological motion has consistently been shown to be a key component of action perception, and a vital contributor to infants' social-cognitive development. If the meaningful interpretation of an action involves mature visual cortical representation of a body moving and a specialized knowledge about the visual properties of biological motion, how does it develop?

The present work intends to contribute for a clearer understanding of the development and of the role of configural processing in interpreting biological motion as a socially relevant stimulus in infancy.

Large developmental changes happen continuously during our first year of life, i.e. during infancy, and the world is full of new things for an infant to learn, and novel changes to accommodate. This is especially true in the development of our visual system (J Atkinson, 1984).

In infancy, the perception of configural relations in biological motion is still immature or emerging, while our social-cognitive abilities are also still forming (Bertenthal, 1993; Bertenthal & Boyer, 2015; F Simion, Di Giorgio, & Bardi, 2011; Francesca Simion & Giorgio, 2015). This is a unique period to investigate and understand configural processing in biological motion and its connections to human social-cognition and brain maturation. When do we start perceiving configural relations in biological motion? Is the ability to perceive configural relations in biological motion linked to infants' selective attention to human actions? Is the perception of biological motion's configural relations sub-served by a specialized cortical response at an early age? These questions, that we intend to answer, will further elucidate us into how humans sense other people's behavior and learn to share meanings and start acting in our complex social world.

1.1 Configural Processing in Biological Motion Perception

The scientific study of the visual perception of an articulated body in motion begun more than 40 years ago, in the early 1970's, by the ground-breaking observations of the Swedish experimental psychologist, Gunnar Johansson (Johansson, 1973).

Johansson created the term "biological motion" to designate the *"motion patterns characteristic of living organisms"* or, more specifically, the *"animal and human motion patterns"*. Biological motion thus includes more than human motion; it includes the motion of all living beings.

Johansson also developed a technique to scientifically investigate biological motion: the point-light technique (Johansson, 1973; Troje, 2013).

The point-light technique is unexpectedly simple but highly reliable since it isolates biological motion information from other sources of visual information. It consists of recording a dozen illuminated dots placed onto the major joints of a person moving against a black background—nowadays, there are algorithms for re-creating point-light displays and motion capture technologies. Either way, the result is a visual stimulus that comprises only a dozen dots in motion, a point-light display (Johansson, 1973).

Johansson's observations with the point-light technique were surprising since—despite the apparent impoverished visual information presented in the stimulus, such as the absence of explicit contours, colors, textures, or even featural information such as eyes, hair or clothes—human observers were able to vividly identify a person from point-light displays within a fraction of a second (Johansson, 1976). The global form of a human in action is rapidly inferred from the relative positions and movements of the dots placed on the joints and limbs in a point-light display. Thus, grounded in the

Gestalt School of Psychology, Johansson was set out to investigate and characterize how the human visual system so rapidly organizes the information contained in the individual and local motions, into the global configuration of a walking human (Johansson, 1973, 1976; Troje, 2013).

Two types of configural relations can be extracted from a point-light display in motion: *local configural relations*, i.e. the spatiotemporal relations between at least two dots in a point-light display—a paradigmatic example of local configural information is the motion of the limbs, e.g. the spatiotemporal relation between the three dots that compose an arm (shoulder, elbow and wrist); and *global configural relations*, i.e. the spatiotemporal relation between all dots that compose the point-light display—corresponding to the global human motion configuration of an action, for example, the form of a person walking in the case of a point-light walker (Bertenthal & Pinto, 1994; Chang & Troje, 2009; Troje, 2013).

Johansson conducted a set of identification tasks, where he varied time of stimuli presentation, or the action being presented; he instructed his participants to describe verbally "something moving" on a screen (Johansson, 1973, 1976). Results were astonishing: 100% of his participants needed solely 200 milliseconds of stimulus presentation to perceptually organize the dots of a point-light walker into the meaningful global percept of a person walking. Moreover, different actions such as running, cycling, dancing, or jumping were also readily identified as fast as in 400 milliseconds (Johansson, 1973, 1976). The walking action was faster to identify (Johansson, 1976) and, considering its functional importance and its frequency in our visual environment—locomotion is the most common human and non-human action—it has been employed more frequently in biological motion perception research. Thus, a point-light display depicting the walking action was specifically termed a point-light walker (PLW).

Johansson's experiments with the point-light technique sparked widespread interest on biological motion. First, because the technique allowed a simple decomposition and careful manipulation of the different perceptual properties (e.g. orientation, configural information, etc.) that characterize biological motion (Blake & Shiffrar, 2007; Masahiro Hirai & Senju, 2020; Troje, 2013). Point-light walkers are the dominant experimental tools for studying biological motion and action understanding (Blake & Shiffrar, 2007; Thornton, 2018). Second, because of the discovery that a point-light display can carry relevant social information, even for young infants (Grossmann, 2015; F Simion et al., 2011). Information of motion alone can carry high-level social meaning. Consequently, research on biological motion perception advanced into an understanding that was far beyond these initial simple identification tasks, requiring a multidisciplinary approach.

Ranging from psychophysics, visual perception, action understanding and social-cognition, developmental psychology, neuroimaging, and even to the new field of behavior epigenetics (that attempts to explain how gene expression is influenced by experiences and the environment) (Wang et al., 2018)—several findings show both the significance and the specificities of biological motion (Blake & Shiffrar, 2007; Masahiro Hirai & Senju, 2020; Troje, 2013).

1.1.1 Models of biological motion perception

Different models or approaches attempt to explain and characterize how the human visual system processes biological motion.

Psychophysics experiments conducted with adults finely characterized the way we respond to biological motion stimuli. These studies found that the simple inversion of a point-light walker makes its identification difficult; the perception of biological motion is thus characterized as being “orientation dependent” (Pavlova & Sokolov, 2000).

Psychophysics experiments also found that the percept of a walking person is salient and resilient to masking noise: observers are fast and accurate in detecting the presence of a point-light walker under various conditions of visual masking (Bertenthal & Pinto, 1994; Cutting, Moore, & Morrison, 1988). Typically, these experiments employ a two-interval alternative forced-choice task. In this task, observers are presented with two types trials: one that contains the point-light walker embedded in a mask (e.g. a set of white dots moving at constant velocity), and an alternate one containing only the visual mask. Observers have to judge which trial contains the target, that is, the walker. Subjects are accurate in detecting the presence of a walker under masking noise even when the mask is composed by a set of white dots moving in the exact same way as the dots of the walker; this is called a scrambled mask (Bertenthal & Pinto, 1994). Correct detection of the walker over a scrambled mask is, however, harder because the display is superimposed over a set of white dots that have the same individual trajectories as the walker (Bertenthal & Pinto, 1994). In this latter case, the authors explain, the correct identification of the walker is dependent on the detection of the global motion configuration of the display (because motion of the individual dots is the same both in the point-light walker and mask, this information is irrelevant for the detection in this task). Despite this, observers are still able to accurately detect the point-light walker under a scrambled mask which resulted in a reinforcement of the importance of global configural processing in biological motion perception (Bertenthal & Pinto, 1994).

Moreover, the same result—detection performance of the walker above change—was also obtained when using moving limbs as masking noise, making also local configural relations uninformative for the detection of the walker (Bertenthal & Pinto, 1994). The authors thus concluded that both individual motion and local configural information is not necessary or obligatory for an observer to identify the familiar configuration of a person walking from point-light walkers. Instead, global configural information is the compelling and major property in biological motion perception (Bertenthal & Pinto, 1994). Nevertheless, Troje & Westhoff (2006) and Chang & Troje (2009) recently demonstrated that there is a contribution from both.

First, Troje & Westhoff (2006) found that the local motion of the feet (two dots placed on each ankle) is essential, as keeping this information intact, despite the spatial scrambling of all the other dots, is enough for adults' correct judgment of the facing direction of a point-light walker (Troje & Westhoff, 2006). The authors demonstrated that adults rely in the local motion of the feet to judge the direction of a point-light walker.

Second, Chang & Troje (2009) found that local and global configural processing are two important but distinct processes with different properties in biological motion perception.

They concluded this from the outcomes of two different psychophysics tasks: one task relied heavily on processing global configural relations (observers had to detect a walker under a scrambled mask), and another relied primarily on local processing (observers had to discriminate the walking direction of both coherent and scrambled walking displays). Both tasks made use of displays of a person walking (point-light walker), of a walking cat, and a walking pigeon. Results from these experiments revealed that: in the first task (that requires the retrieval of global configuration), observers were strongly affected by the walker type (i.e. error rates were lower in the more familiar human form condition) and performance was also more affected by learning (i.e. error rates decreased at the later test blocks); in the second task (more dependent on local processing) performances were not affected by either walker type or learning (Chang & Troje, 2009).

Troje and Westhoff (2006) suggested, therefore, that two distinct and separate processes are in place in biological motion perception: one innate, contained in the local motion of the feet, functioning as a general "life detector", and providing reliable cues for the presence of a walking animal in our visual environment; and another global mechanism, experienced-based, that retrieves the whole body motion of a human in action (Chang & Troje, 2009; Troje, 2013; Troje & Chang, 2013; Troje & Westhoff, 2006).

More recently, a two-process theory for biological motion perception was proposed, combining these findings (that outlined an important role for both local and global configural processes) (Troje, 2008, 2013), with the outputs of studies conducted with infants and point-light walkers, as well as recent neuroimaging data (Masahiro Hirai & Senju, 2020).

The two-process theory (Masahiro Hirai & Senju, 2020) was the first model of biological motion perception that explicitly included developmental data. This is important because an accurate description of the visual mechanisms of biological motion perception must consider how this percept develops, thus, how it changes over time, influenced by visual experience and cortical maturation.

The two-process theory proposes that processing of point-light walkers occurs in two stages during human development: a “step detector” stage; followed by a “bodily action evaluator” stage (Masahiro Hirai & Senju, 2020).

In the “step detector” phase, two types of visual information are processed: (1) the local motion of feet (Troje, 2008, 2013), and (2) feet-bellow-body information, i.e. the processing of the configuration of the feet as being in the lower part of the body (Bardi, Regolin, & Simion, 2014). The authors hypothesize that the processing of these two types of visual information is rapid, pre-attentive and involve sub-cortical networks such as the superior colliculus (midbrain), pulvinar, and ventral lateral nucleus (Masahiro Hirai & Senju, 2020). This “step detector” is also not specific for human motion; it is also sensitive to motions generated by other vertebrates. This system emerges early (it is perhaps innate) and is less dependent of visual experience.

In contrast, in the second stage of processing there is a “bodily action evaluator” system. This system develops gradually as a result of visual experience and cortical development, thus, is not innate and likely matures during the first year of life (Masahiro Hirai & Senju, 2020). It examines configural information in point-light displays (such as the action types) and it selectively responds to human motion, which allows for an individual to acquire specialization for social partners. The “bodily action evaluator” system is sub-served by cortical networks such as fusiform body area (FBA), the extrastriate body area (EBA), inferior frontal gyrus (IFG) and the posterior superior temporal sulcus (pSTS) – see Figure 2.

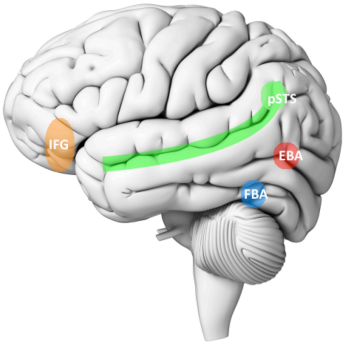

Figure 2. A schematic of the human brain showing the "bodily evaluator system"

A schematic of the human brain showing regions implicated on the processing of the "bodily evaluator system": in orange, the inferior frontal gyros (IFG); green, the superior temporal sulcus (STS); red, the extrastriate body area (EBA); and in blue, the fusiform body area (FBA).
Adapted from Brain and Language course by POINT-LIGHT DISPLAY. Howard, 2020, from http://point-light display.tulane.edu/~h0Ward/BrLg/STS.html, Copyright 2019 by Harry Howard

In sum, although the majority of these models intended to characterize and understand the visual mechanisms that underlie biological motion perception—Johansson's seminal question of *how* (and *why*) our visual system is so efficient at organizing the coherent and meaningful global percept of a human in action out of a dozen moving dots, is still not fully explained (Giese & Poggio, 2003; Masahiro Hirai & Senju, 2020; Johansson, 1976; Lange & Lappe, 2006; Troje, 2013; Troje & Chang, 2013; Wang et al., 2018). Moreover, a critical gap in the majority of the proposed models, is that they only briefly account for the ability of perceiving configural relations during early stages of human development—the two processing theory is a very recent exception (Blake & Shiffrar, 2007; Masahiro Hirai & Senju, 2020). All models stress a remarkable ability of the mature visual system in processing biological motion and biological motion configurations. Nevertheless, knowledge on its development is relevant, if not for anything else, because the few developmental experiments conducted so far with infants indicate that major transitions in the perception of biological motion occur in our first few months of life.

1.2 Development of Biological Motion Perception

Interest in the developmental path of biological motion perception appeared almost 10 years after the seminal studies with the point-light technique pioneered by Johansson (1973), with the publication of the first experiments on biological motion perception conducted with infants by Fox &

McDaniel (1982). Specifically, with the publication of three preferential looking experiments using point-light walkers with two, four and six months-old infants (Fox & McDaniel, 1982).

Infants obviously do not speak or understand instructions, hence, much of what we know regarding infants' social-cognitive development comes from methodological approaches based on their looking behavior (Aslin, 2007; Proffit & Bertenthal, 1990; Teller, 1979)—more recently, with neuroimaging developments, techniques such as electroencephalography (EEG) and/or functional near-infrared spectroscopy (fNIRS) have also been incorporated (Azhari et al., 2020; Lloyd-Fox, Blasi, & Elwell, 2010). Two now classical procedures based on infants' looking behavior are central to infancy research: the infant-controlled habituation procedure and the preferential looking procedure (Aslin, 2007; Frankenhuis, Barrett, & Johnson, 2012).

In a preferential looking procedure, infants are presented with two competing stimuli, a target and a control stimulus, side-by-side (i.e. one on the left and another on the right side of the infant's line of sight), over a series of trials. The amount of time the infant spends looking at the target stimulus determines a preference: if the infant looks more than 50% of total looking time to the target, a preference for the target is determined (and vice-versa); if the infant looks the same amount of time to both stimuli (i.e. circa of 50% of looking time at each stimulus), there is no preference for either stimulus (Teller, 1979). When a preference for a stimulus is obtained, a discrimination between the two stimuli can also be inferred (Houston-Price & Nakai, 2004) – see Figure 3.

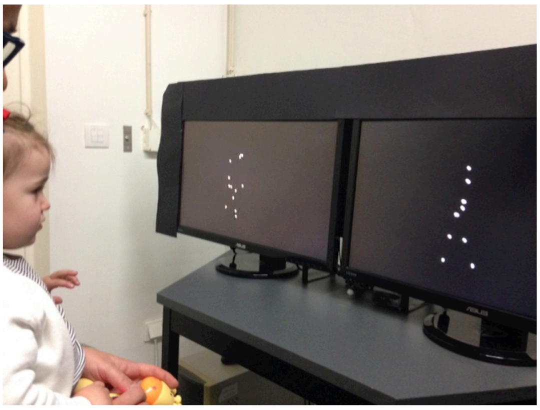

Figure 3. A picture of the preferential looking set-up

Each stimulus is presented on each screen; the infant is seated on his/her parent's lap, in the middle of the two screens, and equidistant from both stimuli. A camera placed in the middle of the two screens records infants' behavior. Measures of the amount of looking time at each stimulus are commonly extracted to determine a preference, but measures of the number of head turns associated to each stimulus, or direction of the first look can also be calculated.

As referred, Robert Fox & Cynthia McDaniel (1982) were pioneers in investigating infants' perception of biological motion; they tested infants in a preferential looking procedure. They were also the few publishing a study using simultaneously point-light displays and a preferential looking procedure, and testing infants during their first months of life—the present work, Bertenthal, Proffitt, Spetner & Thomas (1985), and Sifre et al. (2018), are the other few known exceptions.

Fox & McDaniel (1982)'s preferential looking experiments originated from the adults' psychophysics findings on biological motion perception at the time (Cutting, Proffitt, & Kozlowski, 1978; Johansson, 1973). These adults experiments (reviewed in the previous section) stressed a remarkable ability of the mature visual system in processing biological motion; they also conjectured about an innate or intrinsic capacity of the visual system to process biological motion (Cutting et al., 1978; Johansson, 1973). Thus, to investigate this hypothesis, Fox & McDaniel (1982) tested two, four and six months-old infants to investigate if humans have an early or innate sensitivity to biological motion.

Three cross-sectional preferential looking studies were conducted, contrasting: (1) a coherent point-light walker, to a set of randomly moving dots; (2) a coherent point-light walker, to an inverted point-light walker—in this control stimulus, the intact coherent point-light walker is rotated 180° in the picture-plane, thus, both local and global configural relations are inverted and the display is shown up-side down; and (3) a point-light display of a pair of hands clapping vs. an off-joint hands display—in this latter case, illuminated dots were placed off joints, specifically, markers were placed in the middle of two adjacent joints (Fox & McDaniel, 1982).

Results showed that both four and six months-old preferred the walking motion in comparison with the moving dots and the inverted display, but only six months-old preferred the on-joints clapping motion in relation to the off-joints display. Two months-old infants showed no preferences for either stimulus in all studies (Fox & McDaniel, 1982).

In face of these results, the authors concluded that some post-natal period of visual maturation during the first few months of life is needed for biological motion to be perceived since: two months-old infants revealed no preference for either stimulus; preferences at four months were restricted to the walking action; and only six months-old preferred the on-joints clapping hand motion (Fox & McDaniel, 1982).

The question of innate vs. experienced-based sensitivity to biological motion initiated (Fox & McDaniel, 1982) and accompanied developmental studies on biological motion perception until today (Craighero, Ghirardi, Lunghi, Panin, & Simion, 2020). More recent accounts with newborns suggest a different role for visual experience than the one discussed by Fox & McDaniel in 1982 (Bardi, Regolin, & Simion, 2011; Francesca Simion, Regolin, & Bulf, 2008). While Fox & McDaniel (1982) reported no preference for biological motion in two months-old infants, in an influential study conducted with newborns, Simion, Regolin & Bulf (2008), using a similar set of stimuli, found a preference for looking at biological motion at birth. Studies with newborns suggest that humans orient and process biological motion since their very first days of life but with some limitations.

1.2.1 Predispositions for Biological Motion at Birth

Newborns studies on biological motion mostly conjecture about the existence of an inborn predisposition to prefer biological motion in relation to other kinds of motion (Bardi et al., 2011; F Simion et al., 2011; Francesca Simion et al., 2008).

The starting point for these experiments was again linked to adults' psychophysics findings; in particular, to the more recent adult's findings with feet motion (Troje, 2013; Troje & Chang, 2013; Troje & Westhoff, 2006). These psychophysics experiments with adults conjectured about an innate predisposition of the human visual system to orient or detect local motion, namely, to the motion of the feet. This ability was speculated to be an early adaptive evolutionary behavior that enabled the rapid detection of other locomoting animals in the environment (Troje, 2013; Troje & Chang, 2013; Troje & Westhoff, 2006). Thus, newborns' studies fundamentally begun by questioning if humans have an innate tendency for selecting or preferring biological motion in relation to motion-matched controls.

To test this hypothesis, Simon, Regolin & Bulf (2008) analyzed the looking behavior of two to three days old infants in two preferential looking experiments presenting: (1) an intact point-light walker of a hen walking in place (i.e. walking as if on a treadmill), with a set of non-biological randomly moving dots; and (2) the same intact hen point-light walker, with an inverted version of the display (Francesca Simion et al., 2008). A point-light display of a walking hen was used to account for the remote possibility that two days old infants may have had any visual experience with the human motion; furthermore, if there is an innate predisposition for biological motion at birth, this mechanism would be generalized to the motion of living beings (F Simion et al., 2011; Francesca Simion et al., 2008; Vallortigara, Regolin, & Marconato, 2005).

Results showed that neonates looked longer to the intact hen point-light walker, both in comparison with the non-biological moving stimulus and to the inverted hen (Francesca Simion et al., 2008). Because such young infants had no familiarity to the configuration of the biological motion stimulus presented (i.e., the form of a hen), the authors argued for the existence of an innate perceptual mechanism for the analysis of biological motion (Francesca Simion et al., 2008). In addition, they attributed the conflicting results with the findings of Fox & McDaniel (1982)—that reported no preferences at two months of age—to the duration of the trials employed: Fox & McDaniel (1982) failed to find a preference for the intact display because they used a rather short trial length of 15 seconds (Francesca Simion et al., 2008). A replication of these newborns' preferences for biological motion in relation to random motion, but using the point-light display of a person walking (point-light walker) rather than a hen, was more recently published by another team of researchers (Bidet-Ildei, Kitromilides, Orliaguet, Pavlova, & Gentaz, 2014).

These results with newborns are extraordinary given the limited visual experience of the two-days old infants. However, there are some limitations to the conclusion of an innate predisposition to biological motion.

First, a preference for the intact display over an inverted point-light walker might be explained by an inborn sensitivity to the gravity-dependent dynamics of motion, and not by an innate predisposition to biological motion (Bardi et al., 2014). Furthermore, the two motions (upright and inverted walkers) differ in their orientation and in the amount of motion each stimulus occupies in the screens: the upright display describes an increased amount of motion in the feet region (two limbs) in comparison with the head region (one limb); whereas the opposite occurs in the inverted point-light walker—this might be pertinent in this particular population if we consider that, for instance, looking at the top of the screens and lifting one's head might imply a great motor effort for newborns (Frankenhuis et al., 2012).

Second, the other control stimulus, the non-biologically moving dots, differed from the intact hen point-light walker by two factors: (1) the motion of the individual dots, and (2) the absence of a coherent configuration of motion (the dots in this control stimulus moved in arbitrary directions) (Francesca Simion et al., 2008). Thus, a preference for the hen point-light walker in the relation to random motion can be attributed either to the presence of a coherent configuration, and/or to the specific biological motion features of the single moving dots present only in the intact hen point-light walker (Méary, Kitromilides, Mazens, Graff, & Gentaz, 2007; Francesca Simion et al., 2008).

Considering the aforementioned limitations, Bardi, Regolin & Simion (2011) conducted two new preferential looking experiments with newborns, contrasting the same intact coherent walking motion of the hen but with two new control stimuli: a scrambled hen point-light walker and rigid motion.

1.2.1.1 Newborns process local (but not global) configural relations

An intact coherent point-light walker is composed by individual dots in motion (featural information) that have both local configural relations (i.e. relation between at least two dots in the display, e.g. limbs motion) and global configural relations (i.e. the relation between all the dots that compose the display, which in the human point-light walker corresponds to the form of a person walking). In the case of the newborns studies, they employed the point-light walker of a hen, therefore, the global configuration of this stimulus corresponds to the form of a hen (Bardi et al., 2011; Francesca Simion et al., 2008).

To account for newborns' sensitivity to process only individual features of a point-light walker (i.e. the individual dot motions) vs. the ability to process the relations between those features (i.e. local and global configural processing), two novel manipulations of the intact point-light walker of a hen were implemented in two separate preferential looking experiments: a rigid point-light walker hen, and a scrambled point-light walker hen – see Figure 4 for a schematic of the stimuli.

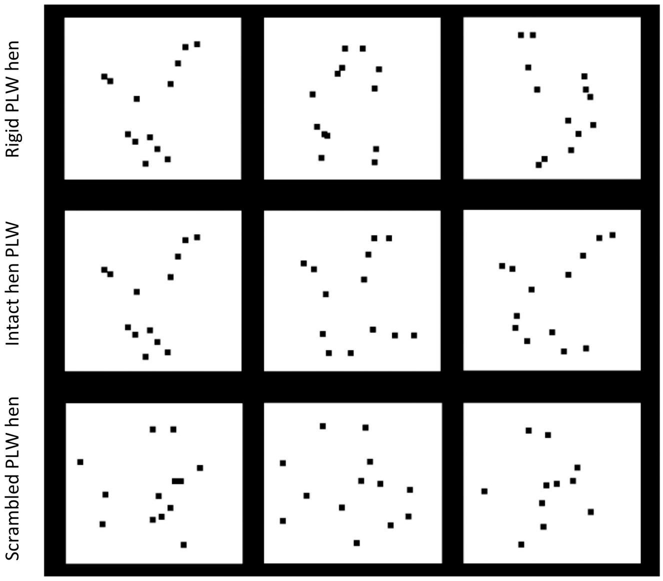

Figure 4. Three samples frames of the three point-light walkers (PLWs) employed in Bardi et al. (2011)

Top – rigid point-light walker hen (a static frame of the PLW was animated to rigidly rotate around its central axis); middle – intact point-light walker of the hen; bottom – scrambled point-light walker hen (the dots' initial locations were spatially randomized disrupting configural processing but its individual trajectories are kept intact).

Adapted from "Biological motion preferences in humans at birth: role of dynamic and configural properties" by Bardi, Regolin and Simion, 2011, Developmental Science, 14(2), p. 355. Copyright 2010 by the Blackwell Publishing Ltd.

Firstly, Bardi et al. (2011) contrasted a coherent point-light walker of a hen with rigid motion (Bardi et al., 2011). The rigid motion display consisted of a single-frame of the intact hen point-light walker animated to move around its central vertical axis producing a rotating hen-like object. This control stimulus depicts a coherent global configuration but no articulated motion, it moves rigidly, close to object motion. Results revealed that newborns spontaneously prefer the intact hen point-light walker in relation to rigid motion.

In the second preferential looking experiment, the authors contrasted the same coherent point-light walker with a scrambled point-light walker (Bardi et al., 2011). In the scrambled point-light walker, randomizing the dots' initial locations disrupts the coherent motion configuration of the hen. Because the dots in the scrambled display are randomly placed, this stimulus is incoherent and there is no possibility of any perceptual grouping of the dots. Both local and global configural relations are disrupted in this stimulus. However, and most importantly, the individual motions of the dots are kept intact and comparable to the intact or coherent point-light walker; featural information is the same both in the scrambled and coherent display (Bardi et al., 2011). The scrambled manipulation is a classic control stimulus from visual perception studies for testing configural processing.

In contrast to the results of the first experiment, newborns looked the same overall amount of time for the two displays, that is, they did not prefer the coherent point-light walker in relation to the scrambled one (Bardi et al., 2011).

This result suggests that we do not process configural relations in biological motion at birth. The authors speculated that it was the presence of the intact motions of the individual dots that determined newborns' looking behavior (Bardi et al., 2011). When the individual motions of the dots are kept intact (as it is the case of the scrambled point-light walker), despite the absence of a coherent configuration (or of any configural information), newborns do not prefer the intact point-light walker (Bardi et al., 2011). Thus, humans at birth do not prefer configural relations (local or global) in biological motion.

To test if newborns are, at least, able to process some level of configural relations in biological motion perception, an infant-controlled habituation experiment was subsequently implemented by the same team, analyzing newborns' discrimination abilities between the same two stimuli, a coherent and a scrambled hen point-light walker (Bardi et al., 2011).

The habituation paradigm is structured on the observation that infants tend to decrease their attention to a stimulus that is presented over a series of trials (habituation phase); when this happens, a new stimulus is shown to the infants (testing phase) (Colombo & Mitchell, 2009; Oakes, 2010; Proffit & Bertenthal, 1990). Thus, in a habituation experiment, infants are repeatedly presented with a stimulus until they reach habituation, i.e. until a certain criterion of response decreases to some pre-established level (usually, when the total looking time on three consecutive trials does not sum to 50% of the total looking of the first three trials) – see Figure 5. At this point, a new stimulus is presented to the infant (testing phase): if the infant's looking time towards the new stimulus increases, there is evidence that the infant discriminated the two stimuli; if there is no increase on infant's looking time with the introduction of the new stimulus, no discrimination between the two stimuli is assumed (Proffit & Bertenthal, 1990) – see Figure 5 for a graphical illustration of an infant's looking behavior during a hypothetical habituation experiment.

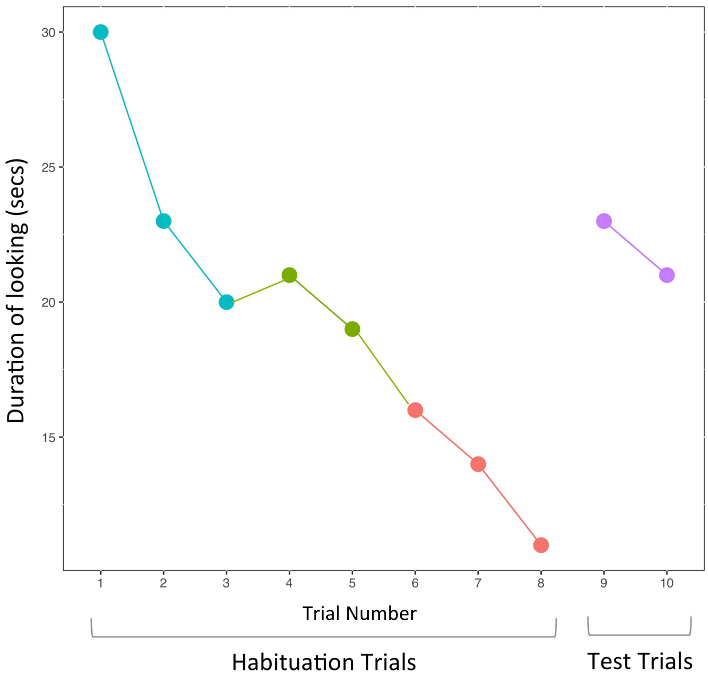

Figure 5. Hypothetical illustration of a discriminative response in an infant controlled habituation procedure.

*From trial 1 to 8, the same habituation stimulus was presented; a second stimulus was introduced on trial 9 and 10. The blue circles correspond to the first three trials; the sum of duration of looking on these three trials is used to calculate the habituation criterion (0.5 * sum of looking on first three trials); then the sum of the most recent three-habituation trials is compared to the criterion value. In this case, the infant reached habituation by summing looking on trials 6, 7 and 8 (red circles), thus, on trial 9 (purple circle), a new stimulus was first presented and the infant looking time increased meaning that the infant discriminated the old vs. new stimulus.*

Three critical details of this procedure must be highlighted: first, the procedure is infant-controlled because the infant determines the time of presentation of the habituation stimulus by the time he/she takes to habituate—this means that *time for habituation* can be used as a measure of learning or encoding the stimulus (Colombo & Mitchell, 2009); second, when testing discrimination between two visual stimuli, the stimulus used in the habituation and testing phase is counterbalanced across infants, meaning that a group of infants is habituated to the target stimulus and another group of infants is habituated to the control stimulus—this makes it possible to extract and compare other measures of the stimuli such as total time for habituation to each stimulus or time of encoding of the two stimuli; second, only discrimination is obtained from this procedure (Proffit & Bertenthal, 1990).

Using an infant-controlled habituation procedure, newborn infants were tested for discrimination between an intact coherent point-light walker of a hen and an scrambled version—newborns showed an increased looking time associated with the introduction of the novel stimulus, therefore, they discriminated the two stimuli (Bardi et al., 2011). No other measures were reported in this experiment.

This result was intriguing because, though newborns show no preference between a coherent and a scrambled point-light walker (they equally turn at both stimuli), they are able to discriminate the two stimuli using an habituation procedure. Considering that a coherent point-light walker is different from a scrambled point-light walker because both local and global configural information is extracted from this stimulus (and not from the scrambled manipulation), newborns must process at least some level of configural relations in biological motion. However, because the scrambled point-light walker lacks both local and global configural information (and the coherent displays has both), it is impossible to conclude if newborns discriminated the two stimuli based on the processing of local and/or global configural relations.

A shift in processing complex visual stimuli from local parts towards the perception of structured wholes is seen in a variety of experiments using distinct visual stimuli (Frankenhuis et al., 2012; Rakison & Butterworth, 1998). Therefore, we speculate that newborns discriminated the two stimuli based on local configural processing. If this is the case, newborns discriminated the coherent point-light walker from the scrambled hen based on the processing of local (e.g. feet motion) but not global configural relations in biological motion (Bardi et al., 2011, 2014; Masahiro Hirai & Senju, 2020; Wang et al., 2018). The ability to process global configural relations (or to retrieve form-from-motion) in biological motion might thus emerge later in development, probably tied to more visual experience with the human motion and to cortical development (Janette Atkinson, 2002).

In any case, the perception of biological motion is limited at birth; in the next section we review studies indicating how, in fact, biological motion (in particular biological motion configural processing) undergoes large developmental changes after birth, during our very first year of life (Bertenthal, Proffitt, & Cutting, 1984).

1.2.2 Developmental Changes in Biological Motion Perception After Birth

In the late 80s and 90s, following the pivotal work of Fox & McDaniel (1982), that emphasized a significant role for visual experience in biological motion perception, a set of key habituation experiments were conducted; these explored the role of visual experience in biological motion perception during infancy—for a complete review of this research see Bertenthal (1993).

A large amount of what we know today about infants' perception of biological motion resulted from this set of infant-controlled habituation studies, testing infants aged three, five, and seven months-old (Bertenthal, 1993; Bertenthal & Pinto, 1994; Bertenthal et al., 1984; Bertenthal, Proffitt, & Kramer, 1987; Bertenthal, Proffitt, Kramer, & Spetner, 1987; Bertenthal, Proffitt, Spetner, & Thomas, 1985; Booth, Pinto, & Bertenthal, 2002; Pinto & Bertenthal, 1996; J Pinto & Shiffrar, 1999). Overall, this research focused on the mechanisms by which the developing perceptual system, in the first months of life, matures and organizes the coherent global percept of a person walking (Bertenthal, 1993; Bertenthal & Pinto, 1994; J Pinto & Shiffrar, 1999). Thus, in these experiments, the more familiar motion of a person walking (not the display of a hen as in the newborns' studies) was employed. Infants were presented with an intact coherent motion of a person walking, projected on the coronal (i.e. frontal-parallel) plane vs. a wide range of visually matched motion controls. Different perceptual properties of the point-light walker that disrupt the global configuration of a person walking were manipulated and tested for discrimination. The aim was to analyze *which* visual perceptual properties shape the perception of biological motion during infancy (Bertenthal, 1993).

As such, using habituation, it was found that infants aged three (Bertenthal, Proffitt, Kramer, et al., 1987), and five months (Bertenthal et al., 1984) are able to discriminate a coherent point-light walker from a spatially scrambled one. These results are in accordance with the newborns findings, as these also found that newborns discriminate (despite not preferring) a coherent walker from a scrambled one (Bardi et al., 2011).

Similarly, the upright orientation of a display appears to be relevant for discrimination at three and five months age: infants at both age groups showed a discriminative response when contrasting an intact upright point-light walker with an inverted point-light walker (Bertenthal et al., 1984).

In an intact point-light walker, the connections between two adjacent dots are rigid since the anatomy of our skeleton is rigid—e.g. the distance between a shoulder and an elbow is constant. Evidence that infants are sensitive to these rigid connections indicates that they are able to perceive a "stick figure" out of the moving dots, thus, they perceive the global configuration of a walking person (Bertenthal, 1993). To analyze if infants are sensitive to these rigid connections between adjacent body joints, Bertenthal, Proffitt & Kramer (1987) created a non-rigid control stimulus where the fixed distances between the joints changed in every frame of the stimulus' presentation. Adults viewing this control report seeing a display whose limbs appear elastic (Bertenthal, Proffitt, & Kramer, 1987) – see Figure 6.

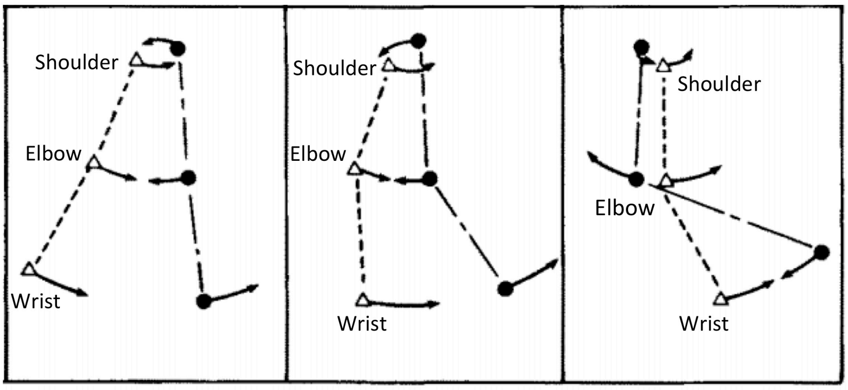

Figure 6. Illustrations of the relative positions of the shoulder, elbow, and wrist in the an intact rigid and non-rigid point-light walker employed by Bertenthal, Proffitt & Kramer (1987)

Relative positions of the shoulder, elbow and wrist of an intact rigid point-light walker (open triangles) and a non-rigid point-light walker (darkened circles). Both the open triangles and the darkened circles represent the three positions of three point-lights corresponding to the shoulder, elbow and wrist. Note that in the non-rigid display, the distances between point-lights change per frame.
Adapted from "Perception of biomechanical motions by infants: implementation of various processing constrains" by Bertenthal, Proffitt and Kramer, 1987, Journal of Experimental Psychology: Human Perception and Performance, 13(4), p. 581. Copyright 1987 by the American Psychological Association, Inc.

However, this manipulation has an important limitation: besides perturbing the rigid connections between the dots, the temporal phase relations of the dots *within* a limb are also perturbed.

Two temporal phase patterns characterize the walking motion: (1) a *within* limbs pattern—there is a synchronized oscillatory motion within the joints that constitute a single limb, i.e., the three dots that compose a limb (e.g. shoulder, elbow and wrist) move in synchrony with respect to one another; and (2) a *between* limbs pattern—the four limbs of a point-light walker (two arms and two legs) oscillate around a single vertical axis (the torso) with adjacent limbs moving in anti-phase directions (e.g. right leg moves in anti-phase relative to the left leg) (Bertenthal, 1993; J. M. Pinto, 1997).

Therefore, to control for this potential confound, a second control, non-rigid stimulus was created, applying the same non-rigid manipulation to the limbs. However, in the two non-rigid control stimuli, total variation between the distances of the joints was equivalent but distances between connected joints differed between the two stimuli on a frame basis. The three stimuli (intact rigidly connected point-light walker and the two non-rigid or elastic point-light walkers) had all different sets of temporal phase relations within limbs but only the intact display had rigid connections between the joints.

Three and five months-old infants were then tested in a habituation task with the three stimuli: an intact rigidly connected point-light walker and the two non-rigid or elastic point-light walkers.

Results from this experiment were unexpected: both three and five months-old discriminated the intact rigidly connected point-light walker from the two non-rigid displays; however, and most importantly, when opposing the two non-rigid displays, only three months-old discriminated the two displays, and the more visually experienced five months-old infants showed no evidence of discrimination (Bertenthal, Proffitt, & Kramer, 1987).

It seems unlikely that three months-old infants are able to discriminate the two non-rigid displays based on the different temporal phase patterns to which the older infants, with a more experienced visual system, would fail to process; plus, adult observers are highly sensitive to these temporal phase perturbations (Bertenthal & Pinto, 1994).

Several hypotheses were proposed to explain these results. The main one conjectured that older five months-old infants were not exploring the rigid vs. non-rigid connections between the joints, instead, they were using the broader presence of a coherent and intact global configuration of a person walking, existent only in the intact display (Bertenthal, 1993).

1.2.2.1 From local to global: a shift from three to five months

To examine infants' sensitivity both to the specific temporal patterns of the walking motion, and to a broader sensitivity to the coherent global human walking configuration present only in an intact display, Berthental (1993) tested three and five months-old infants in another habituation experiment.

In this experiment, infants' sensitivity between an intact walker and a phase-shift point-light walker was tested, that is, a control stimulus in which the temporal patterns of the point-light walker were manipulated (Bertenthal, 1993; J. M. Pinto, 1997).

In the phase-shift point-light walker, both *between*-limb and *within*-limb motions were temporally shifted in respect to the intact display. As a result, in the phase-shift walker, each dot maintained its individual or absolute motion trajectories intact, but the starting location for each point-light was shifted by a random number of animation frames—e.g. the wrist point-light, instead of initiating its trajectory on the first frame of the presentation, started at the tenth frame (ten was the generated random number); this was applied to all dots of the display. Adult observers describe such display as similar to a marionette because connected limb segments do not always move in the same direction (Booth et al., 2002). Furthermore, this manipulation was applied to an intact point-light walker of a person, of cat, and to a point-light walker of a four legged spider, generating six different stimuli: three intact walking motions and three phase-shifted motions (Bertenthal, 1993; J. M. Pinto, 1997). Three and five months-old infants were subsequently tested for discrimination of the intact vs. phase-shifted displays.

Results showed that both three and five months old infants discriminated the intact human point-light walker from its phase-shift version (Bertenthal, 1993; J. M. Pinto, 1997). Nevertheless, only three months-old discriminated the non-human displays from their phase-shift versions—five months-old did not discriminate the cat point-light walker from the phase-shift cat display, and the same result was obtained using the configuration of a spider (Bertenthal, 1993; J. M. Pinto, 1997). Even when the same manipulation was applied to two human-based displays but both shown 180° inverted in the picture plane (inverted point-light walker vs. inverted phase-shift point-light walker), three months-old continued to discriminate the two displays, whereas five months did not exhibit a discriminative response (Bertenthal, 1993).

It seemed thus that five months-old infants were responding specifically to the global motion configuration of a person, confirming the initial hypothesis that the older infants are sensitive to the human form, thus, they process the stimulus at a larger global spatial scale (Bertenthal, 1993). In addition, to verify if a developmental shift in biological motion perception happened only between three and five months of age, the older seven months-old infants were tested in the same task with the non-human displays and its phase-shift versions. Again, seven months-old, like five months, only discriminated the intact point-light walker from its phase-shift version when the global configuration of the display corresponded to a human walking (Bertenthal, 1993; J. M. Pinto, 1997).

Two main conclusions were drawn from these experiments: first, there is a critical developmental shift in biological motion perception from three to five months of age; second, this developmental shift is linked to the ability of the more mature visual system to process the global configuration of a human in action from motion-carried information (Bertenthal, 1993; J. M. Pinto, 1997).

To specifically test these two conjectures, Booth, Pinto & Bertenthal (2002), measured the discrimination abilities of three and five months-old infants but, this time, using two similar global configurations: the point-light display of a human walking (point-light walker) and a point-light display of a human running (point-light runner). Both the point-light walker and runner share the same global human motion configuration (the two stimuli describe a person), and the same temporal phase patterns (synchrony oscillatory motion within the joints, and adjacent limbs moving in anti-phase directions). The two stimuli, however, differ on many other dimensions; for instance, the local motion of the limbs of the runner moves in much greater speed than the limbs of the walker; the degrees of bending of the elbows and knees are also distinct between the two actions (Booth et al., 2002). In spite of these salient differences between the two stimuli, the authors hypothesized that, if five months-old infants are more tuned to the human global configural relations in biological motion, they will not discriminate the two stimuli; whereas three months-old, presumably more sensitive to local information, will discriminate the two displays (Booth et al., 2002).

Findings from this habituation experiment were in accordance with these predictions: five months did not discriminate the point-light walker from the point-light runner but the younger infants did; five months were, thus, less responsive to the differences between the two stimuli than three months-old (Booth et al., 2002).

Unlike the older infants, the discriminative response of the three months old can be explained by the local differences between the two displays. The point-light walker and point-light runner differ only at the level of local relations and the younger infants discriminated the two displays (Booth et al., 2002). Infants at three months seem thus to process biological motion in a more fragmented fashion, being more sensitive to local groupings of point-lights (local configural information), and not to their global configuration (Bertenthal, 1993; Booth et al., 2002; J. M. Pinto, 1997).

Older five months-old infants likely process configural relations over a larger spatial scale thus process the human global motion configuration. There seems to be, thus, a developmental trajectory from local to global (or from "parts-to-whole") in biological motion perception. This is explicit in another habituation experiment conducted by the same team of researchers with three months-old infants (Pinto & Bertenthal, 1996).

In this experiment, the authors conjectured that if three months-old fail to process the global human motion configuration in a point-light walker (because they are tuned to the local configural information of the limbs) then an intact point-light walker should elicit the same response as a set of moving limbs, randomly distributed, and not organized around the torso. Both an intact display and a set of moving limbs have featural and local configural information preserved.

To test this hypothesis, three, five and seven months-old infants were evaluated for discrimination between an intact point-light walker (i.e. unitary axis display) and a divided point-light walker (i.e. a divided axis display) (Pinto & Bertenthal, 1996; J. M. Pinto, 1997) – see 7 for a static illustration of the two stimuli.

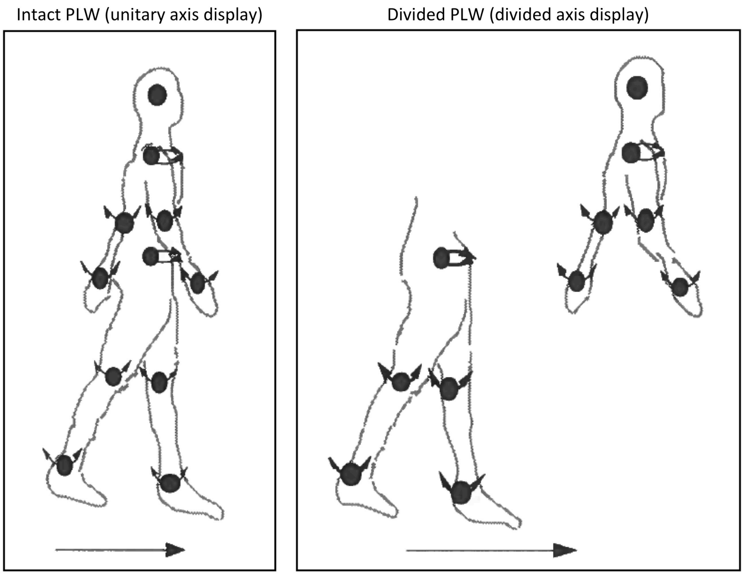
Intact PLW (unitary axis display)
Divided PLW (divided axis display)

Figure 7. Static illustrations of the intact (unitary) point-light walker (PLW) and divided point-light walker employed by Pinto & Bertenthal (1996)

Left – static illustration of the intact point-light walker (unitary axis display).
Right – static illustration of the divided point-light walker (divided axis display).
Only illuminated dots were presented to the infants. The contours illustrated in the figure are only for comprehension.
Adapted from “Developmental changes in infants’ responses to point-light displays of human gait” by Pinto and Bertenthal, 1996, Infant Behavior and Development, (19), p. 677. Copyright 1996 by Elsevier, Inc.

In the intact point-light walker, the limbs are organized along an elongated vertical axis, the torso. In this experiment, the control stimulus consisted in breaking this unitary axis in two halves by the waist level, and show these two halves (upper and lower limbs) horizontally separated as two separate sets of moving limbs (this stimulus was termed the divided axis display) (Pinto & Bertenthal, 1996; J. M. Pinto, 1997).

The prediction was that five and seven months-old infants discriminate the unitary axis (intact point-light walker) from the divided axis display (divided point-light walker) but not three months-old infants. The rationale behind this prediction was that the older infants are able to process the global human motion configural information in point-light walkers (Bertenthal, 1993), thus, they will discriminate an intact display from one that is divided in two halves. In contrast, because limbs' motion was preserved in both stimuli, the less mature visual system of three months-old will not discriminate the two displays because local motion is the same in both stimuli (Pinto & Bertenthal, 1996; J. M. Pinto, 1997).

As hypothesized, three months-old did not discriminate the intact point-light walker from the divided axis display, and the older five and seven months-old discriminated the two stimuli (Pinto & Bertenthal, 1996; J. M. Pinto, 1997). The authors speculated that, for the three months-old infants, the divided and the unitary axis displays are visually equivalent since both stimuli have intact local configural information. Because the younger infants are able to process local motion, but not the global human motion configuration in a point-light walker, they do not discriminate the two stimuli (Pinto & Bertenthal, 1996; Pinto, 1997). The older five and seven months-old infants are able to process global configural information in point-light displays, thus, these infants discriminate the intact display from the divided point-light walker.

More recently, another habituation experiment with six and nine months-old confirmed these conclusions by showing the ability of these infants to perceive human point-light walkers as solid forms, thus, likely processing its global configuration (Moore, Goodwin, George, Axelsson, & Braddick, 2007).

In this habituation experiment, both six and nine months-old infants showed a greater recovery of attention when the solidity of a human point-light walker was violated as it passed through a table, compared to when it passed behind the table; when using a scrambled or an inverted point-light walker, this effect was absent (Moore et al., 2007). Nine and six months-old infants linked a solid form only to the intact upright point-light walker (this was the only stimulus that could not "pass" through a table), suggesting that they perceive the global configuration of the intact point-light walker (Moore et al., 2007).

In sum and to the point, there is a developmental shift in the perception of the walking action between three and five months of age. Newborns and younger three months-old infants are tuned to the local properties of biological motion, regardless of the presence of a human global configuration in point-light walkers; at five months of age, infants appear to become more sensitive to the global configuration (Bertenthal, 1993). In other words, younger infants focus in the local properties of the displays (such as velocities and trajectories of individual or adjacent dots), and only later focus in the more meaningful global human configuration of the walking action (Bertenthal, 1993). The discriminative abilities of five and seven months-old seem to be determined by an extended visual experience with human walking action or, more generally, with the human motion (Bertenthal, 1993).

Although older infants are sensitive to the phase-shifting of a walker (they discriminate an intact point-light walker from its phase-shifted version), when the less familiar configuration of a spider and a cat is used, they do not discriminate these non-human displays from their phase-shifted versions (Bertenthal, 1993; J. M. Pinto, 1997). The same is true for other visual properties of the intact point-light walker, such as its upright orientation: while five months-old are sensitive to the orientation of a point-light walker (Bertenthal et al., 1984), they do not discriminate an upright spider from an inverted one (Bertenthal, 1993).

The extended visual experience with the human gait of the five months likely determines a more narrowed perceptual processing of point-light walkers in relation to younger infants. The intact human form or, more specifically, the global configuration of the human walking action seems to determine the discriminative abilities of infants from five months of age. Whether this sensitivity is translated, from this age, into a higher order social-cognitive processing that includes the recognition of point-light walker stimuli as the representation of a person walking (and to a higher-order cortical processing), is still unclear.

1.3 Biological Motion as a Hallmark of Human Social-Cognition[1]

Social cognition refers to our ability to understand other people, which includes basic perceptual skills that enable us to discriminate people from objects, to more complex abilities such as understanding other people’s actions, emotions, and intentions (Striano & Reid, 2006).

The perception of biological motion has been considered one of the main bases of human social-cognition, as perceiving the motion of others is a fundamental aspect for understanding and interacting with others. Several findings contributed to this assertion.

First, a set of experiments conducted with point-light displays revealed that a notable amount of meaningful social information could be derived from biological motion and point-light displays. We can rapidly perceive what people are doing, how they feel, or what are their intentions—solely by looking at the dynamics of their bodies in motion. Biological motion conveys relevant social information about others.

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[1] The title of this section is the same as Pavlova (2012)

Neuroimaging experiments consistently show that biological motion engages a specialized set of brain areas, very different from other motion stimuli. The perception of biological motion, as well as action recognition, is processed in the superior temporal sulcus (STS)—with a more pronounced activation in the posterior part of the STS and in the right hemisphere (right pSTS) (E. Grossman et al., 2000). Importantly, this region is also heavily associated with other aspects of human social perception and cognition, such as face and voice perception, emotions, dispositions and intentions of others (Deen et al., 2015). The neural mechanisms that support biological motion perception seem also to support other human social-cognitive functions. In addition, these responses start developing in our first year of life (Ichikawa, Kanazawa, Yamaguchi, & Kakigi, 2010; Lahnakoski et al., 2012; Lloyd-Fox, Blasi, Everdell, Elwell, & Johnson, 2011; Lloyd-Fox et al., 2009; V. Reid, Hoehl, & Striano, 2006; V. M. Reid, Hoehl, Landt, & Striano, 2008).

Finally, studies on biological motion perception with infants demonstrate that we selectively prefer to look at biological motion in comparison with other kinds of motion since birth (Bardi et al., 2011; F Simion et al., 2011; Francesca Simion et al., 2008), and that this early attention bias to biological motion is critical for infants' social-cognitive development (Frith & Frith, 1999; Pavlova, 2012).

Altogether, these findings indicate the existence of a perceptual system for analyzing biological motion that is functionally integrated with our social-cognitive abilities since early in life; and how the perception of biological motion is a hallmark of human social cognition (Pavlova, 2012).

1.3.1 Biological Motion Conveys Relevant Information About Others

Biological motion is a rich source of information about others. This is true not only for adult observers but also for human infants.

Adults are fast and accurate in identifying different actions from a single point-light display (Dittrich, 1993; Johansson, 1973, 1976); but they can also identify the gender (Barclay, Cutting, & Kozlowski, 1978; Kozlowski & Cutting, 1977; Runeson & Frykholm, 1983), age (Montepare & Zebrowitz-McArthur, 1988), sexual orientation (Ambady, Hallahan, & Conner, 1999), emotional state (A. P. Atkinson et al., 2004; Brownlow, Dixon, Egbert, & Radcliffe, 1997; Pollick, Paterson, Bruderlin, & Sanford, 2001), intentions (Runeson & Frykholm, 1983), personality traits (Montepare & Zebrowitz-McArthur, 1988; Troje, 2008), or even the identity of a familiar person (Cutting & Kozlowski, 1977; Jokisch et al., 2004; Jokisch, Daum, & Troje, 2006).

The visual motion information contained in point-light displays is also sufficient for adults to understand the interactions between two or more moving displays (Neri, Luu, & Levi, 2006). For instance, observers exposed to displays of two agents dancing or fighting, and to desynchronized versions of these interactions, are more accurate in judging the number of agents presented in the meaningful synchronized interactions (Neri et al., 2006). This reveals that observers are also able to interpret the motions of coordinated interactions solely from motion information.

Developmentally, several experiments also indicate that children and infants decode important social information from biological motion.

Five months-old infants are sensitive to happy and angry emotional content of body movements (Heck, Chroust, White, Jubran, & Bhatt, 2018).

Six months-old can detect the right and left direction of an upright point-light walker but not of an inverted walker (Kuhlmeier, Troje, & Lee, 2010). Also at six months of age, but not the younger four months-old, attribute goals to a point-light walker moving towards to reach a box; but not to an inverted control (Schlottmann et al.; Schlottmann & Ray, 2010).

At twelve months of age, when shown a point-light walker turning to observe a target, infants follow the point-light walker's "gaze" by looking into the same direction that the point-light walker has turned; and, again, this effect is absent if an inverted walker is employed in the same task (Yoon & Johnson, 2009).

Biological motion perception also appears to prime infants' ability to categorize animals in relation to vehicles: twelve months-old that watched a video of a point-light walker, subsequently performed above chance in a animal-vehicle categorization task, whereas infants that watched random motion or an expansion-contraction motion, performed at chance level (Poulin-Dubois, Crivello, & Wright, 2015). Hence, the authors conclude, perception of biological motion facilitated the categorization of animals at twelve months of age (Poulin-Dubois et al., 2015).

During infancy, there seems to be a growing sensitivity to biological motion, which includes the development of configural processing (Bertenthal, 1993), and the ability to perceive relevant social information from the motion of others.

At fourteen months, toddlers prefer or look longer to point-light displays representing non-disrupted social interactions between two people in relation to displays representing disrupted social interactions (Galazka, Roché, Nyström, & Falck-Ytter, 2014). An example of a non-disrupted social interaction stimulus consisted of a video showing a point-light agent falling backwards *toward* another point-light agent; the second point-light agent then caught the falling one before it hit the ground, and pushed her/his back to standing position. In the disrupted pair, the point-light agent fell *away from* the second point-light agent, and the rescue act was not in accordance with the position of the falling point-light agent (Galazka et al., 2014). In addition, preferences for the non-disrupted interactions only happened when upright displays were presented because, when inverted versions of both disrupted and non-disrupted displays were shown, toddlers revealed no preference for either stimulus (Galazka et al., 2014).

Children aged 3 years recognize and discriminate between various point-light displays of different human and animal motions; and recognition of human vs. non-human motion configurations is completely developed at the age of 5 years (Pavlova, Krägeloh-Mann, Sokolov, & Birbaumer, 2001).

Children from 7 to 12 years who scored higher in a biological motion identification task (in this task, they had to identify the facing direction of a point-light walker under masking noise), also scored higher on a subsequent theory of mind task (Rice, Anderson, Velnoskey, Thompson, & Redcay, 2016).

Numerous behavioral experiments indicate that we extract relevant information about others from biological motion. Biological motion is a socially relevant stimulus for adults, children and human infants. Note, however, that these studies have little in common with the initial mechanistic questions about the perceptual organization of the individual and local configurations into the global coherent percept of a person walking (Troje, 2013). Nevertheless, neurophysiology findings indicate that biological motion configuration is processed at the same regions as other high-level social-cognitive functions.

1.3.2 STS Responds to Biological Motion and to Other Social Stimuli

The perception of biological motion recruits different and specialized brain areas, from the occipitotemporal to the prefrontal cortices (inferior frontal gyrus or near premotor cortex) (E. D. Grossman, 2013; Pyles & Grossman, 2013). However, the superior temporal sulcus (STS), specifically, the right posterior extent of the superior temporal sulcus—the right posterior superior temporal sulcus (right pSTS)—is by far, the most reported, and specialized brain area for processing biological motion (Carter & Pelphrey, 2006; Deen et al., 2015; Grezes et al., 2001; E. Grossman & Blake, 2001; E. Grossman et al., 2000; E. D. Grossman, 2013; E. D. Grossman, Battelli, & Pascual-Leone, 2005; E. D. Grossman & Blake, 2002; Lichtensteiger, Loenneker, Bucher, Martin, & Klaver, 2008; Pelphrey et al., 2003; Peuskens, Vanrie, Verfaillie, & Orban, 2005; Pyles & Grossman, 2013)—see (E. Grossman et al., 2000) for a complete review.

The superior temporal sulcus (STS) is one of the longest sulci of the human brain, extending from the inferior parietal lobe anteriorly along the full length of the temporal lobe – see Figure 8 for a depiction of the STS.

Studies investigating brain responses to biological motion have identified that the posterior part of the sulcus, in the right temporal cortex, specifically responds to intact point-light displays.

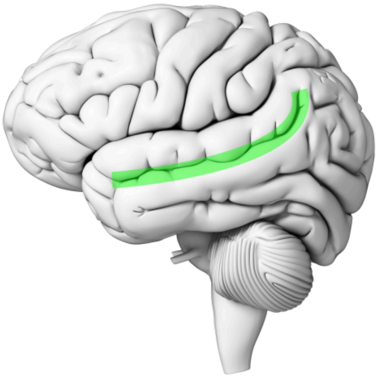

Figure 8. Superior Temporal Sulcus (STS)

Adapted from Brain and Language course by POINT-LIGHT DISPLAY. Howard, 2020, from http://point-light display.tulane.edu/~h0Ward/BrLg/STS.html, Copyright 2019 by Harry Howard

Neuroimaging experiments typically contrast brain responses to the passive viewing of an intact coherent display of a person in action, with an ample number of visually matched controls, such as non-biological motion stimuli (e.g. simple coherent translating motion or rigid object motion), a point-light display inverted in the picture-plane (inverted point-light display), or scrambled point-light displays. Functional Magnetic Resonance Imaging (fMRI) experiments consistently localize an enhanced focus of activity in the right posterior region of the STS associated with the perception of intact biological motion in contrast to these different motion controls (Beauchamp, Lee, Haxby, & Martin, 2003; Deen et al., 2015; Grezes et al., 2001; E. Grossman & Blake, 2001; E. Grossman et al., 2000; E. D. Grossman & Blake, 2002; Peuskens et al., 2005). Point-light displays embedded in masking noise have the effect of reducing right STS neural responses (Grezes et al., 2001; E. D. Grossman, Blake, & Kim, 2004). When repetitive transcranial magnetic stimulation (TMS) is applied onto the right pSTS region, observers become less sensitive to the detection of point-light displays under masking noise (E. D. Grossman et al., 2005). An upright point-light walker elicits peaks of oscillatory magnetoencephalographic (MEG) cortical activity at 170ms, temporally different from responses elicited by motion matched controls, and over the right temporal cortex (Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004). EEG results also reveal topographically similar responses over the right temporal cortex (Jokisch et al., 2004).

In summary, the right pSTS seems to preferentially respond to the intact coherent configuration of biological motion—and this is found in the mature brain using an ample array of motion-matched controls and different neuroimaging techniques. Moreover, fMRI studies conducted with children show that this right STS dominance to biological motion is present and develops during childhood (Carter & Pelphrey, 2006).

Notably, a wider range of studies also implicates the STS in the processing of other socially relevant stimuli. For instance, STS was implicated in the processing of human faces, voice, language, or even human mental states (Allison, Puce, & McCarthy, 2000; Deen et al., 2015; Hein & Knight, 2008; Lahnakoski et al., 2012; Pavlova, 2012). These findings place the STS at the center of human social cognition and bring to light the existence, in the human brain, of a specific brain network for processing information related to others, i.e. for processing social information.

One of the major functions of the human brain is to recognize and interpret social information (Grossmann, 2015). A cortical network of specific brain areas involved in the processing of social information was identified in the human cortex—this network is typically referred as the social-brain network (Adolphs, 1999, 2009; Allison et al., 2000; Deen et al., 2015; Grossmann, 2015). The social-brain network includes a set of structures such as the amygdala, the orbitofrontal cortex, anterior cingulate cortex, and the temporal cortex. The STS, within the temporal cortex, is a key region in the human social-brain network (Adolphs, 1999, 2009; Allison et al., 2000; Grossmann, 2015).

STS was humorously designated the "chameleon of the human brain" (Hein & Knight, 2008) since it responds to: face perception (Ishai, Schmidt, & Boesiger, 2005), voice perception (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000), speech perception (Binder, 2000), audio-visual integration (Beauchamp, Argall, Bodurka, Duyn, & Martin, 2004) or even to higher-level social abilities such as theory of mind (Deen et al., 2015; Gallagher et al., 2000).

This multifunctionality attributed to one of the longest sulci of the human brain, resulted in a debate regarding the functional organization of this sulcus.

On one hand, a modular organization or a regional sub-specialization was proposed. Here, the sulcus has distinct and functionally specialized sub-regions that respond to different and specific social domains; for instance, the posterior extent of the sulcus responds mainly to biological motion whereas more anterior response-locations are activated only during face perception (Deen et al., 2015).

Another hypothesis is that responses to these different social domains overlap within the sulcus, and there are no domain specific sub-regions. Instead, STS would have a more general function of integrating distinctive social information from other functionally connected sub-systems or networks (Allison et al., 2000; Hein & Knight, 2008; Lahnakoski et al., 2012).

Deen, Koldewyn, Kanwisher & Saxe (2015) conducted an fMRI experiment designed specifically to address these two hypotheses (modular organization vs. general function) and investigate STS responses to social stimuli.

In the same set of adults, STS responses elicited by biological motion (point-light displays performing different actions), face and voice perception, to a theory of mind task, and to an auditory story task, were measured (Deen et al., 2015). Results indicated that STS contains both domain-specific sub-regions—organized along a posterior-to-anterior axis and each selectively responding to specific types of social stimuli—and multifunctional regions—that respond simultaneously to different social information. Face and biological motion perception shared resources in a similar region of the posterior part of the STS, but specific responses to biological motion were also found more centrally, slightly posterior to the region responding to faces (Deen et al., 2015).

The authors concluded that STS is both specific and multifunctional in responding to social stimuli thus to biological motion: some areas (or sub-regions) within the sulcus are specifically activated by the intact point-light motion of an action, while other areas are multifunctional, thus, respond both to biological motion and to other social stimuli (Deen et al., 2015). STS seems thus to serve both biological motion perception and, more widely, human social-cognition. Either way, this result is critical since it links biological motion to other social and more complex stimuli. In fact, the right pSTS was appointed as the early biological basis of human social-cognition by its early connecting function to biological motion perception (Pavlova, 2012). Nevertheless, these early connections or infants' cortical responses to biological motion are still vastly unexplored, in particular right pSTS responses to biological motion in the first months of life.

We know that major developmental changes in biological motion perception happen during infancy, as asserted by behavioral measures based on infants' looking time (Bertenthal, 1993). Despite this, cortical responses in infancy to biological motion in the STS (or, particularly, in the right pSTS) are still little investigated.

1.3.2.1. Infancy: STS responses to biological motion

Developmental neuroimaging experiments provide insights on the organization and developmental precursors of adult social abilities thus the social-cognitive neurodevelopmental field is receiving a growing interest (Azhari et al., 2020; Grossmann, 2015). Infants' brain responses to biological motion can elucidate us towards a broader understanding of the processes involved in mature processing of action observation and understanding (and of human social-cognition) because we can investigate these processes while new perceptual, motor and social skills are still being developed (Grossmann, 2015).

A set of studies focusing on the brain mechanisms for processing biological motion during the first half of the first year of life was recently published, including the ones that resulted in this dissertation (Ichikawa et al., 2010; Lisboa, Miguel, et al., 2020; Lisboa, Queirós, et al., 2020; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009)—most of these studies came out from the advances in functional Near-Infrared Spectroscopy (fNIRS).

1.3.2.1.1 Functional Near-Infrared Spectroscopy (fNIRS)

Functional Near-Infrared Spectroscopy (fNIRS) is a non-invasive, neuroimaging technique, especially suitable for infancy research—for a complete review of this technique see Lloyd-Fox et al. (2010) and Wilcox & Biondi (2015).

The fundamental principle behind fNIRS is that the hemodynamic response of the brain in response to a stimulus can be indirectly measured using near infrared light color changes.

fNIRS takes advantage of the relative transparency of biological brain tissue to near infrared light (wavelength between 650-1000nm); this technique consists of emitting infrared-light, that travels through the scalp and the skull, and that it changes according to the level of oxygenation of a particular region of the brain; these light changes are then used to measure the hemodynamic response of the brain and thus determine a significant functional activation (Wilcox & Biondi, 2015). Because infants' brain tissue is more transparent to light in the near infrared part of the spectrum than adults, and infants have less hair, fNIRS is more suitable for infants than for children and adults (Karmiloff-Smith, 2010; Lloyd-Fox et al., 2010).

In comparison with other neuroimaging techniques, fNIRS is able to overcome the challenges that fMRI poses to infants' research and the limits of EEG spatial resolution.

fMRI has a better spatial resolution than fNIRS (Azhari et al., 2020; Lloyd-Fox et al., 2010). Despite this, fMRI is extremely difficult to apply with awake infants because participants need to be motionless during scanning (Azhari et al., 2020; Lloyd-Fox et al., 2010; Nishiyori, 2016). fNIRS, on the contrary, tolerates a substantial amount of movement from participants: infants can be tested while they are awake, typically sitting on their parent's lap and relatively free to move. fNIRS is also effectively superior to fMRI in its temporal resolution since it acquires data at a relative rapid temporal rate; this permits a shorter length of the experimental session which is pertinent when testing infants (Azhari et al., 2020; Lloyd-Fox et al., 2011; Wilcox & Biondi, 2015).

EEG (electroencephalography) has a better temporal resolution than fNIRS, and neuroimaging studies with infants mainly relied upon the use of EEG (Azhari et al., 2020). However, EEG spatial resolution is very limited. The major advantage of fNIRS in comparison with EEG is that fNIRS has a better spatial resolution, allowing the localization of brain responses to specific cortical regions, which is not possible with ERPs (event related-potentials).

fNIRS uses a simple experimental setting and design, similar to EEG/ERPs: infants also wear a cap (or a headgear), and brain activations are reported relative to channels located in the infants' scalp using external brain landmarks – see Figure 9 for a picture of an fNIRS cap on an infant's head model.

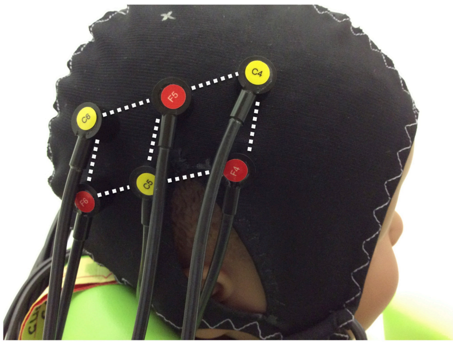

Figure 9. A head model of an infant wearing a fNIRS cap

This cap is composed by 6 optodes: 3 sources (identified in the picture by the red "F" letters), and 3 detectors (identified in the picture by the yellow "C" letters). White dotted lines were drawn in the picture to facilitate the visualization of 7 channels (a connected pair of source-detector).

fNIRS's cap is composed of pairs of sources and detectors; connected pairs of sources and detectors are termed channels (Lloyd-Fox et al., 2010; Nishiyori, 2016). Sources emit infrared light; this light then travels through the infants' head, tissues and scalp, and is detected by nearby detectors.

As previously mentioned, fNIRS measures light changes (or color changes) to determine a functional activation in a specific region of the brain. Roughly speaking, it measures concentrations of blue (corresponding to high levels of oxy-hemoglobin concentration) and red (high level of deoxy-hemoglobin concentration).

When a part of the brain is active, the local firing of neurons produces a complex neurovascular response that results in a large increase in local blood flow, followed by an increase in the oxygen availability of the activated cortical area (Wheelock, Culver, & Eggebrecht, 2019). fNIRS measures the resulting relative changes in local concentrations of oxy-hemoglobin (HbO_2), deoxy-hemoglobin (HHb), and total hemoglobin (HbT) chromophores. Chromophores are the molecules responsible for the color of the blood; these molecules change their color according to the level of blood oxygenation (Lloyd-Fox et al., 2010). Blood oxy-hemoglobin and deoxy-hemoglobin chromophores have different absorption properties of the infrared light thus two different colors—changes in chromophores concentration are thus quantified from light that is emitted by sources and received by detectors located in the infants' scalp (Azhari et al., 2020; Lloyd-Fox et al., 2010). When a stimulus elicits a local neuronal activation, there is an increase in oxy-hemoglobin concentration (fNIRS measures greater concentrations of red light) and a concomitant decrease of deoxy-hemoglobin concentration (fNIRS measures a decrease in the concentrations of blue light) in relation to a baseline (Lloyd-Fox et al., 2010) – Figure 10 shows typical HbO_2 and HHb concentration changes in one channel in a fNIRS functional activation.

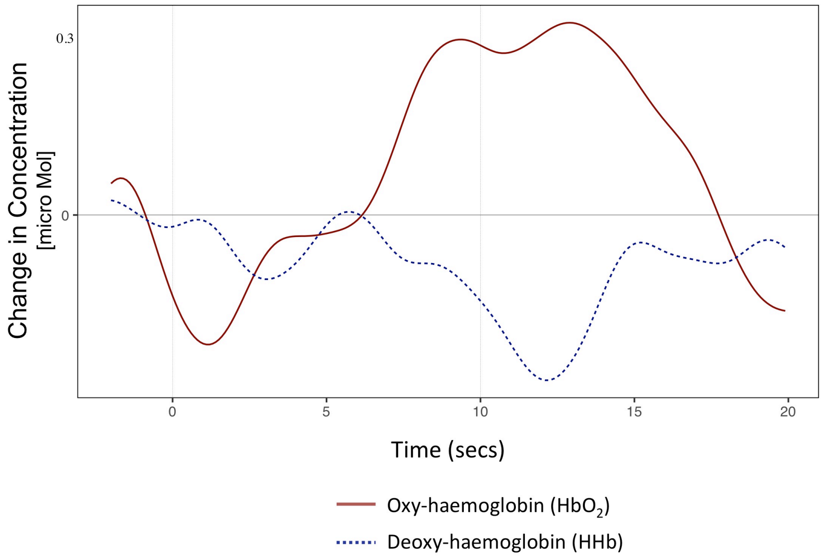

Figure 10. A typical fNIRS hemodynamic response

A typical hemodynamic response associated to a functional activation has been described as an increase in oxy-haemoglobin (HbO_2) and a decrease in deoxy-haemoglobin (HHb). The zero and ten seconds' time-points (both shown with a dotted grey line) mark the stimulus' onset and offset respectively.

fNIRS functional activations are comparable to fMRI BOLD signal—in particular, a significant increase in HbO_2 concentration in fNIRS was demonstrated to be associated with BOLD signal changes in fMRI (Strangman, Culver, Thompson, & Boas, 2002). Therefore, significant HbO_2 concentration changes are considered the most reliable response in the fNIRS literature (Lloyd-Fox et al., 2010; Strangman et al., 2002; Wilcox & Biondi, 2015).

One important limitation of this fairly recent technique is that it is still undetermined how to precisely interpret a hemodynamic response that does not follows this pattern, i.e. how to interpret a significant decrease in HbO_2 and/or a significant increase in HHb (Karmiloff-Smith, 2010; Lloyd-Fox et al., 2010). Another limitation is that, despite its adequate spatial resolution, fNIRS uses external landmarks to subjectively position the cap on the infants' head (Lloyd-Fox, Richards, et al., 2014). Therefore, to link a measured activation to a specific region of interest (ROI), one has to ensure the correct design, placement, and alignment of the cap in infants' head. Even so, linking a significant activated channel to a specific underlying cortical structure in infants is limited by using fNIRS—for more information about this issue see Lloyd-Fox, Richards, Blasi, Murphy, Elwell & Johnson (2014).

Finally, fNIRS experiments with infants typically use a within-subjects experimental block design. In these designs, infants are presented with experimental stimuli that varies from 5 up to 30 seconds, and with baseline stimuli with the same or an extended duration. Trial duration is a critical parameter in fNIRS experiments because the experimental stimulus has to be long enough to elicit the hemodynamic response; on the other hand, the longer each trial, the fewer trials infants will tolerate, and the reverse is also true (Wilcox & Biondi, 2015). Baseline trials have also to be long enough to permit the hemodynamic response to return to its baseline level. Experimental trials in fNIRS experiments with biological motion stimuli typically have a duration of around 16 seconds each (Lloyd-Fox et al., 2009). Nevertheless, more recently, shorter trials have been proved to be effective (Lisboa, Queirós, et al., 2020).

1.3.2.1.1.1 fNIRS studies on biological motion perception

The few fNIRS experiments conducted so far focused on brain responses associated with biological motion employed a within subject block design and tested between four (Grossmann, Cross, Ticini, & Daum, 2013), five (Lloyd-Fox et al., 2011; Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2015; Lloyd-Fox et al., 2009), and seven months-old infants (Biondi, Boas, & Wilcox, 2016; Ichikawa et al., 2010).

In these studies, infants passively watched videos' depicting biological motion and baseline stimuli while their brain activity was being recorded (Biondi et al., 2016; Grossmann et al., 2013; Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox, Wu, et al., 2015; Lloyd-Fox et al., 2009). Infants wore a cap or a headband composed of arrays of sources and detectors positioned over the their temporal-parietal cortices, i.e. circa 10 channels per temporal-parietal lobe.

Despite all of what we know about adults' STS responses to biological motion, the fact is that only few experiments have examined the cortical underpinnings of biological motion during infancy. There are a few EEG studies (Masahiro Hirai & Hiraki, 2005; Marshall & Shipley, 2009; V. Reid et al., 2006; V. M. Reid et al., 2008) but they cannot shed light on STS role on biological motion perception in infancy due to EEG poor spatial resolution (Azhari et al., 2020). We review in more detail previous fNIRS findings in the introduction of Chapter 2 and 3 of this dissertation. Nevertheless, and albeit some limitations (described bellow), the few fNIRS studies on biological motion indicate that a first transition for a right STS dominance in biological perception happens at seven months of age (Biondi et al., 2016; Grossmann et al., 2013; Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009). These studies have, however, some gaps and limitations which motivated some of work presented in this dissertation.

1.3.2.1.1.1.1 Right STS dominance at seven months of age

Overall, results from previous fNIRS experiments suggest that a first transition to a right STS dominance in biological motion happens at around seven or eight months of age: a significant increase in oxy-hemoglobin concentration associated to the point-light display of a surprised face motion (Ichikawa et al., 2010), and to a human hand motion (Biondi et al., 2016) was found only in the right temporal region (and not in the left) in infants aged seven/eight month old; however, Lloyd-Fox et al. (2009) reported bilateral temporal activations to video clips of an actor's upper body moving in younger five months-old infants.

From these results (bilateral temporal activations at five months and solely right at seven months), we can conjecture that a right STS dominance to biological motion appears for the first time between five and seven months of age. However, this was never directly measured in a longitudinal fNIRS experiment testing activations to point-light walkers in five and seven months-old infants.

In fact, these experiments on the hemodynamic response to biological motion in infants did not even use point-light displays. This is a major limitation because most of these studies included more than biological motion information in the stimuli (Biondi et al., 2016; Grossmann et al., 2013; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009).

1.3.2.1.1.1.2 Previous fNIRS studies: gaps and limitations

Overall, most of the previous fNIRS studies on biological motion used video clips of an actor moving as experimental stimuli (Grossmann et al., 2013; Lloyd-Fox et al., 2011; Lloyd-Fox, Wu, et al., 2015; Lloyd-Fox et al., 2009) and not point-light walkers, which is problematic for several reasons.

First, it includes more than motion information in the stimuli: textures, colors, explicit contours, and even facial information are also included. This limits the conclusions about a specific role for biological motion in the measured responses. Furthermore, this visual information maintained in the stimuli is also *per se* associated to activations in similar brain regions and at the same age—e.g. static face perception is associated with right temporal responses in seven/eight months-old (Honda et al., 2010; Otsuka et al., 2007). This confounds biological motion information with the presentation of other social information in the stimuli that we might want to study separately. Ichikawa et al. (2010) is an exception as they employed point-light displays of a moving surprised face expression—but face perception is a particular class of stimuli for the human visual system, including in infancy (Otsuka et al., 2007; F Simion et al., 2011; Slaughter, Stone, & Reed, 2004).

Second, the use of point-light displays enables the identification of *which* perceptual properties of biological motion (e.g. orientation, configural information, etc.) best tap specific brain responses during development. We know that the right pSTS is highly specialized to biological motion in the adults' mature brain because this region preferentially responds to intact point-light displays in relation to motion-matched controls (Peuskens et al., 2005). These controls vary in highly specific motion properties from the intact display, therefore, we know, for example, that the right pSTS is both sensitive to orientation, configural information, and does not respond to rigid motion in the mature brain (Peuskens et al., 2005). How this specialized response to the intact characteristics of biological motion develops is, however, largely unknown.

Third, previous studies also employed control stimuli that varied across many dimensions from the biological motion stimulus—there was no control over the amount of motion, color, contrast, or angular size in both stimuli. For example, videos clips of actors moving their hands or mimicking vowel sounds, were compared with moving mechanical toys (Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009);

an actor dancing was compared with a LEGO figure dancing (E. D. Grossman & Blake, 2002); and a human hand was compared with a mechanical hand motion (Biondi et al., 2016).

Finally, the use of point-light displays better permits the comparison with the adult's fMRI findings with biological motion stimuli (Deen et al., 2015) and with behavioral experiments of biological motion perception in infancy (Bertenthal, 1993; F Simion et al., 2011)—that have mostly employed point-light displays.

In face of these issues, one of the main objectives of the fNIRS experiments presented in this dissertation was to investigate right temporal brain responses in infancy to point-light walkers and motion-matched controls. We intended to, first, assert right STS responses to point-light walkers and then, the right STS degree of specialization to the coherent and intact features of the human walking action. Above all, a preferential response in infants' right STS region to an intact coherent point-light walker suggests a fundamental role of biological motion perception as an early basis of human social-cognition.

1.3.3 An Early Preference for Biological Motion Is a Relevant Social Behavior

Not only human neonates (Bardi et al., 2011; Francesca Simion et al., 2008), but also dogs (Ishikawa, Mills, Willmott, Mullineaux, & Guo, 2018), visually inexperienced chicks (Miura & Matsushima, 2012; Vallortigara et al., 2005), or even fishes (Larsch & Baier, 2018; Nakayasu & Watanabe, 2014) orient or prefer to look at biological motion in relation to other kinds of motions. An early preference for biological motion is important, not only for its survival value but also because it enables social interactions and social learning (Hoehl & Bertenthal, 2021).

An early preference for biological motion, namely, to local motion (such as the motion of the feet) is conjectured to be an adaptive behavior, common to a variety of species, enabling the rapid detection of potential predators or preys in the environment (Bardi et al., 2011; Johnson, 2006; Larsch & Baier, 2018; Francesca Simion et al., 2008; Troje & Westhoff, 2006). In addition to this immediate survival value, a spontaneous preference for looking at biological motion is speculated to contribute to social communication and social cognition (Gerson, Simpson, & Paukner, 2016). For instance, more sociable dogs prefer to look at the approaching motion of a human point-light walker, probably due to a clearer social/biological relevance of the approaching motion, whereas less sociable dogs prefer to look at a lateral view of the point-light walker (Ishikawa et al., 2018). A preferential attention to biological motion is also considered a relevant social behavior for humans, in particular, for infants' social-cognitive development.

Selecting where to look is one of the infants' primary tools for learning about the world, especially at a period where walking, reaching, and most motor actions are unsophisticated (Kretch & Adolph, 2015). On top of this, human infants have a limited attention span and working memory capacities, thus, they must be able to preferentially look at relevant factors in the environment, that are critical for their development (Kretch & Adolph, 2015; V. M. Reid & Striano, 2007; Sanefuji, Ohgami, & Hashiya, 2008; Schachner & Hannon, 2011). Of all the aspects an infant can select to look at in their natural environment, the dynamics of a body in motion is among the most significant, frequent and salient features of their crowded visual environment (Kretch & Adolph, 2015).

Simply by seeking and looking at the motion of people around them, infants gain increasing experience with other people. Looking at other people's motion creates an opportunity to learn how to interpret biological motions, such as learn to decode a gaze or a gesture (e.g. the meaning of a pointing gesture) or even the intentions of certain actions (e.g. predicting that the approaching person intends to interact). Thus, a preferential attention to biological motion was linked to other social capabilities such as theory of mind (i.e. the capacity for attributing intentions to others), and joint attention (i.e. the ability of sharing attention with an adult and an object) (Franchini et al., 2016; Frith & Frith, 1999; Gerson et al., 2016; Pavlova, 2012). In particular, it was empirically shown that children's ability to determine the facing and walking direction of a point-light walker under masking noise was positively correlated with measures of theory of mind (Rice et al., 2016). By directing attention to the motion of their caregivers, infants also increase the chances to initiate or even maintain a social interaction—and the developmental literature shows that early mother-infant social interactions provide the foundations for language development and other cognitive processes (Saxon, 1997). Thus, over time, this selective behavior evolves into social interactions that include more complex, reciprocal and coordinated social behaviors (Hoehl & Bertenthal, 2021).

Infants orient to relevant stimuli in their environments: people moving around them is one of the most available and valuable stimuli they can explore (Gerson et al., 2016). It results that infants actively seek to look at people (Kretch & Adolph, 2015); preferential attention to biological motion in infancy is thought as a precursor of later and more complex social-cognitive abilities; newborns prefer biological motion (Bardi et al., 2011; F Simion et al., 2011; Francesca Simion et al., 2008). Finally, studies also show that infants and children that *do not* prefer to look at biological motion show, on the other hand, that an early absence of a preference for biological motion might compromise their daily-life social perception (Pavlova, 2012). A paradigmatic example is the case of autism spectrum disorder (ASD) children.

Autism spectrum disorder (ASD) is a lifelong, debilitating, neurodevelopmental disorder, characterized by impairments in the social and communicative functioning of the individuals. Social impairments and communicative deficits are considered central characteristics of ASD. At the same time, research on biological motion perception reports an altered preference for looking at biological motion in ASD individuals from early in development (Annaz, Campbell, Coleman, Milne, & Swettenham, 2012; Klin, Lin, Gorrindo, Ramsay, & Jones, 2009; Parron et al., 2008). While typically developing children prefer to look at biological motion, ASD children do not and/or prefer rigid object motion (Annaz et al., 2012; Kaiser, Delmolino, Tanaka, & Shiffrar, 2010; Kaiser & Shiffrar, 2009; Klin et al., 2009). This altered preference for biological motion is conjectured to have cascading effects on the social cognitive development of ASD infants, impacting the development of their social-cognitive abilities.

Klin et. al (2009) tested 2 years old children diagnosed with ASD for preferences between upright point-light displays depicting children's games, such as "peek-a-boo" or "pat-a-cake", and inverted versions of these displays. Contrary to typically developing children or even to mentally delayed children (that both preferred the upright biological motion displays), ASD children showed no preference for either stimuli (Klin et al., 2009).

This absence of a preferential attention to biological motion found at 2 years old was replicated and extended to older ASD children in another study conducted with 3-7 years old. Annaz et. al (2012) investigated preferences for an intact point-light walker of a person and a scrambled control (experiment 1); and for the same intact point-light walker and the point-light display of a spinning top (experiment 2). On both preferential looking experiments, typically developing children preferred the intact point-light walker whereas ASD children showed no preferences on the first experiment, and on the second experiment preferred the object motion (the spinning top rotating) (Annaz et al., 2012).

In contrast with typically developing children, ASD children do not seem to prefer biological motion (Klin et al., 2009). To investigate if this difference is altered from birth, and is affecting visual experiences in these individuals from very early in development, Di Giorgio et al. (2016) decided to test newborns. Newborns at high risk of ASD (i.e. with an older sibling diagnosed with ASD), and newborns at low risk of ASD (i.e. without ASD siblings) were tested for preferences between the point-light walker of a hen and random motion (Di Giorgio et al., 2016). Results from this experiment showed that only newborns at high risk of ASD looked an increased amount of time at random motion in comparison with the intact point-light walker (Di Giorgio et al., 2016).

These results indicate that ASD individuals are on a different developmental trajectory in biological motion perception since very early: newborns at high risk of ASD do not prefer biological motion (Di Giorgio et al., 2016). This is probably generating a set of increasingly atypical experiences for ASD individuals in relation to typically developing infants—and these atypical experiences seem to have effects on their social-cognitive abilities (Annaz et al., 2012; Klin et al., 2009). In favor of this hypothesis, a recent longitudinal experiment conducted with 3 years old revealed that ASD children that exhibited greater attention to biological motion over geometric motion in a preferential looking task at this age, in contrast with children that did not, showed a reduction in the severity of their autistic symptoms one year later (Franchini et al., 2016).

A preference to look at biological motion is important for human social-cognitive development. Despite this, the number of experiments directly measuring preferences for point-light walkers during infancy is scarce.

1.3.3.1 Infants' preferential looking studies on biological motion

As previously reviewed, Fox & McDaniel (1982) were the firsts to investigate perception of biological motion in infancy and the first to use a preferential looking procedure. The main results from these experiments are that two months-old infants show no preferences; both four and six months-old prefer an upright point-light walker in relation to an inverted point-light walker; and only six months-old prefer an on-joint display of a hand moving over the same display with off-joint markers (Fox & McDaniel, 1982). The authors thus concluded that some level of visual experience is needed for infants to prefer biological motion (two months old showed no preferences); and that preferential attention for biological motion becomes increasingly developed with age during the first half of infants' first year of life.

Bertenthal (1993) mostly used infant-controlled habituation procedures to test infants' discriminative abilities in biological motion perception (not preferences). However, the preferential looking procedure has the great advantage of requiring less processing demands than the habituation procedure because the two stimuli are continually present in the screens, hence, the infant does not have to retain in his/her memory the habituation stimulus to compare it with the testing stimulus (Proffit & Bertenthal, 1990). Therefore, Bertenthal et al. (1985) decided to test infants in one preferential looking experiment.

The side-view of point-light walker implicates a natural occlusion of some parts of the limbs during the gait cycle. Bertenthal et al. (1985) tested the sensitivity of both five and eight months-old infants to this natural occlusion of the limbs in the walking action. In a preferential looking experiment, an intact point-light walker (with the natural occlusion of the limbs) was contrasted to a non-occluded point-light walker. This manipulation disrupts the recognition of a person walking in adults (Proffitt, Bertenthal, & Roberts, 1984).

Results indicated that five months-old infants have no preferences but older eight months-old revealed a preference for the intact (naturally occluded) point-light walker (Bertenthal et al., 1985). Again, the conclusion was that preferences for intact displays in biological motion develop with age.

More recently, two new studies were conducted combining point-light displays and the preferential looking paradigm; both studies were longitudinal and followed infants' individual preferences at different points in time.

Kutsuki et al. (2009) tested preferences in infants at four, nine and eighteen months of age between an intact point-light walker and random motion (the same number of dots randomly moving at constant velocity). In this experiment, the authors also scored infants' developmental index using the KIDS questionnaire (Kutsuki et al., 2009). Results of this experiment were presented in a cluster analysis: infants were divided in two clusters according to their total looking time at the intact point-light walker. Thus, two clusters were created that differed in infants preferences for biological motion at nine months: one cluster showed a preference for looking at random motion, while the other cluster preferred the intact point-light walker. Notably, infants from the cluster that preferred the intact point-light walker at nine months also scored significantly higher in their developmental index in relation to the other cluster of infants (infants that preferred random motion at nine months). The authors concluded that a preference for biological motion is not obligatorily associated to the chronological age of the infants, but to an overall developmental capability of the infants at nine months (Kutsuki et al., 2009).

Finally, Sifre et al. (2018) tested longitudinally infants from two to 24 months of age in their preferences towards intact upright point-light displays of an actor playing children's games (e.g. "peek-a-boo") vs. inverted versions of the displays. Five different animations were used and their respective inverted versions; displays were presented with audio recordings of the actions (multimodal stimuli) (Sifre et al., 2018). This was the first study mapping developmental changes in preferential attention to biological motion during the first two years of life. Infants were tested at seven different time points: at the age of two, three, four, five, nine, 15, and 24 months old. As in Fox & McDaniel (1982) study, two months-old did not show any preference, and a preference for the upright point-light displays in relation to inverted displays emerged at three months of age (Sifre et al., 2018). After three months, there was an increase preference for the upright point-light displays across developmental age: older infants tend to look longer to the intact display (Sifre et al., 2018).

Although a preference for biological motion is considered a vital aspect of human social-cognitive development, very few studies have examined preferential attention to biological motion during infancy—we just reviewed the four principal.

Common to the four studies is an increased sensitivity across developmental age on infants' preferences to look at biological motion. Infants' increased visual experience with others might be contributing to this growing attention towards human motion. This greater attention might also be coupled to a growing social and motor development in infants (Sifre et al., 2018). Nevertheless, much still remains to be explained about infants' preferences for human motion in the first year of life.

Fox & McDaniel (1982) and Sifre et al. (2018) found no preference for intact point-light displays at the age of two months in relation to random motion (Fox & McDaniel, 1982) and to inverted displays (Sifre et al., 2018). These results are, though, in contrast with the newborns findings that report a preferential attention to the intact point-light walker at birth (Francesca Simion et al., 2008). Newborns prefer an intact point-light walker in relation to random motion, an inverted walker, and rigid object motion (Bardi et al., 2011; Bidet-Ildei et al., 2014; F Simion et al., 2011; Francesca Simion et al., 2008). Hence, one might conclude that human infants begin by preferring biological motion at birth; then, at two months they show no preferences, to finally prefer again biological motion at around three to five months of age. In short, there seems to be a decline in preference for biological motion at the age of two months (Fox & McDaniel, 1982; Sifre et al., 2018).

But what happens at two months of age that infants show no preferences?

Preferential attention to faces also declines at two months; in this case, it was speculated that at two months occurs a transition between infants' subcortical and cortical processing of faces (Johnson, Dziurawiec, Ellis, & Morton, 1991). Differences in the perception of biological motion from birth to two months might also be explained by a similar cortical transition.

Other important information to consider is that infants preferences for biological motion at birth are limited: when contrasting a scrambled point-light walker, the preference for the intact coherent walker disappears (Bardi et al., 2011). This result indicates that newborns are likely not processing configural relations in biological motion. Instead, newborns might be tuned to the individual motions of the dots; thus the scrambled point-light walker, in contrast with other controls, does not affect newborns' visual preferences because the individual motions of the dots are intact in this stimulus.

We know from previous habituation experiments that three months-old infants begin to process local configural relations and only five months-olds are able to perceive global configural relations in point-light walkers (Bertenthal, 1993). Therefore, following the initial conjecture (i.e. newborns do not process configural relations), we can predict that three and five months will prefer a coherent intact point-light walker in relation to a scrambled point-light walker because these infants are able to process configural relations in biological motion (Bertenthal, 1993).

Hirai & Senju (2020) proposed a two-process theory for the perception of point-light walkers (resumed at the beginning of this General Introduction), where two processes underlie biological motion perception: one that is innate, tuned to the individual motion of the dots (especially to feet motion) and that relies on a subcortical pathway; and another that is learned and is sub-severed by specialized cortical circuits responsible for configural processing of point-light walkers.

Thus, newborns might prefer biological motion because of an orienting mechanism for the individual motions of the dots (such as the motion of the feet); however, this subcortical response is inhibited around the second month of life by the emergence of cortical activity; a preference for biological motion might re-emerge at three months by the cortical processing of local configural relations in point-light walkers (such as the motion of the limbs) (Masahiro Hirai & Senju, 2020). These configural relations then start to be processed at a larger spatial scale, i.e. at its global level, at five months of age (Bertenthal, 1993).

Above all, it is clear that vast developmental changes happen in biological motion perception during the first few months of life that impact infants' preferences for biological motion and likely infants' social-cognitive development. These changes in the perception of biological motion seem to be intimately connected to infants' cortical development and to changes on infants' ability to perceive configural relations in biological motion. Critically, and to the best of our knowledge, no study have examined how these changes affect infants' preferences for a coherent walker after birth; in particular, no study has examined preferential attention for a coherent point-light walker over a scrambled control after birth.

1.4 Main Research Questions

The term "configural processing" refers to any phenomenon that involves perceiving relations among features or parts of a stimulus (Maurer, Le Grand, & Mondloch, 2002). Configural processing in biological motion involves perceiving the relation between at least two dots of a display (local configural information) and/or the relation between all dots of the display that corresponds to the form of a person walking (global configural processing).

Biological motion is a rich source of social information. Fundamental to this seems to be the ability of perceiving configural relations in human motion—observers do not even identify a scrambled point-light walker (i.e. a stimulus with no configural information but with intact featural motion) as a human (Cutting, 1981); only the coherent global motion configuration of a person walking is processed in the right pSTS, a critical node for human social-cognition (Peuskens et al., 2005). However, much remains to be known regarding how humans develop the ability to perceive configural relations in biological motion. The focus of this work is the study of infants' perception of biological motion configuration.

As reviewed throughout this General Introduction, previous developmental studies concerning the perception of biological motion configuration concluded that: (1) humans at birth have an attentional bias to biological motion in relation to other kinds of motions (F Simion et al., 2011)—however, the ability to process configural relations seems to be still immature as newborns have no preferences between a coherent and a scrambled point-light walker (Bardi et al., 2011); (2) with visual experience, infants become increasingly sensitive to configural relations in biological motion; in particular, the ability to process the global configuration of a human walking seems to emerge at five months of age (Bertenthal, 1993); (3) an early preference for biological motion is a critical and fundamental aspect of infants' social-cognitive development (Frith & Frith, 1999; Gerson et al., 2016; Pavlova, 2012)—despite this, it is still unknown whether or when infants develop a preference for the coherent motion of a person walking in relation to a scrambled control; (4) by seven months of age, infants seem to preferentially process biological motion in the right temporal cortex (Biondi et al., 2016; Ichikawa et al., 2010)—however, no fNIRS study have used point-light walkers as stimuli or investigated brain responses to biological motion's configural relations.

The present work intends to find the answers to some of these gaps by combining a multidisciplinary and multilevel approach to study the perception of biological motion during infancy. Our approach is centered around one basic perceptual phenomenon—perceiving configural relations in biological motion—and how the development of this ability relates both to a preferential attention, and to a high-level cortical processing, in the right STS region, of the coherent walking action in infants.

Two distinct but complementary methodological approaches were innovatively combined: a preferential looking procedure—a classic behavioral task from developmental psychology based on infants' looking behavior; and functional near-infrared spectroscopy (fNIRS)—an emergent and promising neuroimaging technique well suited for measuring infants' cortical activity.

In the next two chapters (Chapter 2 and Chapter 3), we present two fNIRS studies conducted with seven months-old infants and point-light walkers. These studies intended to find if biological motion implicates a specialized brain processing, early in development, in the right STS region.

In the fourth chapter, two preferential looking experiments with three to seven months-old infants are presented. The aim of these behavioral experiments was to find when a preference for a coherent point-light-walker in relation to a scrambled point-light walker emerges in infancy.

1.4.1 Infants' Perception of Biological Motion Configuration: Coherent vs. Scrambled Point-Light Walker

To study configural processing in biological motion, the perception of a coherent intact point-light walker is typically contrasted with a scrambled point-light walker. The scrambled point-light walker is a classical control stimulus from visual perception studies specifically used for investigating the role of configural relations. The scrambled manipulation maintains the individual motion of the markers (featural information), while disrupting all configural relations (local and global) in the display.

Most of what we know from development literature on biological motion perception comes from studies based on infants' looking time using point-light walkers (Bertenthal, 1993; Sifre et al., 2018; Francesca Simion & Giorgio, 2015); and most theoretical accounts and/or explanatory models of biological motion perception were proposed to explain the processing specifically of the walking action (Giese & Poggio, 2003; Masahiro Hirai & Senju, 2020; Troje, 2008, 2013). Moreover, locomotion is a common and familiar action, and the human visual system is speculated to process this action earlier than other actions to which it is less exposed (Masahiro Hirai & Senju, 2020). Therefore, in our studies (two fNIRS experiments and two preferential looking) we used only point-light walkers as stimuli.

In the four experiments, we presented walking displays approaching the viewer, while point-light walkers are traditionally presented in a side view. This choice was based on four main factors. First, the frontal view of the stimulus is less complex, since there are no occlusions of the limbs during the gait cycle—and we know that this feature is relevant for infants (Bertenthal et al., 1985). Second, recognition experiments with adults suggest a perceptual advantage for frontal views in relation to side views (Jokisch et al., 2004; Troje, Westhoff, & Lavrov, 2005). For instance, adults' recognition performance of point-light walkers of familiar people is better for frontal than for side views (Jokisch et al., 2004). Third, perception of frontal views of other social stimuli, such as frontal face perception, emerges earlier in infancy than side views (Ichikawa et al., 2019; Nakato et al., 2009). Finally, we conjectured that the motion of an approaching person, as if approaching to interact with the infant, would be more familiar and would increase infants' visual attention to the stimuli and the fNIRS signal intensity. Furthermore, recent studies on biological motion using point-light walkers with infants are also employing frontal approaching views of the displays (Ogren, Kaplan, Peng, Johnson, & Johnson, 2019).

We implemented four studies using point-light walkers (two fNIRS experiments and two preferential looking experiments) to answer two major research questions: *"is biological motion processed in the right STS region in infancy?"* and *"when in infancy emerges a preference for biological motion configuration?"*

1.4.1.1 Is biological motion processed in the right STS region in infancy?

We designed two fNIRS experiments with seven months old infants to specifically address this question, that is, find right STS responses to biological motion in infancy. We hypothesized that the viewing of an intact point-light walker activates the right superior temporal sulcus (STS) at an age where infants perceive global configural relations in biological motion. Behavioral findings with the habituation procedure indicate that this ability emerges at five months (Bertenthal, 1993), thus, seven months-old are experienced in perceiving the global coherent configuration of the human walking action.

Two fNIRS experiments were conducted to measure the hemodynamic functional response in infants' right STS region to the intact frontal motion of a person walking towards the viewer—an upright/coherent point-light walker. Different motion controls of the intact stimulus were used in our two experiments.

In the first experiment, we contrasted an upright point-light walker with both an inverted and a rigid moving point-light walker frame (i.e. a single frame of the coherent display animated to move at constant velocity); stimuli were presented for 16 seconds. In the second experiment, we contrasted the intact display with a scrambled point-light walker; in order to increase the number of trials per infant, we also reduced time of stimuli presentation to 8 seconds in this second experiment.

Chapter 2: Right STS Responses to Biological Motion in Infancy – An fNIRS Study Using Point-Light Walkers, introduces and discuss our first fNIRS experiment. In this experiment, we analyze infants' hemodynamic responses in the right STS region to the perception of an upright point-light walker, inverted, and a rigid moving point-light walker frame (Lisboa, Miguel, et al., 2020). Seven months-old infants passively viewed the three walking displays approaching the viewer while their oxy-hemoglobin (HbO_2) and deoxy-hemoglobin (HHb) concentration in the right STS region was measured using fNIRS. This experiment intended to investigate right STS sensitivity to biological motion in infancy. Specifically, investigate *which* visual characteristics of biological motion contain socially relevant information and thus activate the right STS at this age. Two visual characteristics were studied: the upright orientation, and biological motion' specific non-rigid moving patterns. We hypothesize that the right STS has already some degree of specialization to these features of biological motion at seven months old (Deen et al., 2015; Peuskens et al., 2005).

In Chapter 3: Infants' Cortical Processing of Biological Motion Configuration – An fNIRS study, we looked at whether the same site (right STS region) is sensitive to biological motion configuration (Lisboa, Queirós, et al., 2020). In this second experiment, we used the same fNIRS array as in the previous experiment (nine channels placed over the right STS region) and the same age group (seven months-old) but we contrasted the same coherent or upright display walking in approximation to a scrambled point-light walker. The objective was to investigate if it is the unique motion configuration of a person walking that elicits a significant response in the right STS in infancy.

1.4.1.2 When, in infancy, emerges a preference for biological motion configuration?

Finally, *in Chapter 4: Three months old' preferences for biological motion configuration ans its subsequent decline*, we describe two preferential looking experiments (one cross-sectional and one longitudinal) conducted with three, five, and seven months-old infants.

We know from previous habituation experiments that infants start perceiving the global configuration of a person walking at around five months of age, and that three months old are able to process local configural relations (Bertenthal, 1993). Thus, we began by testing three and five months-old infants in a cross-sectional experiment. In the second preferential looking experiment (longitudinal), we asked parents that participated with their infants at three months in the first experiment to participate again at five and at seven months of age. We also reduced the time of stimuli presentation in this second study.

Our aim was to test when in infancy emerges a preference for a coherent point-light walker in relation to a scrambled point-light walker. We hypothesize that if there is a socially relevant meaning in perceiving global configural relations in biological motion, infants will selectively prefer the motion of a person walking in relation to a scrambled control. In the scrambled point-light walker, there are no configural relations between the dots and the extraction of social meaning of a person walking is impossible, despite the preserved individual motions of the dots.

We end this dissertation with *Chapter 5: General Discussion and Conclusion*. In this section, results from the two converging measures (brain activity and preferential attention) and the four experiments are discussed to conclude about the potential social meaning of perceiving global configural relations in biological motion in infancy.

Chapter 2: Right STS responses to Biological Motion in Infancy – An fNIRS Study Using Point-Light-Walkers

A version of this Chapter is published in Neuropsychologia[1]

Right STS Responses to Biological Motion in Infancy – An fNIRS Study Using Point-Light Walkers

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Abstract

Biological motion perception—our capacity to perceive the intrinsic motion of humans and animals—has been implicated as a precursor of social development in infancy. In the adult brain, several biological motion neural correlates have been identified; of particular importance, the right posterior superior temporal sulcus (rpSTS).

We present a study, conducted with fNIRS, which measured brain activations in infants' right posterior temporal region to point-light walkers, a standard stimulus category of biological motion perception studies.

Seven-month-old infants (n = 23) participated in a within-subject blocked design with three experimental conditions and one baseline. Infants viewed: an intact upright point-light walker of a person approaching the observer; the same point-light walker stimulus but inverted; and a selected frame from the point-light walker stimulus, approaching the viewer at constant velocity with no articulated motion, close to object motion.

We found activations for both the upright and the inverted point-light walkers. The rigid moving point-light walker frame did not elicit any response consistent with a functional activation in this region.

Our results suggest that biological motion is processed differently in the right middle posterior temporal cortex in infancy, and that articulated motion is a critical feature in biological motion processing at this early age.

*Keywords***:** biological motion, right STS, Point-Light Walkers, infancy, fNIRS, neurodevelopment

2.1 Introduction

Fluency in a complex social world requires perceiving the actions of others at the right level of abstraction, not as mere movement but as intentional and goal-oriented; in turn, high-level social cognition entails the visual perception of the movement produced by bodies acting—more generally, the visual perception of the *motion patterns characteristic of living organisms,* or, as it is called in visual and action perception studies, biological motion.

A known neural correlate of biological motion perception in the mature brain is the right Superior Temporal Sulcus (rSTS) (Carter & Pelphrey, 2006; Deen et al., 2015; E. Grossman et al., 2000; Peuskens et al., 2005), an area also linked to other components of our social-cognitive abilities such as face and speech processing, audio-visual integration, and theory of mind (Allison et al., 2000; Deen et al., 2015; Grossmann, 2015; Grossmann & Johnson, 2007; Hein & Knight, 2008; Pavlova, 2012; Zeileis, Wiel, Hornik, & Hothorn, 2008). Presenting a biological motion stimulus to adults using videos of live action or constructed using the point-light display technique systematically leads to right STS activity (Carter & Pelphrey, 2006; E. Grossman et al., 2000; Peuskens et al., 2005). The point-light method in particular—showing only the motion of dots placed on key points of a person in action—has played a major role in behavioral and neuroimaging studies of biological motion (Bertenthal, 1993; Blake & Shiffrar, 2007). It is a de facto standard category of controlled stimulus that preserves the global motion configuration but reduces form information to a minimum (Troje, 2013). A biological motion stimulus is also a proper visual object in that it contains information of both discrete motion (the trajectory of each individual dot) as well as relative motion (the articulated motion of body parts relative to each other, typically the relative movement with respect to a joint, e.g., rotation of the wrist relative to the elbow joint).

In fMRI studies, the right STS area responds to intact canonical point-light displays, but not to a set of motion-matched controls. For example, inverting the point-light display in the picture plane does not elicit the same right STS response as scrambling the initial position of the dots (E. Grossman & Blake, 2001; E. Grossman et al., 2000; Peuskens et al., 2005). The same effect is present when comparing point-light displays with rigid vs. articulated motion: a point-light display that contains articulated motion is associated with greater right STS response than one containing rigid object motion (Beauchamp, Lee, Haxby, & Martin, 2002; Peuskens et al., 2005).

In summary, the right STS in the adult brain is sensitive to the intrinsic motion produced by an articulated body that undergoes specific deformations. This is evidenced by weak activation when presenting: the original motion of each dot in a point-light display, but without the articulated movement part (scrambled display); a display with an inverted orientation (inverted display); and rigid motion.

Considering the importance of biological motion perception for social cognition, and the specificity of the right STS' functional response to biological motion, it seems likely that this specificity also develops in early infancy (Grossmann, 2015; Pavlova, 2012). This hypothesis is supported by the association between biological motion perception in infancy with later and more complex social developmental milestones, such as joint attention and theory of mind (Frith & Frith, 1999; Grossmann & Johnson, 2007; Pavlova, 2012; Yoon & Johnson, 2009), and by the association with the atypical development in autism spectrum disorder (Frith & Frith, 1999; Klin et al., 2009; Pavlova, 2012).

While classic studies of biological motion perception in infancy using behavioral tasks have mapped the most important transitions in the first year (Bertenthal, 1993), only a handful of studies have examined the relevant neurodevelopmental changes. What we know of infancy comes from a few cross-sectional studies using EEG and point-light walkers as stimulus (a point-light display built from a person in the act of walking) (V. Reid et al., 2006; V. M. Reid et al., 2008) and, more recently, fNIRS (Ichikawa et al., 2010; Lisboa, Queirós, et al., 2020; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009).

2.1.1 Neuroimaging Studies of Biological Motion in Infancy

The first ERP study was conducted with 8-month-olds, and contrasted an upright point-light walker with a scrambled point-light walker; the main finding was a significantly greater negative amplitude of response in the right occipitotemporal region, around 200-300ms post-stimulus onset, to the upright stimulus (Masahiro Hirai & Hiraki, 2005). These results were later extended to 5-month-old infants, using several point-light displays presenting different actions (Marshall & Shipley, 2009).

In another study, Reid, Hoehl, & Striano (2006) examined the ERPs of 8-month-olds when viewing the upright and inverted point-light displays of a walking or kicking action. They also found differential activations, with a larger positive peak in the right parietal region associated with the upright displays as compared to the inverted stimuli (V. Reid et al., 2006). Evidence from these ERP studies supports the existence of an early brain processing difference between canonical point-light displays versus scrambled and inverted point-light displays.

Assigning the right STS as the source of the ERP activations, similar to fMRI studies in adults, is difficult (Azhari et al., 2020; Lloyd-Fox et al., 2010; Nishiyori, 2016); EEG cannot specify *which* underlying brain areas generated the measured ERPs (Azhari et al., 2020).

A major change in neurodevelopmental studies in infancy was the introduction of functional near-infrared spectroscopy (fNIRS), which filled an important methodological gap. Similar to fMRI, fNIRS measures the brain's hemodynamic response, has a better spatial resolution than EEG, and does not require the participant to be absolutely motionless, making it an especially suitable imaging technique for infant studies (for reviews, see Lloyd-Fox, Blasi, & Elwell, 2010, and Nishiyori, 2016). Taking advantage of fNIRS' characteristics, recent studies have examined brain responses to biological motion in infancy.

Ichikawa, Kanazawa, Yamaguchi & Kakigi (2010) used point-light displays constructed from the motion of a surprised face expression and reported a significant increase in oxy-hemoglobin concentration in the right temporal area when seven to eight month-olds viewed the upright face, compared to the baseline condition (a static image from the same point-light display). This pattern was restricted to the right temporal hemisphere and the upright stimulus; no significant results were found with the same face inverted (Ichikawa et al., 2010).

Lloyd-Fox et al. (2009) tested 5-month-olds' responses to a live actor's upper body motion relative to moving mechanical toys. Activations to the actor's upper body motion were found bilaterally in a posterior temporal region. In another study, Lloyd-Fox, Blasi, Everdell, Elwell, & Johnson (2011) analyzed 5-month-olds' brain activations specific to the different upper body motions such as hands, mouth, and eyes, but only the hand motion showed a trend associated with bilateral posterior temporal activations at this age.

Grossmann, Gross, Ticini, & Daum (2013) investigated, in younger 4-month-olds, bilateral activations in the superior temporal cortex to the whole-body motion of a live actor and a Lego figure dancing. Congruent pairs (a human actor dancing in a human style; a Lego figure dancing in a robot style) elicited activations on the left temporal cortex; thus, the activations were not specific to biological motion.

Although these fNIRS studies add to previous ERP data on biological motion processing, they are incomplete in addressing a specific functional activation for biological motion in early infancy; we discuss three reasons for this.

First, the majority of these studies used videos of live actors as stimuli, thus including more than motion information (e.g., texture, color, explicit contours, and facial information). In addition, because the point-light technique is a standard method for studying biological motion, the use of point-light displays allows a more direct comparison with previous fMRI findings in adults, as well as with the already extensive behavioral literature on the topic of biological motion perception during infancy (Bertenthal, 1993).

Second, most experiments used control stimuli that varied across multiple dimensions from the main experimental stimuli, e.g., comparing the actions of an actor with moving mechanical toys (Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009); comparing an actor dancing with a Lego figure dancing in a robotic manner (Grossmann et al., 2013); and comparing a human with a mechanical hand (Biondi et al., 2016). This limits the possibility of uncovering *which* perceptual features of biological motion (e.g., orientation, articulation, form information) optimally drive right STS responses in infants and likely contribute to the adult's specialized response in this site to intact upright point-light displays (E. Grossman & Blake, 2001; E. Grossman et al., 2000; Peuskens et al., 2005).

Finally, previous fNIRS experiments focused mainly on face/upper body motions (Biondi et al., 2016; Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009) and on actions that depicted explicit social content, such as actors performing hand games or mimicking vowel sounds (Lloyd-Fox et al., 2009); dancing (Grossmann et al., 2013); or even in point-light displays that depicted emotions, such as point-light display of facial expressions (Ichikawa et al., 2010). The use of live actors performing explicit social actions and/or emotional expressions is justified, since it likely increases the chances of detecting brain activations in the cortical area of interest. However, this method means presenting multiple features to participants that we may wish to study separately when measuring the hemodynamic response to biological motion.

The exception is a recent fNIRS study (by (Lisboa, Queirós, et al., 2020). We measured the right STS response of 7-month-old infants, specifically to a point-light walker. The main experimental comparison was between the point-light walker and a spatially scrambled version of it. In the scrambled point-light walker, the initial dot position was randomized, leaving the individual dot motion unchanged but eliminating the global configuration. Our hypothesis was that the right STS would preferentially respond to a stimulus that depicts both the local configural information and the relevant global configuration of human walking. As hypothesized, we found activations in the right STS region only to the intact upright point-light walker, and not to the scrambled version (Lisboa, Queirós, et al., 2020).

2.1.2 Current Study

In the present study, we measured the hemodynamic response of 7-month-old infants to point-light walkers. The fNIRS array that was used covered the infants' right temporal region and included the right STS. Infants viewed point-light walkers in three conditions and in a within-subject design. The main condition consisted of an intact upright point-light walker; infants also viewed two control conditions: (1) an inverted point-light walker, where only the vertical canonical orientation of the original point-light walker was reversed; and (2) a moving rigid point-light walker frame, made with a single frame from the upright point-light walker, and animated so it approached at constant speed, i.e. without any articulated motion. Since we tested infants with point-light displays, we could investigate *which* basic perceptual features of biological motion (in particular, orientation and articulation) activate the right STS region. We used the point-light display of the walking action—a common but less socially explicit action compared to facial expressions—and we presented it approaching the viewer.

We tested 7-month-old infants because previous fNIRS studies reported a differential hemodynamic response at this age in the right temporal region for the point-light display of a surprised face motion (Ichikawa et al., 2010), as well as for a moving human hand (Biondi et al., 2016). In addition, ERPs studies of infants at this age reported differential activations for intact point-light displays relative to both inverted and scrambled point-light displays (Masahiro Hirai & Hiraki, 2005; V. Reid et al., 2006).

We measured activations only in the right temporal region, where the right STS is located. This region is a neural correlate of biological motion perception in the mature brain, and is sensitive to the specific perceptual features that are only present in the intact canonical point-light walker (Deen et al., 2015). Thus, if infants' functional responses resemble the adult profile (E. Grossman et al., 2000; Peuskens et al., 2005), we hypothesized a significant hemodynamic response—i.e. a significant increase in oxy-hemoglobin concentration in relation to baseline on the right posterior temporal region—to the upright point-light walker only. That is, we expected that neither the inverted point-light walker nor the rigid moving point-light-walker frame would elicit the same response. In summary, at 7 months of age, infants' right STS region activates specifically to a point-light walker in its canonical upright orientation.

2.2 Method

2.2.1 Participants

Twenty-three 7-month-old infants participated in the study (10 females, age range = 214–265 days, mean age = 232 ± 20 days). A further seven infants were tested but were excluded from the final sample due to excessive NIRS signal acquisition problems (n = 1), or for not looking enough (n = 6).

See the “data processing” section for more details on the looking time coding scheme, and on the channel array.

All infants were born full term (37–42 weeks), with normal birth weight (>2500g), and with no hearing or vision impairments. Infants were recruited from local nursery schools or parent meet up groups.

Parents or legal guardians gave informed consent before participating in the study. The study was approved by the University of Minho’s ethics committee.

2.2.3 Stimuli

The complete design included three experimental stimuli, derived from Mouta, Santos, & López-Moliner (2012), and one baseline stimulus (static frames derived from the experimental stimuli).

The three experimental stimuli represented an approaching motion of a male model walking towards the observer and corresponded to: (1) the intact motion of a walker (upright point-light walker), and two manipulations of this motion; (2) an inverted point-light walker; and (3) a rigid moving point-light walker frame.

The original motion data, which corresponded to the approaching upright point-light walker, was captured at 240Hz using a VICON motion capture system and corresponded to the motion of a male model, walking at an average speed of 0.7 m/s, and wearing thirteen markers placed on the head, left and right ankles, knees, hips, wrists, elbows, and shoulders (Mouta, Santos, & López-Moliner, 2012). The markers were rendered as white spheres on a black background. Because the translational component of the walking motion was towards the viewer, the stimulus size varied over time: when seen at a visual distance of 60cm, the point-light walker was 11.8° high x 4.8° wide at the start, and finished its cycle at 21° high x 8.3° wide. To produce the inverted point-light walker, the upright point-light walker animation was rotated 180° in the image plane. Finally, for creating the rigid moving point-light walker frame, the middle frame of the original motion capture data was animated by translating it at a constant speed equal to the upright point-light walker’s average speed (0.7m/s), resulting in an approaching static object, i.e. a point-light walker without articulation and approaching at constant velocity. The baseline stimulus corresponded to a static image taken from either the middle frame of the upright point-light walker or the inverted point-light walker (13.5° high and 5.7° wide) (Ichikawa et al., 2010; Lisboa, Queirós, et al., 2020).

All animations were composited at a 1024*768-pixel resolution and 60Hz frame rate.

2.2.4 Procedure

We used a within-subject experimental block design, with three experimental conditions (upright point-light walker, inverted point-light walker, and rigid moving point-light walker frame), and one baseline condition (a still image); see Figure 11 (upper panel) for a schematic of the block design. An experimental trial for one condition consisted of multiple presentations of the respective point-light display animation, with attention-getters inserted between each individual presentation – see Figure 11 (lower panel). Experimental trials had a total duration of 18s: 4s of the respective point-light display visual stimulus, followed by 500ms of an attention-getter, looped 4 times per trial; see figure for a schematic example of one trial. This exact same procedure, with attention-getters, was applied to baseline trials that always preceded each experimental trial for the same amount of time.

The attention-getters consisted of static fruit images, presented together with pleasant children's sounds (e.g., the sound of a magic wand); see Ichikawa et al. (2010), and Lisboa et al. (2020) for a similar approach. There were five different fruit images of approximately the same size (13.1°x14.0° at 60cm viewing distance) but different colors; each fruit image was presented on a black background simultaneously with one out of five possible children's sounds.

The experimental condition order was counterbalanced; the fruit images were presented in randomized order, as were the sound pairings.

All stimuli were displayed in the center of an ASUS VG248QE-monitor (native resolution of 1920*1080; screen size: 53*30cm) using *Superlab* (Cedrus Superlab 5.0).

During the procedure, the infant passively viewed the stimuli while seated in the parent's lap, at approximately 60cm from the computer monitor, in a room with no windows and with only the dim light from the computer screen. The parent was instructed not to interfere or interact with the infant; the experiment started when the infant was calm and looking at the screen. Above the monitor, a video camera recorded the infant's looking behavior for offline coding of eye fixations.

The experiment was divided into two parts, each lasting 7.2min (18s of baseline plus 18s of experimental trials x 3 conditions x 4 repetitions), with a short interval of around 2min to play with the infant. Trials were consecutively displayed until the end of each experimental part. NIRS recording ended when the infant viewed each experimental stimulus 8 times, or if the infant grew restless or upset; in that case the session would end earlier.

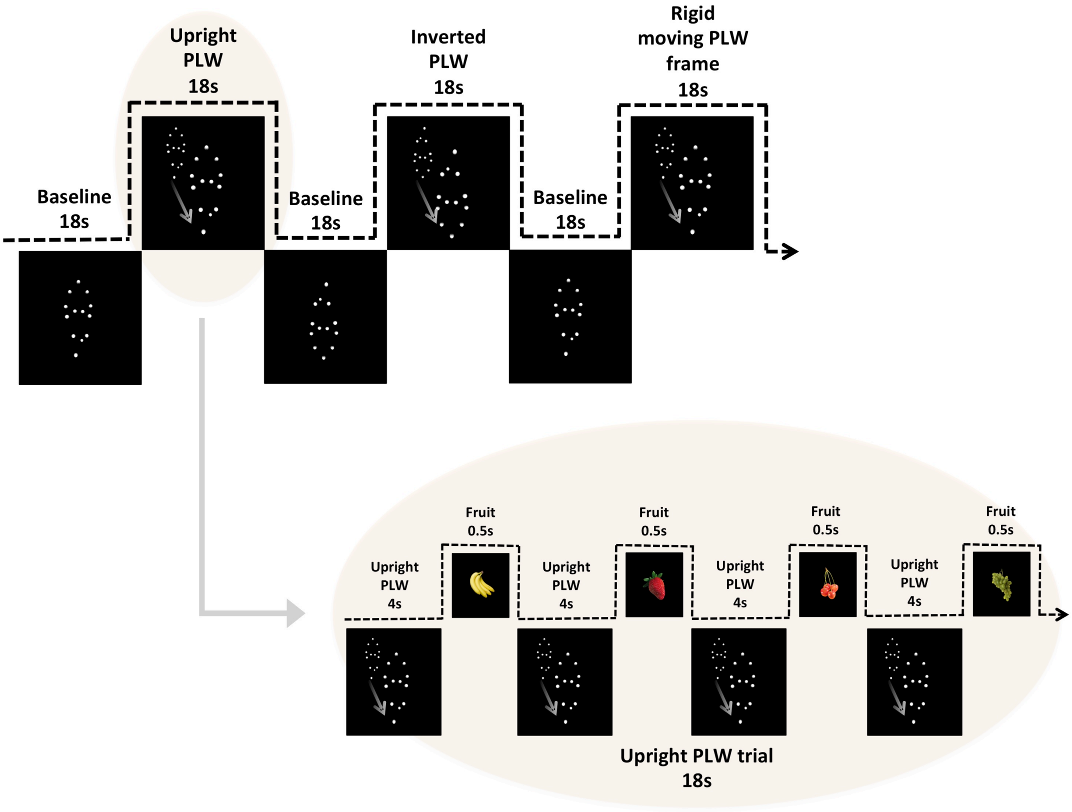

Figure 11. Experimental block design

Upper panel – Block design: the presentation of the three experimental conditions was randomized. A baseline trial always preceded an experimental trial. Both baseline and experimental trials had a total duration of 18s each, together with an attention-getter.
Lower panel – Schematic of a trial: to maintain infants' attention, an attention-getter composed of one fruit image presented simultaneously with a children's sound was inserted every 4s during the presentation of the stimulus and irrespective of whether a baseline or an experimental trial was being presented.

2.2.5 NIRS Recording

All infants were tested with the UCL optical topography system (Everdell et al., 2005). Participants wore an elastic cap (Easycap, GmBH), which was built with reference to the 10-5 system (Jurcak, Tsuzuki, & Dan, 2007), and was composed of three light sources (emitting continuous near-infrared light at two fixed wavelengths of 780 and 850 nm) and three detectors (the system captured data at 10Hz); the setup thus included a total of nine source-detector pairs, i.e. nine channels. The probe was customized to position these nine channels over the right posterior temporal area; see Figure 12 for a schematic representation of the probe array with labeled with the 10-5 system.

Seven out of the nine channels (channels 1, 2, 4, 6, 8, and 9) had 20mm and 22mm source-detector separation, and the two channels that crossed the middle of the array (the longest channels, 3 and 7) had 54/36mm of source-detector separation.

After the infant was comfortably seated, measurements of the infant's head (distance between the *nasion* and the *inion*, distance between the right pre-auricular and the left pre-auricular point, and head circumference) were taken to ensure the correct alignment of the probe on the infant's head, according to the 10-5 system (Jurcak et al., 2007). The cap was placed centrally at the top of *Cz* (central zero point), with channel 2 (corresponding to T8) placed above the right pre-auricular point (Lisboa, Queirós, et al., 2020; Miguel, Lisboa, Gonçalves, & Sampaio, 2017). We located the central midline point (*Cz*) on each infant by first measuring the distance between the *nasion* and the *inion*, and marking the point located at 50% of this total (this was our preliminary *Cz* mark). Then, we measured the distance between right and left pre-auricular points, and marked the point located at 50% of this total. The true *Cz* point was found at the intersection of both marks. In addition, pictures of the infant's cap placement were taken to later confirm the correct location of the channels.

The infants' average head circumference was 44.1, SD = 0.61 cm and the mean nasion-inion distance was 28.9, SD = 0.77 cm.

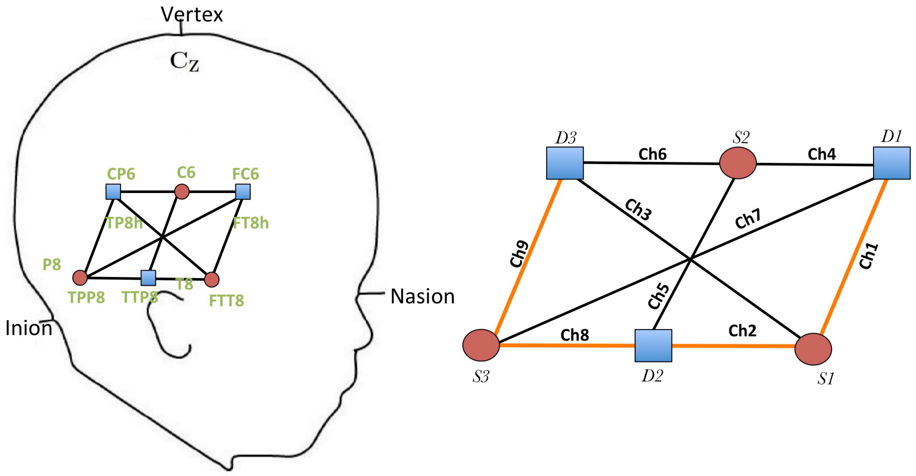

Figure 12. fNIRS array

Left – A schematic infant's head exhibiting the approximate location of the sources/detectors and channels with reference to the 10-5 system: blue squares and red circles indicate the detector and source locations respectively; lines connecting sources and detectors symbolize channels; 10-5 coordinates are superimposed in green.
Right – Detailed scheme of the fNIRS array with channels with significant activations highlighted in orange.

2.2.6 Data Processing

Infant looking behavior was coded offline by two independent coders using SuperCoder (SuperCoder 1.7.1, Purdue University, West Lafayette) and agreement was high: Cohen's $k = .82$, 95% confidence interval [0.73, 0.91], $p < .005$.

For a trial to be considered valid, the infant had to be looking at the screen for at least half of the total time of stimulus presentation (i.e. 8s) (Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015); time spent fixating on the attention-getter fruit images was not included. Trials in which the experimenter or the mother talked were not considered for further examination (Grossmann, Oberecker, Koch, & Friederici, 2010).

Raw data was converted into the NIRS format and analyzed in HOMER2 (Huppert, Diamond, Franceschini, & Boas, 2009). Before any signal processing, we visually inspected raw intensity data, per subject, on all nine channels; this led to the elimination of the two longest channels in the array (channels 3 and 7), since intensity raw data was practically non-existent on both channels and in all participants (Lisboa, Queirós, et al., 2020). In addition, trials that showed high and abrupt signal changes (i.e. when concentration change exceeded ± 15 μMol), were eliminated in all subjects (Hakuno, Pirazzoli, Blasi, Johnson, & Lloyd-Fox, 2018; Lisboa, Queirós, et al., 2020).

Further data corrections and analyses were performed considering only the remaining seven channels and trials, following protocols in previous infant studies that used either the same NIRS equipment and/or the same software (Lisboa, Queirós, et al., 2020; Lloyd-Fox, Széplaki-Köllőd, Yin, & Csibra, 2015; Ravicz et al., 2015).

To be included in the final sample, an infant had to have at least two valid trials per experimental condition; additionally, infants with unusable channel data (beyond channels 3 and 7) were ignored (Ravicz et al., 2015). The mean number of valid trials was 3.83 ± 1.40 for the upright point-light walker condition (N = 88 trials), 4.0 ± 1.68 for the inverted (N = 92 trials), and 3.70 ± 1.29 for the rigid moving point-light walker frame (N = 85 trials).

Data was corrected using a wavelet motion analysis, iqr = .50 (Cooper et al., 2012; Lloyd-Fox, Széplaki-Köllőd, et al., 2015; Ravicz et al., 2015), and was low- and high-pass-filtered with a passband of .50-.010 Hz (Cooper et al., 2012; Ravicz et al., 2015). Next, data from both wavelengths was converted to relative concentrations of oxygenated and deoxygenated hemoglobin, using the modified Beer-Lambert Law and assuming a path length factor of 5 (Duncan et al., 1995).

Mean concentration changes in oxy-hemoglobin (HbO_2) and deoxy-hemoglobin (HHb) were baseline corrected using the 2s prior to experimental stimulus onset, and block averaged using the following time epochs: 2s of baseline, 18s of stimulus onset, and 10s of post-stimulus offset (Biondi et al., 2016).

2.3 Statistical Analyses

The prototypical pattern of activation in fNIRS data that is associated with a functional response is a significant increase in oxy-hemoglobin (HbO_2) and a decrease in deoxy-hemoglobin (HHb) in relation to baseline (Lloyd-Fox et al., 2010). In infant studies, however, this pattern is not consistently observed, and some studies ignore the HHb concentration change when testing for the presence of an activation, as it is the less reliable signal (Lloyd-Fox et al., 2010; Strangman et al., 2002). We modeled both chromophores in order to detect when there is a parallel increase or decrease in concentration, a pattern that is inconsistent with a functional activation (Lloyd-Fox et al., 2010). We first conducted an exploratory data analysis, and visually examined the HbO_2 and HHb concentration change signal across all channels. We did not correct for multiple channel testing. This revealed several channels with candidate activations in at least one condition: channels 2 and 8; and channels 1, 4, and 9 with a weaker increase/decrease of HbO_2/HHb. The activation also had a maximum peak (in absolute value) occurring between 4 and 12s approximately.

Our main analysis consisted of modeling the mean concentration change, using epochs with four seconds of duration after stimulus onset; i.e., individual infants' baseline-corrected NIRS data was averaged in consecutive four-second time windows. In addition, only data from the following time windows was considered:]4, 8],]8, 12],]12, 18]. According to visual analysis of quantile-quantile plots, the dependent variable did not follow a normal distribution at the tails, and we applied a power transformation to the data with an exponent of 5/7; the power-transformed data was used in all analyses.

Modeling followed the approach for longitudinal data analysis (Diggle, Heagerty, Liang, & Zeger, 2002; Mirman, 2016). All models were fitted using the *nlme* package in R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2018). We first explored possible covariance structures by fitting one generalized least squares model to the mean concentration change data, per channel and per chromophore; we used *Time Window* (3 levels:]4, 8],]8, 12],]12, 18]) coded as a categorical variable and *Condition* (3 levels: upright point-light walker, inverted point-light walker, and rigid moving point-light walker frame) as predictors. Analysis of the residuals did reveal serial correlation in the data consistent with an AR(1) or exponential structure; nevertheless, the sample variogram showed that variability from this term was negligible compared to variability between individuals. Thus, we only considered models with fixed and random effects. Because *Time Window* had only three levels (i.e. the number of parameters was low) and we were interested in measuring mean concentration compared to baseline across time windows, our model included a full two-way interaction between *Time Window* and *Condition* in the fixed effects component, and a random intercept per participant in the random effects component. We fitted one linear mixed model per channel and chromophore.

Statistical inference was conducted by computing the 95% confidence interval of a model's estimated mean (estimated marginal means) and a single-tailed test against the baseline of zero (> 0 for the HbO_2 and < 0 for HHb). The single-tailed test was corrected for multiple comparisons using the Sidak method (Šidák, 1967). Mean concentration change inside a time window was considered consistent with a functional activation if the corrected *p*-value for the contrast with baseline was significant, and if the two chromophores were not increasing/decreasing in unison. When at least one condition had a significant activation (inside a time window) we also computed all pairwise comparisons between conditions. All statistical tests were obtained using the R package *emmeans* (R Lenth, 2018). When reporting estimated means and respective confidence intervals we back-transformed the data to the original units.

2.4 Results

Two conditions, upright and inverted point-light walker, yielded significant activations: the upright point-light walker in a more anterior area (channels 1 and 2), and the inverted point-light walker in a more posterior area of the array (channels 8 and 9); see Figure 13. The rigid moving point-light walker frame was not associated with any statistically significant response consistent with a functional hemodynamic activation. Table 1 reports all statistically significant results ($p \leq .05$) in relation to baseline per condition; comparisons between conditions are not reported in this table. Significant activations in relation to baseline, and congruent with a functional response, are described in the following subsections, per condition. Only when a result was statistically significant in relation to baseline in one condition did we compute comparisons between conditions.

Condition	**Chanel**	**Chromophore**	**Time Window (s)**	**Estimated Mean**	**95% CI**	***p* uncorrected**	***p* corrected**
Upright PLW	1	HHb	[4, 8[	-0.225	[-0.470, -0.043]	0.007*	0.010*
			[8, 12[	-0.141	[-0.36, -0.001]	0.044*	0.064
	2	HbO_2	[8, 12[	0.221	[0.011, 0.534]	0.028*	0.042*
	8	HHb	[8, 12[	0.179	[0.003, 0.456]	0.040*	1.000
	9	HHb	[8, 12[	0.150	[0.000, 0.401]	0.053*	1.000
Inverted PLW	1	HHb	[8, 12[	-0.150	[-0.376, -0.004]	0.036*	0.052
			[12, 16[	-0.128	[-0.347, 0.001]	0.058	0.084
	2	HbO_2	[4, 8[	-0.219	[-0.533, -0.010]	0.029*	1.000
			[8, 12[	-0.182	[-0.484, 0.000]	0.053*	1.000
	5	HHb	[4, 8[	-0.164	[-0.434, 0.000]	0.051*	0.074
	8	HbO_2	[4, 8[	0.245	[0.040, 0.527]	0.009*	0.014*
	9	HHb	[12, 16[	-0.177	[-0.436, -0.007]	0.031*	0.046*
Rigid moving PLW frame	8	HHb	[4, 8[	0.205	[0.013, 0.491]	0.025*	1.000
			[8, 12[	0.212	[0.016, 0.499]	0.022*	1.000

Table 1. Significant activations from baseline in the three experimental conditions.

Channels with significant ($p \leq .05$) activations from baseline in the three experimental conditions (upright point-light walker, inverted point-light walker, and rigid moving point-light walker frame; and the three 4s time-windows (]4, 8],]8, 12],]12, 18]); comparisons between conditions are not reported in this table. Note that the uncorrected p-value shown corresponds to the estimated 95% confidence interval and the corrected p-value to a single-tailed test of greater than zero for HbO_2, and below zero for HHb.

2.4.1 Upright Point-Light Walker Condition

In the upright point-light walker condition, HbO_2 concentration at channel 2 was found to be significantly above baseline (i.e. zero) at the [8, 12[time-window, $t(22) = 2.35$, $p < .04$; see Figure 13.

The contiguous channel 1 also revealed a response consistent with a functional activation: a significant decrease in HHb concentration was found at the 4 to 8s time-window, $t(22) = -2.99$, $p < .01$. This response was accompanied by an HbO_2 increase which did not reach statistical significance; see Figure 13.

2.4.2 Inverted Point-Light Walker Condition

In the inverted point-light walker condition, HbO_2 increase in channel 8 was significantly above baseline on the [4, 8[time-window, $t(22) = 2.85$, $p < .05$; see Figure 13.

In the contiguous channel 9, HHb concentration significantly decreased from baseline later, at the [12, 16[time window, $t(22) = -2.30$, $p < .05$; see Figure 13.

On channel 1, from 8 to 12s, HHb decrease in the inverted point-light walker was close to significance, $t(22) = -2.24$, $p = .052$. However, this response was accompanied by a decrease in HbO_2

concentration (see Figure 13) and was thus considered inconsistent with a hemodynamic response and was not further analyzed; see (Lloyd-Fox et al., 2010) for an example of the same approach.

2.4.3 Rigid Moving Point-Light Walker Frame Condition

No significant results were found in either HbO_2 or HHb concentration in relation to baseline and in all time windows.

2.4.4 Comparisons Between Conditions

Channel 2: Increase in HbO_2 concentration at the [8, 12[time window in the upright point-light walker condition was significantly greater in comparison with the other two conditions, i.e. with the inverted point-light walker, $t(176) = 3.43$, $p < .001$, and the rigid moving point-light walker frame, $t(176) = 1.99$, $p < .05$; see Figure 13B.

Channel 1: Decrease in HHb concentration at the [4, 8[time window in the upright point-light walker condition statistically differed from the rigid moving point-light walker frame, $t(176) = -2.74$, $p < .001$, but not from the inverted point-light walker condition; see Figure 13A.

Channel 8: Increase in HbO_2 concentration at the [4, 8[time window in the inverted point-light walker condition significantly differed from the other two conditions, namely from the upright point-light walker, $t(176) = -3.37$, $p <.001$, and rigid moving point-light walker frame, $t(22) = 2.90$, $p < .005$; see Figure 13C.

Channel 9: Decrease in HHb concentration at the [12, 16[time window in the inverted point-light walker condition only statistically differed from the upright point-light walker condition, $t(176) = 2.46$, $p < .05$; see Figure 13D.

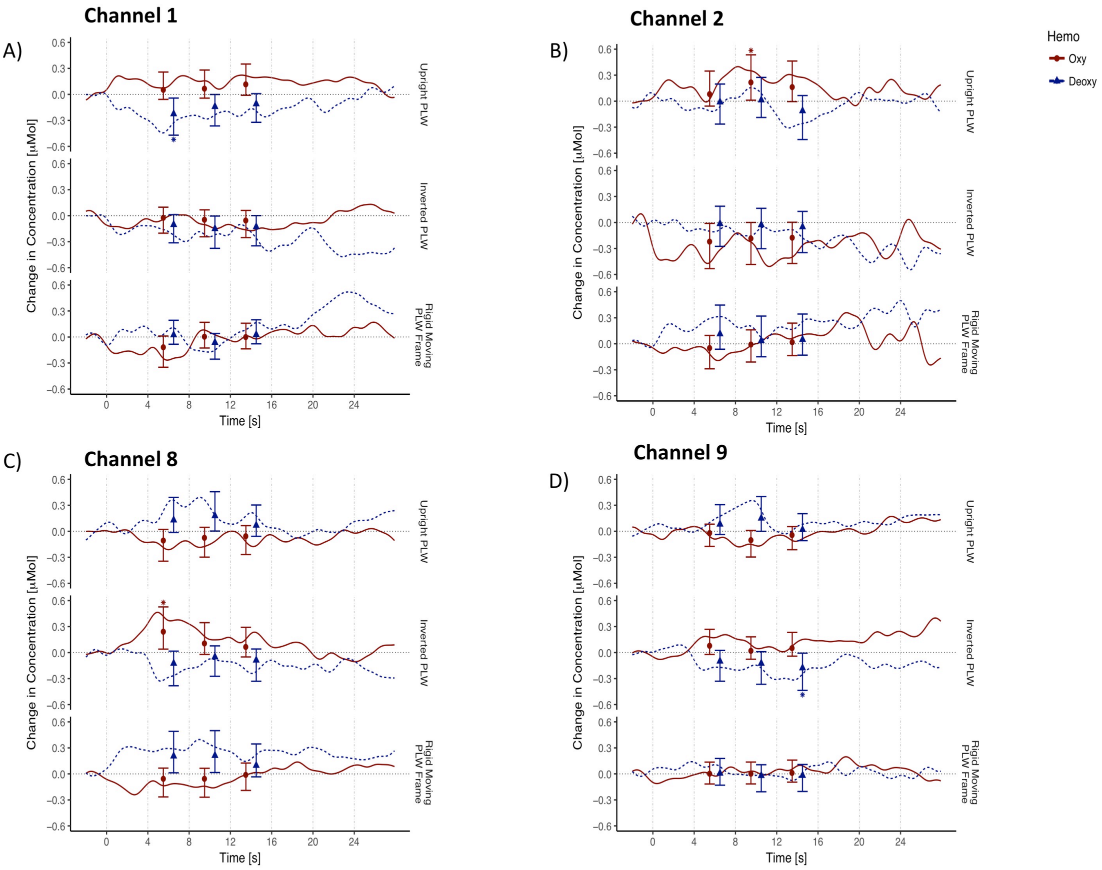

Figure 13. Grand mean average of baseline-corrected HbO$_2$ and HHb concentrations for significant channels in the three experimental conditions.

Grand mean average of baseline-corrected HbO$_2$ and HHb concentrations for the three experimental conditions (upright point-light walker, inverted point-light walker, and rigid moving point-light walker frame) on channels 1 (A), 2 (B), 8 (C), and 9 (D). The zero timepoint marks experimental stimulus onset; total trial duration was 18s. Lines plot the grand mean concentration changes in HbO$_2$ (red line), and HHb (blue dashed line). For the three epochs where we conducted statistical testing,]4, 8],]8, 12],]12, 18], we show the estimated mean and its 95% confidence interval. When the corrected p-value for the comparison with baseline was significant, we placed an asterisk above the respective confidence interval (single-tailed test, greater than zero for HbO$_2$, and below zero for HHb).

2.5 Discussion

Perception of biological motion is a basic perceptual ability necessary for learning about (and interacting with) others, and it is proposed to be a precursor of high-level social cognition (Frith & Frith, 1999; Grossmann, 2015; Pavlova, 2012). Among the network of brain regions preferentially sensitive to social signals, the right STS (superior temporal sulcus) is recognized as a key node in processing social information, including biological motion (Deen et al., 2015; Grossmann, 2015).

In the present study, we examined, in infants, how specific the right STS response is to the perceptual features that characterize biological motion. We measured in 7-month-old infants, using fNIRS, the hemodynamic response in the right temporal cortex to point-light walkers, a well-known class of highly controlled biological motion stimulus. We tested 7-month-olds, since this was the earliest age where brain-processing differences in the right STS region from other biological motion stimuli were previously reported (Biondi et al., 2016; Ichikawa et al., 2010; Lisboa, Queirós, et al., 2020).

In a within-subject design, infants viewed an intact upright point-light walker approaching the viewer, and two controls: an inverted point-light walker (where the canonical orientation was inverted), and a rigid moving point-light walker frame (where a single frame from the original sequence was animated to approach at constant velocity, similar to the motion of a rigid object moving at constant speed).

Results showed that the perception of both the intact upright point-light walker and the inverted point-light walker elicited a response consistent with a hemodynamic functional activation: the upright point-light walker in an anterior area of the array (which corresponds to the right middle-posterior temporal cortex), and the inverted point-light-walker in a more posterior location. Perception of the rigid moving point-light walker was not associated with any functional response in our study, suggesting that the region covered by our array is sensitive to object vs. articulated motion. Most importantly, our study adds novel evidence implicating the right STS in the perception of biological motion.

2.5.1 Activation to the Upright Point-Light Walker

The key finding in our study was the activation to the upright point-light walker; this response was found to be unique for this condition in channel 2 of our array, since it statistically differed from both the inverted and the rigid moving point-light walker frame.

Right STS activation to intact upright point-light displays is one of the most consistent reports in imaging studies of biological motion perception in adults (E. Grossman et al., 2000; Peuskens et al., 2005); underscoring this effect, point-light displays are used as an STS localizer in fMRI studies (Troje, 2013). Although our fNIRS array was specifically designed to cover the right STS, precise localization is not possible with the methodology we used; however, if we consider the neuroimaging findings in adults (E. Grossman & Blake, 2001; E. Grossman et al., 2000; Peuskens et al., 2005) and one spatial coregistering study in infants (Lloyd-Fox, Richards, et al., 2014), then the activations found for the upright point-light walker in our study likely involve the 7-month-olds' right STS. Neuroimaging findings with adults, conducted with fMRI, indicate that the perception of biological motion is specifically processed in the right STS (E. Grossman & Blake, 2001; E. Grossman et al., 2000; Peuskens et al., 2005). Previous coregistering experiments conducted with infants, using the same landmarks with fNIRS, and comparing localized patterns of hemodynamic response in fMRI, located the STS in a similar region to our measured activations (Lloyd-Fox, Richards, et al., 2014).

Previous fNIRS infant studies also found activations to human face and/or upper body motion, but in more posterior temporal locations; these studies, however, were either focused on face motion (Ichikawa et al., 2010), did not use the point-light technique (Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009), and/or used explicit social actions (Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009) in contrast to our use of the walking motion. Our activations to the upright point-light walker in the middle-posterior temporal cortex are, however, consistent with fMRI studies of STS activations in adults to intact biological motion stimuli (Deen et al., 2015), with other infant fNIRS data on human vs. mechanical hand motion (Biondi et al., 2016), and with our recent study in 7-month-olds, using the same fNIRS array, and the same approaching motion of a walker (Lisboa, Queirós, et al., 2020).

In Lisboa et al. (2020), we contrasted an upright point-light walker with a spatially scrambled point-light walker; and found activations associated with the upright point-light walker only, and in the same channel (channel 2) that we report here. Finally, it is worth noticing that the peak of oxy-hemoglobin (HbO_2) increase for the upright point-light walker that we report here (8-12s) also temporally matches other fNIRS studies focused on biological motion perception: Biondi et al. (2016) reported maximum oxy-hemoglobin changes at 8-15s specific for human hand motion in a similar location; similar time periods for biological motion stimuli were found by Lloyd-Fox et al. (2014), Lloyd-Fox et al. (2009), Lisboa et al. (2020), and Ichikawa et al. (2010) in 5- and 7-month-olds.

In sum, our significant findings associated with the upright point-light walker indicate that the right STS region is involved in the processing of an intact walking motion at 7 months of age.

2.5.2 Activation to the Inverted Point-Light Walker

Regarding the inverted point-light walker: although this stimulus only differs from the upright point-light walker in its orientation, we know that this feature (orientation) is salient enough to be used by infants in habituation and preferential looking tasks. Newborns, 4-, 5-, and 6-month-old infants all discriminate, and prefer to look at an upright point-light display rather than an inverted display (Bertenthal, 1993; Fox & McDaniel, 1982; Sifre et al., 2018; Francesca Simion et al., 2008). These behavioral results indicate that infants are sensitive to the orientation of point-light walkers by 7 months of age. Therefore, our initial hypothesis was that the infants' right STS functioning would be comparable to the mature adults' cortex, in which the inverted point-light walker is reported to not recruit its activation (Peuskens et al., 2005). However, our results suggest that this region is implicated in the processing of inverted point-light walkers at 7 months of age; we discuss three different, non-exclusive, research hypotheses to explain this result.

First, it could be that, at this age, the inverted point-light walker is associated with a bilateral response in the STS region (Carter & Pelphrey, 2006; Grossmann, 2015; Ichikawa et al., 2010). Carter & Pelphrey (2006) tested children aged 7 to 10 years in an fMRI study and found an increasing right STS specificity, developing with age, in responding to the perception of an intact walking motion. STS responded more bilaterally in younger children whereas both older children and adults exhibited greater right hemisphere dominance. Ichikawa et al. (2010) also tested responses in the right and left temporal cortex of 7–8-month-olds to the point-light display of an upright and an inverted facial expression of surprise. They found a preferential response in the right temporal cortex to the upright display; in contrast, the response to the inverted face motion showed an increase in concentration of HbO_2 in the left temporal area in relation to baseline, although this difference was not significant (Ichikawa et al., 2010). These two studies did not use point-light walkers as stimuli, which limits direct comparisons. Nevertheless, following on these results, it is possible that the inverted point-light walker is associated with a more bilateral response in the STS region in relation to the upright point-light walker (that is motor right-lateralized) at 7 months of age; this conclusion is, however, outside the scope of this study, as we did not measure left temporal responses.

Reid et al. (2006) measured ERPs and tested inverted and upright point-light displays of walking and kicking in infancy; they indeed reported brain processing differences between the two displays; direct comparison of the reported ERPs and our fNIRS measurements is difficult. EEG and fNIRS are considered the two most suitable neuroimaging techniques to study social cognition in infants (Azhari et al., 2020; Lloyd-Fox et al., 2010), but they are complementary, with EEG's poor spatial precision as one the key differences. In addition, the exact relation between neural activity as measured by ERPs, and the hemodynamic response measured by fNIRS, is still under debate; see, for example, the discussions in (Azhari et al., 2020; Foucher, Otzenberger, & Gounot, 2003; Lloyd-Fox et al., 2010). With the available evidence, we cannot confirm which brain structures underlie the activations in Reid et al. (2006) and their association with our significant results in the right posterior region.

A second hypothesis for our results is that the right STS region is more generally sensitive to the intrinsic motion of an articulated body in motion, even if it is not upright (Thompson, Clarke, Stewart, & Puce, 2005). Though the majority of fMRI research does not support this hypothesis—since it reports a reduced response for inverted point-light displays in the right STS of adults (E. Grossman & Blake, 2001; Peuskens et al., 2005)—there are also a few studies reporting no differences in this region for the inverted control, and arguing for a more general role for the STS in processing articulated motion (Thompson et al., 2005).

A third and final hypothesis is an immature right STS that responds to the common visual properties of upright and inverted displays. In the inverted point-light walker, configural relations between the dots are maintained, plus the stimulus still depicts the body's articulated motion. This might explain the results, especially considering that, in contrast, the rigid moving point-light walker frame did not elicit activations. Articulation is an important dimension of vertebrate motion that distinguishes biological from object motion. This hypothesis is also in accordance with results from Lisboa et al. (2020), that also reported no significant responses in the right STS region of 7-month-olds associated with the visualization of a spatially scrambled point-light walker (where articulation and all configural relations between the dots are disrupted). The developing right STS is perhaps involved in processing configural relations in biological motion (Lisboa, Queirós, et al., 2020), which are present in upright and inverted point-light walkers, but not in either the rigid moving point-light walker frame or in the scrambled point-light walker. More specific responses in the right STS region to the intact properties of biological motion might be an outcome of later development (Grossmann, 2015).

2.5.3 Absence of Activation to the Rigid Moving Point-Light Walker Frame

Lastly, and relative to the rigid moving point-light walker frame condition, the absence of significant responses associated with this condition is a new result in neuroimaging studies of infants. This finding corroborates previous fMRI experiments with adults, showing that STS preferentially responds to articulated motion relative to a stimulus category that corresponded to a human form moving without the internal articulation, similar to our rigid motion condition (Beauchamp et al., 2002).

2.5.4 Contributions and Limitations of the Study

Our knowledge of the neurodevelopment of biological motion perception in infancy is scarce and restricted to a small number of fNIRS studies (that did not use point-light walkers) and cross-sectional studies using ERPs and point-light walkers; see (V. Reid et al., 2006; V. M. Reid et al., 2008) (Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009). The use of the point-light display technique is an important contribution because it isolates motion information from other sources of visual information (Johansson, 1973), and in imaging studies, it enables the precise manipulation of the differences between the experimental and baseline stimuli; new findings can also be compared with the voluminous literature coming from studies in adults. We measured 7-month-olds' hemodynamic response specifically to point-light walkers; the demonstration that the right STS of infants responds to such controlled stimuli as point-light walkers is recent (Lisboa, Queirós, et al., 2020), and this study contributes additional evidence. Another contribution from our study is that cortical activation to the moving rigid point-light walker frame (one of our control stimuli) was never, to the best of our knowledge, tested or compared with an intact point-light display in infants. This manipulation is important, since it maintains a static version of the minimal form information from the original point-light walker, removing all the other visual features characteristic of biological motion, and is similar to rigid object motion.

In addition, we also presented the point-light walker approaching the viewer, while the classic stimuli is a side view. This choice was based on three factors: (1) the frontal view of the stimulus is configurally less complex, since there are no occlusions of the limbs during the gait cycle; (2) recognition experiments with adults suggest a perceptual advantage for frontal views of point-light walkers in relation to side views (Jokisch et al., 2004; Troje et al., 2005); and (3) perception of frontal views of other social stimuli, such as frontal face perception, emerges earlier in infancy than side views, as measured by fNIRS (Ichikawa et al., 2019; Nakato et al., 2009). Considering these factors, we conjectured that the motion of an approaching person, as if approaching to interact with the infant, would also increase infants' visual attention to the stimuli, and the fNIRS signal intensity.

The present study contains a few limitations. Our array was small, restricted to the right temporal cortex; smaller arrays, however, have the advantage of being lighter and more confortable for the infant, capturing a response with less signal to noise ratio, and favoring longer experimental designs (Lisboa, Queirós, et al., 2020; Lloyd-Fox et al., 2011). Our study included three experimental conditions of 18s each; most fNIRS studies conducted with infants contrast only two experimental conditions, (e.g., (Lloyd-Fox et al., 2010). Visual attention in young infants is limited, and our experimental design was at the ceiling level for the 7-month-old infants' ability to collaborate. The distribution of number of valid trials per infant, nevertheless, shows we calibrated the design correctly.

Another possible limitation of our experimental design is the difference between the total amount of motion presented in the rigid moving point-light walker frame and both the upright and inverted-point-light walkers (e.g., the rigid had no intrinsic motion). Nonetheless, in the Lisboa et al. (2020) study, when infants were presented with a scrambled point-light walker that had the exact same total amount of motion as the original point-light walker, there was no significant response. The differences found in our study and in Lisboa et al. (2020) therefore point to the right STS region as sensitive to the distinction of rigid object motion vs. biological motion (and not merely sensitive to the amount of motion), by at least 7 months of age.

2.6 Conclusion

The STS has been intensely studied regarding its connection to social perception and cognition. In this sense, we should underscore that activations along the temporal cortex elicited by biological motion stimuli reported here are also found in other fNIRS studies in infants, conducted with other social stimuli such as: static faces (Otsuka et al., 2007), human face motion (Ichikawa et al., 2010), human vocal sounds (Grossmann et al., 2010), or even multimodal interaction signals (Lloyd-Fox, Széplaki-Köllőd, et al., 2015). There are limits to this comparison since STS is a large sulcus and likely functionally complex (Hein & Knight, 2008); fMRI literature has allocated to STS a more general function: it is likely a multisensory area, specialized in integrating information from multiple sensory modalities (Beauchamp, Argall, et al., 2004; Beauchamp, Lee, Argall, & Martin, 2004).

Future neurodevelopmental studies focused on the first year could shed light on these questions, correlating individual patterns of response to biological motion stimuli in the right STS with other social-developmental skills, and/or addressing the developmental pathway of the STS in processing biological motion.

Two age periods seem relevant, given the available evidence from behavioral and neuroimaging work. The first, suggested by the fNIRS studies conducted so far, is a transition to a right STS dominance; this might happen between 5 and 7 months, e.g. bilateral temporal activations to biological motion were found at 5 months (Lloyd-Fox et al., 2009), and a right temporal dominance at 7/8 months (Ichikawa et al., 2010). This hemispheric specialization also underscores the importance of studying the left STS. The second is a developmental shift observed between 3 and 5 months of age in processing the global human motion configuration; for a complete review see Bertenthal (1993). At 5 months of age, and in behavioral tasks, infants respond specifically to the global human motion configuration present in point-light walkers; 3-month-olds, in contrast, are only capable of processing local motion configurations (e.g., sensitivity to a moving limb but no sensitivity to the disruption of a coherent body in motion) (Bertenthal, 1993). How this developmental shift in biological motion perception between 3 and 5 months-old relates to infants' brain development, and specifically to right STS responses, remains to be investigated.

Our preliminary results suggest that biological motion perception is processed, in infancy, in the right STS, one the one of the central nodes of the social brain network. These results thus indicate that the perception of biological motion is an important precursor of human social cognition.

Chapter 3: Infants' Cortical Processing of Biological Motion Configuration – An fNIRS study

A version of this Chapter is published in Infant Behavior and Development[1]

Infants' Cortical Processing of Biological Motion Configuration – A fNIRS study

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Abstract

Biological motion perception is a key component of action perception, contributing to social cognition in crucial ways. Contemporary neuroimaging studies show that biological motion is processed differently in the human brain from other types of motion. In particular, the right posterior Superior Temporal Sulcus (rpSTS), an area known for its central role in social perception, has been consistently associated with the perception of biological motion in the mature brain. By contrast, most findings investigating the development of biological motion perception in infancy come from behavioral studies, and far less is known regarding the right STS' role in processing biological motion.

The current study used fNIRS to measure brain activation to biological motion in the rSTS region of seven to eight month-old infants. Infants were presented with two conditions: an approaching coherent motion of a person walking (coherent point-light-walker); and a spatially scrambled version of this display, where the global configuration of a person walking was disrupted (scrambled point-light walker).

We found a functional activation, i.e., a significant increase in HbO_2 concentration in relation to baseline, in the right middle-posterior temporal cortex only when infants viewed the coherent point-light-walker. This activation statistically differed from the scrambled display, and no significant activations were found for viewing the scrambled motion.

Our study adds evidence pointing to rSTS' sensitivity to the global human configuration in biological motion processing during infancy. The rSTS seems thus to become functionally specialized in biological motion configuration as early as at seven to eight months of age.

Keywords: biological motion, fNIRS, neurodevelopment, scrambled Point-Light-Walker, right Superior Temporal Sulcus (rSTS)

3.1 Introduction

Our ability to understand and respond to other people’s actions is a distinctive aspect of human’s social cognition. Observing the motion of others is a primary source of dynamic information about their actions (Bertenthal & Longo, 2008), and historically in vision science, action recognition has been associated with the study of biological motion perception.

The term *biological motion* was coined by Johansson in the early 1970s to refer to the intrinsic motion of humans and animals. Johansson (1973) developed a now-classic technique to investigate biological motion: he attached small illuminated dots onto the major joints of a person in action to isolate and study the information revealed by motion from other sources of information such as form, texture, color, or even facial information.

The uniqueness of biological motion perception is vividly demonstrated by point-light displays: although visual information in point-light displays is reduced to a minimum, adult observers need less than half a second to identify the global configuration of a person walking from a point-light walker (i.e. a point-light display depicting walking) (Johansson, 1976).

To perceive a walking person or a human in action from point-light displays, one has to be able to integrate the information contained in the motion of the individual dots into the global form of a person—its global human motion configuration. This perceptual organizational process has been considered a key component of mature biological motion perception and action recognition (Masahiro Hirai & Senju, 2020; Johansson, 1973, 1976; Troje, 2013). Despite this, understanding how the visual system processes configural relations to perceive the global form of a point-light walker (Johansson’s motivation for the creation of the point-light-stimuli) still remains an open question.

One way of analyzing the perception of configural relations in biological motion processing is by comparing the performance of an intact coherent point-light walker with a scrambled point-light walker. A scrambled point-light walker is a standard control manipulation of a coherent display, and consists of randomizing, in the point-light display, the dots’ initial locations. As a result, in a scrambled point-light walker, local configural properties (i.e., the relation between two or more dots such as limb motion), and the global coherent percept of a person in action are absent, although the individual dot motion properties are kept intact. This manipulation thus disrupts both the local and global configurations of the display.

In this context, developmental studies conducted with infants using point-light walkers and behavioral tasks employing the scrambled manipulation have been highly informative about biological motion’s configural processing (Masahiro Hirai & Senju, 2020). Studies conducted with infants at birth showed that newborns both discriminate and prefer an intact coherent point-light walker, over random motion, and over an inverted point-light walker (Francesca Simion et al., 2008). However, when contrasting the coherent point-light walker with the scrambled manipulation, there is no preference for either stimulus (coherent vs. scrambled), although newborns still discriminate between both stimuli (Bardi et al., 2011).

This suggests that the visual system at birth is capable of using visual information to prefer and discriminate the coherent displays but is not integrating the individual motion information to form the global percept of a point-light walker. The ability to process configural relations in biological motion must thus involve a more specialized, late-developing, higher-level processing; hence requiring more visual experience, and cortical maturation (Bertenthal, 1993; Masahiro Hirai & Senju, 2020).

Neuroimaging studies have made important contributions by showing that the superior temporal sulcus (STS), and in particular the right posterior superior temporal sulcus (rpSTS), is involved in the perception of the global human motion configuration in biological motion. Right STS activations have been implicated both in the processing of the higher level information contained in the visual content of an action (Allison et al., 2000), and as a convergence zone between the ventral and dorsal streams, integrating information about form and motion for biological motion (Giese & Poggio, 2003; Kourtzi, Krekelberg, & Van Wezel, 2008; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001).

Multiple studies in adults found higher activation patterns in the right STS region to intact coherent point-light displays in comparison with scrambled versions of the stimuli (Baccus, Mozgova, & Thompson, 2009; E. Grossman & Blake, 2001; Jokisch, Daum, Suchan, & Troje, 2005; Peuskens et al., 2005; Thompson et al., 2005; Vaina et al., 2001).

In addition, the only two neurodevelopmental studies conducted with event-related potentials (ERPs) in infancy, and using coherent vs. scrambled point-light displays, indicate that this role seems to start early in infancy. These two studies examined the neural responses associated with the process of biological motion configuration in eight and five month-old infants.

The first study was conducted with eight month-old infants and found that, during perception of a coherent point-light walker, the amplitude of responses in the right hemisphere were significantly greater for the coherent than for the scrambled point-light walker (Masahiro Hirai & Hiraki, 2005). The second study was conducted in five month-old infants and used a set of point-light displays performing different actions (running, walking, throwing a ball, and kicking a ball), and scrambled versions of the same displays. Results revealed that the coherent point-light displays elicited more positive waveforms at mid-parietal electrodes and more negative waveforms at lateral parietal electrodes in relation to the scrambled displays (Marshall & Shipley, 2009).

These studies are important as they both suggest differential brain responses for coherent vs. scrambled point-light displays; these experiments indicate a differential processing of configural relations in biological motion emerging in the first half of the first year of life (Masahiro Hirai & Hiraki, 2005; Marshall & Shipley, 2009).

However, source localization was not conducted in these experiments; therefore, it is not possible to know the exact cortical location of the reported functional responses. As a result, the right STS role in processing configural relations in biological motion in infancy is still unknown.

Functional near-infrared spectroscopy (fNIRS) was an undeniably important addition to neurodevelopmental studies of social cognition, as this technique has a better spatial resolution than EEG, and is less corrupted by motion artifacts than fMRI (Lloyd-Fox et al., 2010). Plus, fNIRS, like fMRI, records localized patterns of hemodynamic response signal (HbO_2 and HHb); it therefore allows a more fruitful comparison with the already extensive fMRI data on this topic concerning adults (Strangman et al., 2002).

Using this novel method for studying infants' cortical responses to biological motion, a set of recent fNIRS studies has measured brain activations elicited by biological motion in infancy (Biondi et al., 2016; Grossmann et al., 2013; Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009). Importantly, none of these studies investigated the neural processing of configural relations in biological motion perception; thus, none used point-light walkers as stimuli or even contrasted a coherent with a scrambled manipulation.

Lloyd-Fox et al. (2009) tested five months' temporal responses to video clips of a female actor moving her eyes, her mouth, or performing hand games relative to moving mechanical toys. Significant responses were found in both temporal hemispheres in the HbO_2 signal, and they occurred 10 to 18 seconds after the onset of the videos.

Ichikawa, Kanazawa, Yamaguchi & Kakigi (2010) reported a significant increase in HbO_2 concentration in the right temporal area when older, seven to eight month-old infants viewed an upright point-light display of a face moving with a surprised facial expression. This response happened 11 to 17 seconds after stimulus onset, and was restricted to the right temporal hemisphere and the upright stimulus; no significant results were found in left hemisphere or when infants viewed the control stimulus, an inverted version of the same point-light-face (Ichikawa et al., 2010).

Biondi et al. (2016) also measured temporal responses in seven/eight month-old infants to the motion of a human vs. mechanical hand 8 to 15 seconds after stimulus onset, the response to the human hand motion differed from the mechanical hand motion solely in the right middle-posterior temporal cortex.

In sum, although these studies shed light on biological motion processing in infancy, pointing to a right temporal specialization for biological motion present at seven/eight months of age, none addressed the question of perceiving configural relations in biological motion. In particular, it would be ideal to study rSTS responses to biological motion information—and the majority of these studies did not employ the point-light technique, thus including more than motion information in the stimuli (Biondi et al., 2016; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009). Because they did not use point-light displays, control stimuli varied across multiple dimensions from the main experimental motion stimulus—e.g. comparing the actions of an actor versus moving mechanical toys (Biondi et al., 2016; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009); or a human versus a mechanical hand (Biondi et al., 2016). The only exception is the Ichikawa et al. (2010) study, but the stimuli studied are limited to activations to a point-light display of a surprised face motion—and face perception is a particular topic on developmental research (Francesca Simion & Giorgio, 2015).

In conclusion, it is still unexplored how the infant's right STS, a critical node in processing social stimuli (Allison et al., 2000; Deen et al., 2015; Grossmann & Johnson, 2007), responds to an important type of controlled stimuli, point-light-walkers, or to such a relevant perceptual property as the configural relations in biological motion.

Here we present a novel study specifically addressing the right STS' role in infancy in the perception of configural relations in point-light walkers. In a within-subject design, we measured the hemodynamic response in seven/eight month-old infants' right temporal region, using fNIRS, to an intact coherent point-light walker (a more socially relevant stimulus, since it depicts the local motion configuration of the limbs, and the global motion configuration of a person walking) vs. a scrambled point-light walker (a stimulus that maintains the individual motion of the dots, but breaks its local and global configuration).

The rationale for measuring only the right temporal region at seven/eight months of age has three parts: (1) our fNIRS array was small, composed of 9 channels – but smaller arrays have the advantage of capturing a signal with fewer motion artifacts and with better overall quality, since they are more comfortable and lighter for the infant (Lloyd-Fox et al., 2010); (2) we measured the right temporal region, taking into consideration that configural relations in biological motion are processed in the right STS in the mature brain (Peuskens et al., 2005; Vaina et al., 2001), thus we speculate that, likewise, infants' differential processing of coherent vs. scrambled point-light displays happens specifically in this region; and, finally, (3) previous neurodevelopmental studies conducted with fNIRS indicate differential processing of biological motion stimuli also occurring only in the right temporal cortex and specifically at this age (Biondi et al., 2016; Ichikawa et al., 2010). In addition, we know from previous ERPs studies that seven to eight month old infants show brain process differences in relation to a coherent point-light walker versus a scrambled point-light walker (Masahiro Hirai & Hiraki, 2005).

We hypothesize an increase in oxy-hemoglobin (HbO_2) concentration in the right temporal cortex associated with the observation of the coherent global configuration of the intact point-light walker; we also hypothesize that this response will be absence in the scrambled point-light walker condition.

3.2 Method

3.2.1 Participants

The final sample consisted of 17 (n = 17) typically developing infants with no hearing, visual, or any other reported clinical condition (birth weight > 2500g; gestation period > 37 weeks; Apgar score > 7). Infants were aged between seven and eight months of age (5 females, mean age = 7 months and 24 days, SD = 12 days); the attrition rate was 29.2 % – see Table 2 for a complete characterization of our sample. Seven more subjects were tested but data was excluded due to equipment failure (n = 1), or because they did not satisfy the inclusion criteria (n = 6) – see the inclusion criteria on section 3.2.4 NIRS Recording and Data Processing. Subjects were recruited through direct contact with their parents. All parents gave informed consent of the procedure and the study was approved by the University of Minho ethics committee.

Final sample characterization	
Number of infants	17 (5 females)
Age at birth (weeks)	39 weeks (8 days)
Age at study (months, days)	7 months and 24 days (12 days)
Weight at birth (g)	3141.27 (522)
Height at birth (cm)	48.55 (2.52)
Cesarean deliveries	2 (12.5%)
Apgar score	9.27 (0.44)
Head circumference (cm)	44.67 (1.58)
Nasion-inion distance (cm)	27.45 (1.67)
Age of the mother (years)	34.28 (3.31)
Age of the father (years)	34.87 (5.41)

Table 2. Final sample characterization Standard Deviations appear in parentheses after the mean, except for cesarean deliveries, which are presented in an absolute number followed by the percentage.

3.2.2 Stimuli and Experimental Design

Two point-light walkers approaching the viewer's frontal plane were used: (1) a coherent intact point-light-walker; and (2) a spatially scrambled version of this display – see Figure 14 for a schematic of the stimuli. The coherent point-light walker consisted of a male model (13 dots) walking two steps from the back to the front in the frontal plane—for details on motion acquisition and stimulus construction see Mouta, Santos, and López-Moliner (2012). The area covered by the stimulus in visual angle ranged between 13° 41' x 5° 43', initially, and 24° 48' x 24° 48', at a viewing distance of 50 cm.

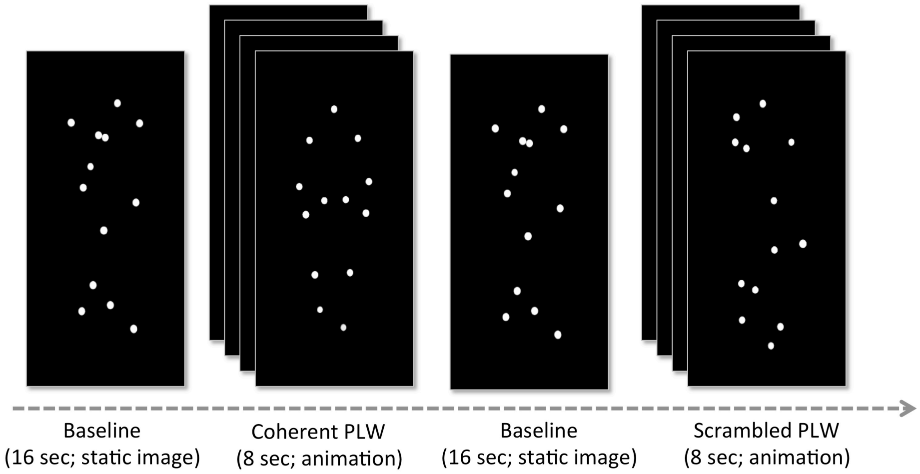

Figure 14. A schematic representation of the stimuli and the experimental design

The scrambled point-light walker was created by randomizing the initial positions of each of the dots corresponding to the joints of the original intact point-light walker. Thus, the individual motion paths of each dot were exactly the same as in the coherent display, but all spatial relations between the dots, local configural (e.g. relation between two or more dots), and global (the relation between all dots), were perturbed in the scrambled point-light walker.

The point-light walker stimuli were presented on an ASUS VG248QE-monitor (native resolution of 1920*1080; screen size: 53*30cm) by rendering the point light displays using *Superlab* (Cedrus Superlab 5.0); stimulus presentation was done at a frame rate of 60 frames per second and 1440 x 900 pixels resolution.

The baseline stimulus consisted of the presentation of a static image. This image corresponded to a selected middle frame, generated from a separate scrambled point-light walker (i.e. not from the scrambled stimulus used in experimental trials). Thus, the baseline stimulus corresponded to a static image of a fixed number of white dots (i.e., 13 dots) on a black background, arranged in randomized positions. All stimuli (baseline and experimental) occupied an approximately equal visual angle.

Subjects participated in a within-subject block design that comprised two experimental conditions (coherent walker and scrambled walker) and one baseline condition (static image) – see Figure 14 for a schematic of the experimental design. Infants participated in 16 blocks in total: 8 blocks in which the coherent point-light walker was presented, and another 8 with the scrambled walker. Each block consisted of a baseline period, where the static image was presented for 16 seconds, and an experimental period, where one of the motion stimuli was presented for 8 seconds. The presentation order of the blocks was randomized. The baseline period was longer than the experimental period to allow the hemodynamic response, initiated during the experimental condition, to return to its baseline level (Lloyd-Fox et al., 2010); at least 10 seconds after the experimental stimulus offset seems to be needed for the hemodynamic response to return to baseline (Taga, Asakawa, Maki, Konishi, & Koizumi, 2003).

In both periods (baseline and experimental), an image of a fruit synchronized with pleasant children’s sounds (500 milliseconds’ duration) were introduced every 2 to 4 seconds to draw and keep the infant’s attention on the screen—see Ichikawa et al. (2010) for a similar approach. Fruit presentation increased the baseline period from 16 seconds to 18 seconds, and the experimental period from 8 seconds to 10 seconds.

3.2.3 Procedure

When parents arrived at the laboratory, they were asked to answer a short socio-demographic questionnaire; at the same time, the experimenter measured the infant’s head (head circumference, nasion-inion, and ear-to-ear distance) and marked the *Cz* point (Miguel et al., 2017) – see Table 2 for more details of the measurements.

Next, they moved to the experimental room, which was dimly lighted, and the infant sat on their parent's lap; the experimenter then correctly aligned the cap on the infant's head. The cap was placed centrally on the top of *Cz,* with channel 2 (corresponding to T8) placed above the preauricular point (Miguel et al., 2017). Photos of cap placement were taken in order to confirm the correct location of the array – see Figure 15A for a picture of the cap on an infant's head.

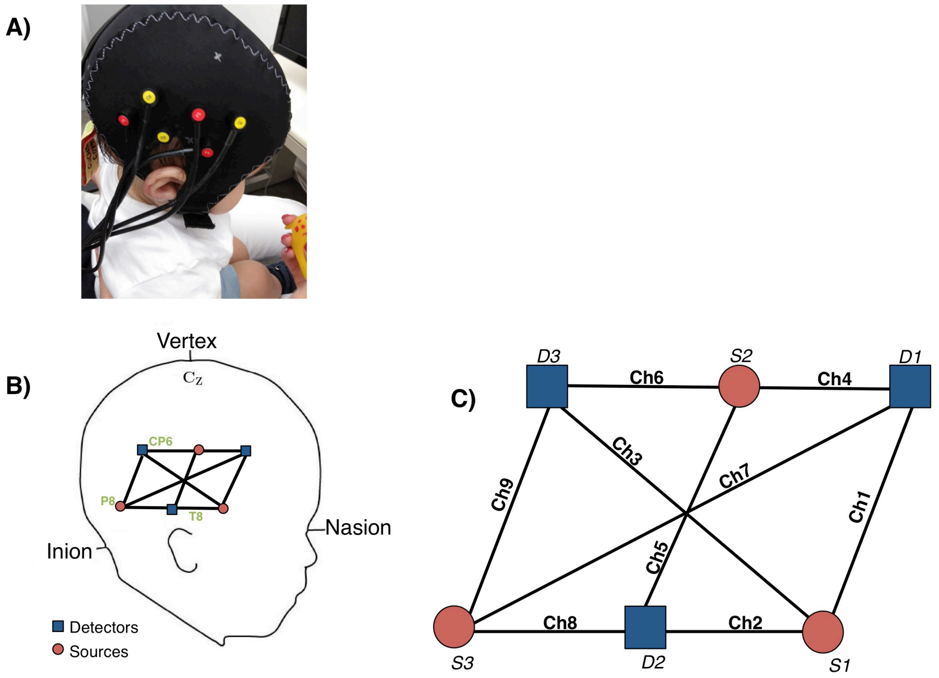

Figure 15. Illustration of the fNIRS array

A – A photo of the cap on an infant's head.
B – A schematic infant's head exhibiting the approximate location of the sources, detectors, and channels, with reference to the 10-5 system: blue squares and red circles signalize the detectors and sources location respectively; lines connecting sources and detectors symbolize channels; 10-5 coordinates are superimposed in green.
C – A detailed scheme of the fNIRS array with the numbered channels; being too long, channels 3 and 7 did not capture practically any signal and were not analyzed.

When the infant was calmly seated, the experimenter triggered the beginning of the experiment. A camera placed below the computer's screen recorded the infant's eyes for off-line coding of their looking behavior. The hemodynamic response was recorded while the infant passively watched the stimuli; rubber toys and/or a pacifier were allowed when needed to help the infant stay calm and focused during the procedure. Parents were instructed to refrain from interacting with the infant, and no talking was allowed during the recording.

To prevent the infant from becoming tired and/or fussy, a pause to play with the infant was introduced in the middle of the procedure, i.e., after 8 blocks of stimuli presentation, approximately 4 min.

The experiment ended when the infant watched all 16 blocks (lasting approximately 8 min), or when they became too bored or fussy to continue.

3.2.4 NIRS Recording and Data Processing

We used the UCL optical topography system (Everdell et al., 2005) to record the hemodynamic response in the right temporal region. Infants wore an elastic cap (Easycap, GmBH), composed of 9 channels, that was built using as reference the 10-5 system (Jurcak et al., 2007).

All 9 channels were dispersed over the right temporal area, in the approximate location of the right STS (Lloyd-Fox, Richards, et al., 2014). The array was thus composed of 3 emitters/sources (that emitted continuous near-infrared light at two fixed wavelengths of 780 and 850 nm), and 3 detectors (that captured data at 10Hz) – see Figure 15B and C for a schematic representation of the array. The two channels that crossed the middle of array (the longest channels, 3 and 7) had a 54–36mm source-detector separation and the other seven channels (channels 1, 2, 4, 5, 6, 8, and 9) had 2022mm.

For an infant to be included in the final sample, the following inclusion criteria had to be satisfied: (1) all channels had usable data (not including the longest channels, 3 and 7) (Ravicz et al., 2015); (2) looked at the experimental stimuli for at least 5 seconds in each trial (Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015); and (3) had at least 2 valid trials per experimental condition. Trial number per subject could range from 2 to 8 trials. Mean number of trials per subject was 4.18, SD = 1.47 in the coherent point-light walker condition, and 4.88, SD = 1.58 in the scrambled point-light walker condition.

All data transformations were conducted using HOMER2 (Huppert, Diamond, Franceschini, & Boas, 2009). Raw data was converted into *.nirs* format for analysis and each channel's signal was, first, visually inspected. The longest channels, 3 and 7, were eliminated from all processing and analysis because they had practically nonexistent-recorded data in all infants. Trials with high and abrupt signal changes in which concentration changes exceeded ± 15 μMol were also eliminated (Hakuno et al., 2018).

To correct for motion artifacts, we followed the hybrid approach of the spline interpolation method and Savitzky–Golay filtering; this method is implemented in HOMER2, and is detailed in (Jahani, Setarehdan, Boas, & Yücel, 2018). After motion correction, the signal was band-pass filtered with a high pass of 0.01 Hz and a low pass of 0.5 Hz.

Data from both wavelengths was then converted to relative concentrations of oxygenated (HbO_2) and deoxygenated (HHb) hemoglobin, using the modified Beer-Lambert Law with a path length factor of 5 (Duncan et al., 1995).

Finally, HbO_2 and HHb concentrations were baseline corrected using the final 2 seconds of baseline trials, i.e., the mean concentration in the 2 seconds before the experimental trial onset was subtracted from the experimental trial signal. Data was then block averaged from -2 seconds before the onset of each experimental trial (baseline) and +10 seconds after the experimental trial's offset (i.e., 20 seconds in total of signal after stimulus onset).

3.3 Statistical Analysis

The prototypical functional activation pattern in fNIRS consists of an increase in oxy-hemoglobin (HbO_2), and a concomitant decrease in deoxy-hemoglobin (HHb) concentration in relation to baseline (Lloyd-Fox et al., 2010). This pattern involves a change in both chromophores, but a significant increase in HbO_2 concentration has been systematically found as the most reliable response signal (Lloyd-Fox et al., 2010; Strangman et al., 2002). Nevertheless, we opted to report data on both chromophores. Moreover, a parallel increase or decrease in the two signals has been described as a response that is inconsistent with a functional activation (Lloyd-Fox et al., 2010). All statistical analyses were performed using the R programming language (R Core Team, 2013).

We first performed an exploratory analysis by plotting the grand-average hemodynamic change, from stimulus onset to 20 seconds after, for both HbO_2 and HHb in the two conditions (coherent and scrambledpoint-light walkers), and per channel. The visual inspection of the hemodynamic response in both conditions revealed a response that is consistent with a functional activation for the coherent point-light walker in five channels (channels 1, 2, 4, 5, and 6), and in only one channel (channel 1) for the scrambled point-light walker. Channels 8 and 9 did not reveal any consistent response – see Figure 16 for a depiction of the hemodynamic response in all seven channels. The range of maximum concentration changes observed across infants and conditions for HbO_2 and HHb occurred between 6 and 18 seconds.

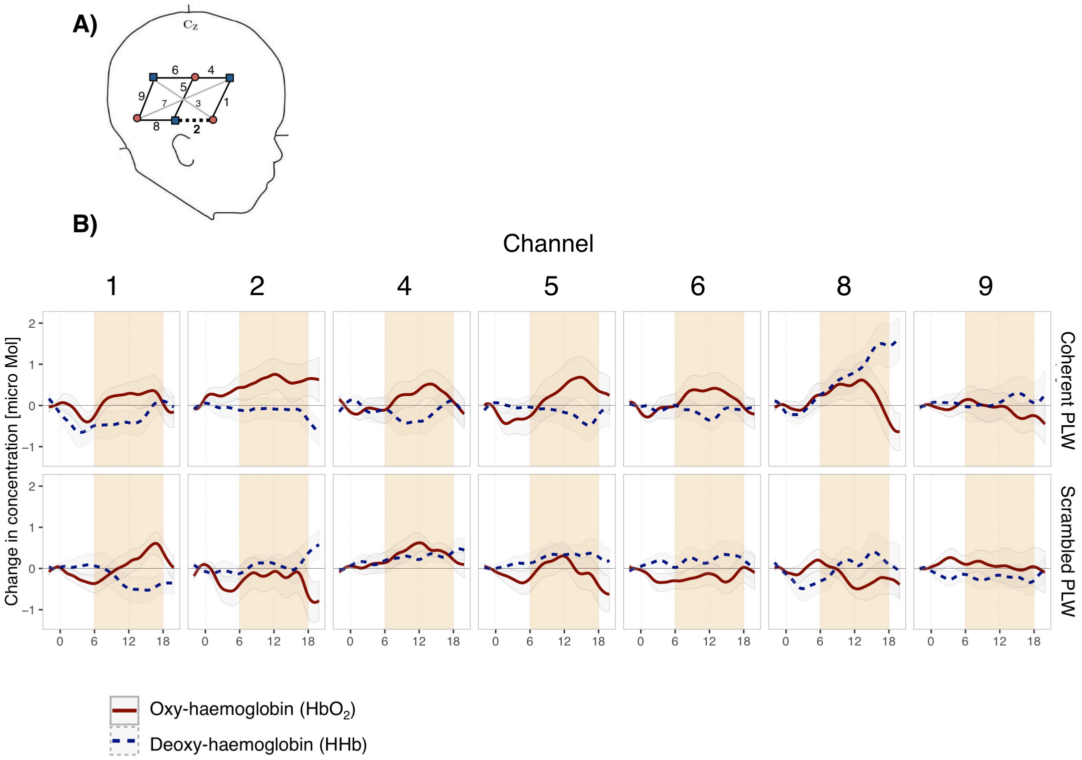

Figure 16. Grand-mean average of baseline-corrected HbO_2 and HHb concentrations on the seven channels for the two experimental conditions (coherent and scrambled point-light walker)

A) A model of the infants' head with the array: blue squares and red circles symbolize, respectively, the detectors and sources locations; lines connecting sources and detectors symbolize channels; channels are numbered in the array; a significant increase in HbO_2concentration associated with the coherent point-light walker condition was found at the [12, 18[time-window on channel 2 (dotted in the model).

B) Grand-mean average of baseline-corrected HbO_2 and HHb concentrations for the two experimental conditions (coherent point-light walker and scrambled point-light walker) in the seven channels (raw data at 10Hz) – channels 7 and 3 were excluded from processing and analysis because no data was captured in these channels. Numbers on the top identify the respective channel. The zero time-point marks experimental stimulus onset; we plotted the 20secs response signals after trial onset. Lines plot the grand mean concentration changes in HbO_2 (full red line) and HHb (dashed blue line); the shaded ribbon around the lines marks 1SE (with variance estimation done by pooling data at each time point). The yellowish shaded area, from 618 seconds, demarks the maximum signal changes in all channels.

The main analysis consisted of modeling the mean concentration change in the seven channels (1-6, 8-9) in the two conditions, and in three consecutive 6-second epochs. Channels 3 and 7 were not processed or included in the statistical analysis because they did not capture any signal data. The following *time-windows* after stimulus onset were thus considered:]0, 6],]6, 12] and]12, 18]. The maximum range of concentration changes happened between 6 and 18 seconds, based on visual inspection of the grand-averaged hemodynamic responses, and in accordance with previous work published regarding a similar task (Ichikawa et al., 2010). We also included the]0, 6] time window, adding one extra parameter to the model; including this window also adds data contributing to the variance estimation in the model. In addition, by analyzing the whole signal we can assess more information regarding the signal changes over time.

Because data did not follow a normal distribution (by analysis of the quantile-quantile plots), we applied a power transformation (exponent of 5/7), and the power-transformed data was used in all subsequent analyses.

Modeling followed the approach for longitudinal data (Diggle et al., 2002; Mirman, 2016). We fitted one linear mixed model to the mean concentration change data with fixed (*Time-window* and *Condition*) and random effects, per channel, and per chromophore. Thus, our model included a full two-way interaction between *Time-window* (3 levels:]0, 6],]6, 12], and]12, 18]) and *Condition* (2 levels: coherent point-light walker and scrambled point-light walker) in the fixed effects component, and a random intercept per participant in the random effects component. All models were fitted using the *nlme* package in R (Pinheiro et al., 2018).

Statistical inference was performed in the modeled data using the package *emmeans* in R (Russell Lenth, 2018). For each time window, we computed a confidence interval using the model's estimated mean and variance, and the comparison with the baseline is captured by the uncorrected *p*-value. In order to determine if there was a significant activation, we further computed a single-tailed test against the baseline of zero (> 0 for the HbO_2 and < 0 for HHb) for the two conditions and three epochs. Within one channel and chromophore, all single-tailed tests were corrected for multiple comparisons using the Sidak method (Šidák, 1967). Mean concentration change inside a time window was considered consistent with a functional activation, if the corrected *p*-value for the contrast with baseline was significant, and the two chromophores were not increasing/decreasing in unison. Only when at least one condition had a significant activation (inside a time window), did we compute a pairwise comparison between the two conditions. Only significant results are reported in the *Results* section.

3.4 Results

Only the coherent point-light walker was associated with a significant activation in relation to baseline. This activation was measured in the anterior area of the array (channel 2), in the right middle-posterior temporal cortex. As hypothesized, the scrambled point-light walker did not elicit any significant response.

In the coherent point-light walker condition, HbO_2 concentration in channel 2, right below T8 (Jurcak et al., 2007), was found to be significantly above baseline (i.e., zero) at the [12, 18[time-window (*t*(16) = 2.34, *p* = .048). Because the coherent point-light walker produced significant activation in this time-window, we also computed a pairwise comparison of the estimated mean concentration changes in HbO_2 in the coherent vs. scrambled point-light walker in this channel. The estimated mean concentration change in HbO_2 concentration was significantly greater (*t*(80) = 2.16, *p* = .03) in the coherent point-light walker in relation to the scrambled point-light walker at the [12, 18[time-window – see Figure 17 for a more detailed depiction of the modeled hemodynamic signals in both conditions in this channel. In addition, this increase in HbO_2 concentration in channel 2 was also accompanied by a decrease in HHb, but that did not reach significance. All other statistical analysis revealed no significant result.

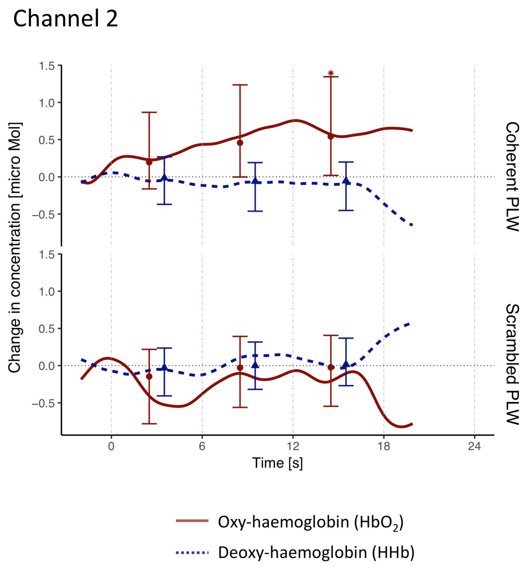

Figure 17. Grand-mean average of baseline-corrected HbO_2 and HHb concentrations on channel 2 for the two experimental conditions (coherent and scrambled point-light walker)

The zero time-point marks experimental stimulus onset. Lines plot the grand mean concentration changes in HbO_2 (red line) and HHb (blue dashed line). For the three epochs in which we conducted statistical testing,]0, 6],]6, 12],]12, 18], we show the estimated mean and its 95% confidence interval. The corrected p-value for the comparison with baseline is highlighted with an asterisk above the respective confidence interval (single-tailed test, greater than zero for HbO_2 and below zero for HHb).

3.5 Discussion

The current experiment was, to best the best of our knowledge, the first demonstrating the right temporal cortex involvement in the processing of configural relations in biological motion during the first half of the first year of life.

Significant responses to a coherent point-light-walker over a scrambled point-light walker were measured, using fNIRS, in the right middle-posterior temporal cortex of seven to eight month-old infants—and this site, where the right STS is located, has been reported as a primary location for processing global configural relations in biological motion in the mature brain (Peuskens et al., 2005; Vaina et al., 2001). Thus, one of the main findings of our study is that the brain regions involved in the analysis of biological motion configuration in the mature brain seem to be functionally specialized by at least seven months of age.

Despite fNIRS having better spatial resolution than EEG, precise localization of cortical structures is still difficult (Lloyd-Fox et al., 2010), e.g. spatial registration of the collected data onto an atlas was not possible in our study. However, the increase in HbO_2 concentration in the coherent point-light walker condition at seven months of age is likely associated with the right STS structure for three reasons. First, an increase in HbO_2 concentration (our measured response signal) was found to be the response signal in fNIRS most strongly correlated with fMRI changes (Strangman et al., 2002). Second, our significant increase in HbO_2 concentration cannot be simply attributed to other motion-sensitive adjacent areas, such as MT/V5, because our activation was specific to the coherent walker and was not elicited by the scrambled moving display. Finally, previous coregistering studies, using the same landmarks with fNIRS and comparing localized patterns of hemodynamic response in fMRI in infancy, found that channels located around T8 likely measure the right STS structure (Lloyd-Fox, Richards, et al., 2014).

A differential neural processing of biological motion configuration adds supporting evidence to the few previous neuroimaging studies conducted so far with point-light stimuli which showed a differential processing of coherent vs. scrambled point-light displays at the same age using ERPs (Masahiro Hirai & Hiraki, 2005). However, considering fNIRS's higher spatial resolution (Lloyd-Fox et al., 2010), we extend these results by implicating the right temporal cortex, and the right STS, in processing configural relations in biological motion at seven/eight months of age.

This is relevant because the STS, and in particular the right STS, is a key node in the neural processing of many aspects of social perception and cognition, starting early in life (Allison et al., 2000; Deen et al., 2015; Grossmann & Johnson, 2007). In this sense, other fNIRS studies conducted in infancy and early childhood have found significant activations in the right STS region associated with different socially-relevant stimuli, such as: static face processing in five to eight month-old infants (Otsuka et al., 2007), human face motion in four and eight month-olds (Grossmann et al., 2008; Ichikawa et al., 2010), human vocal sounds in seven month-olds (Grossmann et al., 2010), multimodal interaction signals in six month-olds (Lloyd-Fox, Széplaki-Köllőd, et al., 2015), and even joint attention in twelve to fourteen month-old infants (Hakuno et al., 2018). In typical development, the ability to perceive a person in action from motion information has been tightly linked to the development of other social abilities; the perception of biological motion has also been conjectured to be a precursor to later and more complex social abilities such as joint attention or theory of mind (Frith & Frith, 1999; Pavlova, 2012). Therefore, our results add evidence to biological motion's role in social cognition in early development: our activations to the coherent point-light walker were found in the right STS region, which overlaps with the neural processing of other important social abilities at similar age groups, and even to more complex social-cognitive abilities in older infants. Our significant increase in HbO_2 concentration was only associated with the processing of the coherent walker, and it statistically differed from the scrambled point-light walker, which indicates that it was the articulated motion configuration of a person walking that elicited such cortical response.

Second, we used a smaller trial duration in relation to previous fNIRS studies that also focused on the study of biological motion (Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009): for instance, Lloyd-Fox et al. (2009) presented video clips of an actor for 16 seconds, whereas in the present experiment, stimuli presentation was half that time, i.e., 8 seconds. Our results thus indicate that 8 seconds of stimuli presentation is sufficient to elicit the typical hemodynamic response in biological motion perception, which has the critical advantage of increasing the number of valid trials per infant. This is significant considering the complexity of both the measurements and the apparatus, and the young age of the participants (Lloyd-Fox et al., 2010; Nishiyori, 2016).

There are, however, some limitations to this study. One is the size of our array: we only recorded responses in nine channels placed over the right temporal region. In addition, responses were measured in only one age group of seven/eight month-old infants. Future studies should examine frontal and left-temporal activity at different developmental ages (Carter & Pelphrey, 2006; Grossmann et al., 2013; Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009). Previous fNIRS research suggested a temporal right-specialization for biological motion emerging between five and seven to eight months of age: Ichikawa et al. (2010) and Biondi et al. (2016) reported right hemisphere dominance in face and hand motion at seven/eight months-old, as opposed to Lloyd-Fox and colleagues (2009), who found bilateral temporal activations to video clips of female actors in motion in younger, five month-old infants. This issue could be addressed by considering longitudinal samples with younger age groups and, in particular, right and left temporal responses to biological motion. However, the aim of the current experiment was to study right STS responses to configural relations and not to investigate the development of hemispheric temporal lateralization in biological motion. Our results do suggest that the right STS is sensitive to configural relations in biological motion perception at seven/eight months of age.

Another limitation is the sample size that restricts the statistical inference techniques that can be applied to the full dataset; this is an issue in the majority of fNIRS studies, as recently reviewed (Azhari et al., 2020).

Finally, our sample had a male-female imbalance, since we had only five female infants out of seventeen participants. Nevertheless, this imbalance regarding the sex of our participants is unlikely to undermine our results, since studies with children and adults suggest an advantage of females over males in the perception of point-light displays: e.g., in a fMRI study, female brain responses to coherent versus scrambled point-light displays were enhanced relative to male subjects (Anderson et al., 2013); see also (Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000; Sokolov, Krüger, Enck, Krägeloh-Mann, & Pavlova, 2011). Therefore, this limitation in our sample does not seem to bias the main conclusion of the paper—in fact, despite the reduced number of female participants, a significant response associated with only the coherent point-light walker was still found.

In conclusion, we found that by at least seven months of age, the right middle temporal cortex, where the right STS is located, is part of the network that processes the global human configuration in biological motion. This finding supports a linking relation between the development of a basic perceptual ability and the activity of one of the central nodes in processing high-level social abilities, such as the capacity to interpret and understand the actions of other agents in a complex social world.

Chapter 4: Three months-old' preferences for biological motion configuration and its subsequent decline

A version of this Chapter will be submitted for publication

Three months-old' preferences for biological motion configuration and its subsequent decline

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Abstract

To perceive and identify the action of others via biological motion, it is essential to perceptually organize local moving body parts into the whole configuration of a human body in action. Adult observers are fast and accurate in doing so (Johansson, 1973). Much less is known about how the ability of perceiving the configural relations in biological motion develops. We investigated the development of this ability in three to seven months-old infants in two preferential looking experiments.

We measured preferential attention between the coherent motion configuration of a person walking (coherent point-light-walker) and a scrambled point-light walker, both in a cross-sectional (experiment 1), and a longitudinal preferential looking experiment (experiment 2).

Contrary to our initial hypothesis, a preference for the coherent point-light walker was present at three months and both five and seven months old did not show any preference.

We discuss our results in terms of the different perceptual, motor and attentional processes available at each age group, and how they dynamically interact with selective attention towards the coherent motion of a person walking during the first year of life.

Keywords: Social cognition, biological motion, preferential looking, configural relations, point-light-walkers

4.1 Introduction

Infants are active perceivers, selecting from all potential loci in the environment where to direct attention. There is so much to learn about others that infants begin to select and direct attention to moving people around them since very early. In this context, one of the most important classes of stimuli in the environment that is frequently preferred, is the visual information contained in an articulated body in motion or, in other words, biological motion (Adolph & Berger, 2006).

Our visual system is particularly tuned to biological motion. First, in just a few milliseconds, we can identify the configuration of a human in motion out of a dozen dots placed on the major joints of a moving person: adults are incredibly fast and accurate in biological motion configural processing, i.e. at representing the global form of a human from the parts of a moving body (Johansson, 1973). Biological motion is also processed differently in the human brain from other types of motion (Carter & Pelphrey, 2006; E. Grossman & Blake, 2001; E. Grossman et al., 2000; Lisboa, Miguel, et al., 2020; Lisboa, Queirós, et al., 2020; Peuskens et al., 2005). Finally, but most important, biological motion is a rich source of social information about others: we can identify what people are doing, how they feel or what are their intentions, solely by looking at the dynamics of their bodies in motion (A. P. Atkinson et al., 2004; Dittrich, 1993; Johansson, 1973, 1976; Jokisch et al., 2004; Runeson & Frykholm, 1983). There are no static people and perceiving emotions, intentions or even the meaning of an action is fundamentally tied to perceiving human movement.

All of this might explain, at least in part, why infants begin to select and prefer biological motion from the very moment they are born (Bardi et al., 2011; Francesca Simion et al., 2008).

4.1.1 Infants Prefer Biological Motion

Infants need to observe and devote a great deal of time attending to important stimuli in their environments, from which they have so much to learn about (Pavlova, 2012). Human infants seek or prefer to look at biological motion since birth (Bardi et al., 2011; F Simion et al., 2011; Francesca Simion et al., 2008).

By looking at biological motion, infants learn to decode and interpret the meaning of others' actions and intentions (Frith & Frith, 1999; Pavlova, 2012); it also enables them to learn and expand their motor repertoire (Boyer & Bertenthal, 2016; Sanefuji et al., 2008). A preference to look at biological motion is considered a central social behavior that occurs during infancy.

On the other hand, a failure in a preference for biological motion is conjectured to be one disrupting element of infants' social-cognitive development.

Children diagnosed with autism spectrum disorder (ASD)—a disorder characterized by a lack of social and communicative abilities—do not prefer biological motion in relation to other kinds of motion (Annaz et al., 2012; Klin et al., 2009). This early absence of a preference for biological motion in ASD likely has cascading effects in these children' social development (Klin et al., 2009). In a recent study testing newborns, the absence of a preference for biological motion was conjectured to be an early biomarker for ASD (Di Giorgio et al., 2016). This study found that newborns with familial risk for ASD (i.e. who have an older sibling diagnosed with ASD), unlike newborns at low risk for ASD (i.e. who do not have an older sibling diagnosed with ASD), showed no preference for biological motion in relation to random motion (Di Giorgio et al., 2016).

In typically developing infants, a measurable preference for biological motion is present at birth (F Simion et al., 2011). Studies with newborns show that two-day-old infants spend more time looking at a point-light walker of a hen than to non-biological motion stimuli— a point-light walker is a point-light display depicting the walking action. Furthermore, newborns are sensitive to inversion in biological motion stimuli, preferring to look at the upright point-light walker of a hen compared to an inverted version of the same stimulus (Francesca Simion et al., 2008).

However, biological motion perception is still immature at birth (Bidet-Ildei et al., 2014; Proffit & Bertenthal, 1990; Sifre et al., 2018): when using another type of control stimulus, a spatially scrambled display (scrambled point-light walker), where only the original dots' positions are randomized, there is no preference for the coherent intact walker (Bardi et al., 2011). Although newborns show no preference for either stimulus (coherent vs. scrambled), the two are discriminated in an habituation task (Bardi et al., 2011). This result is critical as it shows that the developmental path of biological motion perception is far from being completed at birth: newborns equally turn at a scrambled and a coherent point-light walker; nevertheless, only the coherent point-light walker has the coherent and socially relevant global configuration of a person walking.

4.1.2 Perceiving Configural Relations is Critical for Biological Motion Perception

Perceiving configural relations is a basilar ability in biological motion perception and one of the first steps for understanding human actions (Bertenthal & Longo, 2008). To uncover the meaning of an action, first, we have to perceptually organize the individual constituents of a point-light display (dots or sets of dots) into a unique and coherent global configuration of a person in action. Configural processing is thus a fundamental component of biological motion perception, and one of things that makes biological motion, a socially relevant stimulus (Thompson, 2012).

The perception of configural relations in biological motion is typically studied by contrasting a coherent intact point-light walker with a spatially scrambled point-light walker.

The scrambled control is a classical manipulation from visual perception studies and it consists in randomizing the position of the individual elements that compose the visual stimulus. In the case of biological motion (and of point-light displays) the initial positions of the dots are scrambled or randomized. As a result, the scrambled point-light display has the same set of individual moving dots as the original display, with each dot's individual trajectory preserved, but all configural relations between the dots are disrupted. Both local and global configural relations are disrupted in the scrambled manipulation.

Both local and global configural relations are extracted from a coherent point-light walker. Local configural relations refers to the coherent temporal-spatial relations between two or more dots of the display—e.g. a single articulation of a limb, i.e. the relation between three dots placed over the shoulder, elbow, and wrist that compose a moving arm (Bertenthal, 1993); global configural relations refers to the coherent relation between all the dots of the display, that correspond to the form of a person walking in the case of a point-light walker (Bertenthal, 1993; Bertenthal et al., 1984). Because there is no configural relations in the scrambled point-light walker, adults observers describe this stimulus as an array of independent entities, namely, a moving swarm of bees; they typically do not report even seeing human motion (Cutting, 1981).

Developmentally, a set of infant-controlled habituation experiments suggest that the ability to perceive configural relations in point-light walkers emerges between three and five months of age (Bertenthal & Pinto, 1994; Bertenthal et al., 1984; Bertenthal, Proffitt, & Kramer, 1987; Bertenthal, Proffitt, Kramer, et al., 1987; Bertenthal et al., 1985; Booth et al., 2002; Fox & McDaniel, 1982; Pinto & Bertenthal, 1996; J. M. Pinto, 1997) – for a complete review see Bertenthal (1993).

In these habituation experiments, five months-old infants specifically respond to the global configuration of the human walking action; in contrast, three-month-olds, more tuned to local configural information, seem to respond instead to the presence of moving limbs in the display (Bertenthal, 1993). While three-month-olds are sensitive to the relation between just subgroupings of point-lights (local configural information), five-month-olds are able to process stimuli at a larger spatial-temporal scale, at its global level (Bertenthal, 1993; Bertenthal & Pinto, 1994; Booth et al., 2002). For instance, in one particularly representative habituation study, Pinto & Bertenthal (1996) tested three and five-months-old infants for discrimination between an unitary axis point-light walker (which corresponds to the intact display), and a divided axis point-light walker – see *Figure 7. Static illustrations of the intact* *(unitary) point-light walker and divided point-light walker employed by Pinto & Bertenthal (1996)* in *General Introduction* for a representation of the two stimuli.

In the divided axis display, the principal vertical axis of organization of the coherent point-light walker was divided in two halves by the waist level; this stimulus consisted in the presentation of the two halves at the same time (upper and lower body) horizontally spatially separated (Pinto & Bertenthal, 1996). The unitary axis corresponds to the coherent intact point-light walker. Importantly, discrimination between the two stimuli implies global configural processing: both stimuli have intact individual moving dots and intact local configural information (both the unitary and the divided axis displays have an equal number of intact subcomponents corresponding to the limbs), but only the intact display has a global configuration that corresponds to a person walking (Bertenthal & Longo, 2008; Pinto & Bertenthal, 1996; J. M. Pinto, 1997).

Results showed that five-month-olds discriminated the two stimuli but three-month-olds did not (Pinto & Bertenthal, 1996). At five months, infants seem to process the global human motion configuration and consequently they discriminated the intact from the divided axis display. Instead, three-months-old infants, more tuned to the local configural relations in point-light displays, such as the motion of the limbs (that were preserved in both stimuli), did not discriminate the two displays (Pinto & Bertenthal, 1996; Pinto, 1997).

Finally, and in accordance with these results, neurophysiological studies testing infants also show early brain-processing differences between scrambled and coherent point-light displays at eight (Masahiro Hirai & Hiraki, 2005), seven (Lisboa, Queirós, et al., 2020), and at five months of age (Marshall & Shipley, 2009). In particular, Lisboa et. al (2020) found activations associated to the perception of a coherent point-light walker (but not to a scrambled point-light walker) in seven months-old infants, and in the right STS region, the same region where adults process configural relations in biological motion. These results indicate that at least at seven months, infants are able to process configural relations in biological motion.

4.1.3 Current Study

Perception of biological motion requires processing configural relations (Masahiro Hirai, Chang, Saunders, & Troje, 2011; Masahiro Hirai & Senju, 2020; Troje, 2013). Newborns do not prefer a coherent point-light walker in relation to a scrambled control, i.e. a display that only maintains the individual dot motions and disrupts all configural relations (Bardi et al., 2011). This finding indicates that infants at birth are unable to process configural relations in biological motion. Nevertheless, perceiving configural relations is an essential step for understanding human actions, emotions, and intentions, in short, to interact and communicate with others.

Previous habituation experiments indicate that three months process local configural information and that five months-old infants are sensitive to the global configuration of a person walking (Bertenthal, 1993); there is also evidence of brain-processing differences between a coherent and a scrambled point-light walker at seven months of age (Lisboa, Queirós, et al., 2020). These results indicate that the ability to perceive configural relations in biological motion likely develops in infancy.

Here, we present two preferential looking experiments testing preference for biological motion configuration in infancy. These preferential looking experiments intended to answer to the following question: when do infants begin to represent configural relations in biological motion and, therefore, prefer a coherent point-light walker in relation to a scrambled control?

To answer this question, our two preferential looking experiments tested three to seven months-old infants. In the first experiment, cross-sectional, we tested three and five months old; and in the second experiment, longitudinal, we tested three, five and seven months old. In both experiments, we presented a coherent intact point-light walker alongside a scrambled point-light walker, and measured the amount of time infants looked at each display.

We hypothesize that, because the ability to process the global human motion configuration in biological motion emerges in infancy, particularly at around five months of age, and three months old process local configural information (Bertenthal, 1993), a preference for a coherent point-light walker in relation to a scrambled walker would emerge around this developmental period. Infants turn their attention to stimuli that are important; we hypothesize that, if infants at five months are able to process the meaningful and coherent global configuration of a person walking, they might also prefer this stimulus in relation to a scrambled control.

4.2 Experiment 1: Cross sectional study with 3 and 5-months-old infants

4.2.1 Method

4.2.1.1 Participants

Fifty infants (N = 50) took part in the experiment: N = 27 infants with three months-old (10 females, M = 104.3 days, SD = 10.9, age range = 89.0 – 128.0) and N = 23, five months-old infants (13 females, M = 166.6 days, SD = 10.3, age range = 143.0 – 188.0).

At three months of age, only data from n = 17 infants was processed (37.0% attrition rate): one infant was excluded due to technical problems, three due to fussiness, and six did not pass the two looking criteria – more details on the looking criteria are in the *Data coding and processing* section. At five months of age, the final sample comprised n = 17 infants (26.09% of attrition rate): two infants were eliminated due to technical problems, and four infants did not pass the looking criteria.

All infants were born full-term (at least 37 weeks of gestation and birth weight > 2500g), and had no family history of neurological disorders or reported hearing or vision problems. Infants and parents were recruited from pediatrician clinics, public health centers, and pregnancy gymnastic classes. All parents gave their written informed consent before participating. University of Minho ethics committee approved the study.

4.2.1.2 Stimuli

Two motion stimuli were used in this study: (1) an intact coherent point-light-walker, and (2) a spatially scrambled version of this display.

The coherent point-light walker was captured using a VICON motion capture system at 240Hz (Mouta et al., 2012). It consisted of 13 white spheres placed on the major joints (head, right and left shoulders, hips, ankles, knees, wrists, and elbows) of a female model walking against a black background (Mouta et al., 2012). The 13 spheres measured each 0.68° of visual angle at 50cm of visual distance. The point-light walker described a frontal approaching motion (1.34 m/s), walking two steps or one complete step cycle (2 seconds) as if on a treadmill, i.e. with the translational displacement removed. The stimulus measured 21.31° in height and 8.53° in width at a visual distance of 50cm.

The scrambled point-light walker was created by randomizing the initial position of the 13 dots that composed the coherent point-light walker's dots, inside of a bounding box with approximately the same width and height as the original coherent point-light walker. Both stimuli (coherent and scrambled) had the same duration and an equivalent angular size (the scrambled point-light walker measured 22.29° in height and 7.97° in width). The scrambled point-light walker consisted of an elongated random displacement of the dots, where all spatial-temporal relations between the dots were disrupted. Both local (the spatial-temporal relation between at least two dots) and global (the spatial-temporal relation between all dots that compose the coherent display, that corresponds to the form of a person walking) configural relations were perturbed in the scrambled display.

Despite this, the number, size, luminance and velocity profile of the individual moving dots were the same in both stimuli. The individual motion of each dot was kept intact in the scrambled point-light walker.

The two point-light-walkers were animated in Blender, an open source 3D graphics program (Community, 2016).

4.2.1.3 Procedure

Preference between the two motion stimuli (coherent and scrambled) was assessed by a preferential looking procedure. The implemented procedure followed the one described by Bidet-Ildei et al. (2014).

The main apparatus consisted of two side-by-side identical computer screens (6.5 cm apart, screen size: 53x30 cm, ASUS VG248QE monitor, with a resolution of 1920x1080, 144Hz) placed in a room with no windows, and illuminated only by a dimly light located behind, and in the middle of the two screens. The screens were framed with black cardboards and a webcam (model HP HD 4310, 30Hz) was placed in the middle of the screens only for online tracking of the infant's behavior during the experiment. Infants' looking behavior during stimuli presentation was recorded by a second high-definition video camera (Panasonic HC-V777, sampling frequency of 50Hz) also placed in the middle of the screens – see Figure 18 for a schematic representation of the apparatus. Control of the experiment (starting a new trial, rendering the stimuli, synchronization with the camera recording) was achieved using custom-made software. The two point-light walker stimuli were presented, one on each computer monitor, at a resolution of 1920 x 1080 pixels, and rendered in real-time using Blender 2.78 and at 60 Hz.

During the experiment, infants sat on their parent's laps, 50 cm away from the middle of the two screens. Parents were instructed to: (1) refrain from interacting with the infant—they were specifically told to not interact with the infant and only smile if the baby searched for their face; (2) maintain the infant centered on his/her lap; and, finally, (3) not turn their own body or head to either side of the screens and to fixate the middle of the two screens.

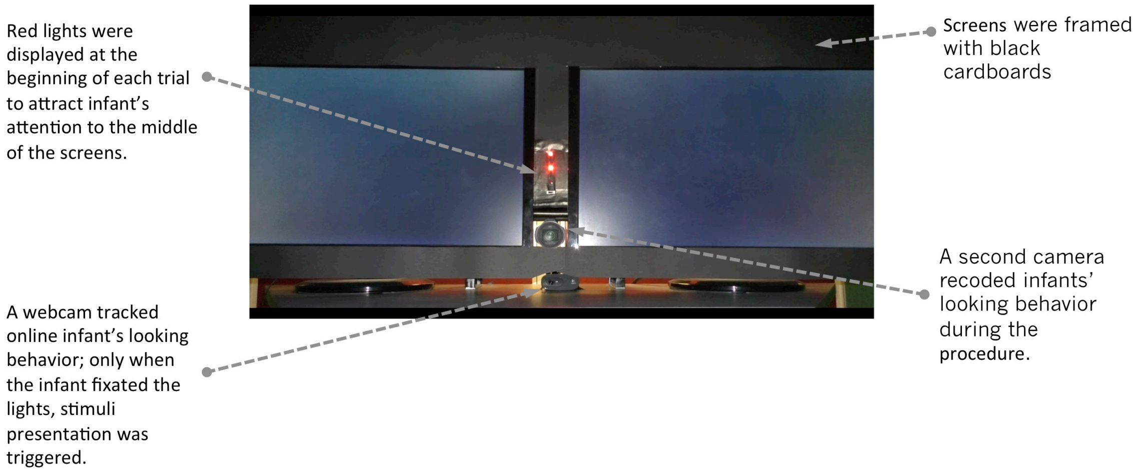

Figure 18. A picture of the apparatus of the preferential looking

Once the infant was calm and seemed ready, the experiment started. Each trial was structured as follows: the apparatus started by displaying three small red lights, equidistant from the two stimuli, in sync with an enjoyable toy sound, to attract infants' attention to the middle of the two screens. Once the infant looked at the lights, i.e. to the middle, the experimenter triggered the beginning of a trial (the experimenter tracked the infant's looking using the webcam). The actual experimental period consisted of presenting the two motion stimuli simultaneously, one per screen (Bertenthal et al., 1985; Bidet-Ildei et al., 2014). The two stimuli were separated by 46.6 cm horizontally (42.98° at 50cm of visual distance) and left/right position for the coherent and scrambled point-light walker was counterbalanced across trials per individual subject; the order of the trials was also randomized per subject. Infants saw a total of 6 trials with 60 seconds of duration each (Bidet-Ildei et al., 2014). To reach 60 seconds of trial duration thepoint-light walkers were looped, thus, each step cycle (2 seconds of duration) was looped 30 times. The experiment lasted approximately 6 minutes.

4.2.1.4 Data coding and processing

To be included on the final sample, infants had to: (1) show sufficient looking, i.e. at least 50% of the time looking at any screen (Bidet-Ildei et al., 2014); and (2) do not show any side bias, i.e. have at least 10% of looking time at each screen (Bidet-Ildei et al., 2014; Golinkoff et al., 2002).

A trained human coder, unaware of the experimental design or of which stimuli were on each screen, coded infants' eye fixations. Infants' fixations were classified according to three categories: (1) looking at the right stimulus from the midline of the screens; (2) looking at the left stimulus from the midline of the screens; and (3) looking elsewhere. Fixation time towards the coherent point-light walker was calculated per trial and transformed into a proportion by dividing the amount of time spent looking at the coherent point-light walker by total looking time spent looking at scrambled or coherent point-light walker. This proportion of looking at the coherent point-light walker per trial was then averaged per subject. The distribution of the proportion of time looking at the coherent point-light walker, in both age groups, followed a normal distribution (confirmed by visual inspection and a Shapiro-Wilk test) and there was homogeneity of variances, hence, we used parametric statistics.

4.2.2 Results

A preference for the coherent point-light walker was assessed by comparing the grand mean proportion of time looking at the coherent point-light walker to chance level (.50), i.e. a proportion of looking at the coherent point-light walker that is not statistically different from .50 indicates no preference for either stimulus. We compared the grand mean proportion of looking at the coherent point-light walker to chance level at three and five months of age; we also compared grand mean proportion of looking at coherent point-light walker between the two age-groups. Main results are in Figure 19.

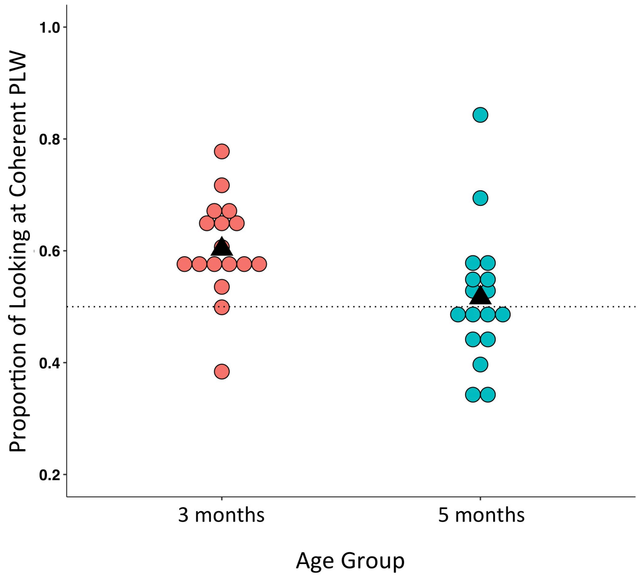

Figure 19. Proportion of looking at the coherent point-light walker (PLW) in Experiment 1 at three and five months of age

Each dot represents the proportion of looking at the coherent point-light walker per subject. Infants at three months are denoted by orange dots, and blue dots denote five months. Mean group proportion per age group is represented by the black triangle. The doted horizontal line marks the 0.50 proportion, i.e. equal looking at both stimuli and no preference.

Three-month-olds preferred to look at the coherent point-light walker: grand mean proportion of looking at the coherent point-light walker, M = .60, SD = .08, was significantly above chance, *t*(16) = 4.77, *p* < .001). As can be seen in Figure 19, the proportion of looking at the coherent stimulus was above .50 in all subjects at this age, except for two infants. In contrast, five-month-olds did not prefer to look at the coherent point-light walker, M = .52, SD = .12, *t*(16) = .55, *p* = .59. Infants did not show a systematic preference for the coherent or the scrambled point-light walker at five months.

The two groups also significantly differed, with grand mean proportion of looking at the coherent point-light walker being significantly higher at three when compared to five months, *t*(32) = 2.38, *p* = .02.

4.2.3 Discussion

We intended to find when, in infancy, a preference for a coherent point-light walker over a scrambled point-light walker emerges. Results from this first experiment are important as they indicate that a preference for the coherent point-light walker emerges at three months of age. This is a relevant and innovative finding of our study.

Nevertheless, and in contrast with our initial hypothesis, the older five months-old infants did not show any systematic preference. This result was unexpected since we conjectured a preference for the coherent point-light walker at five months, considering previous habituation studies demonstrating these infants' abilities in processing the global human configuration in point-light walkers (Bertenthal, 1993). We found a decline in the preference for the coherent point-light walker at five months of age.

4.2.3.1 Three months-old prefer coherent point-light walkers

Previous preferential looking experiments report that newborns show no preference between a coherent and a scrambled point-light walker (Bardi et al., 2011). Our observation of a preference at three months adds further evidence by showing that the first few months of experience are important in preferential attention to biological motion. We attribute this preference to the ability of three months old to process local and not global configural relations in biological motion (Bertenthal, 1993; Pinto & Bertenthal, 1996; Pinto, 1997).

Sensitivity to local configural information is more likely to explain the significant increased looking time to the coherent point-light walker in these younger infants for several reasons. First, a preference for the intact display does not necessarily imply that the global human motion configuration of the coherent point-light walker is being processed: all configural relations between dots are removed in the scrambled point-light walker, but both global and local configural information can be extracted from the coherent point-light walker (Bertenthal, 1993; Pinto & Bertenthal, 1996; Pinto, 1997). For instance, local configural motion information contained in the limbs is only available in the coherent point-light walker and not in the scrambled control. Three months old might have thus preferred the coherent point-displays due to the presence of limbs.

Second, previous habituation experiments conducted with three and five months-old infants concluded that three months-old are more tuned to local configural information in biological motion (Bertenthal, 1993). For example, three months-old were unable to discriminate a coherent point-light walker from a stimulus that consisted of a collection of limbs randomly displayed (Pinto, 1997) or from a divided axis point-light walker (Bertenthal, 1993; Pinto & Bertenthal, 1996; Pinto, 1997). Apparently, when the motion of the limbs is preserved in the stimulus, three-months-old infants do not discriminate the coherent point-light walker from its control (Bertenthal, 1993). Local configural information seems thus to be a key perceptual feature for biological motion perception at three months of age.

Finally, it is worth mentioning that, considering the nature of the preferential looking procedure (Houston-Price & Nakai, 2004), and because three months-old showed a preference in our study, we can also infer that these infants discriminate a coherent from a scrambled point-light walker. In order to prefer one of the stimulus, infants have to discriminate the two stimuli (Houston-Price & Nakai, 2004). This result is consistent with previous habituation experiments that found the same, i.e. the ability to discriminate a scrambled from a coherent point-light walker at three moths (Bertenthal, Proffitt, Kramer, et al., 1987). In fact, these habituation experiments reported that both three (Bertenthal, Proffitt, Kramer, et al., 1987) and five (Bertenthal et al., 1984) months-old discriminate the two stimuli. However, preference is not the same as discrimination. Discrimination does not implies a preference (we can discriminate two stimuli without having a preference for any) but a preference for a stimulus implies an ability to discriminate the two stimuli (Houston-Price & Nakai, 2004). Therefore, despite discriminating a coherent point-light walker from a scrambled point-light walker (Bertenthal et al., 1984), older five months-old infants in our sample did not show a systematic preference for the coherent point-light walker.

4.2.3.2 No preference for the coherent point-light walker at five months

In our study, only three-months-old showed a preference for the coherent point-light walker, five months revealed no systematic preference for either stimulus. This result was unexpected since previous habituation experiments reported that both at three and five months discriminate a coherent from a scrambled point-light walker (Bertenthal, 1993; Bertenthal et al., 1984; Bertenthal, Proffitt, Kramer, et al., 1987). We do not intend to conclude that five months lose abilities that were available to the younger infants. Thus, one alternative hypothesis to explain this result is that this decline in preference for the coherent point-light walker might be explained by some parameter of the procedure that is not so well adjusted to the older infants.

We analyzed graphically the individual fixation patterns of the two age-groups in time per trial; and five-month-olds showed a more "exploratory" looking behavior in terms of an increased number fixations towards the stimuli; three months-old exhibited less shifts but longer fixation bouts between the two stimuli – see Figure 20 for a depiction of the fixation per infant in the two age-groups.

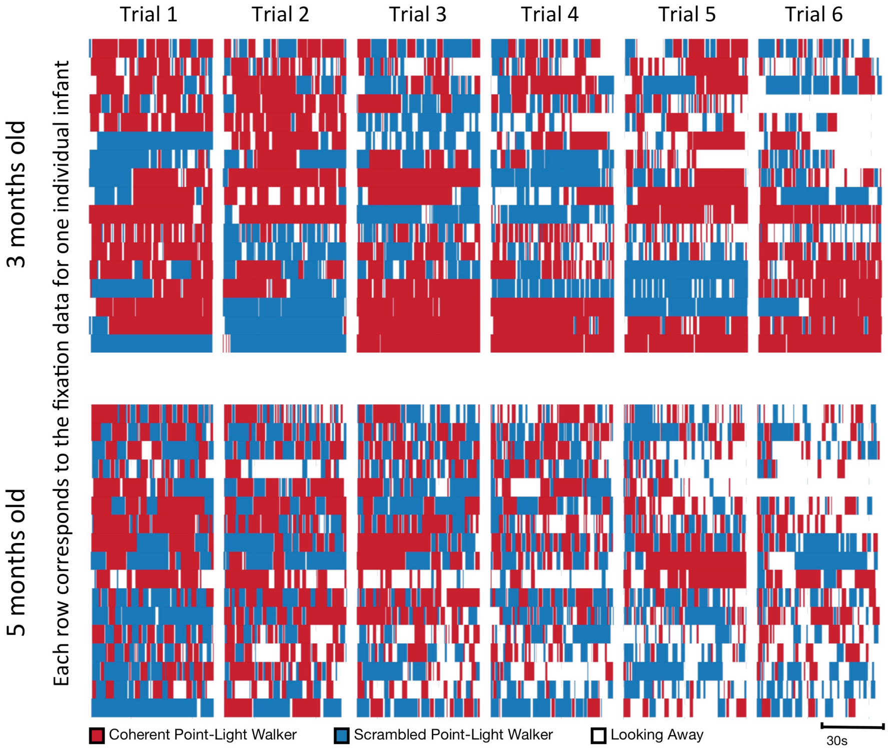

Figure 20. Visualization of fixation time series' data of all participants at three (upper panel) and five months (lower panel) and in all trials of Experiment 1.

Each row of colored tiles corresponds to one individual infant and each horizontally contiguous block of color corresponds to a sustained bout of fixation towards the coherent point-light walker (red), the scrambled point-light walker (blue) or away (white). Trial duration was 60seconds and the start of each trial was synchronized in the visualization. The vertical ordering of infants was calculated by applying hierarchical clustering (Ward's method) to the vector composed of proportion of looking at coherent PLW per trial. A gap between trials was placed to help the visualization; inter-trial pause took only a few seconds and was controlled by the infant's behavior.

We calculated the number of fixations per minute, and five months (mean number of fixations per minute = 14.02, SD = 4.11) differed from three months-old (M = 9.96, SD = 5.28) because they produced more fixations than the younger infants, *t*(32) = 2.50, *p* = .02. The two groups also differed in their proportion of total looking time to the screens, *t*(32) = 2.30, *p* = .03, with five months (proportion of total looking time: 0.71, SD = .12) spending less time looking at any stimulus than the younger infants (M = .81, SD = 0.12)—though infants at both age-groups were measurably engaged in the task, since they had to look at least 50% of the time to either screen.

Considering the fixation data analysis, we conjectured if 60 seconds of trial duration might be too long for five-month-olds. Trial duration in preferential looking experiments with biological motion stimuli varies greatly across the literature: while some studies conducted with newborns (Bidet-Ildei et al., 2014; Méary et al., 2007; Francesca Simion et al., 2008) and older infants (Sifre et al., 2018) employed 60 seconds of trial duration, other studies with four to twelve-month-olds employed less time, varying between 10.5 seconds (Christie & Slaughter, 2010; Kutsuki et al., 2009) to 15-20 seconds (Bertenthal et al., 1985; Fox & McDaniel, 1982; Sanefuji et al., 2008). Trial duration is a critical parameter that must be adapted both to the infant's age and the infant's speed of encoding the stimuli—older infants tend to encode visual stimuli faster than younger infants (Houston-Price & Nakai, 2004). Therefore, it makes sense that the older five months infants need less time of stimuli presentation.

Thus, we decided to conduct a second preferential-looking experiment with the goal of replicating our main finding with five-month-olds but using a reduced trial duration. We also wondered if this difference in performance (preference at three vs. no preference at five) is specific to five months or if it is present at older age groups, likely reflecting the developmental shift previously reported between three and five months of age (Bertenthal, 1993). Therefore, we also included a new age group of seven months-old infants in this second preferential looking experiment. Specifically, we decided to ask parents that participated in the first experiment with their infants at three months to come again both at five and at seven months of age. This second experiment is thus longitudinal.

4.3 Experiment 2: Longitudinal study with 3, 5, and 7 months-old infants

4.3.1 Methods

4.3.1.1 Participants

We contacted parents that participated in the first experiment when their infant was three months to come again to participate at five (mean age = 171 days, SD = 12.42, age range = 155.0-193.0 days, 6 females) and seven months (mean age = 228.75 days, SD = 11.29, age range = 212.0-254 days, 8 females)—except for one infant that started participating at five months. Thus, N = 28 infants were enrolled in this study: 27 infants participated since the beginning at three months and one infant began participation at five months-old and returned at seven months. To be included on final sample, an infant had to have usable data in at least two time points.

The final longitudinal sample consisted of n = 17 infants: n = 14, three months old; n = 14, five months old; and n = 16, seven months old. From the first to the second experiment, three subjects were excluded from final sample at three months of age because: (1) parents did not come to participate again (n = 2); and (2) one subject did not have usable data in any of the other two time-points. However, two infants that participated at three months of age in experiment 1 (but were excluded due to the two looking criteria in this time point), were now included at five and seven months of age since they had usable data on these two-time points. Plus, at five months of age, one infant missed data collection session, and two were eliminated due to technical problems. Only one infant missed participation at seven months of age.

All parents signed the consent form and the University of Minho ethics' committee approved the study.

4.3.1.2 Stimuli

We used the same stimuli as in experiment 1.

4.3.1.3 Procedure

The same procedure applied to experiment 1, except that trial duration for infants at five months was reduced from 60 seconds to 20 seconds, and infants participated in a total of 12 trials instead of 6. At seven months of age, each infant participated in 12 trials of 15 seconds each.

4.3.1.4 Data coding and processing

We applied same processing done for experiment 1 was used in this study. To be included in the final sample, infants had to pass the same two looking criteria as in experiment 1. In addition, only infants with usable data from at least two time-points were included in our longitudinal sample. Fixation time to the coherent point-light walker was again calculated per trial and transformed into a proportion; this proportion was then averaged per subject. Proportion data followed a normal distribution.

4.3.2 Results

The main finding is evident in Figure 21: the grand mean proportion of looking at the coherent point-light walker at five and seven months of age is close to chance level, M = .52, SD = .06, and M = .51, SD = .05 respectively. In contrast, grand mean proportion at three months of age was above chance, M = .60, SD = .09.

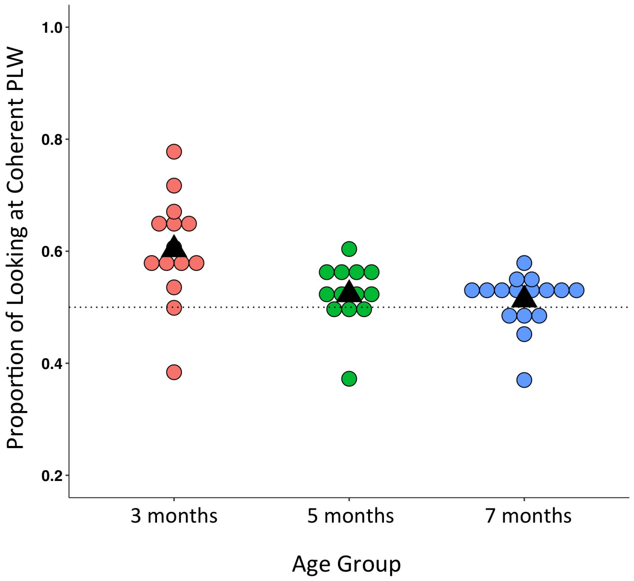

Figure 21. Proportion of looking at the coherent point-light walker (PLW) in Experiment 2 at three, five and seven months of age

Each dot represents the proportion of looking at the coherent point-light walker per subject. Infants at three months are denoted by orange dots, green dots denote five months, and blue seven months-old. Mean group proportion per age group is represented by the black triangle. The doted horizontal line marks the 0.50 proportion, i.e. equal looking at both stimuli and no preference.

To determine mean differences in the proportion of looking at the coherent point-light walker between the three time points, we fitted our longitudinal data for mean proportion of looking at the coherent point-light walker, with a linear mixed-effect model. Data was modeled using the *nlme* package in R (Pinheiro et al., 2018) using age in months (3 levels) as a fixed effect and a subject-level intercept as a random effect – see Figure 22 to see the model estimates over the three time points.

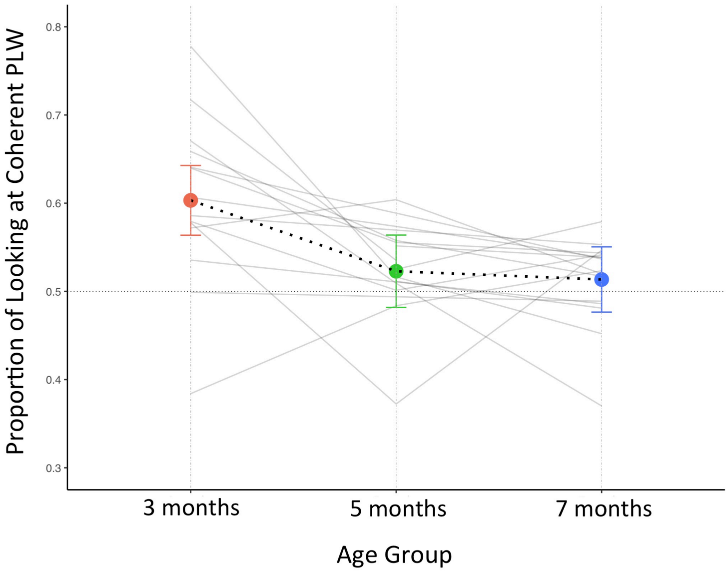

Figure 22. Model-based mean estimates of proportion of looking at the coherent point-light walker at three (orange), five (green) and seven (blue) months of age superimposed onto infants' longitudinal raw data (in grey).

The horizontal doted line denotes the 0.5 proportion, i.e. equal looking at both stimuli and no preference. Error bars are displayed through mean dots.

We tested whether the mean proportion of looking at the coherent point-light walker was different from chance in the three age groups, by computing a 95% confidence interval of the model's estimated mean proportion and a single tailed test (adjusted for multiple comparisons using the Bonferroni correction) against .50. Confidence interval and test was obtained using the R package *emmeans (Russell Lenth, 2018).*

Mean estimates from the model confirmed preferential attention to the coherent point-light walker at three months of age but absent at five and seven months; mean proportion of looking at the coherent point-light walker was significantly above chance at three months, $t(16) = 5.54$, $p < .001$, but not at five $t(16) = 1.18$, $p = .26$, or seven months, $t(16) = .77$, $p = .45$.

We also compared the estimates of the mixed model between the three age groups: proportion of looking at the coherent point-light walker was significantly greater at three months both when comparing with five, $t(24) = 2.99$, $p < .01$, and seven months-old infants, $t(24) = 3.52$, $p < .05$. Finally, differences between the five and seven months were not significant, $t(24) = .026$, $p = 1.00$.

4.3.3 Discussion

This second experiment was important for two main reasons. First, it replicates the results found on experiment 1 at five months using a reduced trial duration: mean proportion of looking at the coherent display was at chance level in both experiments. Second, we extended this result to seven months-old infants. Three months old prefer a coherent point-light walker in relation to a scrambled control; both five and seven months old showed no preferences for either stimulus.

Altogether, these results suggest that configural relations in biological motion perception begin to be extracted as early as three months of age, and add further evidence for a developmental shift happening between three and five months in biological motion perception (Bertenthal, 1993). Several hypotheses might explain this decline in preference for the coherent walker at five months.

4.3.3.1 Three months-old prefer configural relations in biological motion perception

The main finding of our study is that at three months, infants prefer to look at a coherent point-light walker in relation to a scrambled point-light walker. To the best of our knowledge, this is the first study that measured preferences for biological motion configural relations in infancy.

Both local (e.g. the articulation of one arm represented by three dots, shoulder, elbow and wrist) and global configural information can be extracted from the coherent point-light walker; in contrast, the scrambled point-light walker does not depict any coherent configuration. Considering previous habituation experiments with three months-old and point-light walkers (Bertenthal, 1993), we reason that this preference is because these infants are processing local, and not global configural information in biological motion. Processing the spatial-temporal dynamics of a whole body moving is perhaps more complex than process moving body parts.

4.3.3.2 Replication of no preference for the coherent point-light walker at five months

Mean proportion of looking at the coherent point-light walker at five months was at chance level both in experiment 1 and 2. We replicated this result in two preferential looking experiments, conducted with two independent samples of five months-old infants.

From the first to the second preferential looking experiment, we reduced trial duration from 60 seconds to 20 seconds. Despite this, in both experiments, we found no preferences. Thus, the absence of a preference at five months is not explained by an inappropriate trial duration in the preferential looking procedure. In fact, the introduction of a shorter trial duration reduced variance of the data in relation to the 0.50 chance level, from experiment 1 (SD = .60) to experiment 2 (SD = .12)—compare five month-olds data in Figures 19 and 21. Infants' individual responses in experiment 2 (with a reduced trial duration) were less variable, and variance was significantly larger in the experiment 1 in relation to experiment 2, $F(16, 12) = 4.76$, $p < .01$. Thus, 20 seconds of trial duration seems to be a more adequate parameter for the five months-old infants in this task. This makes sense since the older the infants, the faster they tend to encode visual stimuli (Houston-Price & Nakai, 2004), thus, this result might indicate that five month-olds need less exposure than three-month-olds to process point-light walkers.

However, our finding at five months is at odds with Sifre et al. (2018) findings and even to our initial hypothesis. We conjectured that five months would prefer the coherent stimulus considering their ability to process the global human configuration in point-light walkers (Bertenthal et al., 1984). Moreover, Sifre et al. (2018) tested longitudinally infants from two to 24 months of age in their preferences towards an intact upright point-light displays of an actor playing children's games (e.g. "peek-a-boo"), and inverted versions of the displays—and they found an increase preference for the upright point-light displays emerging at three months, and increasing across developmental age. Direct comparisons between the two studies are limited by the fact that Sifre et al. (2018) used multimodal stimuli (i.e. visual and audio), while we used visual-only stimuli; but the main difference here is that Sifre et al. (2018) used inverted point-light displays.

In contrast with our control stimulus, an inverted point-light display has configural coherence thus both local and global coherent configurations. Also, in the inverted display, the individual motions of the dots are inverted, and in the scrambled point-light walker they are maintained intact. The use of inverted point-light displays as control stimuli also has two more important caveats. First, preferences for the upright point-light displays might simply be explained by an infants' sensitivity to gravity-dependent dynamics of motion (and these are not specific to biological motion). Second, the two motions (upright and inverted point-light walker) differ in the region with the highest amount of motion they occupy in the screens: the upright display has an increased amount of motion in the feet region (two limbs) in comparison with the head region (one limb); whereas the opposite occurs in the inverted point-light walker (Frankenhuis et al., 2012). Conclusions regarding comparisons between our findings and with Sifre et al. (2018) results should take into consideration these limitations. Instead of an increase in preference for the intact display across developmental age, as Sifre et al. (2018) reported, we found a developmental shift in biological motion perception happening between three and five months of age.

4.3.3.3 Developmental shift in preferential attention to biological motion between three and five months of age

Reproducing previous findings with the habituation procedure (Bertenthal, 1993), we have identified a developmental shift between three and five months in the perception biological motion configuration: three months preferred the coherent point-light walker in relation to a scrambled point-light walker whereas both five and seven months-old did not show any preferences. Furthermore, we found two different patterns of looking behavior between the younger vs. the older five and seven months old infants. More specifically, we found the same pattern of looking behavior observed in five months in experiment 1, with higher frequency of shifts of fixation between the two stimuli, in the current experiment both at five and seven months – see Figure 23 and Figure 24.

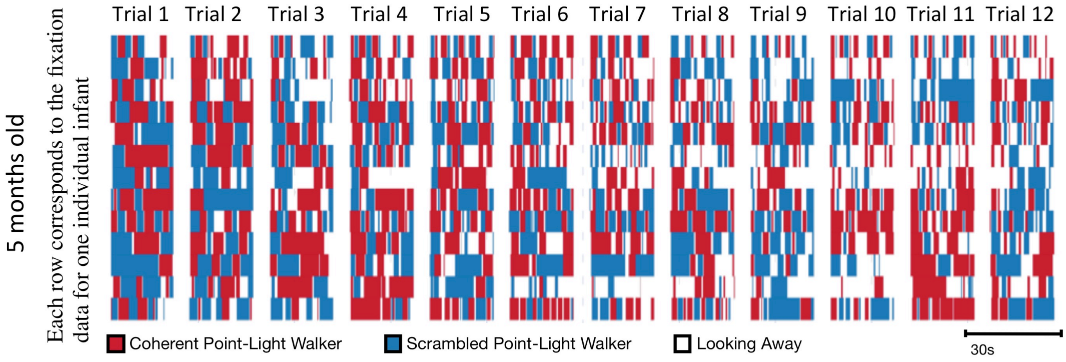

Figure 23. Visualization of fixation time series' data of all participants at five months in all trials of Experiment 2

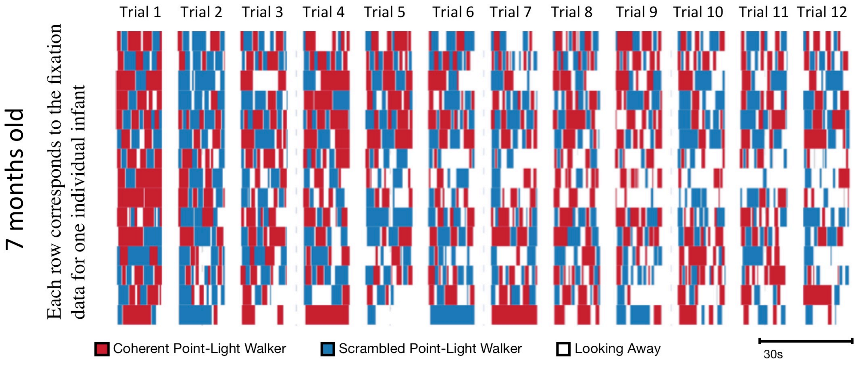

Figure 24. Visualization of fixation time series' data of all participants at seven months in Experiment 2

Each row of colored tiles corresponds to one individual five (Figure 23) and seven (Figure 24) months infant and each horizontally contiguous block of color corresponds to a sustained bout of fixation towards the coherent point-light walker (red), the scrambled point-light walker (blue) or away (white). Trial duration was 20 seconds at five months and 15 seconds at seven months and the start of each trial was synchronized in the visualization. The vertical ordering of infants was calculated by applying hierarchical clustering (Ward's method) to the vector composed of proportion of looking at coherent point-light walker per trial. A gap between trials was placed to help the visualization; inter-trial pause took only a few seconds and was controlled by the infant's behavior.

We compared the number of fixations per minute in this experiment between three (M = 8.77, SD = 4.58) and five months (M = 19.15, SD = 4.99); and between three and seven months (M = 19.52, SD = 5.45). Both five, *t*(9) = 6.15, *p* < .001, and seven months-old, *t*(12) = 5.90, *p* < .001, showed higher number of fixations relative to the younger three months-old infants. Five and seven months-old infants did not differed in their number of fixations towards the stimuli per minute, *t*(11) = .85, *p* = .41. Also as in the previous experiment, three months-old infants (M = .85, SD = .12) exhibited a significantly higher proportion of total looking time in relation to five (M = .65, SD = .11), *t*(9) = 4.38, *p* < .05, and seven months-old (M = .67, SD = .11), *t*(12) = 4.26, *p* < .05. Again, the two older age groups did not significantly differ, *t*(11) = .88, *p* > .05.

In sum and to the point, five and seven months-old infants seem to exhibit a similar pattern of looking behavior that is distinct from the younger infants. Three months old infants, in contrast with the older infants, prefer the coherent point-light walker. Based on these results and analysis, we propose three hypotheses, not mutually exclusive, to explain these differences: (1) the exogenous vs. endogenous balance in selective attention is different between three and five/seven months of age; (2) the stimuli's level of perceptual complexity, from the infant's perspective, varies across the two age-groups; and (3) a preference for the coherent point-light walker emerges later in development in a *U*-shape developmental curve linked to infants' motor development.

The exogenous vs. endogenous balance hypothesis considers that selective attention to the stimuli in our task and in the two age groups is being mediated by different balances between exogenous and endogenous: at three months attention is balanced to be more exogenous and at five/seven months more endogenous. Three months attention is more exogenous or stimulus-driven, that is, more controlled by the external characteristics of the stimuli; at five and seven months, infants gain a more endogenous control of their attention and are internally directed (Bertenthal & Boyer, 2015; Reynolds, 2015). Thus, it could be that three months' selective attention in our task was more driven by the "low level" visual features of the coherent point-light walker (such as the depiction of configural coherence or a vertical symmetry in this stimulus); whereas, the older infants, likely less controlled by these salient visual features of the coherent stimulus, engaged in a more "exploratory" looking behavior switching their fixations between the two stimuli.

Our second hypothesis refers to the level of complexity of the two stimuli. The scrambled point-light walker seems to be a more complex visual stimulus than the coherent point-light walker at three months. Bertenthal, Proffitt, Kramer, et al. (1987) tested three months old infants in an infant-controlled habituation procedure, and reported that three months took longer to habituate to the scrambled in relation to the coherent display. This result indicates that three months took longer to encode the scrambled point-light walker suggesting that this stimulus is visually more complex for these infants (Bertenthal, Proffitt, Kramer, et al., 1987). We know that infants do not prefer stimuli that are either too simple or too complex and prefer stimuli with intermediate levels of complexity (Kidd, Piantadosi, & Aslin, 2012). Thus, three months old infants turn their attention to the coherent point-light walker, that is, the stimulus with an intermediate level of complexity for their visual system to process. In contrast, the scrambled point-light walker might be a visual competitor of more comparable complexity to the coherent point-light walker in the older infants; therefore, five and seven months old equally look at both stimuli.

The final and third hypothesis is related to the action-perception and action-execution link (Bekkering et al., 2009; Iacoboni et al., 1999; Rizzolatti & Craighero, 2004). Infants' own action experience seems to be related to infants' visual preferences: crawling infants prefer to look at a crawling motion and walking infants prefer a walking motion (Sanefuji et al., 2008); ten-weeks old infants, who experienced the stepping reflex, produced greater ERP activity when viewing an upright coherent point-light walker relative to an inverted walking motion—this effect was not found on infants that did not experience the walking reflex (V. M. Reid, Kaduk, & Lunn, 2017). Thus, we conjecture that a preference for the motion of a person walking (coherent point-light walker) in relation to a scrambled control might emerge later in development, around 14-19 months of age, with experienced walking infants. The experience of walking might thus provide a unique learning opportunity for walking infants (Loucks & Sommerville, 2013) that might change their selective attention to the global human motion configuration of point-light walkers. To test this hypothesis, experienced walking infants could be tested in the same preferential looking procedure.

4.3.4 Conclusion

In our studies, we found that three months old prefer a coherent point-light walker in relation to a scrambled control; nevertheless, this preference declined at five months. Multiple reasons might concur to explain this decline in preference for the coherent walker in our study; we have identified and discussed some that seem more relevant. However, more studies with different techniques need to be conducted to understand the development of a selective attention to biological motion configuration.

Our studies are relevant since they bring to the discussion how the study of basic perceptual phenomena is important to inform us or contribute to the understanding of higher-level human social abilities. In this sense, the emergency of a sensitivity to the global human motion configuration in biological motion perception might not only mirror a new basic sensory skill available for infants (Bertenthal, 1993), but also reflect a new selective social attentive behavior that is critically linked to infants' upcoming abilities to produce different actions, as well as interpret them in a complex social world (Bertenthal & Boyer, 2015; Bertenthal & Longo, 2008; Booth et al., 2002; Frith & Frith, 1999; Loucks & Sommerville, 2013; Pavlova, 2012; Sifre et al., 2018).

Chapter 5: General Discussion and Conclusion

We have an extraordinary ability to readily detect, recognize, and extract complex social information from human motion, even when the visual cues are comprised solely of a few point-lights attached to the major joints of a body in motion. The perception of biological motion involves different processing levels, from the processing of the motion of individual dots, to the relation between sets of dots (local configural processing), and to higher levels of integration in which sets of dots (for example, limbs) are perceptually configured into a whole body in action (global configural processing). We then are able to extract intentional actions or a person's internal and subjective state solely from biological motion (Moore et al., 2012). Despite its basic perceptual nature, perceiving configural relations in biological motion is a key aspect of human action understanding (Bertenthal & Longo, 2008; Moore et al., 2012).

In the present dissertation, we studied, in infancy, the development of local and global configural processing of the human walking motion. For that, we conducted four experiments with infants aged from three to seven months, focused on the developmental path of the perception of configural relations in biological motion. Our approach was based around one core perceptual mechanism—perceiving configural relations—and two experimental tasks: a neuroimaging measure of cortical activity using fNIRS (Chapter 2 and 3), and a behavioral measure of preferential attention (Chapter 4). We aimed to answer to two main questions: "is biological motion processed in the right STS region during infancy?" and "when, in infancy, emerges a preference for biological motion configuration?"

5.1 Is Biological Motion Processed in the Right STS Region During Infancy?

To answer to this question, two neuroimaging experiments with seven months-old infants were conducted using functional near-infrared spectroscopy (fNIRS) (Lisboa, Miguel, et al., 2020; Lisboa, Queirós, et al., 2020).

In the two experiments, infants passively watched an intact coherent motion of a person walking (coherent point-light walker) while their cortical activity was recorded (nine channels placed over the right STS region). This activity was then contrasted with responses associated to three motion-matched controls: an inverted point-light walker, a rigid moving point-light walker frame (Chapter 2), and a scrambled point-light walker (Chapter 3). We tested seven months-old infants because previous fNIRS studies indicate that a first step to a right STS dominance in biological motion occurs at this age (Biondi et al., 2016; Ichikawa et al., 2010; Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009).

In our experiments, visualization of both the upright/coherent point-light walker and inverted point-light walker activated areas within the right STS region of seven months old. The locations of the activations within the right STS region for each display were however different: the coherent point-light walker activated a region within the middle-posterior temporal cortex and the inverted point-light walker in the posterior temporal cortex. These responses, that corresponded to a significant increase in oxy-hemoglobin concentration in relation to baseline, also significantly differed from the other motion conditions: the coherent point-light walker differed from the inverted, rigid point-light walker frame, and scrambled point-light walker; and the inverted point-light walker significantly differed from both the upright and rigid moving point-light walker frame. Both the scrambled point-light walker and the rigid moving point-light walker frame did not elicit any significant response.

These results link the perception of point-light walkers to infants' right STS functioning and they indicate that this site already has some degree of specialization to biological motion at least at seven months of age.

5.1.1 The Coherent Point-Light Walker is Associated with Right Middle-Posterior Temporal Cortex Functioning

Previous fNIRS experiments used video clips of an actor's upper body motion as stimuli to study infants' brain responses to biological motion (Lloyd-Fox et al., 2011; Lloyd-Fox et al., 2009)—however, see Ichikawa et al. (2010). Using video clips of an actor includes more than biological motion information in the stimuli, limiting conclusions concerning right STS specialization to human motion in infancy.

One of the main innovative aspects of the present work was that we were the firsts measuring the brain hemodynamic response in infancy to point-light walkers. Moreover, since we used the point-light technique, we could specifically investigate *which* basic visual properties of biological motion activate infants' right STS region. We could thus study the degree of specialization of this cortical site at seven months of age.

To the date, only a few EPRs studies employed point-light walkers to measure brain responses to biological motion in infancy (Masahiro Hirai & Hiraki, 2005; M Hirai, Watanabe, Honda, & Kakigi, 2009; Masahiro Hirai, Watanabe, Honda, & Kakigi, 2013; Marshall & Shipley, 2009; V. Reid et al., 2006; V. M. Reid et al., 2008). These ERPs studies found brain-processing differences between intact coherent point-light displays and a set of motion-matched controls, both at seven and at five months of age. However, it is not possible to assert from these ERP experiments, the location of the measured response-signals—EEG has a low spatial precision (Azhari et al., 2020; Lloyd-Fox et al., 2010). Therefore, it was still unknown whether the right STS—a critical node in human social cognition—is involved in the perception of point-light displays in infancy.

Ours were the first studies demonstrating that the perception of the coherent/upright point-light walker is associated with the activation of infants' right middle-posterior temporal cortex. This response was found in two independent fNIRS experiments, with two distinct seven months-old samples. Furthermore, activations associated with the coherent point-light walker significantly differed from an inverted point-light walker, and a rigid moving point-light walker frame (described on Chapter 2) (Lisboa, Miguel, et al., 2020), and a scrambled point-light walker (Chapter 3) (Lisboa, Queirós, et al., 2020). The two studies have much in common but they differed in the motion controls used and in other relevant aspects.

5.1.1.1 Comparison between the two fNIRS experiments

In two fNIRS experiments we analyzed infants' hemodynamic responses in the right STS region while seven months old viewed an approaching motion of a person walking or a motion-matched control. In both experiments, we used the same fNIRS array (9 channels placed over the right temporal region) and tested seven months-old infants. In two independent samples, we found identical results: a significant activation to coherent/upright point-light walker in the right middle-posterior temporal cortex. This adds reliability to our main finding. However, there are also important differences between the two experiments.

In the first experiment (Chapter 2), stimuli was presented for 16 seconds, while in the second experiment (Chapter 3), we reduced experimental stimuli presentation to 8 seconds. This difference is important because we found that 8 seconds of stimuli presentation is sufficient to elicit the same hemodynamic response. Previous fNIRS experiments conducted with infants and biological motion stimuli used longer trial durations (Biondi et al., 2016; Lisboa, Miguel, et al., 2020; Lloyd-Fox et al., 2011; Lloyd-Fox, Papademetriou, et al., 2014; Lloyd-Fox et al., 2009). A reduced trial duration can critically increase the number of valid trials per infant. Therefore, as expected, the mean number of valid trials per infant increased from the first to the second experiment.

There are also differences in the temporal interval where we found significant responses between the two experiments, likely associated with these changes in the design. In the first experiment (Chapter 2), significant activations were captured 12 seconds after the presentation of the upright point-light walker; in the second experiment (Chapter 3), trial duration was shortened thus significant responses were measured earlier, there is, 8 seconds after stimulus on-set.

Despite these differences, the key finding is that in both experiments we measured significant activations in the right-middle posterior temporal cortex associated to the coherent point-light walker. This result is consistent with the two-process theory of biological motion processing (Masahiro Hirai & Senju, 2020). This theory postulates that the processing of intact configural walking displays involves some degree of visual experience, and the activation of high level cortical networks (Masahiro Hirai & Senju, 2020). In accordance, we found activations in the right temporal cortex and in seven months-old infants. Our results thus add evidence to two-process theory of biological motion processing (Masahiro Hirai & Senju, 2020) and, most importantly, they indicate that the coherent configuration of a person walking is a relevant social stimulus for infants at least at seven months of age.

5.1.1.2 Neural mechanisms that support biological motion also support other social-cognitive functions

As reviewed in Chapter 1. General Introduction, several findings suggest that the perception of biological motion is an essential part of human social-cognition. Underscored by the general finding that humans extract socially relevant information from point-light displays, right STS involvement in biological motion perception is also a strong indicator of the socially relevant meaning of this percept. Our fNIRS experiments extended this cortical report to infancy.

The right STS is implicated in the processing of other socially relevant abilities in adults, such as face processing, theory of mind, or language (Carter & Pelphrey, 2006; Deen et al., 2015; Peuskens et al., 2005). Developmentally, the perception of biological motion was conjectured to be a precursor of later and more sophisticated social abilities, such as joint attention and theory of mind (Carter & Pelphrey, 2006; Frith & Frith, 1999; Pavlova, 2012). Nevertheless, no previous study had demonstrated right STS involvement in the perception of point-light walkers in infancy.

Our studies show that human infants process biological motion in the right STS region thus they add evidence to the conjecture that biological motion is an important precursor of human social-cognition. Furthermore, our significant activations associated with the coherent point-light walker were located in similar or adjacent to regions that are also linked to other social-cognitive abilities in infancy and toddlerhood (Hakuno et al., 2018; Hyde, Simon, Ting, & Nikolaeva, 2018; Ichikawa et al., 2010; Miguel, Gonçalves, Cruz, & Sampaio, 2019; Otsuka et al., 2007).

Previous fNIRS studies conducted in infancy and early childhood have found significant activations in the right STS region associated with: static face processing in five and eight month-old infants (Otsuka et al., 2007), human face motion in four and eight month-olds (Grossmann et al., 2008; Ichikawa et al., 2010), multimodal interaction signals in six month-olds (Lloyd-Fox, Széplaki-Köllőd, et al., 2015), theory of mind (Hyde et al., 2018), human vocal sounds in seven month-olds (Grossmann et al., 2010), affective touch in twelve months-old (Miguel et al., 2019), and joint attention in twelve to fourteen month-old infants (Hakuno et al., 2018). Our results thus indicate that the perception of point-light walkers shares resources in the infants' brain with other social-cognitive abilities. In other words, we found that the neural mechanisms that support biological motion perception also support other social-cognitive functions in infancy and toddlerhood.

5.1.2 The Inverted Point-Light Walker is Associated with Right Posterior Temporal Cortex Functioning

The mature human visual system is highly sensitive to the orientation of point-light displays. Biological motion perception is characterized as being "orientation dependent", meaning that, inverting the orientation of a point-light display is enough to disrupt its identification (Pavlova & Sokolov, 2000). fMRI studies also show that upright point-light walkers elicit greater responses in the right STS relative to inverted point-light walkers in the mature brain (E. Grossman & Blake, 2001).

Experiments based on infants' looking behavior (using both habituation and preferential looking procedures) demonstrate that infants are sensitive to the orientation of point-light displays (Bertenthal, 1993; Fox & McDaniel, 1982; Francesca Simion et al., 2008). Neurodevelopmental studies also suggest that inversion is processed differently in the infant's brain. For example, Ichikawa et al. (2010) reported significant activations in the right temporal cortex of seven months-old infants associated to the upright point-light display of a surprised face expression; the inverted face expression did not elicit any significant response (Ichikawa et al., 2010).

Considering the exposed, our initial hypothesis was that the inverted point-light walker would not be associated with a significant response in the right STS region of seven months-old infants. However, we found that the observation of this stimulus elicited a significant activation in the posterior temporal cortex (Lisboa, Miguel, et al., 2020). This response, found earlier, 4 to 8 seconds after stimulus on-set, significantly differed from the upright point-light walker, and the rigid moving point-light walker frame (the other two conditions of the study).

We discuss four hypotheses to explain this result: (1) there is a more general function for the human right STS in biological motion perception, thus, the right STS is sensitive to an articulated body in motion, independently of its orientation (Thompson et al., 2005)—this hypothesis is less likely considering that most adults' fMRI experiments report a greater right STS response associated to intact point-light walkers (E. Grossman & Blake, 2001); (2) there are different processes within infants' right STS responding to different biological motion information; (3) the inverted point-light walker is associated with a more bilateral temporal response, in infants, in relation to the upright point-light walker (that is more right-lateralized) (Ichikawa et al., 2010); and (4) specificity to biological motion in the right STS is gradually developing, and at seven months of age this area is not as specific (or is less differentiated) as adults' cortical responses. The last three hypotheses are not mutually exclusive and are detailed next.

5.1.2.1 Different processes within infants' right STS are in place

We observed different locations within the infants' right temporal region associated with our two significant conditions (Lisboa, Miguel, et al., 2020); this might be informative. In our study, the coherent point-light walker was associated with a significant increase in oxy-hemoglobin concentration in the right middle-posterior temporal cortex and the inverted point-light walker in the right posterior temporal cortex.

Regions within the adults' right STS can respond differently to biological motion and motion-matched controls—for example, Grèzes et al. (2001) reported significant responses associated with rigid motion (the point-light display of a rotating cube) located posteriorly in the STS compared with the ones elicited by an upright point-light walker (Grezes et al., 2001). Likewise, in our results, the right middle-posterior temporal cortex might be involved in the processing of the coherent point-light walker whereas more posterior locations in the right STS with the processing of the inverted point-light walker. These different locations could be associated to a differential processing where more posterior parts of the right temporal cortex are less differentiated and respond more generally to other features of biological motion.

Jokisch et al. (2005) also found both temporal and spatial differences in adults' perceptual analysis of biological motion. In their study, two negatives ERPs associated with the perception of frontal-view point-light walkers were measured: one at an earlier peak (at 180ms after stimulus onset) associated solely to a coherent/upright point-light walker (but not to a inverted or scrambled point-light walker); and a second later one (between 230 and 360ms) with a larger amplitude for both the upright and inverted point-light walker (but not for a scrambled display). They performed a source localization analysis in this second peak and located these responses in right fusiform gyrus and in the right superior temporal gyrus (Jokisch et al., 2005), which overlaps with our observed responses (Lisboa, Miguel, et al., 2020). Thus, the authors interpreted their findings in the following way: the first peak reflects a rapid identification of the highly familiar human figure, and the second one might be associated with a more specific analysis of motion patterns providing biologically relevant information. These spatial and temporal differences reported by Jokisch et al., (2005) might also reflect a processing that was also captured by our measured activations to the coherent and inverted displays (Lisboa, Miguel, et al., 2020).

More specific conclusions regarding the different location and the temporal dynamics (fNIRS has a low temporal resolution) of our responses should be taken carefully. More studies need to be conducted, manipulating the orientation of point-light stimuli and right STS locations.

5.1.2.2 The inverted point-light walker is associated with a more bilateral temporal response

We measured cortical responses to point-light walkers in the right temporal cortex of seven months-old infants. However, it is critical for future studies to measure more regions of interest, namely, left temporal responses.

Neuroimaging studies conducted in the mature adult brain show that presenting biological motion stimuli to adults systematically leads to strongly right lateralized activity in the pSTS (Grezes et al., 2001; E. Grossman & Blake, 2001; Pelphrey et al., 2003). Yet, few studies have examined the developmental course of this inter-hemispheric difference in STS responses to biological motion.

There is only one fMRI experiment conducted so far; this study found that school-age children's activity, when passively viewing human motion, is more bilateral (or less right-lateralized) than adults—even so, the right pSTS responded over twice as much to the biological motion condition in children when contrasted with other conditions (Carter & Pelphrey, 2006).

In infancy, even less is known—there is only one fNIRS experiment conducted with seven months-old analyzing right and left temporal responses to point-light displays of face motion (Ichikawa et al., 2010). This experiment found that an upright point-light display of a face elicits significant activations in the right temporal cortex of seven months-old in relation to baseline; and this difference was not found in the left temporal cortex (Ichikawa et al., 2010). The inverted point-light display of the face in this study showed an increased oxy-hemoglobin concentration in the left temporal cortex but that did not reach statistical significance in relation to baseline (Ichikawa et al., 2010).

We did not measure left temporal responses but we can conjecture that the inverted point-light walker in our study might be associated to an increased oxy-hemoglobin concentration in the left temporal cortex. Thus, the inter-hemispheric difference in STS responses at seven months old might be greater for the upright point-light walker than for the inverted point-light walker. Responses associated with the coherent point-light walker would be more right specialized in comparison with the functional responses associated to the inverted point-light walker.

Finally, it is worth noting that measuring more regions or interest is also vital in understanding infants' cortical functional development and even adult cortical functioning: comparing the complexity of the adults' brain functioning to only one region of interest, and in one specific age group is very limited (Karmiloff-Smith, 2010).

5.1.2.3 Right STS is infancy is less differentiated than adults

Another possible explanation for our significant findings is that, at seven months of age, the right STS is simply less differentiated than the adults, and is not orientation-dependent, thus, is responding to the common visual characteristics or properties of the upright and inverted point-light walkers.

Both the upright and inverted point-light walker produce complex patterns of articulated motion, and both have a coherent configural relation between the dots. In contrast, stimuli that do not possess one or both of these visual features did not elicit significant activations in our study, e.g. the rigid moving point-light walker frame and the scrambled point-light walker (Lisboa, Miguel, et al., 2020; Lisboa, Queirós, et al., 2020).

The rigid display do not depicts articulated motion or a human motion configuration; the scrambled point-light walker do not depicts articulated motion or even a coherent motion configuration. Therefore, it could be that, at seven months of age, the right STS is responding to human configural motion information, independently of its orientation. These results indicate, at the very least, that biological motion configural processing is a central feature of biological motion perception. Corroborating this conclusion, fMRI experiments with adults report greater right STS responses to an inverted point-light walker in relation to a scrambled point-light walker, outlining right STS role in biological motion configural processing (E. Grossman & Blake, 2001).

More specific and differentiated responses in the right STS region to the intact properties of biological motion might be an outcome of later development (Grossmann, 2015).

5.1.3 Cortical Specificity to Biological Motion Develops Gradually

It is a fact that the human brain still undergoes large developmental changes from infancy to adulthood. In particular, we know that cortical responses to biological motion change from childhood to adulthood (Carter & Pelphrey, 2006; M Hirai et al., 2009; Masahiro Hirai et al., 2013; Lichtensteiger et al., 2008).

Longitudinal experiments using ERPs report that responses to coherent vs. scrambled point-light walkers only reach adult level in children at the age of 10 years old (M Hirai et al., 2009; Masahiro Hirai et al., 2013). fMRI experiments located these developmental changes in the STS (Carter & Pelphrey, 2006; Lichtensteiger et al., 2008).

Carter & Pelphrey (2006) used fMRI to compare brain responses to biological motion in children aged 7- to 10-year-old and adults. Of all regions activated in this study, the only one showing developmental change was the STS: adults' responses were more right lateralized whereas children responses were more bilateral (Carter & Pelphrey, 2006). Lichtensteiger et al. (2008)' fMRI findings are also in line with these results: they found that biological motion-related functional activity is enhanced in adults in relation to 5- to 7-years old children, specifically in the right STS. This increased specificity in the right STS across age during childhood was hypothesized to be due to multiple of factors, including maturation, additional experience with biological motion, or even to an overall increase in social skills (Carter & Pelphrey, 2006).

In conclusion, children's cortical responses to biological motion seem to be still developing. Measurements of children and adults in the same experiment indicate that cortical activity in biological motion shifts from being bilateral and more widespread during childhood to a more localized profile with age (Lichtensteiger et al., 2008). If the right STS is not adult-like in children, one can infer that it is also not during infancy.

5.1.3.1 The development of a right STS specificity to biological motion in infancy

As reviewed in the General Introduction and in the introduction of Chapters 2 and 3, knowledge on infants' cortical development in response to biological motion is limited. This is, in part, related to the scarcity of neuroimaging techniques sufficiently adequate for infants—fNIRS was a relatively recent addition (Azhari et al., 2020; Lloyd-Fox et al., 2010). Moreover, no previous study approached the perception of biological motion in infancy by applying point-light walkers. Our results add to the understanding of infants' cortical processing to biological motion since we used point-light displays; however, we only tested one age group, and specific conclusions about developmental changes in infancy are impossible based solely in our two studies. Truly developmental questions focus on progressive change thus compare different age groups (Karmiloff-Smith, 2010).

We only tested seven months old infants with point-light displays but we conjecture that a first transition to a right temporal dominance in biological motion develops, in infancy, at seven months of age: Lloyd-Fox et al. (2009) reported activations in both temporal hemispheres to video clips of moving actors at five months, and Ichikawa et al. (2010), a right temporal dominance to the presentation of point-light displays of moving faces at seven months (Ichikawa et al., 2010; Lloyd-Fox et al., 2009). Nevertheless, these two studies used different motion stimuli. The next step in studies of biological motion perception in infancy is to conduct fNIRS longitudinal experiments, testing various age groups during the first year of life, and employing point-light walkers to investigate cortical changes in the temporal cortex. We hypothesize that cortical responses to point-light walkers will gradually increase in their specificity during infancy (Masahiro Hirai & Senju, 2020). Thus, developmental changes during the first year of life might include a gradually more specific right-STS response (Carter & Pelphrey, 2006; Lichtensteiger et al., 2008) and/or a more differentiated response to biological motion visual features in the right STS region; for instance, a more mature response in older than seven months old infants that does not respond to inverted point-light walkers.

5.2 When, in Infancy, Emerges a Preference for Biological Motion Configuration?

In Chapter 4, we focused on understanding when a preference for a coherent point-light walker over a scrambled control emerges in infancy. For that, we conducted two preferential looking experiments using the same stimuli as in our fNIRS experiments, i.e. motion of an approaching walking person, i.e. a point-light walker. The first experiment (experiment 1) was cross-sectional and tested three and five months-old infants. The second experiment (experiment 2) was longitudinal, and we asked parents that participated in experiment 1 at three months to return with their infants at five and seven months to participate in the same procedure with a reduced trial duration.

Results from both experiments revealed that a preference for the coherent point-light walker over a scrambled point-light walker emerges at three months of age. However, both five and seven months old showed no preference for either stimulus—mean proportion of looking at the coherent display was at chance level in the two older age groups. The absence of a preference at five months of age was replicated in two independent studies with two different samples of five months old; therefore, this behavior is not explained by an inappropriate trial duration in the preferential looking procedure. On the other hand, two differential looking behaviors were observed between three vs. five and seven months old infants: three months-old preferred the coherent point-light walker, and revealed a smaller number of fixations on the screens, and an extended proportion of time looking at the screens during the task; the older infants did not show a preference for either stimulus, and revealed a more "exploratory" looking behavior, with an increase number of fixations, and shorter fixations between the two stimuli.

These results were unexpected since we found a decline in preference for the coherent stimulus in the older infants. If we were to only consider the older infants data and the simplest interpretation of a preferential looking task: we found no evidence for the ability to process global human motion configuration in the older infants—a result at odds with previous habituation experiments that found it to be present at least at five months of age (Bertenthal, 1993); and with our fNIRS data (Lisboa, Queirós, et al., 2020). Furthermore, previous preferential looking experiments conducted with upright and inverted point-light displays showed an increased preference across developmental age, starting at three months of age (Sifre et al., 2018).

Nevertheless, our results mirror the developmental shift found in biological motion perception between three and five months of age (Bertenthal, 1993). In addition, we replicated our null result (no preferences in the older infants) in two studies, and in two age groups of five and seven months old, increasing the reliability of these results.

We propose three developmental and non-mutually exclusive hypotheses for understanding this shift in preference for configural relations at three vs. five/seven months of age: (1) differential attentional processes are differently balanced in the two age-groups; (2) the stimuli's level of perceptual complexity, from the infant's perspective, varies across the two age-groups; and (3) a preference for the coherent point-light walker emerges later in development in a *U*-shape developmental curve, linked to infants' ability to walk (i.e. a perception-action link).

5.2.1 Developmental changes in selective attention: the exogenous vs. endogenous balance is different between three and five/seven months of age

Three and five/seven months-old infants show two distinctive patterns of looking behavior in our preferential looking task: the older infants changed more between the stimuli, and three-month-olds exhibited less number of fixations but longer fixation bouts. We speculate that these differences might reflect different attentional processes, which might partially explain the different preferences.

Behavioral and neurophysiology studies in infancy suggest that from birth until around three months, infants mostly rely on a reflexive, stimulus-driven, exogenous selective attention; a more endogenous or voluntary control or intentional allocation of attention begins to emerge at around five months of age (Bertenthal & Boyer, 2015; Reynolds, 2015). Thus, three-month-olds' visual attention is more automatic and reflexively drawn to salient features of the visual stimuli; infants at this age have a more exogenous orienting and their attention is more controlled by salient visual features of the stimuli (Bertenthal & Boyer, 2015; Reynolds, 2015). In contrast, at five-month-old, infants begin to regulate their visual fixation and scanning better (more of an endogenous orienting), have a more exploratory visual behavior, and they also need less exposure to a visual stimuli to process it (Reynolds, 2015).

In this sense, selective attention towards the coherent point-light walker might have relied at three months of age, in a more stimulus-driven attentional process, where low-level visual properties of the coherent point-light walker, such as depiction of configural coherence or a vertical symmetry (not present in the scrambled point-light walker) controlled the infants' visual attention. Five and seven month-olds, with more developed perceptional and attentional systems are less controlled by these low level visual properties of the stimuli and thus might internally balance their attention in a more "exploratory" looking behavior.

5.2.2 Perceptual Complexity of the Stimuli: the scrambled point-light walker is visually too complex for three months-old

Previous habituation experiments with point-light displays have established an important developmental shift for biological motion perception emerging between three and five months of age (Bertenthal, 1993). According to these studies, infants begin to process the global human configuration in point-light walkers at around five months of age, and the younger three months-old infants are more tuned to local configural information (e.g. limbs motion evoked by the articulated movement of three dots) (Bertenthal, 1993). Importantly, in their habituation study with three months-old infants, Bertenthal, Proffitt, Kramer, et al. (1987), also reported that infants at three months process or encode both stimuli very differently during the habituation phase: infants that were habituated to the scrambled point-light walker took longer to reach habituation and showed a fluctuating habituation pattern, while infants in the coherent condition, habituated faster and exhibited a continuously decreasing habituation pattern (Bertenthal, Proffitt, Kramer, et al., 1987). According to the authors, this behavior suggests that the scrambled point-light walker might be a more complex stimulus than the coherent point-light walker to encode at three months (Bertenthal, Proffitt, Kramer, et al., 1987)—analysis of five or seven months' habituation patterns were not reported (Bertenthal et al., 1984).

Thus, at three months of age, the scrambled point-light walker is likely a complex stimulus (Bertenthal, Proffitt, Kramer, et al., 1987); as a result, infants might be attending to the stimulus that has an optimal level of complexity for their visual system to process and learn (Kidd et al., 2012; Köster, Kayhan, Langeloh, & Hoehl, 2020): in the case of three-months-old infants, the coherent point-light walker.

For the more mature visual system of the five and seven months-old infants, the coherent point-light walker might not represent a stimulus with such an optimal level of complexity for the older infants to learn (Bertenthal, 1993). Mature processing of coherent point-light walker in relation to a scrambled point-light walker at seven months of age was confirmed in our fNIRS experiment: the coherent point-light walker (but not the scrambled display) activated the right middle-posterior temporal cortex at seven months (Lisboa, Queirós, et al., 2020)—an area known to process configural relations in the mature brain (Blake & Shiffrar, 2007; Deen et al., 2015; Peuskens et al., 2005). However, if the coherent point-light walker is too simple for the five/seven months prefer, on the other hand, the scrambled display might still represent a too complex visual stimulus for these infants—this stimulus does not even depict any configural coherence. As a result, both the coherent and the scrambled point-light walker might be equally competing for the older infants' attention, one for being too simple, the other for being too complex, and none with an intermediate level of complexity at this age to capture five/seven months-old infants' preferences (Kidd et al., 2012; Köster et al., 2020).

In order to test this hypothesis and understand which are the levels of complexity for processing both the coherent and the scrambled point-light walker at the three age groups, a habituation experiment could be conducted in which the habituation patterns and time for habituation are measured and compared in the three groups. We hypothesize that the scrambled point-light walker will still represent a complex visual stimulus for the older infants to process, i.e. with an increased time to reach habituation, though the older infants will reach habituation to the coherent point-light walker faster than three months.

5.2.3 Perception-Action Link: a preference for the coherent point-light walker emerges in experienced walking infants

Five and seven months-old might not prefer the coherent point-light walker simply because they are still not able to process the global human configuration in point-light walkers and this ability might emerge later in development—although the majority of previous behavioral (Bertenthal, 1993) and neurophysiology (Masahiro Hirai & Hiraki, 2005; Lisboa, Queirós, et al., 2020; Marshall & Shipley, 2009) research conducted with coherent and scrambled point-light displays suggests the opposite. In favor of this hypothesis, and in accordance with our results, Christie & Slaughter (2009) reported that nine, but not six months-old infants preferred a coherent body motion rather than a scrambled body motion. This study however used very distinct stimuli than the ones employed in our experiments: they used animated static photos of human bodies (not point-light displays) whose head oscillated left and right and limbs went up and down, and they did not use real motion-captured data (Christie & Slaughter, 2010). Nevertheless, considering the reported preference for the coherent body stimulus at nine months, and the absence of a preference at six months, we can speculate that, likewise in our experiment, more visually experienced infants, older than seven months, could show a preference for the coherent point-light walker in a *U*-shaped developmental curve. Furthermore, nine months-old infants are more developed in terms of their locomotor abilities (e.g. most infants are able to crawl at this age) in relation to six or seven months—and not only visual experience but also motor experience seems to play a role in the perception of biological motion (Bertenthal & Longo, 2008; Hauf, Aschersleben, & Prinz, 2007; V. M. Reid et al., 2017).

Specifically, infants' own action experience is closely related to how infants perceive and visually select actions to look at. Crawling infants prefer to look at a crawling motion vs. walking motion, and walking infants prefer the walking motion vs. crawling motion (Sanefuji et al., 2008). Neuroimaging findings report that fourteen to sixteen months-old infants, more experienced with crawling than walking, show a stronger electrical brain response for the visualization of a crawling motion in relation to walking (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008); and ten-weeks old infants, who experienced the stepping reflex, produced greater ERP activity when viewing an upright coherent point-light walker relative to an inverted walking motion—this effect was not found on infants that did not experience the walking reflex (V. M. Reid et al., 2017).

Studies investigating motion perception in the mature brain also substantiate this linking hypothesis by suggesting that both the production and observation of an action share resources, namely, within a particular class of sensorimotor neurons, the human mirror neuron system (Bekkering et al., 2009; Iacoboni et al., 1999; Rizzolatti & Craighero, 2004). There is now solid evidence linking action observation and action execution, i.e. perceiving the actions of others shares resources with executing movements, and the infant's motor capabilities are known to contribute to general action perception.

Thus, we conjecture that a preference for the motion of a person walking (coherent point-light walker) in relation to a scrambled control might emerge later in development, around 14-19 months of age, with experienced walking infants. The experience of walking might thus provide a unique proprioceptive information (Loucks & Sommerville, 2013) that will change infants' attentional bias to the global human motion configuration in point-light walkers.

To test this hypothesis, older walking infants could be tested in the same preferential looking procedure. To the best of our knowledge, our two preferential looking experiments were the first measuring the development of a preference for biological motion configuration after birth.

5.3 Connecting all the Dots: Final Remarks and Future Directions

Biological motion perception is an extraordinary ability, encompassing not only basic, "low-level" processing of visual information, such as perceiving configural relations, but also the ability to understand emotions, intentions or beliefs from human movement (Moore et al., 2012; V. Reid, 2011). Understanding and predicting the actions of others entails, first, configural processing of the movement produced by bodies acting. Configural processing is a key component of biological motion perception and of action recognition, thus, an important contributor to social cognition in several ways.

The present work investigated three to seven months old infants' ability to perceive configural relations in biological motion. Both cortical responses and selective attention to a coherent point-light walker against a scrambled point-light walker were measured.

In Chapters 2 and 3, we investigated right STS responses to biological motion configuration in seven months old using fNIRS; and, in Chapter 4, the development of a preferential attention to a coherent point-light walker in relation to a scrambled control, in three, five and seven months old.

The use of both behavioral (Chapter 4) and neuroimaging correlates (Chapters 2 and 3) of biological motion configural processing in infancy was a differentiating and innovative factor of this work. Thus, the joint discussion of the four experimental studies using two complementary techniques but the same controlled experimental stimuli is key.

The ability to perceive configural relations in point-light walkers was reported to emerge at three months with five months developing the ability to perceive global configural relations (Bertenthal, 1993). We speculated that this would be linked both to a differential cortical processing in the right STS region of a coherent point-light walker (Chapters 2 and 3); and to a preferential attention to a coherent walker in relation to a scrambled walker (Chapter 4).

Our fNIRS experiments indicated that seven months-old infants, more experienced with the global configuration of a person walking than younger three moths old infants (Bertenthal, 1993), respond differently to a coherent point-light walker in relation to a scrambled control in the right middle-posterior temporal cortex (Lisboa, Miguel, et al., 2020; Lisboa, Queirós, et al., 2020). The perception of global configural relations of a walking person seems thus to be sub-served by the functioning of the right STS at seven months. Nevertheless, and in contrast with our initial hypothesis, these infants did not prefer a coherent point-light walker in comparison with a scrambled point-light walker: both seven and five months old showed no preferences. Only infants at three months exhibited selective attention towards the coherent point-light walker (Lisboa, Basso, Santos, & Pereira, in prep.). Our behavioral results seem to be at odds with our neurophysiological findings: seven months old show a differential cortical response but not a behavioral preferential response. The main question following this apparent contradiction is: what do these infants actually perceive from point-light walkers?

On one hand, fNIRS findings indicate that seven months old are able of integrating motion with the human configuration of an action: they process the coherent point-light walker in the right middle-posterior temporal cortex, an area known for its role on human social-cognitive perception; this cortical response statistically differed from a set of motion-matched controls, including a scrambled point-light walker (Lisboa, Queirós, et al., 2020) or rigid object motion (Lisboa, Miguel, et al., 2020); adults process configural relations in biological motion at the same site (Baccus et al., 2009; E. Grossman & Blake, 2001; Jokisch et al., 2005; Peuskens et al., 2005; Thompson et al., 2005; Vaina et al., 2001). If seven months-old infants perceive the human form from point-light walkers, it would make sense that they would prefer to look at a coherent, and socially relevant configuration of a person walking, in relation to a scrambled point-light walker. However, this was not the case (Lisboa et al., in prep.). Next, we argue that this absence of a preference can be explained by multiple factors and does not necessarily mean that infants are not able to process configural relations, or that the underlying cortical mechanisms are not functioning (Janette Atkinson, 2002).

First, three months old prefer the coherent point-light walker, indicating that younger infants are able to process and prefer at least some level of configural information. In addition, as identified and previously discussed, there are many possible interpretations for this shift in the preferential response between three vs. five/seven months old infants—e.g. a different balance between exogenous and endogenous selective attention processes, the stimuli might represent different perceptual complexity for the two age groups, the different motor development of the infants might impact their preferences. All of this might be determining where the three and five/seven months old infants prefer to look at and none of these explanations implicates that the older infants are not able to perceive the global configuration of the human walking action.

Second, simple looking time measures provide very limited "yes/no" information about the infants' social-cognition. Thus, a lack of preference cannot directly assert the absence of an ability (Haith, 1998). It is vital to have different methods or different ways of tackling the same experimental question; evaluating or characterizing human development based on the results of one method is obviously very limited. Multiple measures can inform whether our results are a function of methods variance or of more general factors (such as attention that should remain invariant across different methods). There are limited methods available to study infants' development (Janette Atkinson, 2002; Wilcox & Biondi, 2015): our fNIRS measurements were fundamental as they provided a different context for the seven months-old configural abilities, despite the absence of a behavioral preference in these infants. Nevertheless, more convergent variables, measured with different techniques would add to our main experimental questions and would help disambiguate our findings. Other possible measures/methods of interest might include: habituation (Oakes, 2010; Proffit & Bertenthal, 1990), heart rate variability (Colombo, Richman, Shaddy, Follmer Greenhoot, & Maikranz, 2001) or eye tracking and pupillometry (Jackson & Sirois, 2009; Joshi & Gold, 2020). In particular, equipping the infant with an eye tracker in the same preferential looking procedure does not highly increases instrumentation and could inform whether infants focus or scan the displays differently in time.

Finally, we could have searched for more information regarding the particular development of the infant, namely, his/her motor and social-cognitive development and abilities (Kutsuki et al., 2009). Is the infant able to grasp an object? When did the infant begin to grasp? Is the infant able to crawl or walk? Since when? How socially developed is the infant? These and other information could bring to light important individual differences that might explain differential looking patterns or distinct cortical oxy-hemoglobin concentrations (even within the same age group). Chronological age is one possible developmental descriptor but might not be always the best one. In addition, biological motion research may well benefit from exploring individual differences and their covariation with other perceptual, cognitive, and motor skills—there is a lack of research on this subject.

Future studies should also consider longitudinal designs. The large body of literature in social-cognitive development presents major discontinuities in the understanding of early developmental social-cognitive abilities. This fragmented understanding of social-cognitive development stems in part from studying social cognition in a piece-meal approach, not in the context of mutually interacting systems of attention, perception, and action that change over time, and develop individually with or through brain maturity (Bertenthal & Longo, 2008; Thelen & Smith, 1996). Future studies should consider follow longitudinally right STS lateralization to biological motion during the first year of life while measuring infants' motor and social abilities as well as their selective attention to the coherent motion of a person walking.

There is still much to investigate about infants' perception of biological motion configuration and, more generally, about infants' social cognitive development. This thesis underscored the role of basic perceptual phenomena, such as biological motion configural processing, in high-level social-cognitive development in infancy. It also showed that there are multiple challenges facing perceptual and social-cognitive systems in extracting meaning from human motion—any developmental account of the understanding of human social-cognition needs to take into consideration the development of sensitivities in multiple layers of meaning. At the end, we were able to accomplish the ultimate goal of science with this work: answer to research questions with more interesting research questions.

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