Studying brain development in infants by eye measurements: visual perception and visual attention

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This thesis is presented by

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To obtain the degree of Doctor from the University of Barcelona, Doctoral program in Biomedicine

Supervisors

Dr. Rachel V. Gow   **Dr. Hans Supèr**

Acknowledgements

Thanks to

The teachers who remained open, collaborative and attentive to whatever was needed.

To the parents who decided to take part in the study and trusted me and the aim of the work.

The babies for their participation and the gift of being in their presence. I owe it to them the development of the present thesis.

For all those who I may not be explicitly mentioning but are part of the helping hands and support throughout my trajectory.

Thanks!

FLAVIA

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Abstract

In the first years of life, there is a dramatic unfolding of cognitive abilities supported by the progressive control of gaze behaviour. The early development of oculomotor control is presumably closely tied to the maturation of the attention system. Vergence eye movements are the movements of the eyes in opposite directions, which subserve binocular vision and depth perception. Previous studies have suggested a correlation between vergence and orienting attention (Puig, Pallarés, Zapata, & Puigcerver, 2016; Solé Puig, Pérez Zapata, Aznar-Casanova, & Supèr, 2013; Super, Marco, Perez Zapata, Canete Crespillo, & Sole Puig, 2014). The neural structures involved in the vergence system, for instance the Frontal Eye Fields (FEF), Superior Colliculus (SC), pulvinar of the thalamus and Posterior Parietal Cortex (PPC) overlap with those of the attention orienting system. This is of relevance as studying how children allocate their visual attention to relevant stimuli is a direct measure of cognitive abilities. Vergence has been studied in our research group as a measure of cognitive processing (e.g. Sole Puig et al., 2013, 2015, 2016; Esposito et al., 2018, 2019; Varela et al., 2018). In these studies, vergence responses were observed during top-down and bottom-up generated shifts of visual attention, where attentional load positively correlated with the strength of the vergence response (Sole Puig et al., 2013). The notion of a role for vergence in attention is supported by the observation of a correlation of eye vergence responses with the neural activity encoding shifts of visual attention (Solé Puig et al., 2016). Besides attention, vergence relates to memory processing as well. Memorized stimuli are accompanied with stronger vergence responses when compared to stimuli that are forgotten (Sole Puig et al., 2016). These observations motivated our current studies in younger children, to contribute to a better understanding on the impact of vergence eye movements in cognitive development early on. This PhD study consists

exploring the association between the changes in the angle of vergence eye movements' and orienting attention responses in early childhood. With eye tracking methodology, Face perception and Visual Short-Term Memory (VSTM) were evaluated as fundamental milestones of cognitive development. 130 young children aged 6-36 months were recruited from two regional kindergartens. Face images versus scrambled face images on one hand, and repeated objects versus novel objects' images on the other hand, were introduced as visual presentations, to tackle basic cognitive functions that we hypothesize are based on orienting attention. The first study addressed face processing. A series of prototypical static human face images with neutral expression were presented from a validated face database and compared it with their computerized scrambled version. We observed that vergence eye movements' responses were enhanced to face stimuli when compared to scrambled face stimuli. The study on Visual Short-Term Memory contends with the ability to temporarily hold information and form transient representations of objects. In turn, establish whether children utilize this visual information to anticipate future events. We presented two coloured objects on screen and randomly repeated one of them and a novel one separately. We observed that for the repeated object presentation, not only did vergence response increase, but also the order of image type correlated with the enhancement in vergence modulation.

Thus far, to the best of my knowledge, this is the first PhD study of its type evaluating vergence eye movements to assess attention-orienting responses in early childhood.

Resumen

En los primeros años de vida existe un gran despliegue de habilidades cognitivas respaldado por el control progresivo de la mirada. El desarrollo temprano del control oculomotor está asociado al desarrollo de la atención. Los movimientos oculares de vergencia consisten en el movimiento de los ojos en direcciones opuestas que dan lugar a la visión binocular y la percepción de profundidad. Previamente, hemos sugerido una correlación entre la vergencia y la orientación de la atención (Puig et al., 2016; Solé Puig et al., 2013; Super et al., 2014). Las estructuras neuronales involucradas en el sistema de vergencia, entre ellas, los campos oculares frontales, el colículo superior, el pulvinar del tálamo y la corteza parietal posterior se superponen con las del sistema de orientación de la atención. Esto es relevante ya que el estudio de cómo los niños despliegan y distribuyen su atención visual a los estímulos relevantes del entorno es una medida directa de sus capacidades cognitivas. De este modo, la orientación de la atención puede arrojar luz sobre el desarrollo cognitivo a posteriori. La vergencia ha sido estudiada en nuestro grupo de investigación como una medida del procesamiento cognitivo (Sole Puig et al., 2013, 2015, 2016; Esposito et al., 2018, 2019; Varela et al., 2018). En estos estudios, se observaron respuestas de vergencia durante los cambios en la atención visual generados de arriba hacia abajo y de abajo hacia arriba, donde la carga atencional correlacionó positivamente con la amplitud en la respuesta de vergencia (Sole Puig et al., 2013). La noción de un papel de la vergencia en la atención se basa en la observación de una correlación en las respuestas de vergencia ocular con la actividad neuronal que codifica los cambios en la atención visual (Solé Puig et al., 2016). Asimismo, la vergencia está relacionada con la memoria. Los estímulos memorizados se ven reflejados en respuestas de vergencia más pronunciadas en comparación con los estímulos no retenidos en la memoria (Sole Puig et al., 2016). Este

estudio doctoral consiste en explorar la asociación entre la modulación en el ángulo de vergencia y la orientación de la atención en la infancia. Mediante la metodología de seguimiento ocular, el procesamiento de caras y la memoria visual a corto plazo (MVCP) se evaluaron como hitos fundamentales del desarrollo cognitivo. Se reclutaron 130 niños de 6 a 36 meses de edad de 2 jardines de infantes regionales. Por un lado, presentamos imágenes de caras frente a imágenes de puzles de caras, y en la otra tarea, imágenes de objetos repetidos frente a objetos nuevos. El primer estudio abordó el procesamiento facial. Una serie de imágenes estáticas prototípicas de caras humanas con expresión neutral se compararon con su versión computarizada. Observamos que las respuestas de vergencia aumentaron frente a los estímulos de caras en comparación con los estímulos de puzles de caras. Por otra parte, el estudio sobre la memoria visual a corto plazo tiene relación con la capacidad de mantener temporalmente la información y formar representaciones transitorias de objetos. Asimismo, queríamos observar si los niños utilizan esta información visual para anticipar eventos futuros. Para ello, presentamos simultáneamente dos objetos de colores en la pantalla y luego repetimos uno al azar y otro nuevo, por separado. Hemos observado un incremento en la modulación de la vergencia en el caso de los objetos repetidos y asimismo correlacionado el incremento en la vergencia con el orden de presentación de la imagen.

Este es el primer estudio doctoral de su tipo que proporciona información novedosa acerca de la vergencia para evaluar las respuestas de orientación de la atención visual en la primera infancia.

Glossary

A   Amygdala

ASD   Autism Spectrum Disorder

ADHD Attention Deficit Hyperactivity Disorder

BA   Brodmann Area

C   Cingulate

2-D   Two-Dimension

3-D   Three-Dimension

DLPFC Dorsolateral Prefrontal Cortex

DS   Dorsal Striatum

ERP   Event Related Potential

FEF   Frontal Eye Fields

FEFs   Frontal Eye Fields for saccades

FEFv Frontal Eye Fields for vergence eye movements

GLM General Linear Model

GP   Globus Pallidus

IPD   Inter-Pupillary Distance

LGN   Lateral Geniculate Nucleus

MRF   Mesencephalic Reticular Formation

MT   Medial Temporal area

MVCP (esp) Memoria Visual a Corto Plazo

OFC   Orbitofrontal Cortex

PEF   Parietal Eye Fields

PPC   Posterior Parietal Cortex

Pulv   Pulvinar

RF   Receptive Field

SC   Superior Colliculus

SEF   Supplementary Eye Field

T/TH   Thalamus

V1   Primary (striate) Visual cortex

V4   One of the visual areas in the extrastriate visual cortex

VLPC   Ventral Lateral Prefrontal Cortex

VS   Ventral Striatum

VSTM Visual Short-Term Memory

List of figures

B: schematic explanation of the angle of vergence eye movements spanned by the visual angle formed by the right and left eye vectors

C: Task design scheme in a visual recognition memory paradigm

El verdadero viaje de descubrimiento consiste,

no en buscar nuevos paisajes,

sino en mirar con ojos nuevos

Marcel Proust

(1871-1922)

1. Introduction

Eye movements are the expression of the prioritized pattern of information by the oculomotor system. Progressive gain in oculomotor control enables babies to direct their attention to extract the most relevant visual information from their surroundings and to communicate with their conspecifics. Visual orienting responses can thus potentially yield insight into the development of attentional orienting and selection processes.

Vergence eye movements, where the eyes rotate in opposite directions, bring the two lines of sight to an intersection at a focus point in space. Two main reasons support eye vergence as the focus of the present thesis: the locus of attention while fixation is maintained has been the preferred way to study attention because the retinal locations of stimuli are not altered, covert shifts of attention do not produce a disruption in perceptual input, and therefore introduce no demand to bridge perceptual disruption. Recently, it was suggested that vergence eye movements have a role in covert orienting of visual attention (Solé Puig, et al., 2013; Puig, et al., 2013).

Attentional control has been defined as the ability to keep a representation or goal actively in mind in the face of conflict (Kane & Engle, 2002; Rueda et al., 2004). In this line, from 6 months old on, infants can learn predictable sequences of events, and an important development takes place in regards to the ability to overcome distracting information between 18 to 24 months of age (Clohessy et al., 2001; Garon et al., 2008).

Visual attention, which has a pivotal role in the cognitive processing of sensory information, is a driver of VSTM (Astle & Scerif, 2011). Regions involved in the control of eye movements, such as the FEF, Lateral Intraparietal area and SC are also involved in covert visual-spatial attention (Moore & Fallah, 2001; Murthy, Thompson, & Schall, 2001; Powell & Goldberg, 2000). Some researchers have even questioned the meaningfulness of the distinction between visual–spatial attention and visual–spatial working memory (Awh & Jonides, 2001; Medendorp, 2006).

As investigating eye movements has been a promising approach to uncover the role of VSTM in early attentional processes, our interest in the developmental origins of VSTM has led us to ask how young children encode and maintain visual information over brief intervals. Since vergence reflects the function of the brain, quantitative assessment of these eye movements can reveal fundamental information regarding the brain's underlying control strategy. An understanding of how vergence is controlled in young healthy individuals has been our utmost goal. We wanted to explore the association between the maturation of the attention system and increasing gaze control, by orienting responses as the baseline of cognitive development. The present dissertation is focused on testing face perception and memory recognition in young children to observe whether the relative changes of vergence signal correlate with orienting visual attention.

If, as Piaget argued, children are actively engaged in the construction of their own knowledge, visual behaviour is amongst the main pillars of cognitive development. Thus, visual attention processing shall be observed through vergence eye movement modulation.

1.1 Eye movements

In everyday life, we constantly shift our gaze in different directions and in different depths, to look at different objects in 3-D space. Of the multiple ways that the visual system has for exploring the surrounding environment, several eye movements either maintain or bring the object of interest onto the fovea, the central part of the retina specialized in detailed visual processing. Gaze shifts in direction and depth involve components of both vergence eye movements and saccades or most usually a combination of both.
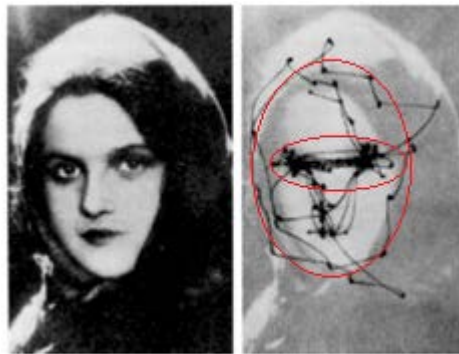
Figure 1. An example of visual exploration where a subject explores the photography for a minute. Black lines represent saccade trajectories and black dots are the fixations. Hairline was highlighted in red as fundamental reference for face identification and well as eyes representing the most informative region explored. Adapted from Yarbus (1967).

Saccades are the fast movements used to change fixation rapidly. They are conjugate movements—i.e., the eyes move in the same direction. We normally make an average of 3 to 4 saccades per second and fixate for 300–400 ms at a time, to take in the information at the fovea and to decide where to fixate next. Several processes are believed to take place during this period, such as a shift of visual attention to the new target, disengagement of oculomotor fixation, and computation of the metrics of the movement (Yang, Bucci, & Kapoula, 2002). Perhaps the preparation state necessary to initiate a

saccade depends on the distance at which the eyes verge. Precise estimation of the distance to an object and the distance between objects around us is important for our interactions with our surrounding environment (Foley, Ribeiro-Filho, & Da Silva, 2004). For correctly defining the distance of an object, both its position and orientation needs to be determined (Gilinsky, 1951; Westheimer, 1996). This point provides a reference frame which, in turn, provides the contextual information of the object located in space (Merker, 2013). The neural processing of distance and position of objects is termed Visual Space. An accurate representation of the physical space is only possible if both the physical and visual space have accurate mapping. However, properties of the geometry of visual space seem to vary as a function of the available depth cues.

1.1.1 Vergence

Vergence (or disjunctive) eye movements refer to the simultaneous movement of both eyes in opposite directions. Convergence is the inward rotation of the eyes, moving from far to close, nasally. Divergence is the outward rotation of the eyes, starting from close and moving to far, temporally. Vergence eye movements subserve proper binocular fixation and fusion to allow for binocular vision and depth perception.
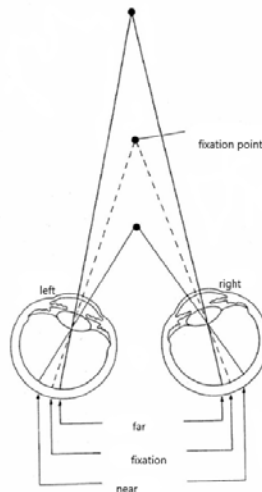
Figure 2. Vergence eye movements. Pure symmetric vergence response showing sequential components: starting from the tonic vergence position (outer pair of solid lines), it proceeds with an initial accommodative vergence component movement (inner pair of solid lines), which is then followed by the reflex component (commonly referred to as fusional or disparity convergence) movement (pair of dashed lines) to finally bifixate on the near target. Adapted from Maddox (1893).

Vergence could be dissected in four linearly additive sequential components: tonic, accommodative, reflex and voluntary. Tonic vergence is the initial component of vergence which shifts the eyes from an anatomic resting position to a more convergent physiological position of rest; likely reflecting baseline midbrain neural activity. Accommodative vergence is the blur-driven component. Reflex vergence responds to the presence of retinal disparity, i.e. the angular difference between target angle and bifixation angle. It has been commonly referred to as fusional vergence by clinicians who emphasize its function (Hofstetter, 1945), and named disparity vergence by bioengineers who emphasize its stimulus control properties (Kenyon, Ciuffreda, & Stark, 1980), which reduces the residual amount of vergence error to a minimum. The fourth component, voluntary convergence, is attributed to "knowledge of nearness" of the target (Jiang, Hung, & Ciuffreda, 2002). Usually, binocular disparity and retinal image blur are considered the primary physical stimuli to the vergence and accommodative systems. Still,

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some reports show that vergence eye movements may be evoked by stimuli that give the impression of being nearer or further than the point of convergence, in the absence of disparity or accommodation cues, labelled as proximal vergence (Howard, 2004).

1.1.1.1 Vergence cues: disparity

To navigate successfully in 3-D space, it is necessary to recognize objects and to know their spatial relationship relative to each other and to oneself. The geometrical properties of the two retinal images give rise to disparity, as each eye sees a slightly different view of the world given the horizontal separation between them. By comparing the views of the two eyes one can perceive which of two objects is closer and how much closer it is. If the object is far away, the disparity of that image falling on both retinas will be small. If an object is near, the disparity will be large. Vergence eye movements activate disparity cells at the foveal region (Kapoula, Isotalo, Müri, Bucci, & Rivaud-Péchoux, 2001). The most precise cue to depth perception depends on disparity and is called stereopsis. It requires that the two eyes fixate the same object, or place in space so that the two retinal images can be fused into a single percept. Before combining the images of each eye to form a unified perception of depth, the visual system first has to match the two retinal images. Solving the correspondence problem (i.e. what is the counterpart in one eye of a particular point on the retina of the other eye) is essential for stereopsis. Binocular vision allows for stereoscopic vision as well as enhanced visual resolution.

1.1.1.2 Vergence: a two-stage processing system of visual perception

Pure vergence eye movements, i.e. without a saccadic eye movement, have been proposed as a double control system (Cullen & Van Horn, 2011), composed of a fast open-loop transient movement that is ballistic in nature which brings the eyes near the target position, followed (after approx. 200 ms) by a slower, closed-loop (sustained) movement that is under visual feedback control and reduces the residual error (or fixation

disparity) to a few minutes of arc, i.e. within Panum's fusional area (Collewijn, Erkelens, & Steinman, 1997; Semmlow, Hung, Horng, & Ciuffreda, 1993, 1994). This component, due to its non-ballistic behaviour, provides flexibility.

Whether or not vergence eye movements are programmed by perceptual information is controversial. Some studies show a clear dissociation between depth perception and vergence eye movements (Erkelens, 2001; Masson, Busettini, & Miles, 1997; Teichert, Klingenhoefer, Wachtler, & Bremmer, 2008; Wismeijer, Van Ee, & Erkelens, 2008). However, other evidence demonstrates perceptual effects on vergence eye movements (Hoffmann & Sebald, 2007; Wagner, Ehrenstein, & Papathomas, 2009). For instance, researchers suggested a percept-driven versus data-driven eye movement control (Wagner et al., 2009). The data-driven would be an automatic eye movement system for rapid successions of fixations; whereas the percept-driven would be a deliberate schema-driven vergence system that accounts for stable fixations based on the perceptual state of the observer. We could associate the perceptual state to the fourth component of vergence, voluntary vergence, evoked by stimuli that give the impression of being nearer or further than the point of convergence. We speculate that percept-driven vergence could be the interface through which attentional mechanisms select relevant perceptual information from the external world.

1.1.1.3 Neurobiology of the vergence eye movements system
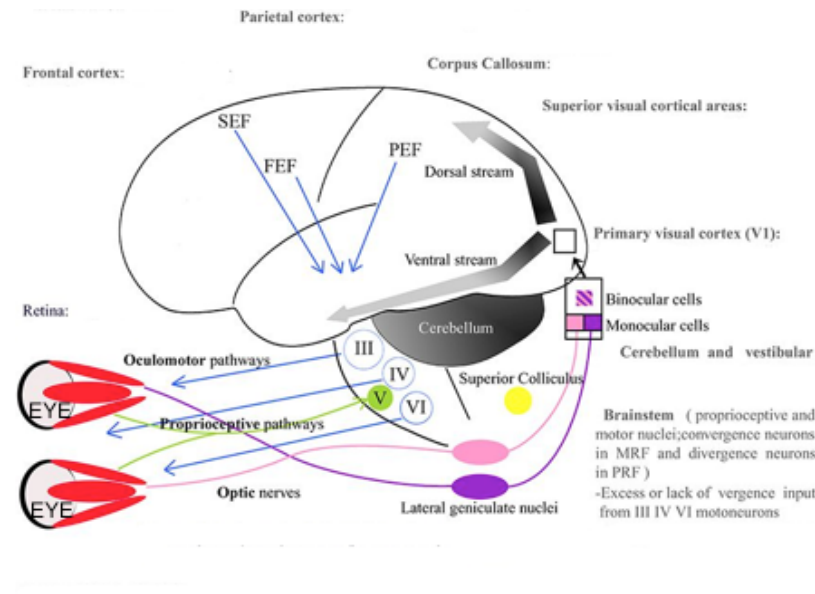
Figure 3. The vergence system. Structures implicated: Supplementary eye fields (SEF). Frontal Eye Fields (FEF). Parietal Eye Fields (PEF). III, IV, V, VI motoneurons. Primary visual cortex (V1). Midbrain Reticular Formation (MRF). Pontine Reticular Formation (PRF). Adapted from Daw (2014).

Neurons in the MRF, part of a broader pathway, which includes the frontal and parietal regions of the cerebral cortex and cerebellum (Gamlin, 2002; Mays, 1984) encode vergence eye movements commands and project to the oculomotor nucleus. The SC, a gaze control centre that integrates visual and motor signals, receives direct anatomical connections from V1. These projections may convey the perceptual information that is required for appropriate gaze shifts (Pérez Zapata, Aznar-Casanova, & Supèr, 2013). In the rostral part of the SC eye fixation is controlled and changes in vergence eye movements angle are encoded (Van Horn, Waitzman, & Cullen, 2013).

1.1.1.4 Neurobiological Commonalities and differences of the vergence and saccadic systems

If we compare vergence eye movements and saccadic system's localization within the brain, differences in vergence eye movements rely within the midbrain and anterior portion of FEF, while saccadic activity lies in the posterior portion of FEF (Alkan, Biswal, & Alvarez, 2011). In terms of commonalities, vergence eye movements and saccade retinal maps are proximal within the FEF (Yang & Kapoula, 2011). Similar functional activation has been found in the SEF, dorsolateral prefrontal cortex (DLPFC), ventral lateral prefrontal cortex (VLPFC), lateral intraparietal area, cuneus, precuneus, anterior and posterior cingulate and cerebellar vermis.
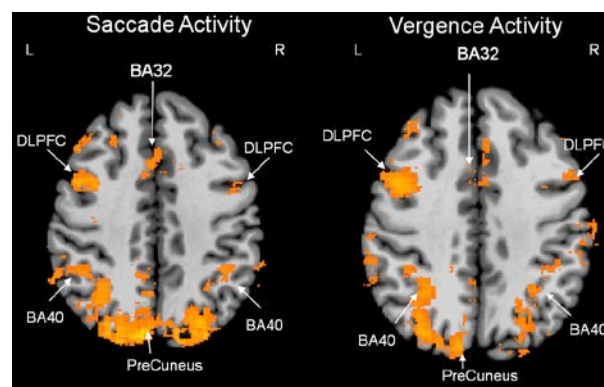
Figure 4a. Functional activation for the saccade (left side) and the vergence eye movements data set (right side) showing typical commonality. DLPFC = dorsolateral prefrontal cortex and BA = Brodmann Area. Adapted from Alkan et al. (2011).
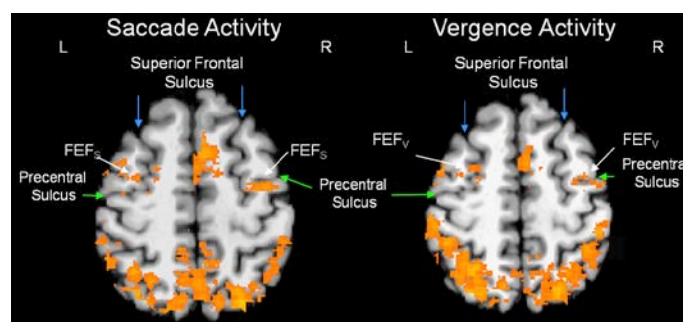
Figure 4b. Functional activation for the saccade (left side) and the vergence eye movements data set (right side) showing typical commonality. FEF= frontal eye fields. Adapted from (Alkan et al., 2011).

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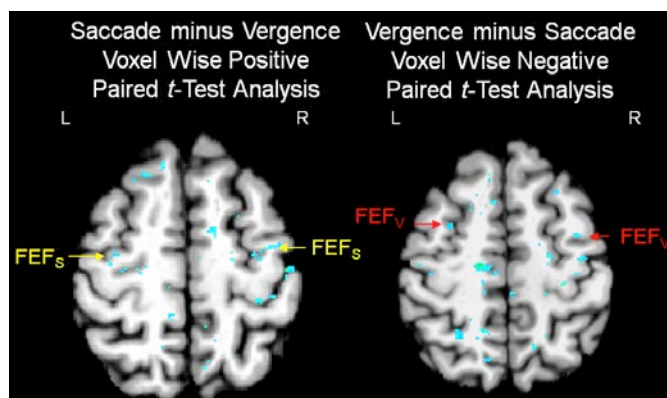
Figure 5. Axial images showing differentiation between the functional activity of the frontal eye fields (FEF) from saccade (left) and vergence eye movements (right) superior to the bicommissural plane for all images. Adapted from Alkan et al. (2011).

1.1.1.5 Interaction between saccadic and vergence eye movements system

There is controversy on whether vergence eye movements starts prior to saccade or not (Kumar, Han, Dell'Osso, Durand, & Leigh, 2005; Mays & Gamlin, 1995) and whether vergence eye movements simply add to the saccade or is a central "facilitation" (Kumar et al., 2005) or peripheral enhancement (Alvarez, Alkan, Gohel, Douglas Ward, & Biswal, 2010). Vergence eye movements, is a much slower movement reaching speeds of 20°/s. When vergence eye movements are accompanied by saccades they are speeded up, whereas the saccadic component is slowed down (Zee, Fitzgibbon, & Optican, 1992). Notwithstanding these claims, in a study by Jainta and colleagues (2011) they found that the contamination of vergence trajectories by saccadic intrusions did not change with repeated exposure to stimuli (Jainta, Bucci, Wiener-Vacher, & Kapoula, 2011). Neither the frequency of saccades nor their amplitude were affected. Somehow, repetition improves vergence movements, which is not simply due to an increase in the number or amplitude of saccade intrusions (Coubard & Kapoula, 2008; Semmlow, Chen, Granger-Donetti, & Alvarez, 2009).

1.1.1.6 Vergence and development

During the first postnatal years, certain anatomical and physiological conditions are required for the normal development of vergence eye movements, such as orientation and direction selectivity. These variables need to be in coordination before stereopsis develops so that the binocular cells will have similar inputs from the two eyes. If the two eyes are not properly aligned, double vision takes place. There is ample evidence, from animal physiology and clinical experience, that the binocular organization of the visual cortex remains highly modifiable for a period after it is initially established (Daw, 1995). The maintenance of binocular functions depends on a critical synergy between mechanisms that detect binocular relationships in the images from the two eyes, and the motor mechanisms that control alignment. The human binocular system, and thus the neural system for vergence eye movements develop during the first few years of life and vary in relation to postnatal experience (Jando et al., 2012). Infants must achieve a balance in their use of the independent and coupled components of accommodation and vergence eye movement responses in a dynamic environment if they are to achieve single and clear vision simultaneously.

Vergence eye movements are seen at 1 month of age. Still, more pronounced movements occur at 2 and 3 months, when a steady improvement takes place (Aslin, 1988; Hainline & Riddell, 1995; McMurray & Aslin, 2004) in response to an object moved slowly toward or away from the infant. There is an increase in the number of adequate vergence eye movements at 4–5 months. It is around this age, when stereopsis is developing (Mitkin & Orestova, 1988). Vergence eye movements may be driven by accommodation and blur, at all ages, and the gain increases with age, but how strong disparity is as a cue before the onset of stereopsis is not completely clear (Bharadwaj & Candy, 2009). A number of studies have suggested that the interdependent coupling of

accommodation and vergence eye movements is present in early infancy, although Frick and colleagues (Frick, Colombo, & Saxon, 1999) found that early on (3-4 months), the latency of shifts of fixation from a central to a peripheral target showed great variability. They suggested from this a link with the development of the neural attention system related to the frontal lobe, which controls the ability to engage or disengage from fixation. Infants between 5 and 10 weeks of age have been shown to generate vergence eye movements responses to accommodative stimuli (Aslin & Jackson, 1979), but it is thought that the blur detection that drives accommodation may have limited sensitivity due to limited spatial vision (Green, Powers, & Banks, 1980). By approximately 3 months of age, infants demonstrate the ability to dynamically change their accommodation and vergence eye movements. With all cues present, typical human accommodative latencies are in the order of 300-400ms, while vergence eye movements latencies are between 100 and 200ms. Like adults, the developing visual system could also use combinations of retinal blur (primary cue for accommodation) and disparity (primary cue for vergence eye movements) to drive these near-motor responses (Aslin & Jackson, 1979b; Bharadwaj & Candy, 2008; Bobier, Guinta, Kurtz, & Howland, 2000; Currie & Manny, 1997).

The accuracy and peak velocity of vergence eye movements is that of an adult by approximately 4.5 years of age, only the duration remains to be improved which happens at around 8 years old (Yang & Kapoula, 2004). While the critical period for acuity in humans lasts from a few months of age to 6–8 years, the critical period for binocular vision and stereopsis peaks at a few months of age. This explains why binocular function should be studied as early as possible.

Throughout infancy and toddlerhood there is a dramatic unfolding of cognitive abilities characterized by the progressive development and emergence of gaze control, which relies on the flexibility to shift response set or focus of attention.

1.2 Visual attention

Attention is the process that selects particular stimuli for further evaluation. It is currently conceived as a network of interrelated systems that are organized into distinct levels and instantiated in different neural areas (Atkinson & Braddick, 2012). For instance, the subcortical or vigilance system, engaged in alertness and sustained attention. The posterior or basic attention system, on visual spatial orienting, responds automatically to modality-specific stimuli and moves attention to selected locations for further processing, subserved by the PPC, the pulvinar region of the thalamus, and the SC in the midbrain. These brain structures work as a network to mediate attention shifts, responsible for automatic orientation (disengaging, moving, engaging) of visual attention in response to motion, change or other visual cues. Finally, the anterior or executive system regarding volitional control and conflict resolution, recruits resources for goal-directed behaviour. It has been argued that at least three critical postnatal periods of attentional development in infancy: the first involves the period from birth to 2-3 months of age, when the development of alertness takes place; the second involves the period from 3 to about 6 months, when the orienting system emerges; the third refers to the period from 6 months to 12 months when executive attention is starting to gain control (Colombo, 2001)

1.2.1 How does visual attention affect visual perception?

Visual attention exerts a wide variety of effects on neuronal responses in the visual cortex (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000; Reynolds & Chelazzi, 2004). Neuronal responses adapt according to attention processing (Khayat, Niebergall, & Martinez-Trujillo, 2010; Martínez-Trujillo & Treue, 2002; Reynolds & Chelazzi, 2004; Reynolds, Pasternak, & Desimone, 2000).

The receptive field (RF) of an individual sensory neuron is located in the particular region of the sensory space in which a stimulus will modify the firing of that

neuron. In other words, increases in visual sensitivity and acuity alter the neurons' receptive fields' structure in early visual cortex development (Carrasco, 2011; Reynolds & Chelazzi, 2004; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). It has been suggested that this acts through multiple mechanisms, such as (i) enhancement of sensory signal-to-noise ratios by increasing gain and response reliability (Reynolds et al., 2000) and (ii) by dynamically adjusting certain properties of the receptive field, for example, their size (Desimone & Duncan, 1995) and position (Womelsdorf et al., 2006) in order to meet the specific behavioural demands of the observer (Carrasco, 2011). These mechanisms appear to be implemented at early stages of visual processing—for instance, by selectively increasing spike rate early on during development in the thalamus (McAlonan, Cavanaugh, & Wurtz, 2008) and by narrowing the tuning for spatial position in V1 neural populations (Fischer & Whitney, 2009). The neurons' response is biased towards the attended stimulus and attenuated for the unattended, as if the neuron's RF contracted around the attended stimulus (Ghose & Maunsell, 2008; Lee & Maunsell, 2010).
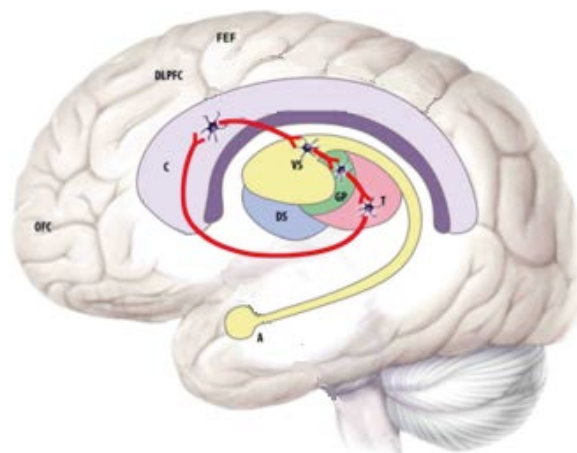
Figure 6. Attentional circuits: FEF frontal eye fields, *A* amygdala, *C* cingulate, *OFC* orbitofrontal cortex, *DLPFC* dorsolateral prefrontal cortex, *DS* dorsal striatum, *VS* ventral striatum, *GP* globus pallidus, *T* thalamus. Adapted from Tamietto & de Gelder (2010).

1.2.2 Attention and oculomotor processes

Visual attention may produce a bias in the inherent stochastic displacements of retinal images by inducing correlations of successive displacements. Eye movements would facilitate these shifts in visual attention and constrain the set of all possible eye movements to only the most immediately relevant potential targets (Awh & Jonides, 2001).

Usually, we move our eyes so that the fovea coincides with the attended location, for attention and fixation to match. It is well documented that eye movements and spatial attention are closely linked, with a shift of attention preceding each shift of gaze (Deubel & Schneider, 1996; Irwin & Andrews, 1996; Kowler, Anderson, Dosher, & Blaser, 1995). In this regard, research has supported a relationship between orienting visual spatial attention and programming of saccades (Doré-Mazars, Pouget, & Beauvillain, 2004; Juan, Shorter-Jacobi, & Schall, 2004). Yet, a key finding in research about visual attention is that the orientation of attention can differ from the orientation of gaze position, as where someone fixates does not tell us whether they are attending or not. This is so because we are able to shift attention covertly to the periphery of our visual field without making an eye movement. Attention can in this way reduce the performance difference between the fovea and the periphery by enhancing spatial resolution (Treisman & Gelade, 1980). Recently, vergence eye movements have been associated to covert orienting attention in children and adults (Solé Puig, et al., 2013; Solé Puig et al., 2015) and its modulation in time correlated with brain activity (Puig et al., 2016). Due to our limited perceptual processing capacity, covert attention would serve the role of accelerating the rate of visual attention processing. This could be achieved by enhancing the representation of the relevant percepts while diminishing the lesser ones in the visual environment (Hawkins et al., 1990; Liu, Stevens, & Carrasco, 2007; Lu & Dosher, 1998; Posner, 1980), including

enhanced spatial resolution at the attended location (Anton-Erxleben & Carrasco, 2013), as well as increased contrast sensitivity (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Ling & Carrasco, 2006), speed of information accrual (Carrasco, Giordano, & McElree, 2004; Carrasco & McElree, 2001) and grouping (Scholte, Spekreijse, & Roelfsema, 2001).

In relation to the neural structures, part of the visual orienting attention system overlap**s** with vergence eye movements. For instance, the rostral SC encodes changes in vergence eye movements angle (Van Horn et al., 2013) and also has projections to the amygdala via the pulvinar (Tamietto & de Gelder, 2010) mediating orienting responses (Carlson, Reinke, & Habib, 2009). The PPC is involved in visually guided movements and attention control (Mishkin & Ungerleider, 1982). On the other hand, the planification and control of eye movements takes place through the cerebellum-cerebral loop. The cerebellum being implicated in the maintenance of predictive activity (Ghajar & Ivry, 2009) and cerebellar vermis structures such as the pyramid indirectly involved in covert visual attention via oculomotor control mechanisms (Yarbus, 1967). In addition, as evidenced in previous research (see figures 4a,b;5&6), neurobiological structures common to the saccadic and vergence system, such as the DLPFC support attention, planning, spatial orientation and behavioural restraints (Badre & Wagner, 2005; McDowell, Dyckman, Austin, & Clementz, 2008). Also, the VLPFC is implicated in working memory and task switching (Schendan & Stern, 2008). In turn, the posterior cingulate cortex is involved in visuospatial encoding and attention (Dean, 2004), as well as the parietal lobe (Bisley & Goldberg, 2010; Herrington & Assad, 2010).

1.2.2.1 Developmental aspects of attention and oculomotor processes

How do infants extract just the information from the vast array of potential objects accessible during a single fixation? (Aslin, 2013).

The development of visual attention in infancy and toddlerhood is concurrent with neurological maturation and developmental changes in behaviour (Johnson, 2001). As from birth and for a while infants are restricted by their inability to move around on their own, therefore visual attention is important for their exploration of the environment and for gaining knowledge about the world. In fact, one of the earliest appearing skills in infancy is the development of oculomotor control (Hofsten & Rosander, 1997; Rosander & Von Hofsten, 2002). Oculomotor control enables infants to direct their attention to extract visual information in the environment (Rosander & Von Hofsten, 2004) and is also crucial for social communication (Guastella, Mitchell, & Dadds, 2008).

The ability to selectively attend has been related to the orienting system. Orienting attention through overt or covert eye movements would allow an infant to learn to cope with and organize the enormous amount of surrounding information. At 3-4 months, infants show evidence of selective attention, as they use the identity of a central cue to preferentially orient to targets on the left or right side (Johnson, Posner, & Rothbart, 1991). Selective attention is one of the primary means to optimize attention processing. It is important for any task that requires cognitive control, which involves selecting and restricting the amount of sensory information that should be attended to for further processing (Posner & Boies, 1971). Gaze shifting during the first 6 months of life is primarily reactive and strongly governed by novelty (Blaga & Colombo, 2006; Dannemiller, 2005). But children increasingly gain more gaze control and are able to disengage their gaze from one stimulus and direct it to another (Hood & Atkinson, 1993). For example, 1- to 2-month-old infants exhibit a series of very long look durations, when viewing static stimuli and they have limited capacity to orient to single targets. By the age of 3 months, there appears to be a greater proportion of shorter look durations, thought to reflect a reduction in the early difficulties that they encounter with disengaging their

attention – known as "sticky fixation" or "obligatory attention" (Johnson, et al., 1991).
By 4 months, problems with disengaging from static stimuli have largely disappeared
(Johnson, et al., 1991).

1.2.2.2 Orienting attention

In order to increasingly develop the control that they exert on their environment,
infants progressively learn on orienting attention through eye movements, both overtly
and covertly. This ability is significantly improved when they can form representations
of temporarily occluded objects and use their experience to make predictive eye
movements (Johnson & Shuwairi, 2009; Kochukhova & Gredebäck, 2007).

Orienting attention to selectively process certain stimuli on a neural level,
involves two networks: the temporal parietal junction and the frontal eye fields (Posner
& Huang, 2011). Interestingly, the temporo-parietal junction integrates tactile, visual and
proprioceptive sensory input with interoceptive information that allows an appreciation
of spatial orientation in 3-D and balance.

Infants younger than 6 months orient predominantly to salient stimuli
characterized by features such as motion, contrast, patterning and visual complexity
capturing attention (Dannemiller, 2000). With the infant's increasing ability to shift
attention between stimuli, by 6 months of age, the orienting system becomes fully
functional (Hood & Atkinson, 1993; Johnson et al., 1991; Rothbart, 1996; van de Weijer-
Bergsma, Wijnroks, & Jongmans, 2008). Components of visual orienting in early infancy
involve contingency learning, anticipatory looking and disengaging (Johnson et al., 1991).
Overall, facilitatory and inhibitory components are required in the process of attention
orienting. This development allows the child to make future-oriented predictions and to
increasingly act in a goal-directed manner (Diamond, 2002; Jurado & Rosselli, 2007;
Zelazo, Carlson, & Kesek, 2008). The early development of cognitive control is

presumably closely tied to the maturation of the attention systems (Clohessy, Posner, & Rothbart, 2001; Garon, Bryson, & Smith, 2008; Rueda et al., 2004). Hence, the maturation of the attention system and thus the increasing gain control in orienting responses shall impact on age-related changes in encoding and retention of relevant contextual information. During the latter half of the first year, infants begin to develop more volitional control over their attention, and this development continues well into childhood (Colombo, 2001; Courage et al., 2006; Posner, Rothbart, & Thomas-Thrapp, 1997; Ruff & Capozzoli, 2003). Furthermore, attention control processes have been suggested to be the unifying construct underlying cognitive control not only in children (Garon et al., 2008; Lehto, Juujärvi, Kooistra, & Pulkkinen, 2003) but also in adults (McCabe, Roediger, McDaniel, Balota, & Hambrick, 2010; Miyake et al., 2000). Attention processes are of importance for cognitive control, as these processes appear to be involved in performance on a variety of tasks (Baddeley, 1986, 2002; Eigsti et al., 2006; Kane & Engle, 2002).

Related to the changes in children's attention and control of eye movement, the bias for faces becomes robust and resistant to distraction during the second half of the first year. This development is thought to take place because of the child's increasing experience and the neural maturation of the attention system (Posner et al., 1997; Ruff, Capozzoli, & Saltarelli, 1996). Development of visual attention in early development involves continued enhancement of the executive attention system and integration with the orienting system (Ruff et al., 1996), as the direction of gaze often guides actions (Land, Mennie, & Rusted, 1999). It has been shown that from early infancy to early childhood the orienting system serves as the cognitive and emotional control system. Tummeltshammer and Kirkham (2013) found that by 8 months old, infants may be able to separate learnable visual targets from distractors, and guide attention to support their

learning so that they start exercising cognitive and emotional control (Tummeltshammer & Kirkham, 2013). In 6-7 months old children, self-regulation depends upon orienting attention (Sheese, Voelker, Posner, & Rothbart, 2009). The orienting system thus constitutes the basis of and is therefore a prerequisite for executive attention to develop.

1.3 The development of Visual Short-Term Memory (VSTM)

Before infants can deploy attention effectively, they must determine which events are advantageous to attend to and which provide no meaningful or reliable information. VSTM emerges by 4 months old. It allows infants to form stable representations despite the relatively fragmented visual input (blinks, saccades and occlusions). Infant memory development is characterized by age-related changes in a number of basic memory processes including encoding, retention, and retrieval (Morgan & Hayne, 2006). The infants' ability to detect changes in location is dependent on their developing sensitivity to spatial reference frames to have salient landmarks. Between 4 and 6 months old infants can use location memory to plan eye movements to a sequence of targets or to learn predictable sequences of events presented at 2 different locations (Gilmore & Johnson, 1997; Gilmore, Johnson, Simion, & Butterworth, 1998; Haith, Wentworth, & Canfield, 1993). By 6 months old, infants can remember location in a variety of contexts that likely engage different memory systems. Infants are sensitive to statistical regularities, such as cross-situational co-occurrences and inter-event contingencies, and use these relations to form associations, program saccades and detect reliable cues (Kirkham, Slemmer, Richardson, & Johnson, 2007; Wu & Kirkham, 2010). Human learners make inductive inferences based on small amounts of data (Xu & Garcia, 2008), following this claim, the role of visual experiences throughout development is to serve as datasets for infant learners (Bertenthal & Campos, 1990).

1.3.1 VSTM, attention and eye movements

VSTM plays a central role in ensuring that the eyes are directed efficiently to goal-relevant objects in the world (Finger & Daffner, 2012). For attending to prioritary stimuli, Baddeley argued that spatial working memory might rely on implicit eye movement programs (Baddeley & Hitch, 1974). Moreover, Smyth and Scholey suggested that short-term maintenance of spatial information involves covert shifts of attention, i.e. focal shifts of spatial attention to memorized locations (Smyth, 1996; Smyth & Scholey, 1996).

The input for vision is divided into a series of discrete spatio-temporal episodes because there are perceptual gaps between individual fixations, and therefore a memory for the visual properties of the scene must be maintained across each eye movement (Treisman & Gelade, 1980). A role of attention would be constructing bound object representations at the level of perception (Kahneman, Treisman, & Gibbs, 1992). This would make essential information explicit, bringing it to the foreground and allowing it to be smaller and manipulated more quickly. Because more processing resources are devoted to behaviourally important objects than to less important ones, the relevant objects are more likely to become encoded into VSTM (Bundesen, Habekost, & Kyllingsbaek, 2005). VSTM system is considered to be a feedback mechanism. Thus, the oculomotor system, attention-guided behaviour and visual short-term memory (VSTM) representations are interconnected (Hollingworth, Richard, & Luck, 2008).

1.4 Rationale for the studies on Face perception and VSTM

Most of our viewing is conducted while we fixate our gaze. Eye movements drive the fovea to fixate each part of a scene for processing sensory information with high resolution. However, during gaze fixation, the eyes are never completely still and different fixation eye movements are described. Yet, little is known about the role of these fixation eye movements in visual information processing (Martinez-Conde, Macknik, &

Hubel, 2004). The main role of vergence eye movement is to obtain and maintain single binocular vision using sensory information (Howard & Rogers, 1995). The human binocular system, and thus the neural system for vergence eye movements, develop during early childhood (Jando et al., 2012). A variety of behavioral and electrophysiological studies agree that the onset of functional binocular interaction in human visual cortex normally occurs between 10 and 16 weeks of age in infants (Braddick, 1996) and that visual sensitivity increases with cortical and foveal maturation in the first 6 months of life (Braddick & Atkinson, 2011).

Oculomotor structures form part of the attention circuits. The maturation of the attention system and oculomotor control form the basis of cognitive development. Eye vergence can be considered as a modulatory oculomotor process (Aslin, 1993), which can be observed at early developmental stages (Jandó et al., 2012). At around 4 months old stereopsis emerges, i.e. the perception of depth based on the small horizontal differences between the images projected onto each eye, which is governed by vergence. At these developmental stages, infants also show good ocular alignment (Braddick, 1996) and an increase in vestibular and proprioceptive information. These developmental milestones contribute to framing their visual perception and action in the world (Hainline & Riddell, 1995). Visual maturation continues throughout early childhood, as binocular control may have a more extended developmental period (Jandó et al., 2012).

If binocular control does not adequately develop, it may lead to a deficit in visual attention (Fawcett, Wang, & Birch, 2005). For example, children suffering from attention problems, like ADHD (Granet, Gomi, Ventura, & Miller-Scholte, 2005; Solé Puig et al., 2015; Varela Casal et al., 2018); and ASD (Milne, Scope, Pascalis, Buckley, & Makeig, 2009) have atypical or poor binocular control. Children with attentional problems have shown poor vergence responses when orienting attention (Solé Puig et al., 2015). From

these findings, it was suggested that eye vergence responses during gaze fixation may as well have a role in attentional processing of visual information (Super et al., 2014). Solé Puig et al. (2013) reported that vergence is not only guided by the physical attributes of visual stimuli but also strategies of information processing. Vergence responses were observed during top-down and bottom-up generated shifts of visual attention, where attentional load positively correlated with the strength of the vergence response (Solé Puig et al., 2013). Solé Puig and colleagues observed that during central fixation the eyes briefly converged after orienting visual attention to a peripheral stimulus. This was not the case when attention was not directed to the target (Solé Puig, et al., 2013). Furthermore, stimulus saliency positively correlated with the strength of vergence responses (Solé Puig, et al., 2013) where highly salient stimuli elicited stronger vergence responses. Moreover, a role of vergence in attention is supported by the observation of a correlation of eye vergence responses with the neural activity encoding shifts of visual attention (Puig et al., 2016). The attention related vergence responses showed a positive correlation with the strength of ERPs at parietal locations (Puig et al., 2016).

Given the limited amount of processing resources and the overwhelming amount of incoming information, infants learn to prioritize those stimuli that are most informative among the ones they are frequently exposed to (Leppänen & Nelson, 2009). Human faces are one of the most significant visual stimuli to mankind, in the context of interactions, as human beings are social (Taylor, Batty, & Itier, 2004). The relevance of perceiving faces lies in that they provide information, particularly on danger and reward (Peltola, Leppänen, Palokangas, & Hietanen, 2008). Attention bias for faces can be used to examine the neural correlates of attention and may be a way to monitor early neurodevelopment in infants (Leppänen, 2016).

Vergence responses were also observed when correctly perceiving and memorizing visual stimuli, especially when the repeated stimulus was correctly identified, but not when stimuli went unseen or were forgotten (Solé Puig, et al., 2013; Solé Puig, Romeo, Cañete Crespillo, & Supèr, 2017). The VSTM system can create memory representations rapidly, based on object perception and mediated by visual attention (Hollingworth & Henderson, 2002; Matsukura & Vecera, 2009). VSTM is needed to store perceptual information for long enough so that it can be integrated with new perceptual information (Hollingworth et al., 2008). This information is then used every time we blink, make a saccadic eye movement, compare objects, or when occlusion occurs (Hyun, Woodman, Vogel, Hollingworth, & Luck, 2009). Visual attention, which has a pivotal role in cognitive processing of sensory information, is a driver of VSTM (Astle & Scerif, 2011). It also strongly relates to recognition memory (Reynolds, 2015) where it can assist in encoding visual information into memory and influence already stored information (Griffin & Nobre, 2003). Visual attention and VSTM are already present right after birth and continue to develop during the early years of childhood (Courage & Howe, 2004; Rose, Feldman, Futterweit, & Jankowski, 1997; Rose et al., 2004). By 6.5 months, young children can form object representations, and use the features of those representations to individuate objects—likely components of VSTM representations. Up to until 8 months, young children become able to store multiple items (Morgan & Hayne, 2006). Ross-Sheehy found preferences for changing displays at set sizes 2 and 3 in 10 and 13-month-old young children, indicating that they have a VSTM capacity that is sufficient to distinguish between changing and unchanging displays of arrays with up to 3 items (Ross-Sheehy, Oakes, & Luck, 2003).

As eye vergence relates to and possibly has a role in attentional selection, we speculated that attention related eye vergence responses shall be present at the early stages of childhood and it was proposed that eye vergence could have a role in attention orienting responses in face perception and memory recognition in early childhood. To test this, we applied a face perception task by introducing static human faces together with their scrambled version. Based on the previously mentioned research on visual attention and VSTM, we have also applied a paired comparison memory recognition task that allowed discrimination between a familiar/repeated object and a novel object.

2. Objectives and hypotheses

This PhD study evaluated face processing and the overlap between attention and memory, using an eye-tracking methodology to study young children's ability to orient preferentially to prioritized stimuli. To address the research questions, the participants' eye tracking recordings and the dynamic of their visual responses were analysed.

The overall aim of this PhD study was an investigation into the early development of attention orienting and incipient cognitive control in early childhood, through vergence eye movements modulation in time. The primary objective was to find out whether vergence eye movements' responses provide further insights into the understanding of attention processing. The general hypothesis was that attention and oculomotor processes are greatly intertwined in the brain from early on. For this reason, the modulation of vergence eye movements could be the by-product of attentional modulation driven by visual inputs.

The specific objectives were:

In the study of face processing, the main aim was to assess visual orienting responses through vergence eye movements modulation in time, by comparing eye vergence responses for static human face images and their scrambled version.

The following specific hypothesis were formulated for the benefit of the study:

1.   Vergence eye movements' signal would correlate with different attention orienting responses across the two conditions: face and scrambled face images.

2.   Building on previous research, it was predicted that there would be a significant correlation between the attentional response to faces and vergence signal changes in time in young children aged 6-36 months old.

3.   The attentional modulation would correlate with covert orienting to the visual input and translated into an attention-induced enhancement of vergence signal; an increase in the attention-induced vergence signal would correlate with the processing of prioritized information, for instance, in this task, face images.

The study on Visual Short-Term Memory outlined the study of orienting attention and its overlap with encoding, maintenance and retrieval of information by analysing vergence eye movements' responses for repeated and novel objects' images.

1.   Vergence eye movements signal would correlate with different attentional responses, in repeated stimuli vs. novel stimuli.

2.   Building on previous research, it was predicted that there would be a significant correlation between the attentional response to memorized objects and vergence eye movements' signal changes in time in young children aged 12-36 months old.

3.   The attentional modulation would correlate with covert orienting to the visual input and translated into an attention-induced enhancement of the vergence eye movements' signal; an increase in the attention-induced vergence eye movements' signal would correlate with further processing for familiar objects.

3. Materials and Methods

These are the principles that guided the decision-making process in relation to the definition, delimitation, data collection and analysis of this PhD study.

3.1 Ethics

Research was conducted in young children, as only in this way could we fully exploit the large plasticity of the developing brain to study visual perception and attention mechanisms.

Informed consent and assent

For the process of obtaining the permission by proxies, parents/guardians or appointed guardian, written informed consent was an exclusion criterion throughout all studies. Participants' parents/caregivers were informed in written and oral form on the key objectives of the study, the procedures that had to be followed, and the foreseeable discomforts, as well as the potential benefits clearly indicated in the information sheet and the consent form. They were informed on their rights regarding voluntary participation, to ask questions on the nature, risks and impact of their participation, the protection of confidential data and the possibility to withdraw at any time.

When applying for ethical approval from the competent University of Barcelona Ethics Committee, detailed information was provided on the procedures that were used for the recruitment of participants (e.g. number of participants, inclusion/exclusion criteria, indirect incentives for participation, the risks and benefits for the participants, etc.) and the nature of the material collected (e.g. personal data).

Care and protection of research participants

All study procedures were designed to minimise any potential discomfort. No examination was conducted against the will of the participant or the caregiver. The researcher secured to foster a continuous dialogue with participants and informed them of anything new related to the studies.

Privacy issues

Protection of research participants' confidentiality. The European Guidance for Healthcare Professionals on Confidentiality and Privacy in Healthcare and the Directive 95/46/EC (and its revision) on the protection of individuals with regard to the processing of personal data and on the free movement of such data was applied and respected. All study procedures followed this guideline.

All documents and data were handled with strict confidentiality. Names and person-related data were subject to the conditions of the national Protection Acts and European Directives and rules. All personal data (e.g. name) was kept strictly separated from completed data collected through the experimental set up. Each individual was assigned a unique code number (UCN), and this UCN was devoid of any identifying data. The UCNs served as the primary identifiers and thus were used throughout.

The following are the studies that have been contextualized in their theoretical background for the purpose of this PhD study. Later on, the procedures for data collection are exposed and, later, the analysis procedures used. This section presents the context that defines the two cases of study and continues to expose the set of criteria and procedures.

3.2 Participants

We recruited typically developing boys and girls, from a public kindergarten in Barcelona, aged 6 to 36 months. In the paired comparison recognition memory procedure, forty-three young children, 12 to 36-month-old (26.75±7.33); 14 girls (26.57±6.56) and 29 boys (26.93±8.11) composed the final sample. We grouped participants in 4 age groups (12-18 months-old: 9 children; 19-24 months-old: 9 children; 25-30 months-old: 10 children; 31-37 months-old:15 children) to study possible developmental effects. The grouping criteria is based on previous research that indicates that the control of attention is not fully developed until 18 months of age (Rueda et al., 2004). In addition, the ability to overcome distracting information develops between 18 and 24 months (Clohessy et al., 2001). Furthermore, visual attention and VSTM become more flexible and more stable around 18-24 months old (Robinson & Pascalis, 2004).

In the case of the face perception procedure, the final sample consisted of 39 young children, 22 boys and 17 girls. (mean ± SD: 27.6 ± 8.1 months).

The peculiarity of working with a sample of young children relies in that there are added constraints and considerations to take into account. In the sample studied, we could not count on the possibility of exposing young children to controlled stimulus contingencies over an extended period of time, as they usually get bored and opt out of the testing situation. In general, the easier the task and more varied the stimuli the longer an infant or young child will cooperate. We shall also mention the limitations on the instructions given, if any; the risks on them not understanding the indications provided

by the experimenter, whenever possible, as well as the developmental stages that they are going through, which influence both their visual and attentional response.

Selection criterion:

All infants were born full-term, were in good health, and had no visual nor neurological disorders, as informed by the parents and the kindergartens' director. Parents signed a written informed consent for their child's participation, in accordance with the Helsinki Declaration. The Ethics Committee of the University of Barcelona approved of the study.

Inclusion criteria

Signed informed consent,

Born full-term,

Good health, with no visual nor neurological disorders.

Exclusion criteria

Any accommodative problems, such as strabismus or nystagmus.

3.3 Apparatus

The methodology we used was based on remote eye-tracking technology, a binocular remote eye-tracking system to monitor gaze position at a sample rate of 30 Hz (X2-30 Tobii Technology AB, Sweden). This technology has enabled assessing the attentional measure of gaze behavior early on (Wass, Smith & Johnson, 2013). It is a non-invasive technique to measure visual processing and visual behavior in infancy, that offers much higher spatial (~1° of visual angle) and temporal resolution (typically between 30-500 Hz) in comparison to video coding. When it comes to remote, non-intrusive eye tracking, the most commonly used technique is pupil centre corneal reflection (PCCR). The basic concept is to use a light source to illuminate the eye causing highly visible reflections, and a camera to capture an image of the eye showing these

reflections. The image captured by the camera is then used to identify the reflection of the light source on the cornea and in the pupil. We can then calculate a vector formed by the angle between the cornea and pupil reflections—the direction of this vector, combined with other geometrical features of the reflections, is then used to calculate the gaze direction. There is evidence where changes in pupil size have been associated with attentive processing (Porter et al., 2007).

Stimuli were presented on a 41 x 23 cm flat PC monitor with a display resolution of 1024 x 768 pixels, synced with the X2-30 Tobii eye-tracker. Gaze behaviour was monitored throughout the trials on a separate laptop screen to ensure continuous data recording and to monitor the quality of the ongoing task.

3.4 Procedure

The experiments were performed within a quiet room and under dimmed lighting conditions to avoid external noise. Children sat comfortably at 60 cm of the PC monitor on which the stimuli were presented and the eye-tracking camera was mounted below the monitor (see Fig. 7,8). The seat was raised and lowered to standardize the position of each child's eyes, parallel relative to the screen. During testing, unless required for reassurance, experimenter and parent /teacher were out of view from the child. The adult did not interact with the child unless necessary. Side panels were placed around the equipment to reduce visual distraction away from the monitor.

The equipment was calibrated at the beginning of each experiment per participant. For calibration, a large moving coloured rattle image (9.5° x 7.2°) with musical soundtrack (rattle) played through stereo external speakers placed on both sides behind the screen. Calibration was performed at 5 corner points and was considered accurate with at least 1000 ms of gaze fixation to collect 30 gaze points at each calibration location within a radius of 50 pixels from the centre of the image. Fixation generally refers to the

time between saccadic eye movements when the eyes are relatively stable (as they can also be bracketed by blinks, smooth pursuit and other eye movements). During a fixation, several cognitive processes may occur: foveal visual information is processed and encoded in working memory, the next saccade target is selected from peripheral visual stimuli and the oculomotor program required to bring the target into foveal vision is prepared (Rayner, 1998). Fixation is made up of the conflict between demands for keeping the eyes stationary (in order to encode foveal visual information) and disengaging attention to shift to peripheral targets (Findlay & Walker, 1999).

After calibration was successfully completed, the presentation of visual stimuli began.

3.4.1 Face processing

From the FACES database (Ebner, Riediger, & Lindenberger, 2010) we chose 12 adult male and 12 adult female images with neutral facial expression. Each face image was pixeled by dividing the face image into sub-images (20 x 20 pixel blocks) and generating a random matrix of these sub-images. Overall, 24 face and 24 scrambled face images were used. From these 48 images in total, each of them was presented one time, in random order, during the visual presentation to prevent from habituation.

Each trial consisted in the presentation of a face or scrambled face image (size 19.68° x 20.71°) for 1000ms at the centre of the screen on a grey background (Fig.7). After an additional 1000ms of inter-trial interval (mask), a new sequence started automatically. Every 6 trials an attention grabber appeared centrally to reengage the infant in the visual presentation, which consisted on a dynamic cartoon (size 19.68° x 20.71°), centrally presented for 1000ms along with musical soundtrack. The entire visual presentation lasted for 48 trials. Infants freely looked at the images and most of them completed the session in less than 3 minutes.
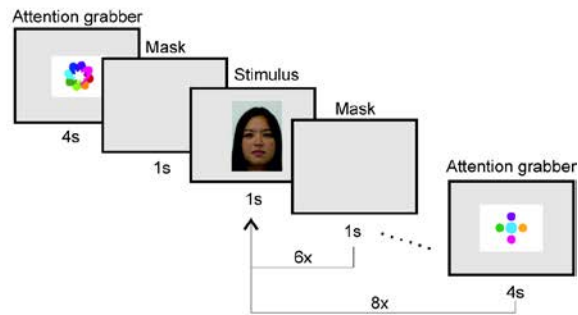
Figure 7. Experimental procedures and explanation of the angle of eye vergence. A) Image of the experimental set-up. B) Task design scheme. C) Example of face and scrambled face image. D) The angle of eye vergence relates to the distance of the focus point to the eyes.

3.4.2 Visual-Short-Term Memory

After calibration was successfully completed, the task started. Each trial started with the presentation of a sample array containing two-coloured cartoon images (approx. size 12°x12°) of daily objects (see Figure 8) presented for 2.5 seconds followed by a retention interval consisting of a grey mask for 1 second. After the mask ended, a sequence of two consecutives images (single-item) was presented. One of the objects belonged to the previous sample array and the other one was a completely novel object. Each object was presented for 1 second, followed by a grey mask of the same duration. The sequence of the single-item (for repeated and novel images) was random. After every 6 trials the attention grabber, a looming cartoon with an accompanying sound to engage the participants' interest, was presented for 4 seconds. Each trial consisted of a new set of images. Therefore, none of the images were repeated across trials in order to target more specifically VSTM (Oakes, Baumgartner, Barrett, Messenger, & Luck, 2013; Ross-Sheehy et al., 2003). Each participant completed an average of 30 trials within approximately 3 minutes.
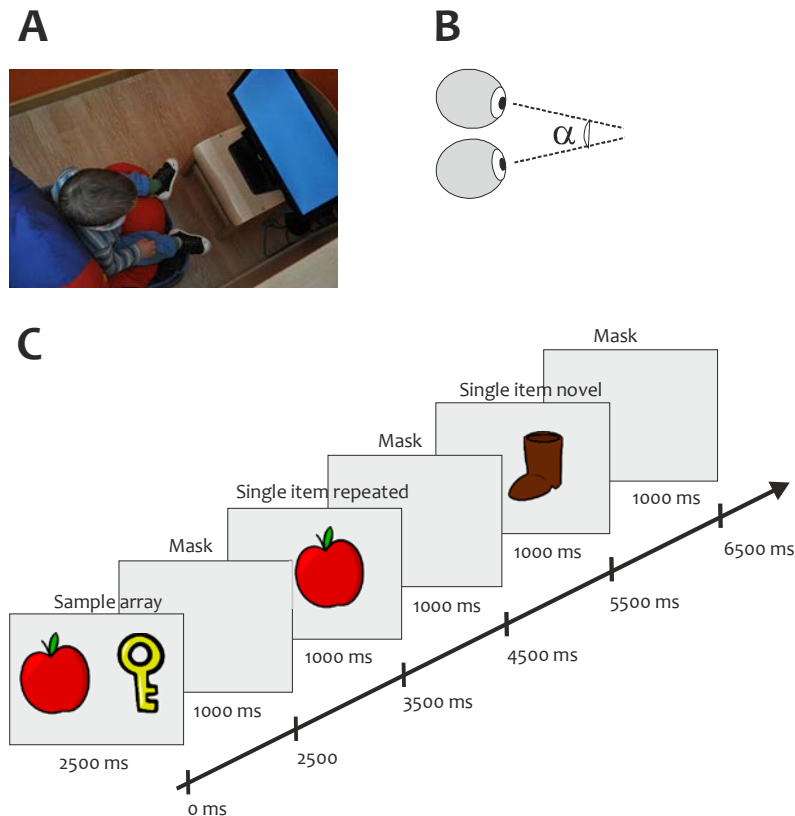
Figure 8. Experimental design **A**: Example of setup. **B**: Schematic explanation of the angle of eye vergence spanned by the visual angle formed by the right and left eye vectors. **C**: Task design scheme, adapted from a visual recognition memory paradigm.

3.5 Data preparation and statistical analysis

The study of eye movements and coding of fixation data were performed with software written in Python. Each raw signal was cleaned using the eye tracker's validity score feature, which assigns a score to every sample estimating the accuracy and the quality of the eye position. The validity codes are provided by the Tobii eye-tracker and are based on how certain the image/position of an eye is captured. This is related to the Purkinje images the tracker uses to estimate the position of an eye. Thus, an instance in which the tracker detects all Purkinje images and produces a position, is assigned a score of 0. Scores of 1, 2 and 3 are uncommon, but correspond to the detection of fewer Purkinje images and thus, the production of worse approximations for distance/position/pupil size. A score of 4 is produced when the tracker is completely unable to detect the eye (for

instance, a closed eye). There is a score for both eyes, hence left and right validity scores. Low validity scores usually happen during saccades and blinks. Only 0 score lectures were left (approx. 80% of total per signal). The first phase of analysis was an automated identification of non-fixation data, comprising blinks, saccades, fixations shorter than 100ms, and fixations away from the target image which were filtered out in the relevant data segment. A fixation is considered when the change in eye position is less than 7 mm, lasting for at least 100 ms. We calculated the vergence responses by measuring the angle between the gaze vectors of both eyes. To calculate the vectors, we used the 3-D eye coordinates and 2-D gaze coordinates in the same reference frame provided by the Tobii X2-30 software. The vergence point is defined as the 'near-intersection' point of the two gaze lines. The calculation of the vergence angle is done by the following cross-product formula:

Where E refers to the eye coordinates and S the gaze coordinates, *L/R* denote left/right.

$$\cos \theta = \frac{|\overline{E_L S_L} \cdot \overline{E_R S_R}|}{\|\overline{E_R S_R}\|\|\overline{E_L S_L}\|}$$

On the other hand, we are aware that pupil size is quite sensitive to stimulus low-level features such as contrast, luminance or complexity, as well as cognitive processing. For this reason, when we designed the task procedure, we tried to keep these features similar across stimuli. However, during the actual experiment we did not check whether luminance was uniform. During data analysis, the pupil signals were normalized by subtracting the mean of the first 200 ms in each trial (same procedure as with vergence).

3.5.1 Face processing

After computing the vergence responses, we split the data into 2 conditions (*face* and *scrambled face*) and averaged the data across trials. Before averaging, the offset was removed, i.e. for each trial the initial vergence value was extracted from the time series to detect attentional related vergence modulation in time.

Statistical analysis. Vergence responses of all trials were also analysed per time sample therefore conditions were compared at each time interval, using a t-test with a significance level of p=0.05 (Solé Puig, et al., 2013). As in our previous studies (Sole Puig et al. 2013a, b, 2015, 2016) eye fixation behaviour and behavioural responses per time sample were analysed using a t-test. The vergence distribution per time sample is represented in the figures to visualize the differences in vergence modulation. We applied a t-test to compare image type (face or scrambled face) and assess whether or not there were significant differences between the conditions.

3.5.2 Visual-Short-Term Memory

Due to poor quality, vergence data from two participants was excluded from the analysis. After computing the vergence responses, we took for each subject all vergence values of all trials per condition (repeated/novel), considering order of image presentation, within a time window of two seconds, from the onset of the mask that precedes the single-item probe. Finally, we calculated the mean vergence across subjects. Before averaging, the offset was removed, i.e. for each trial the average vergence responses during the first mask presentation were extracted from the time series to detect attentional related vergence responses to the repeated and novel images. The obtained signal was then smoothed using a moving average with a 200 ms window. Vergence responses were averaged over a window of 400 ms prior to stimulus onset (pre-stimuli responses) and 400 ms after stimulus onset (post-stimuli responses). The same trials we

used for vergence analysis were also used for pupil analysis. Before averaging, the offset was removed in the same way we did for the vergence responses and the signal was normalized by dividing it by its maximum.

Statistical analysis. Due to the many variables of interest involved in this task, for instance, repetition effect, time window effect, order effect, age and gender or participants, a linear-mixed effect modelling approach was applied to the vergence responses. In order to determine the effects of repetition, time window, order, age and gender on vergence responses, we considered "repetition", "time", "order", "actual age" and "gender" as continuous (or fixed) factors and "participant" as a random factor. We used age as a continuous factor, given the number of participants divided into the different developmental age groups that could reduce statistical power to the sample. This model handles simultanesoulsy co-variates, experimental conditions and the variability observed across items and subjects.

4. Results

4.1 Face processing

4.1.1 Gaze behaviour

First, we analysed gaze behaviour, i.e. location, duration, and number of fixations for face and scrambled face images. We generated fixation maps from the locations of eye positions (Fig. 9). Maps show fixation regions within the middle area of the face image corresponding mainly to the eye regions. A clear triangle pattern where eyes, nose and mouth are predominantly fixated was not observed. In spite of this, as reported before, there exists a tendency to move the eyes towards the centre-of-gravity of the visual configuration (Coren & Hoenig, 1972; Findlay, 1982; Vitu, 1991). In line with this, a certain bias towards the centre of the visual display has been observed. For scrambled images, a relatively similar pattern of gaze locations was found (Fig. 9) mainly with central fixations.

The average duration and number of fixations were calculated for face and scrambled face images separately. The fixation durations were 180ms±102 (mean±std) for face images and 184ms±105 (mean±std) for scrambled face images, which were not statistically different. Likewise, the average number of fixations did not differ between conditions. For face images, the average number of fixations was 1.31±0.29 (mean±std) and 1.31±0.21 (mean±std) for scrambled faces. Significant differences in fixation behaviour between gender and age were not observed.
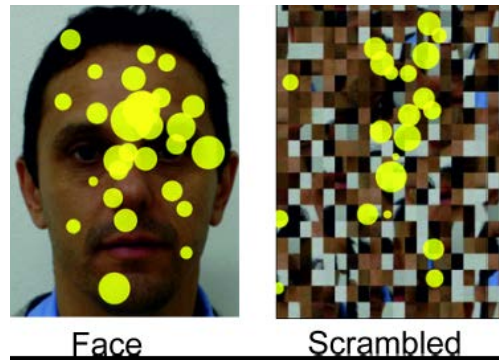
Figure 9. Examples of fixation maps for both face images (on the left) and scrambled faces (on the right) which show the region of gaze fixations (coloured blobs).

4.1.2 Eye vergence responses

Next, we analysed eye vergence responses while gazing at the images. The data revealed that vergence angle increases i.e. eyes converge, a few hundred milliseconds after the onset of the face image. This was noticeable in the *face* condition (Fig. 10). At the time of stimulus removal, vergence responses started decreasing sharply, i.e. the angle of eye vergence became smaller. Even though the average vergence response to face stimuli is very small, it is significantly stronger when compared to the response to the scrambled face images. In figure 10 the black lines indicate the significant ($p<0.05$) time points. Per trial we averaged the vergence responses over a 300-800ms time window after stimulus onset when the difference between the two conditions was strongest. The average vergence response (mean±std: $0.008°±0.003°$) to face stimuli was significantly stronger ($t=2.0$; $df=103$; $p=0.025$ CI$=±0.00048$) than the average response to scrambled face images (mean±std: $0.002°±0.0029°$).

We assessed possible developmental changes in vergence responses by carrying out a linear regression analysis. We obtained a rather flat line ($y =- 0.00088x+ 0.02$).

No difference in vergence responses between boys and girls was observed in the face condition ($t=-0.2839$; $df=68$; $p=0.61$) nor in the scrambled face condition ($t= 0.8160$; $df=68$; $p=0.79$).

50
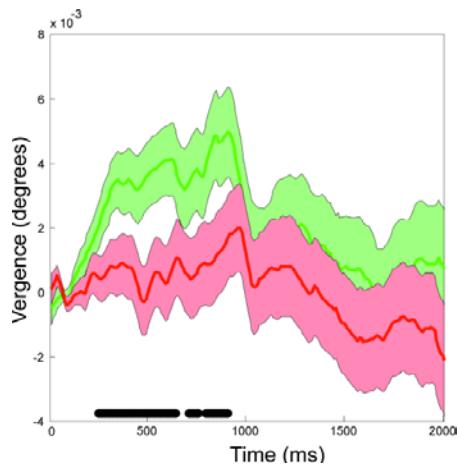
Figure 10. Mean vergence response to face (green line) and to scrambled face images (red line). Shaded areas represent SEM. Black dots denote time samples were responses are significantly (p<0.05) different. Time is from face stimulus onset.

4.1.3 Pupil size

The assessment of pupil size did not yield differential responses between stimulus conditions.

4.2 Visual-Short-Term Memory
4.2.1 Gaze behavior

To assess whether the duration or number of fixations impacted performance for repeated or novel presentations of single items, we analysed fixation behaviour during the sample array (i.e. the two simultaneous coloured cartoon images) separately for the to-be-repeated image and the not-to be repeated image depending on the display side (left/right from midline). The results showed (Figure 11) that the average number of fixations (mean±std: 1.12±0.80) on the side corresponding to the to-be-repeated image was similar to the number of fixations on the side of the not-to-be-repeated image (mean±std: 1.16±0.94). The average fixation duration on the side corresponding to the to-be-repeated image (mean±std: 237.08±51.67ms) was neither statistically different from the fixation duration on the side of the not-to-be-repeated image (240.88±57.97ms).

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Overall, when pairs of images were presented simultaneously in the sample array, children showed similar duration and number of fixations per corresponding display side of the screen.
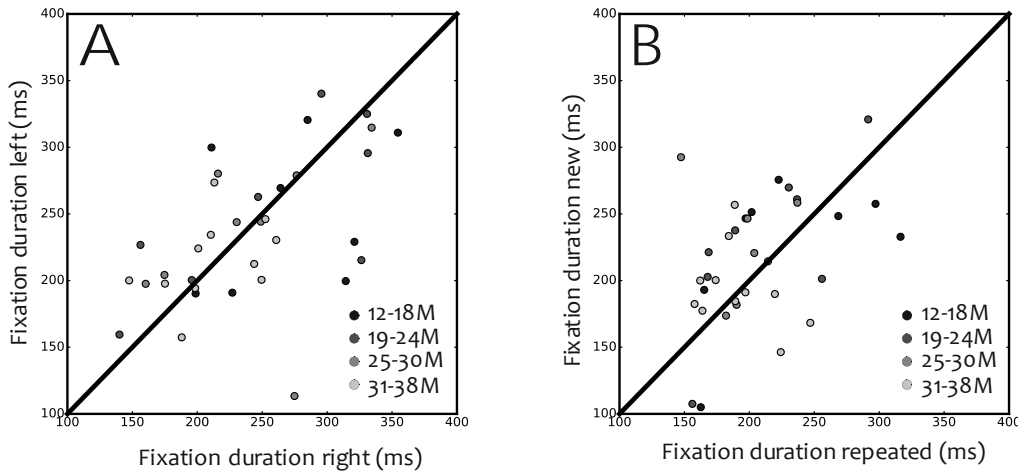
Figure 11. Mean fixation duration per subject. Different grey-scale (from light grey to black) colours were used to group each subject according to age. We grouped participants in 4 age groups (12-18 months old: 9; 19-24 months old: 9; 25-30 months old: 10; 31-36 months old: 15) to study developmental effects. **A:** Average fixation duration when looking at the right image of the stimuli pair versus the fixation duration when looking at the left image. **B:** Average fixation duration for repeated versus new images.

The average duration and number of fixations were also calculated for the novel and repeated images separately (single-item probe). The average fixation duration was 224.61±115.52ms (mean±std) for novel images and 250.78±122.39ms (mean±std) for repeated images (Figure 11). The difference was not statistically significant (p=0.37). Neither the number of fixations turned out significantly different (mean±std; repeated images, 1.39±0.32; novel images, 1.40±0.32; p=0.25).

We were also interested in knowing whether there is an effect due to the order of image presentation. We found that the number of fixations to the repeated item depended on whether it appeared on the first or second order of image presentation. When the repeated image was presented first (repeated 1st) the average fixation number (mean±std:

1.36±0.35) was reduced (p<0.05) compared to the fixation number to the repeated image (mean±std: 1.42±0.33) when presented second (repeated 2nd). The average fixation number did not turn out to be significantly (p=0.45) different in the novel condition between order of presentation (novel 1st; mean±std: 1.38±0.36; novel 2nd; mean±std: 1.42±0.33). The average fixation duration to the repeated item was not significantly (p=0.45) different when the repeated item was presented first (repeated 1st; mean±std: 231.73±125.07ms) than when presented second (repeated 2nd; mean±std: 264.43±127.07ms). This was also true for the novel items (novel 1st; mean±std: 214.55±100.37ms; novel 2nd; mean±std: 236.72±130.81ms; p=0.20).

4.2.2 Eye vergence responses

Next, we analysed the angle of eye vergence while children looked at the novel and repeated images (single-item probe). A convergence response was observed, which started around 500ms prior to the onset of the single item and reached a maximum of 0.1-0.3 degrees around stimulus onset. (Figure 12). Around 500ms after stimulus presentation, the eyes started to diverge towards baseline level. The increase in the angle of eye vergence occurred for repeated and novel images.
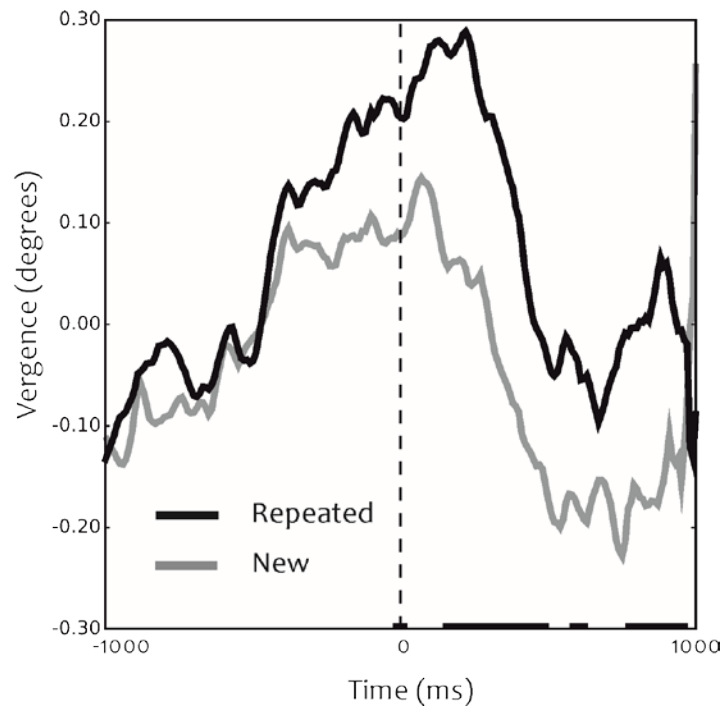
Figure 12. Vergence eye movements. Mean vergence responses to repeated (familiar) and novel items. Vertical dotted line depicts the onset of the image. Time is from stimulus onset. The lines at the bottom depict the time samples when the vergence angle significantly ($p<0.05$) differs between repeated and novel conditions.

During the image presentation (after image onset), the average vergence response was stronger to repeated images that the vergence response to novel ones (Figure 12; see black horizontal lines at the x-axis). This effect of image type on vergence responses was significant ($t=-2.38$, $df=2797$, $p=0.017$, CI= -1.22, -0.120). The factor 'age' was significant ($t=5.00$, $df=2797$, $p=5.9e-07$, CI= 0.012, 0.029). The effect of gender type on vergence responses was not significant ($t=1.4078$, $df=2797$, $p=0.15929$, CI=-0.034445, 0.20983).

We then analysed the vergence responses to repeated and novel images as a function of the order of stimulus presentation. We therefore separately calculated the vergence responses to the first and second image. For both first and second images, a pre-stimulus vergence response was observed. The strength of the pre-stimulus responses to

novel as well as to repeated images was similar when they were presented as the first image (Figure 13). However, the strength of the pre-stimulus vergence response to the second stimulus was stronger if the image was a repeated one (Figure 13; see black horizontal lines at the x-axis). The post stimuli responses were stronger for repeated stimuli, independent of presentation order (Figure 13). There was an effect of image type on window (pre/post stimulus) condition (t=2.52, d= 2797, $p = 0.011$, CI= 0.071, 0.57).
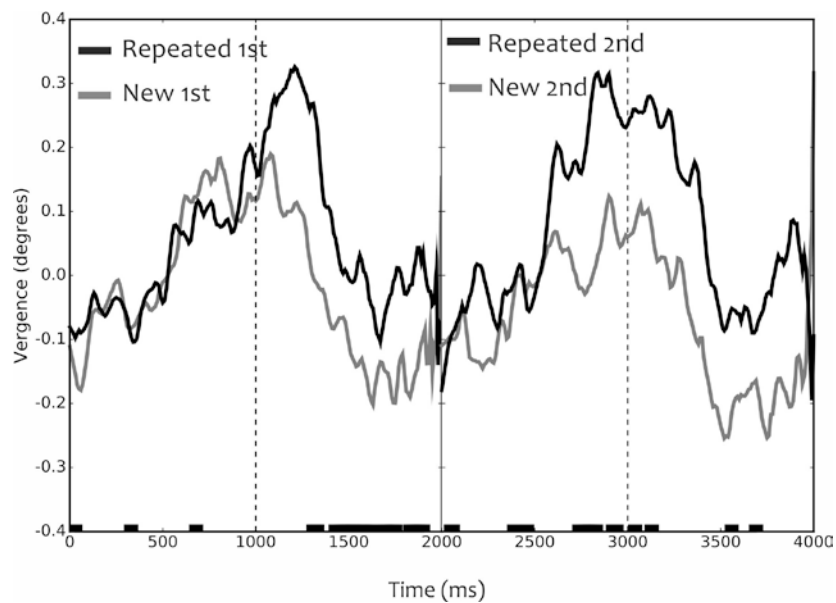
Figure 13. Vergence responses during the trial. Vergence reponses to first and second image presentation. Vertical dotted lines depict the onsets of the images. Time is from start of the trial (from mask onset 0-1000ms; from stimulus onset (random single item probe) at 1000-2000ms; mask from 2000ms-3000ms and stimulus onset from 3000-4000ms). The lines at the bottom depict the time samples when the vergence angle significantly (p<0.05) differs between repeated and novel conditions.

4.2.3 Pupil size

We therefore analysed the changes in pupil diameter. For both repeated and novel items pupil began dilating around 300ms before stimulus onset, reaching peak values at approximately 400ms after presentation of the single item. The results on the modulation in pupil size show that it is similar for repeated images and novel items (Figure 14).
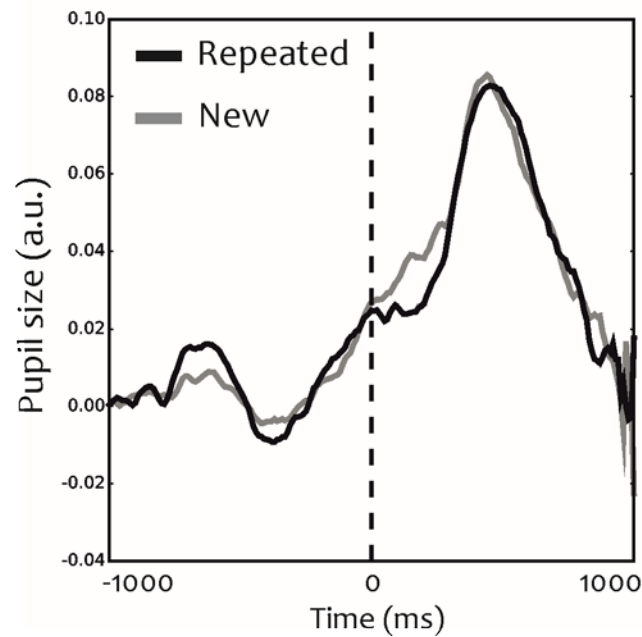
Figure 14. Pupil size. Pupil responses to repeated and novel items. Vertical dotted line depicts the onset of the image. Time is represented previous to and from stimulus onset. No samples where vergence responses differed significantly between conditions were detected.

5. Discussion

In this PhD study, we observed vergence responses in time in a face perception and a paired comparison memory recognition task in young children, to further understand the mechanisms involved in attention processing early on in development. We wanted to study the correlation between the maturation of the attention system and the increasing gaze control, by studying vergence eye movements' modulation and its correlation with attention orienting responses as pillars of fundamental cognitive abilities' development. The focus was on vergence eye movements as previous reports suggested that its modulation in time reflects perceptual and attentional processing of visual information (Puig et al., 2016; Solé Puig et al., 2013, 2015, 2017). Visual attention is of value considering that the study of a previous developmental stage can shed light on the underlying mechanisms of a later developmental stage (Papageorgiou & Ronald, 2013).

This PhD study rests upon two theoretical assumptions. First, attention and oculomotor processes are interrelated processes. Second, the early development of gaze control is closely tied to improvements in attentional control.

The overall results showed that infants process both stimuli, faces and scrambled faces on one hand; and repeated and novel objects on the other hand, in a different fashion. A significant enhancement in the modulation in time of eye vergence responses has been observed, specifically in the case of faces and repeated objects. This could point towards an attention orienting response when presented with a more relevant stimulus or its prioritized processing, reflected through vergence eye movements.

5.1 Face processing

5.1.1 Gaze behavior in face perception

In the face percepcion task, we found that the fixation duration for face images and for scrambled face images were not statistically different. Likewise, the average number of fixations did not differ between conditions. We did not find a correlation between gaze

fixation duration and vergence responses, in line with previous studies (Solé Puig et al., 2017). In support to this observation, one key finding in research about visual attention is that the orientation of attention can differ from the orientation of gaze position, as where someone fixates does not tell us whether they are attending or not. This is so because we are able to shift attention covertly to the periphery of our visual field without making an eye movement. Due to our limited perceptual processing capacity, covert attention would serve the role of accelerating the rate of visual attention processing. The neural structures, part of the visual orienting attention system overlap with vergence eye movements (Carlson, Reinke, & Habib, 2009; Tamietto & de Gelder, 2010; Van Horn et al., 2013). Attention can in this way reduce the performance difference between the fovea and the periphery, possibly by enhancing the representation of the relevant percepts while diminishing the lesser ones in the visual environment (Hawkins et al., 1990; Liu, Stevens, & Carrasco, 2007; Lu & Dosher, 1998; Posner, 1980), included enhancing spatial resolution (Anton-Erxleben & Carrasco, 2013; Treisman & Gelade, 1980).

The advances in infant attention based on further brain development and experience lead to more efficient processing of objects, faces, and visual patterns. Some researchers, indicate that infants require less time to demonstrate novelty preferences across this age range (Richards, 1997; Rose, Feldman, & Jankowski, 2004). Others state that beyond six months of age, infants display shorter looking to basic stimuli, such as black and white geometric patterns, but begin to display longer looking to more complex stimuli such as faces and objects (Courage et al., 2006).

5.1.2 Vergence responses in face perception

The eyes converged more when presented with the face image, as compared to the scrambled face image. The data revealed that vergence angle increases a few hundred milliseconds after the onset of the face image. This could be explained as biologically

significant stimuli are prioritized by the attention system. As predicted, the increased allocation of attention to highly relevant stimuli lead to enhanced processing of such stimuli and triggered synchronized changes in vergence responses. Face images and scrambled face images were comparable in terms of colour range, and luminance. Except that the scrambled stimulus contained no higher order structure and thus it represents a "noise" stimulus, generated from the same face within the array created to match its low-level visual properties (Halit, Csibra, Volein, & Johnson, 2004). This points out that even if the abstract display was highly salient, it did not contain the clear structure of meaningful elements found in a face that infants are familiarized and have experience with (Hunnius & Geuze, 2004). This also supports findings demonstrating an advantage in the properties of face-like images which were defined as more detectable and congruent compared to scrambled images (Macchi Cassia, Valenza, Simion, & Leo, 2008). Thus, the magnitude of the attentional modulation might be highly correlated with subjective arousal.

The results from vergence modulation in time may also have revealed that the bias for faces becomes more robust and resistant to distraction during the second half of the first year. The strengthening of the attentional hold for faces during the second half of the 1st year may relate to emerging functionality of prefrontal systems involved in active control of attention, resulting in selective enhancement of responses to competing stimuli (Bonnefond & Jensen, 2012). A similar interpretation has been proposed for increases in sustained attention to patterned stimuli in infants between 6 and 12 months (Courage, Reynolds, & Richards, 2006). A developmental tendency or pattern was not observed, possibly due to the age range evaluated, where this discriminating capacity might have been present earlier. Human newborns make differential responses to a face-like pattern compared to their response to non-facial rearrangements of these blobs (Morton &

Johnson, 1991). Mark Johnson and John Morton (1991) have used a distinction between prototype face perception and recognition of individual faces in their theory of face perception in infancy. It is debated as to whether some subcortical area, such as the pulvinar, within an oculomotor orienting circuit may operate at birth and underlie the preferential orienting response to faces in newborns. Tracking a stimulus further and for longer, which is the differential response of a newborn to the face-like configuration of three blobs, may represent an initial bias in the attentional salience system; this may in turn bias later face recognition systems to allow elaborate discrimination of faces and facial expressions in older infants. Because obligatory fixations are typically observed at around 1 and 2 months, and the capacity to disengage and shift spatial attention from one stimulus to another is well developed by 6 months (Hunnius & Geuze, 2004), the most likely interpretation of maintaining attention on faces, especially in older infants, is that this bias involves active suppression of responses to other distracting stimuli.

Research performed in adult population have shown gender differences, in that men treat information differently (Bayliss, di Pellegrino, & Tipper, 2005) than women, who have been found to perform better in episodic memory tasks involving face recognition (Yonker, Eriksson, Nilsson, & Herlitz, 2003). We considered gender-specific differences in the attentional bias toward face stimuli, a biologically salient trigger, together with a female tendency towards emotional expression and sensitivity, as suggested by (Kring & Gordon, 1998). From previous research, we expected that stimuli of such emotional significance would increase the allocation of attention and lead to enhanced processing and perceptual analysis, reflected in vergence responses. Results were found accordingly, except that no difference in vergence responses between boys and girls was observed in the face condition nor in the scrambled face condition.

5.1.3 Pupil size in face perception

We observed pupil size modulation for faces as well as for scrambled faces. However, differences in pupil diameter were not observed between conditions. In previous tasks (Solé Puig, et al., 2013, 2015) we found changes in pupil diameter but these changes were not related to orienting attention nor to the observed vergence responses. Our current findings are in line with these previous observations, while other research, contrary to our results, indicates a correlation between pupil changes and arousal or cognitive processing (Karatekin, 2007; Porter et al., 2007; Rosa, Oliveira, Alghazzawi, Fardoun, & Gamito, 2017).

5.2 Visual-Short-Term Memory

5.2.1 Gaze behaviour in VSTM

In this study, we found no clear differences neither in duration nor frequency of fixations, for either repeated or novel items. When pairs of images were presented simultaneously in the sample array, children showed similar duration and number of fixations per corresponding display side of the screen. We only observed a reduced number of fixations to the repeated objects when presented first, in the single-item probe. This may suggest that children did not display any initial preference for location (left or right side of the screen), or object type (repeated or novel objects). Looking preferences at population level may appear to be random despite individual infants showing clear familiarity or novelty preferences (Bogartz & Shinskey, 1998). In addition, models of infants' attentional preferences (Hunter & Ames, 1988) show that random looking behaviour should not be equated with a failure to discriminate. Moreover, individual infants pass through a period between preferring familiarity and preferring novelty when both attract their attention equally, which will appear as random looking (Roder, Bushnell, & Sasseville, 2000).

5.2.2 Vergence responses in VSTM

We assessed eye vergence in children while looking at novel and repeated object images. The results of our current study show that both repeated and novel images elicited vergence responses. Still, during the image presentation, the average vergence response was stronger to repeated images, as of recognition, when compared to the vergence response to novel ones. Hence, the effect of image type on vergence responses was significant, indicating a relation between vergence and visual memory. As we have previously mentioned, in a study by Jainta and colleagues (2011) they found that the contamination of vergence trajectories by saccadic intrusions did not change with repeated exposure to stimuli (Jainta, Bucci, Wiener-Vacher, & Kapoula, 2011). Neither the frequency of saccades nor their amplitude were affected. Somehow, repetition improves vergence movements, which is not simply due to an increase in the number or amplitude of saccade intrusions (Coubard & Kapoula, 2008; Semmlow, Chen, Granger-Donetti, & Alvarez, 2009). This would explain why significant differences in vergence modulation for familiar objects were found but not for novel ones, in addition to not observing significant changes in gaze behaviour. VSTM is present right after birth and from early childhood, as children can distinguish between changing and unchanging displays (Courage & Howe, 2004; Rose et al., 1997, 2004). We therefore argue that the observed differential vergence responses between repeated and novel stimuli reflect VSTM. This idea agrees with the reported observation of vergence responses to correctly remembered images in adults (Solé Puig et al., 2017).

If memory was reflected in the vergence responses, we speculated that the image type (repeated or novel) of the first presentation would affect the vergence responses to the second presentation and have an effect on vergence responses during the pre and post stimulus periods. Indeed, interactions between the order of presentation (first and

second) and image type (novel and repeated), as well as interactions between time window (pre and post-stimulus presentation) and image type were reported. For both image types, pre-stimulus vergence responses were noticed where the strength was a function of presentation order. We suggest that the increased vergence responses reflect preparatory or attention processing. Our finding of vergence responses during the mask period, prior to the presentation of the repeated or novel image could represent an element of anticipation once children infer the sequence due to the format of serial repetitions (Fiser & Aslin, 2002). Anticipatory vergence responses also occurred prior to behavioral responses in a memory task, which were stronger when the responses were correct (Solé Puig et al., 2015). Moreover, the induced vergence responses when orienting visuospatial attention after cueing (Solé Puig, et al., 2013) could be considered as a preparatory phase for subsequently processing the target stimulus.

We aimed to evaluate the extent to which differences in allocation of attention at encoding could explain differences in VSTM between children of different ages. We observed that the factor 'age' was significant. More specifically, with increasing age, children were able to manage increased levels of information, as the oldest age clusters showed improvements in attention control through enhanced vergence modulation. However, developmental patterns with the current data may not be accounted for, as there was heterogeneity in the age range tested, reduced power in separating age clusters and therefore a decreased number of participants per group. A role of attention in VSTM tasks has been demonstrated in infants (Ross-Sheehy, Oakes, & Luck, 2011). Attention may be a vehicle by which information is stored in memory (Schmidt, Vogel, Woodman, & Luck, 2002). Yet, little is known about the principles that govern the attentional process required for perception and memory. Reynolds, Courage, & Richards (2010) showed that the cortical areas controlling attention to stimuli may be similar to cortical areas controlling

recognition memory. The conceptualization of VSTM control as equivalent with visual attention forms part of a larger claim that VSTM and attention are simply two terms to describe the same selective mechanism (Chun, 2011; Cowan, 2001; Gazzaley & Nobre, 2012; Kiyonaga & Egner, 2013; Theeuwes, Belopolsky, & Olivers, 2009; Wheeler & Treisman, 2002). As it has been pointed out in previous research, the attention orienting system serves as the cognitive and emotional control system with the executive system to start exercising cognitive and emotional control from around 18 to 24-months of age (Posner, Rothbart, Sheese & Voelker, 2012). This task has demonstrated that important improvements in attention and its control take place. Our current findings show attention related eye vergence already at early developmental stages and support a role of eye vergence in visual attention and memory. This is relatively an advanced ability, as it involves keeping the object's representation in mind over the delay and forming an expectation to correctly anticipate the object's reappearance. The nuclei that are responsible for vergence eye movements receive direct input from cortical areas involved in attention control. Therefore, attention, vergence and VSTM circuits appear to be coupled, indicating shared neural control mechanisms.

Taking into account previous research on gender differences in the adult population for object recognition (McGivern et al., 1998), we speculated an increased allocation of attention to objects in the female group, which would trigger synchronized enhanced changes in vergence responses. Nonetheless, sex differences with the current data may not be accounted for, possibly due to a gender bias in recruitment conditions.

5.2.3 Pupil size in VSTM

We observed that stimuli evoked modulation in pupil size for repeated and novel images. In contrast to vergence responses, pupil responses to repeated and novel stimuli did not differ. Moreover, they showed a different temporal pattern than the vergence

responses. A difference in response patterns between pupil and vergence was previously reported (Solé Puig, et al., 2013b; Solé Puig et al., 2015). Thus, even though changes in pupil diameter provide a momentary, involuntary and unbiased measure of arousal and cognitive load (Karatekin, 2007; Porter et al., 2007; Rosa, Oliveira, Alghazzawi, Fardoun, & Gamito, 2017) and the neural mechanisms that control vergence as well as pupil size are linked, the attention related vergence responses cannot solely be explained by changes in pupil size.

5.3 Covert attention and the relevance of vergence eye movements in bran function

The modulations in the angle of vergence eye movements in time obtained in both tasks, point towards significant attentional orienting and visual processing differences. Our observations of vergence modulation in time when evaluating face processing and recognition memory procedures, show a transient peak response. We suggest that the relative changes of vergence signal are a way of monitoring endogenous processes, as changes in focusing are associated with internal shifts of attention. Thus, we speculate that the perceptual state of the observer would be reflected in the attentional hold of the object, correlated to vergence modulation. The sites computing final oculomotor decisions are located in the FEF and SC, structures already described to be overlapping with the orienting system and vergence eye movements' neurobiological substrates (Gottlieb & Balan, 2010), which are active during covert shifts of attention. Retinal projections to the primary visual cortex (V1) diverge first to different subcortical visual centers in parallel, including —among others— the lateral geniculate nucleus (LGN), the SC and the pulvinar (Kaass & Huerta, 1988). In contrast with the LGN, which acts as a first-order relay of retinal signals to V1 (Guillery & Sherman, 2002), the widespread bidirectional connectivity of these two visual centers with nearly all visual areas indicates that they are not simply passive relays (Casanova, 2004).

The attention system maturation interacts with increasing gaze control, therefore orienting responses progressively transition from purely reflexive to more volitional, goal-directed actions (Johnson, 2001). Vergence eye movements may encode signals of visual selection, representing a form of attention orienting and possibly incipient motor plans. The impact of selective attention on Event Related Potential (ERP) components like the visual P100 would be leading to larger amplitudes if a stimulus appears at an attended location as compared to an unattended location (Luck, Heinze, Mangun, & Hillyard, 1990), but directing attention towards certain features of objects rather than their spatial location leads to later effects, starting at about 150 ms (Hillyard & Anllo-Vento, 1998). Vergence signal has been observed as a modulation with a transient peak response, possibly related to stages of stimulus encoding such as the one represented by the P300, a positive deflection in the ERP, which peaks around 300 ms (200-400ms) after stimulus onset. It is the most prominent ERP component sensitive to cognitive processing (Verleger, 1988). The P300 is elicited when subjects attend to a stimulus and when they discriminate the stimulus feature. The amplitude of the P300 reflects the probability and task relevance of a stimulus, which is generated in distributed neural systems (Hillyard & Anllo-Vento, 1998), while P300 latency reflects the duration of stimulus evaluation (Donchin & Coles, 1988). This indicates that orienting attention responses and oculomotor processes are tightly coupled, as we have hypothesized and aimed to study herein. Vergence eye movements could be a valid measure for evaluating visual behaviour early on, as young children already present significant volitional, strategic control over their visual behaviour. It could serve as a reliable parameter to provide information on visual orienting responses, suggesting an association with attention processing.

5.4 Limitations

The original aims of this study were highly ambitious, as we wanted to develop and test a cognitive battery, which examined: (1) emotion perception (2) joint gaze (3) face processing, (4) memory, and (5) audiovisual speech integration. Following expert advice, the emotion perception and joint gaze tasks were discarded for inclusion in the project. Another part of the study recruited a school-age cohort of children aged 8-14 years to assess attentional differences using the Posner Paradigm. Together with the audiovisual speech integration task, these materials are under current revision and thus were not included herein.

Limitations that may have impacted the current results rely in that we have implemented an accessible methodology through an eye tracker device of low-level resolution (Tobii 30Hz), which may have had an effect on the quality of the vergence signal recorded. In our sample, there was heterogeneity in the participants' age. For instance, in the memory task, by separating per age clusters, which intended to replicate developmental patterns in visual processing, we have significantly reduced the number of participants to be analysed in each group, therefore substracting power. Females did not show stronger vergence responses, when compared to males. This could be possibly due to a bias in recruitment, as there were 14 girls and 29 boys, a 1:2 ratio. As suggested by Colombo (2001), single-age point measurements of early attention and cognitive abilities may not be the optimal research strategy for understanding how these early milestones lay the ground for cognitive abilities in later years. Instead, a more advantageous approach may be by implementing repeated measurements. Thus, a potential limitation of the current thesis is the lack of longitudinal data that would have enabled a more accurate description of the developmental changes. In spite of all this, due to the doctoral program time constraints, we specifically incorporated the age groups that

were important to consider in terms of attention development and increasing gaze control. Some of the findings based on this PhD study have also been informative for the planning of future work. It would be necessary to measure impact factors and other indicators in future studies, such as Cohen's d effect, betas, correlations, which would improve the understanding on the significance of the results and their impact in the observed population overall.

6. Conclusions

6.1 Face processing

In this task, no significant results were found in gaze behaviour. Neither scan paths nor heat maps for face vs. scrambled faces, showed significant differences in the number of fixations.

Children showed an average vergence response to face stimuli that was significantly stronger to the average response to scrambled face images. This differential modulation may indicate a differential attention processing in face perception. In spite of the differential processing, vergence responses did not differ between the male and female population under these experimental conditions. When correlating sex and age, it did not result in significant differences either. A correlation between gaze fixation duration and vergence responses was not observed.

Differences in pupil diameter were not found between face and scrambled face images, thus pupil modulation may not be the cause of vergence responses.

6.2 Visual-Short-Term Memory

In this task, we found no clear differences neither in duration nor frequency of fixations, for either repeated or novel items. We only observed a reduced number of fixations to the repeated objects when presented first.

Both repeated and novel images elicited vergence responses. Children showed on average a stronger vergence response to repeated single item probes. For both image types, pre-stimulus vergence responses were noticed where the response strength was a function of presentation order. The strength of the pre-stimuli responses depended on the image condition, i.e. whether the second image was a novel or a repeated one. If the stimulus appearing second within the visual sequence was a repeated one, then the pre-stimulus vergence response was stronger when compared to a novel one. There was an effect of image type on pre and post-stimulus responses for repeated images. We observed that the

factor 'age' was significant. However, developmental patterns with the current data may not be accounted for. Sex differences were not significant.

For both repeated and novel items pupil began dilating around 300ms before stimulus onset, reaching peak values at approximately 400ms after presentation of the single item. The modulation in pupil size was similar between repeated images and novel items and thus no significant differences were found.

Overall, our results on eye vergence responses enhanced at specific times and for significant stimuli (i.e. faces and familiar objects), indicate that attention-orienting responses underlying face perception and processing, as well as memory recognition, are critical for brain development. This is in line with other researchers who propose an integrative view of cognitive control (Banich, 2009; Garon et al., 2008; McCabe et al., 2010; Miyake et al., 2000), where attention is considered the cornerstone of cognitive development.

6.3 Implications of the thesis

This PhD study suggests a basis for the use of vergence eye movements as a tool for measuring attention in infants, toddlers and young children, which may help provide new insights into attention and perceptual processing. The present findings hopefully motivate further research to examine changes in early cognitive processing in relation to attention orienting and its correlate in vergence responses as the basis of attention control later on. Cognitive development needs to be understood as a cyclic process, where attention influences learning, and learning guides attention. For instance, some studies have already demonstrated that during the first year of life, infants at risk behave differently from control groups in simple visual orienting paradigms that measure components of visual attention (Elsabbagh et al., 2009). Individual differences in infant's

attention could predict both concurrent and future indices of cognitive status (Colombo, Kapa, & Curtindale, 2010). There is evidence to support that there is continuity of attentional style during the first year of life (Colombo et al., 2010) as well as continuity of attention from infancy through toddlerhood to pre-adolescence (Rose, Feldman, Jankowski, & Van Rossem, 2012). Furthermore, distinct developmental profiles indexing the control of visual attention may characterize subgroups of infants at risk. Sacrey et al., (2013) found that the development of visual attention shows different patterns in infants, who later receive a diagnosis of Autism Spectrum Disorder (ASD). Many developmental disorders have been linked to deficits in attentional processing, such as in ASD (Elsabbagh et al., 2009); specific language impairment in adolescents (Lum, Conti-Ramsden, & Lindell, 2007); developmental dyslexia (Facoetti, Paganoni, Turatto, Marzola, & Mascetti, 2000); and Attention Deficit Hyperactivity Disorder (ADHD) (Dalsgaard, 2013).

6.4 Future directions

Using eye movements could be useful to assess functional brain development in infants, towards a better integration of scientific knowledge into etiological models and a more direct translation into preventive health care, as well as the creation and monitoring of healthy growth interventions. This is the baseline for our investigation that is further motivated by the creation of a battery of tests in the future, where attention processing underlies the individual's cognitive profile.

1.Using eye movements to assess functional brain development in infants

Providing an example of how studying individual differences in infant attention can facilitate the identification of individuals at risk for developing certain neurodevelopmental disorders The ultimate goal of this effort is to develop objective quantitative tools for the detection of developmental delays in early childhood. As a

lomgitudinal study, provide tools that might be deployed in primary care paediatrician's offices. As part of a larger effort in implementation science, as a contribution to health care not only from the medical point of view but also including the families and all the agents implicated in the child's upbringing.

2. Using eye movements, to assess individual differences in infancy

Eye tracking will enable us to ask new questions about development. This represents the starting point of a long-term project where we are to incorporate the lessons learned from the studies performed. Correlate vergence eye movements modulation in different cognitive assessment tasks with conventional tools of infant development evaluation such as Bayley Scales of infant development; Mullen Scales of Early Learning; The Fagan test of Infant Intelligence or Vineland Adaptive Behaviour Scale at 6, 12, 18, 24 and 36 months to obtain standardized measures of adaptive function.

7. References

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