Social Perception in Infancy: A near infrared spectroscopy (NIRS) study

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Abstract

The capacity to engage and communicate in a social world is one of the defining characteristics of the human species. While the network of regions that compose the social brain have been the subject of extensive research in adults, there are limited techniques available for monitoring young infants. This study used near infrared spectroscopy to investigate functional activation in the social brain network of 36 five-month-old infants. We measured the haemodynamic responses to visually-presented social stimuli in the temporal lobes. A significant increase in oxyhaemoglobin was localised to two posterior temporal sites bilaterally, indicating that these areas are involved in the social brain network in young infants.

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While the network of regions that together compose the social brain have been the subject of extensive research in adults, their origins in infancy largely remain obscure. Part of the reason for this lack of knowledge is methodological. For a variety of reasons, it is very difficult to scan awake and conscious infants in functional MRI protocols that involve visual presentations. Further, while electroencephalography (EEG) measures give good temporal resolution, their spatial resolution remains comparatively poor. A newly developed non-invasive imaging method, Near Infra-Red Spectroscopy (NIRS), can potentially bridge this methodological gap. In this study we demonstrate that NIRS can be used to investigate visually-induced activity in regions of the social brain in young infants.

Over the last decade, there has been an increasing interest in a particular region of the adult human social brain network, the superior temporal sulcus (STS). Once thought of as a 'biological motion detector' responding to any eye, mouth, hand or whole body movements, it has recently been associated with more complex functions, such as implied motion in static images, intentionality of actions and the social relevance of actions (Calvert et al. 1997; Gallagher & Frith, 2004; Grezes et al, 2001; Hoffman & Haxby, 2000; Lotze et al, 2006; Mosconi, Mack, McCarthy & Pelphrey, 2005; Puce, Allison, Bentin, Gore & McCarthy, 1998; Saxe, Xiao, Kovacs, Perrett & Kanwisher, 2004; Vaina, Solomon, Chowdhury, Sinha & Beliveau, 2001). Puce and colleagues (Puce, Allison, Bentin, Gore & McCarthy, 1998) were amongst the first to describe functional activity to perceived eye and mouth movements in the posterior temporal portion of the STS in

humans. These authors proposed that the STS is responsible for processing dynamic components of the face. Further, a study using static point light displays of figures walking, kicking etc. found that transcranial magnetic stimulation (TMS) over the right posterior STS disrupted perception of the movements whilst having no effect when applied over another motion sensitive area, MT/V5 (Grossman, Batelli & Pascual-Leone, 2005). Recently, Lotze and colleagues (Lotze et al, 2006) revealed a differential response in STS to expressive hand gestures (waving) and/or body referred movements (combing hair) compared with isolated hand movements (i.e. using a key), supporting the view that there is increased activation in STS with increased social relevance.

Within the extent of the STS, different areas appear to be specialised for different types of stimuli. Studies that involve perceived eye movements find a focussed area of bilateral activation around the posterior STS, often in the right hemisphere, while responses to hand and mouth movements show more widespread activation extending anteriorly, and often in the left hemisphere (for a review of several studies see Allison, Puce & McCarthy, 2001 and Pelphrey, Morris, Michelich, Allison & McCarthy, 2005). Moreover, research suggests that the right posterior STS may be more sensitive than the left to the type of social motion perceived; mutual vs averted gaze (Pelphrey, Viola & McCarthy, 2004), congruent vs incongruent gaze (Mosconi et al, 2005), expressive vs instrumental gestures (Gallagher & Frith, 2004).

Whilst much functional MRI research has been done on biological motion processing and associated activity in the temporal posterior lobe in adults, there are limited techniques available for monitoring functional brain activation in infants. Specific spatial localisation of brain activity has not been investigated extensively during infancy

because techniques such as fMRI cannot accommodate mobile, awake infants. Near infrared spectroscopy (NIRS) is a non-invasive optical technique, which provides the opportunity to measure the haemodynamic response to neuronal activation in a range of different subjects including awake infants. With this optical technique, the light migrates from sources on a sensor pad located on the head, through the skin, skull and underlying brain tissue, and is then detected by sensitive detectors on the same sensor pad (for early NIRS work see Chance et al, 1993; Jöbsis, 1977). Changes in blood oxyhaemoglobin (HbO_2), deoxyhaemoglobin (HHb) and total haemoglobin (HbT= HbO_2 + HHb) in the underlying cortex are measured by detecting changes in reflected near-infrared light. The concentration of these chromophores (the molecules that are responsible for the colour of the blood due to their absorption of light at different wavelengths) change according to the metabolic demand of the neurons in a given cortical region, thus enabling functional brain activation to be measured. A typical haemodynamic response to cortical activation is an increase in blood flow leading to an increase in HbO_2 and a (relatively smaller) decrease in HHb as it is displaced from the veins, leading to an increase in HbT. Previous work suggests that the properties of the vascular response measured by NIRS is comparable to the BOLD (blood oxygen level dependence) response seen in MRI research. However, there is ongoing debate concerning which chromophore changes most closely map the BOLD response (for review see Obrig & Villringer, 2003; Ferrari, Mottola & Quaresima, 2004). Though there is a causal relationship between changes in deoxyhaemoglobin (HHb) concentration and the BOLD signal, Strangman and colleagues (Strangman, Culver, Thompson and Boas, 2001), found the strongest correlation between BOLD fMRI changes and oxyhaemoglobin (HbO_2). Moreover, while adult NIRS studies

show HbO_2 and HHb responses consistent with BOLD fMRI signal changes, infant data reveals a less consistent pattern of activation (Baird et al, 2002; Sakatani, Chen, Lichty, Zuo & Wang, 1999; Meek et al, 1998; Wilcox, Bortfeld, Woods, Wriuck & Boas, 2005; Zaramella, et al, 2001). Therefore in NIRS research it is appropriate to investigate both oxy- and deoxy-haemoglobin changes in response to a given stimulus.

Initial studies using single channel NIRS to monitor functional activation in infants used standard visual (chequerboard) and auditory (pure tone) stimuli (Meek et al, 1998; Sakatani et al, 1999). More complex stimuli have now been investigated using a range of different multi-channel NIRS optical topography systems (i.e. Blasi et al, 2007; Otsuka et al, 2007; Pena et al, 2003; Shimada & Hiraki, 2006). Whereas single channel systems were limited to measuring just one location, multi-channel optical topography allows simultaneous measurements across an array of channels enabling spatially localised activation across a larger area of the cortex to be investigated. In addition, by adjusting the configuration of the sources and detectors it is possible to potentially discriminate responses at different depths of the cortex by using channels with several different separations. For example, in a recent study on face perception, we found a more widespread haemodynamic response (increase in HbO_2) to faces, compared with visual noise in the occipital area in four-month-old infants (Blasi, et al, 2007). Furthermore a larger number of channels with a significant increase in HbO_2 were found at the deepest depth, suggesting that there may be some discrimination in the response as a function of depth relative to the cortical surface.

Multi-channel arrays may also be used in several locations simultaneously to measure differential responses over differing brain regions. A recent study used two

arrays located over the temporal lobes to investigate neural activation in five to eight month-old infants. Otsuka and colleagues (Otsuka et al, 2007) found differential responses to face inversion between hemispheres in response to static images of upright and inverted faces. For upright faces an increase in HbT and HbO_2 was observed in the right hemisphere indicating a lateralised inversion effect. Indeed the authors suggest that this response could reflect activity associated with face perception in the STS. Though this study investigated static faces without implied motion, the rapidly changing face stimuli within trials (5 faces per 5 second trial) could have caused a response in the STS. However, limited conclusions can be drawn about the spatial localisation of the response as the reported effects are based on grouped data across all channels in each lateral array. The findings support the need to further investigate the temporal lobes, and the role it plays in an infant's social brain network.

The purpose of the current study was to investigate whether young infants show a haemodynamic response over the posterior temporal lobe to a complex social stimulus involving biological motion. To maximise the potential response and maintain the infants' attention, the biological motion condition comprised of naturalistic video clips of human movements involving eyes, mouth and hands. In Experiment 1 this was compared to complex but static images of transport, which served as the baseline condition. In Experiment 2 a further condition, a dynamic non-social stimulus, was introduced. We chose to study five-month-old infants to facilitate comparison with previous NIRS studies. To investigate this question, two sensor pads were placed over the temporal lobe on each hemisphere. The posterior half of the sensor pad lay over the scalp locations T3-T5/T4-T6 while the anterior half of the pad extended toward F7/F8 (according to the 10-

20 system, Jasper, 1958). The placement of the sensor pads allowed us to make predictions about the spatial localisation of the response using the findings of adult fMRI studies in this field. If the infants' functional activation to biological motion perception resembles that of adults' then we hypothesise that localised activation will occur in response to the social stimuli in the posterior half of each sensor pad near to scalp locations T5 and T6. As the stimuli used in this study included both eye, mouth and hand movements we further predict that there will be bilateral activation rather than any overall lateralisation effect as has been suggested in earlier research (for review see Allison et al, 2000; Pelphrey et at, 2005). However if five-month-old infants do not yet possess a specialised STS we predict no differences in activation between the human moving video clips and the control static transport images.

Experiment 1

Method

Participants

Twenty-four five-month-old infants took part in the study (13 females and 11 males; age 154 ± 8.7 days old). A further two infants participated but were excluded from the study as they failed to look at the stimuli for the minimum number of six trials; all other infants completed the whole study. All parents volunteered by responding to advertisements and gave written informed consent to participate. The study protocol was approved by the appropriate Ethics Committee. The infants were from a varied ethnic and socio-economic background, predominantly white (British/non-British) or British black (mixed/African/Caribbean).

Procedure

The infants sat on their parent's lap and were encouraged to watch the stimuli displayed on a 46-inch plasma screen with a viewing distance of approximately 100cm. The experiment ended when the infants became bored or fussy. The experimental condition consisted of full colour life-size social video clips of female actors who either moved their eyes left or right, their mouth in silent vowel movements, or performed hand games; 'Peek-a-boo' and 'Incy Wincy spider'. These were presented in an ABA format (six seconds, four seconds and six seconds, designed to keep the infant's attention). The baseline condition consisted of full-colour still images of different types of transport (i.e. cars, helicopters) presented randomly for a pseudo-random duration (1 – 3 seconds). These images were selected to be colourful, complex and interesting, and ensured that infants remained attentive to the screen. Note that NIRS studies with adults use a blank screen as the baseline but this is not possible when working with infants, therefore the static images act as the baseline for the activated period containing the social video clips. The overall surface area of the displayed experimental stimuli and baseline stimuli were equivalent, and subtended a visual angle of approximately 12 degrees.

The sequence of stimulus presentation is illustrated in figure 1. The session began with a rest period (30 secs minimum) during which the infant was shown shapes in the four corners of the screen to familiarise them with the general experimental setup. Following this the trials alternated one after the other, i.e. a 16 second experimental trial followed by a 16 second baseline trial. In addition, during every third trial, music was played to help maintain the infant's overall engagement with the task. Thus, music was

played at an approximately equal number of experimental and baseline trials for each infant. If necessary, occasional alerting sounds were used to draw the infant's attention back to the screen. The experimental trials and baseline trials were presented consecutively three times each, followed by a preferential looking trial. For this, a social still image and a transport still image of equal size were presented for five seconds, one on the left and one on the right of the screen. Following this, a further six consecutive experimental and baseline trials were presented, and then a further preferential looking trial (this time with the human and transport images displayed on the opposite side of the screen to the first preferential looking trial). Thereafter, consecutive experimental and baseline trials were displayed repeatedly until the infant became bored or fussy (see figure 1 for an overview of this procedure).

Data acquisition and array placement

To investigate cortical activation, NIRS measurements were made using the UCL topography system (Everdell et al 2005). The multi-channel system uses two wavelengths at 770nm and 850nm in a frequency multiplexed approach allowing rapid data acquisition of the attenuation signal from the reflected near infrared light. The array of channels are designed and adapted for each study protocol, allowing flexibility in the source detector geometry and locations of the arrays. Eight optodes, in a ten-channel (source-detector pairs) arrangement with an inter-optode separation of 20mm were placed on the temporal lobe on each hemisphere in custom-built arrays and head gear (see figure 2). The midpoint of the lower row of channels lay over scalp location T3 on the left hemisphere and T4 on the right. The schematic map (figure 2) shows an estimation of the 10-20

system scalp locations, using available anatomical landmarks for the five-month-old infants. The posterior area of each pad lies approximately over the scalp locations T5/T6, analogous to the region of interest (the STS area reported in adult MRI studies).

Data rejection

To assess whether the infants were looking during each trial we recorded their eye movements and coded looking time off-line. This was the first step in the selection of valid trials. For a trial to be considered valid, the infant had to be looking at the screen for at least 4 seconds prior to the experimental trial onset and for a minimum of 80% of the following experimental trial period. A minimum of six valid experimental trials was required to include an infant in the study.

Following this, the recorded NIR attenuation measurements for each infant were analysed and trials or channels were rejected from further analysis based on the quality of the signals. Criteria for channel rejection included the presence of: (1) large movement artefacts assessed by measuring the coefficient of variation (CV) of the signal. Channels were excluded if the CV of the attenuation measurement for each wavelength exceeded 10% or if the difference in CV between the attenuation measurements for the two wavelengths ($|CV_{770} - CV_{850}|$) exceeded 5%. These changes in CV could be due to movement of the pads and hat, differential occlusion of the source fibres for each wavelength or a loose fibre in the pad; or (2) high frequency noise beyond the limits of physiological effects, where the normalized high frequency power (nHF) is greater than 35% of the total power of the signal (see Kirjavainen et al, 2001). For each infant, the channels that survived these rejection criteria were analysed for trial selection. The trial

selection analysis identified sharp changes in the signal caused by sudden movements rather than a generally noisy channel from a continuously moving infant as identified by measuring the coefficient of variance. Following data conversion from attenuation to concentration data (a full description is given in the following 'Data Analysis' section), trials that contained changes in HbO_2 concentration that exceeded a predefined range (± 5 μM during the baseline trials, and ± 15 μM during the experimental trials where artefacts in the signal may occur in addition to activation), were removed from the data set. The minimum number of valid experimental trials for each channel was six.

Data analysis

For each infant, the attenuation signal (from the reflected near-infrared light) was low-pass filtered, using a cut off frequency of 1.8Hz. The data was then divided into blocks consisting of 4 sec of the baseline trial (still transport images) prior to the onset of the 16 sec experimental trial (human video clips), plus the following 16 sec baseline trial (still transport images). This 36-second block of attenuation data was detrended with a linear fit between the first and last 4s of the 36 sec block. Within these 4 sec segments we assume that all effects of the experimental stimulus have subsided (Blasi et al, 2007). The data was then converted into changes in concentration in HbO_2 and HHb using the modified Beer Lambert law (Delpy et al, 1988) and assuming a differential pathlength factor for infants (5.13; Duncan et al., 1995).

Following this, valid experimental stimulus trials were averaged together for each infant, and a time course of the mean change in HbO_2 and HHb was compiled for each channel. These average time courses for each infant were then compiled into a grand

averaged time response curve of the haemodynamic response (across all infants) for each channel. A time window (region of interest) was selected between 10 and 18 seconds post experimental stimulus onset. This period of time was selected to include the range of maximum changes observed across infants for HbO_2 and HHb. Statistical comparisons of the response to experimental vs baseline trials across all infants were made using the valid data for each channel. One sample t-tests were performed during the specified experimental trial time window, to compare the maximum change (or amplitude) in HbO_2 and HHb with the mean of the baseline trial.

Results

According to the criteria previously described, valid data was obtained from 24 of the 26 infants tested. The mean number of experimental trials recorded in these infants, was 9.6 and the mean length of the recording session was 6 minutes 30 seconds. The proportion of valid channels across the group of infants was 76% in the left lateral pad and 82% in the right lateral pad. The preferential looking task indicated that there was a significant preference for the experimental stimulus over the baseline stimulus (exp = 80.2%, baseline = 19.8%, $p < 0.001$, $t = 5.766$, paired t test).

A one sample t-test of the maximum increase (or amplitude) in HbO_2 in response to the experimental stimuli (during the specified time window 10-18s post stimulus onset) revealed a significant increase from the baseline in HbO_2 in two channels (ch14: $t = 2.356$, $p < 0.05$, $df = 18$; ch28: $t = 3.117$, $p < 0.01$, $df = 23$. Note that the degrees of freedom differ as recordings on ch14 were achieved in only 19 of the total 24 infants). These two channels were located in the most posterior area of the pads, over the T5 and

T6 scalp locations (see figure 1). Within these two channels, a Sign test revealed that across the group, infants were significantly more likely to have an increase in HbO_2 in response to the experimental stimuli (ch14: N = 18, p = 0.048, ch28: N= 24, p = 0.01) There were also an additional two channels that reached borderline significance at the most anterior area of the pads, (ch2: t = 2.037, p = 0.055, df = 16, ch16: t = 1.83, p = 0.08, df = 20). There were no significant changes in the concentration of HHb across infants. Table 1 gives a summary of these results.

The grand averaged time courses of the haemodynamic changes in HbO_2 and HHb for channels 14 and 28 are shown in figure 3. The time courses display the response across infants to the experimental condition followed by the baseline condition. Alongside the significant increase in HbO_2 concentration in both channels, the non-significant HHb concentration changes vary, with channel 14 showing a decrease and channel 28 a slight increase. The latency of the maximum change in HbO_2 in both channels occurred at approximately 13-15s post stimulus onset, towards the end of the trial.

Discussion

Changes in the concentration of HbO_2 showed a significant increase in response to the social dynamic stimuli in two channels located in the posterior area of the pad over each hemisphere, scalp locations T5 and T6 (10-20 system). The location of this activation is consistent with findings of previous fMRI research with adults (for review see Allison et al, 2000; Pelphrey et al, 2005). The findings support the possibility that

five-month-old infants may already activate a restricted temporal region for the visual processing of social stimuli.

However, an alternative interpretation of is the results from Experiment 1 is that the significant response seen in the posterior channels of the lateral pads is attributable to activity in MT/V5 rather than an area of the brain responsible for processing social stimuli such as STS. MT/V5 is a motion sensitive area of the visual cortex located near to posterior STS, which responds to dynamic stimuli (Henning, Merboldt, & Frahm, 2005; Nogushi, Kaneoke, Kakigi, Tanabe & Sadato, 2005; Watanabe, Kakigi, Miki & Puce, 2006). As the experimental stimuli differed from the baseline in both the social nature of the images and in the dynamic motion involved in Experiment 1, we cannot determine which aspect of the dynamic social stimulus elicited the effect observed. Therefore a second experiment was designed to investigate this question. To explore the importance or otherwise of complex dynamic motion for the activations observed, in Experiment 2 we contrasted two experimental conditions; the first was the same social dynamic video used in the first experiment; and the second was a non-social dynamic video that involved complex and nested motion patterns. We predict that the posterior temporal effect observed in Experiment 1 would be evident in Experiment 2 for the social dynamic stimuli but not for the non-social dynamic stimuli. This result would allow us to support the hypothesis that the observed activation can be attributed to social processing occurring in the STS.

Experiment 2

Method

Participants

Twelve five-month-old infants took part in the second experiment (6 females and 6 males; age 146 ± 6.4 days old). A further seven infants participated but were excluded from the study (four failed to look at the stimuli for the minimum number of trials; two became fussy and in a further one the NIRS head gear was improperly placed). All parents volunteered by responding to advertisements and gave written informed consent to participate. The study protocol was approved by the appropriate Ethics Committee. The infants were from a varied ethnic and socio-economic background, predominantly white (British/non-British).

Procedure

The same procedure was used as in Experiment 1, but with two alterations. Experiment 2 compared two experimental conditions; social dynamic and non-social dynamic. The social dynamic stimuli were the same as in Experiment 1, while the non-social dynamic stimuli were video clips of machine cogs and pistons and moving mechanical toys. These stimuli were selected because they involved complex interacting curvilinear motion patterns that served as a good control for biological and facial motion. The two experimental conditions were presented sequentially with the baseline trials occurring between each experimental trial (see figure 1).

In addition the preferential looking trial was presented at the same two intervals (i.e. one after six trials and a further one after the twelfth trial), however instead of comparing the social stimulus to baseline, a still image of each of the experimental conditions was displayed, i.e. social vs non-social.

Data acquisition, array placement and data rejection

This followed the same methods as Experiment 1, but with one amendment to the data rejection criteria. As there were two types of experimental condition in Experiment 2, infants watched a lower number of trials per condition even though the overall looking time was comparable. Therefore, in Experiment 2 we required a minimum of three valid trials for each experimental condition (social dynamic or non-social dynamic).

Data analysis

This followed the same procedure as that used in Experiment 1. In addition to the one sample t-tests performed on each separate experimental condition (social dynamic or non-social dynamic versus baseline) a paired t-test was also performed in each channel to compare the activation in response to the two different conditions. As in Experiment 1, these analyses were conducted on the maximum change in HbO_2 and HHb compared with baseline, during the specified experimental time window (10-18s post experimental stimulus onset).

Results

According to the criteria previously described, we included data from 12 of the 19 infants tested. The mean number of experimental trials recorded in these infants was 5 social dynamic trials and 5 non-social dynamic trials, and the mean length of the recording session was 6 minutes, similar to that of Experiment 1. Due to a technical fault in the left lateral pad, channels 1 and 3 were excluded from seven of the infants' data, though all of these infants still met the exclusion criteria described earlier. The proportion of valid channels across the group of infants was 67% in the left lateral pad and 77% in the right lateral pad. The preferential looking task indicated that there was a significant preference for the social stimulus over the non-social stimulus (dynamic social = 71.6%, non-social dynamic = 28.4%, $p < 0.05$, $t = 4.419$, paired t test).

Group effects for the social dynamic experimental condition using a one sample t-test of the maximum increase in HbO_2 in response to the stimulus (during the specified time window 10-18s post stimulus onset) revealed a significant increase from baseline in HbO_2 concentration in 9 channels (see table 2). 5 of the 9 channels were located in the posterior region of the pads in each hemisphere (ch11, 14, 25, 27, 28). Two of these 5 channels are the same two channels that were found to have a significant increase in HbO_2 in response to the social dynamic stimuli in Experiment 1 (ch14 and 28). The remaining four channels with significant activation were located in the anterior regions of each lateral pad (ch1, 15, 16, 17). Two of these four channels showed borderline significance in response to the social dynamic stimuli in Experiment 1 (ch1, 16).

Group effects for the non-social dynamic experimental condition using a one sample t-test of the maximum increase in HbO_2 concentration in response to the stimulus

(during the specified time window 10-18s post stimulus onset) revealed a significant increase from the baseline in HbO_2 in two channels (ch15 and 26; see table 2). These channels were located in the right lateral pad, one of which located in the anterior region, was also found to be active during the social dynamic experimental condition. There were found to be no significant changes in HHb concentration during either experimental condition.

Finally, a paired sample t-test to compare the difference in the maximum increase in HbO_2 from baseline during each experimental condition revealed a significant difference between the response for the social dynamic and the non-social dynamic stimuli in two channels (see table 2). These two channels, 14 and 28, displayed a significantly larger increase in HbO_2 to the social dynamic stimuli compared to the non-social dynamic stimuli. These two channels are the two most posterior channels in each pad and are the same channels that were found to have a significant increase in HbO_2 in response to the social dynamic stimuli in Experiment 1.

The grand averaged time courses of the haemodynamic changes in HbO_2 and HHb for channels 14 and 28 (the channels found to show a significant difference in the haemodynamic response across experimental conditions) are shown in figure 4. The time courses display the response across infants to each experimental condition followed by the baseline condition. During the social dynamic experimental condition, alongside the significant increase in HbO_2 concentration in both channels, the non-significant HHb concentration changes vary, with channel 28 (right hemisphere) showing a decrease in HHb whilst channel 14 (left hemisphere) first showed a slight increase in HHb followed by a decrease. The latency of the maximum change in HbO_2 in both channels occurs at

approximately 15-16 seconds post stimulus onset just as the stimulus is ending, a similar finding to that of Experiment 1. In contrast, during the non-social dynamic experimental condition the haemodynamic time courses show two different trends in these two channels. In channel 14 (left hemisphere) both HbO_2 and HHb concentration show a slight increase over the time course. Whereas in channel 28 (right hemisphere) the HbO_2 and HHb show the opposite trend to the response observed to the social dynamic stimuli; the HbO_2 concentration decreases across the time course, whereas the HHb concentration increases.

Finally, figure 5 shows a schematic map of the sensor pads for each hemisphere highlighting the significant HbO_2 changes seen across infants. A schematic map is shown for each Experiment (1 and 2), with separate maps for each statistical comparison (social dynamic versus baseline (Experiments 1 and 2), non-social dynamic vs baseline (Experiment 2), and social versus non-social (Experiment 2)) illustrating the spatial distribution of the significant responses. This figure highlights the clustered effect in the posterior and anterior regions seen in response to the social dynamic stimuli (figure b).

Discussion

The findings of Experiment 2 reveal several significant effects in support of our hypotheses. Firstly, there were significant haemodynamic increases in HbO_2 in response to the social dynamic stimuli in the posterior region of each sensor pad, localised to scalp locations T5 and T6 (10/20 system). These effects replicate those obtained in Experiment 1. Additionally, a consideration to be addressed by Experiment 2 was whether the posterior haemodynamic change observed in response to the social dynamic stimuli could

be attributed to MT/V5, a general motion sensitive area, rather than attributed to a social-stimulus specific response in the STS.

In Experiment 2 the non-social dynamic stimuli did not reveal any significant HbO_2 concentration changes in the posterior channels that showed significant effects in response to the dynamic social stimuli in Experiment 1 and Experiment 2. Further, when the response to the dynamic social stimuli was directly compared to that to the non-social dynamic stimuli, a significant difference was found between the two conditions in bilateral posterior channels. The social dynamic stimuli had a significantly greater increase in HbO_2 compared with the non-social dynamic stimuli in the most posterior channels of the pads near to scalp locations T5 and T6 (10/20 system). These findings provide further support for the hypothesis that infants as young as five months of age have a specialised area of the temporal cortex activated by dynamic social stimuli. The location of this neural activity identified by the significant haemodynamic changes is consistent with the findings of fMRI studies on STS activity in adults in response to social stimuli (for review see Allison et al, 2000; Pelphrey et al, 2005).

An unpredicted region of activation in response to social dynamic stimuli was also found in the most anterior area of the pad over each hemisphere, with grand averaged HbO_2 haemodynamic changes approaching significance in Experiment 1 and exhibiting significant increases in response to the social dynamic stimuli in Experiment 2. Moreover, a significant increase in HbO_2 was also found in one of these significant right anterior channels in response to the non-social dynamic stimuli, indicating a more general response property.

General Discussion

We have used optical topography to detect differences in stimulus processing in five-month-old infants. Our results demonstrate greater neural activation, as measured by relative changes in the haemodynamic response, in regions of the posterior lateral pads in response to dynamic social stimuli. This area corresponds approximately to scalp locations T5 and T6, which are located over the region of the STS where neural activation is found in adults in response to social stimuli. These findings provide further support for the hypothesis that infants as young as five months of age have a specialised area of the temporal cortex for processing social dynamic stimuli. In further support of this hypothesis, neural activation as measured by haemodynamic change in HbO_2 to the non-social dynamic stimuli, was not evident in the posterior region of the pads. These findings are in accord with an adult fMRI study by Beauchamp and colleagues, who observed a greater response in the superior temporal cortex to moving human stimuli compared with moving tools (Beauchamp, Lee, Haxby and Martin, 2002).

Interestingly, a more widespread response to the social dynamic stimuli was observed in Experiment 2 compared with Experiment 1 (i.e. Exp 2 had a greater number of channels with significant haemodynamic changes). One difference between the first and second experiment was the number of successful trials that the infants attended to; reducing in number from an average of 10 trials in Experiment 1, to 5 trials in Experiment 2. This was an unavoidable consequence of adding a second experimental

condition. Is it possible that as the stimulus presentation continues, the infant's neural responses adapt to the stimuli becoming reduced in amplitude over time? The adaptation of neural responses to repeated stimulus events has been identified using a number of measures from single unit recording to functional MRI (Krekelberg, Boynton & van Wezel, 2006). Taking this into consideration, we re-ran the group analyses for Experiment 1, including only the first 5 trials from each infant. We found that the number of significant channels increased from ch14 & 28, to ch14, 25, 28 in the posterior region and ch2, 15, 17 in the anterior region of the lateral pads. This finding suggests that infants' neural responses do indeed adapt to the stimuli, as has been found in fMRI studies with adults (several mechanisms have been proposed for this effect - habituation leading to suppression of temporally repetitive stimuli (Grill-Spector & Malach, 2001); priming of selective neurons (Schacter & Buckner, 1998); inhibition of non-selective neurons (Li, Miller & Desimone (1993)), and/or that the response lowers as infant's become less attentive to the stimuli. Interestingly this effect was found to not occur as strongly in the posterior areas of the lateral pads, as significant channels were found in Experiment 1 over the full set of trials.

The anterior activation discussed above occurred extensively in response to the social dynamic stimuli (i.e. 4 channels, left and right hemisphere), and to a lesser extent in response to the non-social dynamic stimuli (1 channel in right hemisphere), in a region approximately between scalp locations T4, F4 and F8. There are several cognitive processes and associated neural activity evident in adults that could provide tentative interpretations for this anterior cortical activation. Though research into neural activation in response to biological motion and social dynamic stimuli has primarily focussed on

posterior temporal areas such as STS, often additional activation is found in an anterior temporal/inferior frontal region of the cortex. For example, a study by Saygin and colleagues (Saygin, Wilson, Hagler, Bates & Sereno, 2004) of biological motion perceived in point light displays found bilateral activation in the inferior frontal gyrus. This activation is in a similar area to the region of anterior activation found in response to the social dynamic stimuli in the current study. The authors conclude that this frontal activity reflects the recruitment of action observation networks and provides a possible interpretation for the anterior location of activity in the present study. Further, a meta-analysis of functional neuroimaging studies (Pelphrey et al, 2005) of biological motion suggests that mouth movements are often associated with anterior temporal and/or left area of the STS while eye gaze is often associated with posterior temporal and/or right area of the STS. Moreover in an fMRI study conducted to support this meta-analysis, Pelphrey and colleagues also found that mouth and eye movements (but not hand movements) caused bilateral activation in the middle and inferior frontal gyrus (Pelphrey et al, 2005). It is evident that perception of differing social movements can cause neural activation in different locations of the cortex in adults. Though the current study used a variety of social movements in the video clips (hand, eye and mouth) potentially allowing us to investigate such effects, the clips were mixed together during each 16 second trial and so separate haemodynamic responses for each type of social movement could not be assessed. It is clear that further developmental research is needed to investigate whether the spatial localisation of the haemodynamic responses observed in this study could potentially differ across varying social actions, or whether the localised areas of neural activation reported in adult research will not yet be evident in infancy.

Although far greater anterior neural activation was observed in response to the social stimuli, some effect was also seen in response to the non-social dynamic stimuli, which was restricted to the right hemisphere. Research on spatial working memory as evidenced in a recent study by Imaruoka and colleagues (2005) may offer a further explanation for this neural activity. These authors investigated neural responses to a multiple component object permanence-tracking task in which participants were required to maintain a coherent percept of a multiple component object either while it was stationary or dynamic. During the dynamic condition there was significant activation in the ventral frontal cortex strongly lateralised to the right hemisphere, a region of the cortex similar to the activation found in the current study to the non-social and social dynamic stimuli. In support of this finding, a meta-analysis by D'Esposito and colleagues (1998) concluded that activity in the ventral frontal areas in response to spatial working memory tasks is often strongly lateralized to the right hemisphere. Further to this, the ventral frontal cortex including the inferior frontal gyrus is within the frontoparietal network which is often associated with a range of diverse cognitive demands including goal directed and stimulus driven attention (Corbetta & Shulman, 2002; Culman et al, 1998; Duncan & Owen, 2000; Jovicich et al, 2001).

As to our knowledge there are currently no other infant neuroimaging studies of this nature, we have to rely on research with adults to provide support or an explanation for our findings. Potentially, infants could be responding to the multi component dynamic objects used in the current study in the same way that adults do using such processes as spatial working memory, goal directed and stimulus driven attention or action observation networks (for the social dynamic stimuli). Further developmental research is

needed to investigate whether the ventral-frontal spatial localisation of the haemodynamic responses observed in this study could be attributed to any of the processes outlined above.

We have demonstrated that young infants may already show activation of a specific area of the temporal cortex in response to social stimuli, evidenced by localised oxyhaemoglobin responses in the posterior channels of the temporal pads bilaterally. We were however, unable to detect any significant decreases in deoxyhaemoglobin in response to the social stimuli. While adult NIRS studies show HbO_2 and HHb responses consistent with BOLD fMRI signal changes (i.e. a decrease in HHb and parallel increase in HbO_2), infant data reveals a less consistent pattern of HHb changes in response to neural activation (Baird et al, 2002; Sakatani, et al, 1999; Meek et al, 1998; Wilcox et al, 2001). It is uncertain whether in infants the standard decrease in HHb should be expected, and is a matter of much controversy. Related to this, there is also ongoing debate concerning the ideal pair of wavelengths to use for NIRS measurements (Boas, Dale & Franceschini, 2004; Sato, Kiguchi, Kawaguchi & Maki, 2004; Yamashita, Maki & Koizumi, 2001), and in particular how the wavelengths of the source lasers may effect the accurate measurement of HHb changes. Indeed, it is possible that the wavelengths of the source lasers in the multi-channel system used in this study may not be as sensitive to HHb changes as to the estimation of HbO_2. We are currently investigating this wavelength dependent response and this debate is being addressed in future generations of NIRS systems.

Despite these technical issues, we can clearly measure HbO_2 haemodynamic responses to social and non-social dynamic stimuli. Further work with this technique may

help us understand whether infants display differential cortical responses to differing types of social stimuli and whether we can associate this activity with the STS, as has been shown in fMRI studies with adults.

Does the activation of posterior temporal regions to social dynamic stimuli in 5-month old infants imply the early specialisation of the cortical social brain network? While other studies are consistent with the rapid specialisation of regions of the cortical social brain network (Grossman et al. submitted), a large body of electrophysiological and fMRI data indicates relatively gradual specialisation of key components of the adult social brain network, such as the fusiform face area (e.g. De Haan et al, 2002, Cohen-Kadosh & Johnson 2007). Although the degree of specialisation of the posterior temporal areas remains to be investigated in more detail, one possibility is that regions of the social brain critical for detecting communicative situations specialise before other aspects of social brain function (Grossman & Johnson 2007). The findings of this study highlight the exciting potential of optical topography as a tool for studying these critical issues in developmental cognitive neuroscience.

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Figure Legends

Figure 1: A timeline of the stimuli for a) Experiment 1 and b) Experiment 2.

Figure 2: a) A lateral and birds eye view of an infant wearing the sensor pads and head gear. b) A schematic view of the sensor pads on both hemispheres with the approximate location of the channels shown in relation to the 10-20 system.

Figure 3: Experiment 1 - Grand averaged time course of the haemodynamic response across infants for the two most posterior channels on the left (a) and the right (b) lateral pad.

Figure 4: Experiment 2 - Grand averaged time course of the haemodynamic response across infants for each experimental condition (social dynamic and non-social dynamic) for the two most posterior channels on the left (a) and the right (b) lateral pad.

Figure 5: A schematic view of the sensor pads with channels showing a significant group effect for HbO2 (maximum increase in HbO2 from baseline) highlighted in red; a) Experiment 1 – social dynamic; b) Experiment 2 – social dynamic; c) Experiment 2 – non-social dynamic; d) Experiment 2 – non-social dynamic vs social dynamic.

Table 1

Mean maximum changes in HbO_2 and HHb concentration (μM) across infants during the window of activation 10 – 18 sec post experimental stimulus onset; one sample *t* tests; *p < 0.05; statistically significant increase in HbO_2 or HHb concentration compared to baseline.

Left lateral pad							**Right lateral pad**						
	Δ[Hb0$_2$] μM			**Δ [HHb] μM**				**Δ [Hb0$_2$] μM**			**Δ [HHb] μM**		
Ch	*Mean*	*t*	*p*	*Mean*	*t*	*p*	**Ch**	*Mean*	*t*	*p*	*Mean*	*T*	*p*
1	0.31	1.40	0.18	0.20	1.32	0.20	15	0.21	1.39	0.18	-0.26	-1.68	0.11
2	0.48	2.04	0.055	0.28	1.16	0.26	16	0.34	1.83	0.08	0.01	0.31	0.76
3	0.26	0.90	0.38	0.09	0.09	0.93	17	0.32	1.22	0.24	-0.09	0.02	0.99
6	0.18	0.73	0.48	-0.04	-0.40	0.69	20	-0.10	-0.46	0.65	0.11	-0.07	0.95
7	0.15	0.76	0.46	0.11	1.60	0.13	21	0.37	1.93	0.07	0.15	0.09	0.93
8	-0.02	-0.58	0.57	0.16	1.04	0.31	22	-0.30	-1.51	0.16	0.26	0.06	0.96
11	0.08	0.64	0.54	-0.01	-1.20	0.25	25	0.29	1.30	0.21	-0.25	-1.86	0.08
12	0.05	0.21	0.84	0.15	0.779	0.45	26	-0.02	-0.07	0.92	-0.09	0.64	0.54
13	0.10	0.40	0.69	-0.11	-1.10	0.29	27	0.24	0.90	0.38	-0.05	0.55	0.59
14	0.43	2.36	0.03*	-0.25	-1.01	0.33	28	0.59	3.12	0.005*	0.17	1.64	0.11

Table 2:

Group data of the statistical analyses and mean maximum changes in HbO_2 : The results are shown for the channels with a statistically significant increase in HbO_2 concentration compared to baseline during the window of activation 10 – 18 sec post experimental condition onset (one sample *t* tests; *p < 0.05).

Social dynamic experimental condition (one sample t-test)							
Left lateral pad				**Right lateral pad**			
	Δ[Hb0$_2$] µM				**Δ [Hb0$_2$] µM**		
Ch	*Mean*	*t*	*p*	**Ch**	*Mean*	*t*	*p*
1	2.16	4,54	0.045*	15	0.92	3.79	0.003*
11	0.88	2.48	0.035*	16	0.61	2.74	0.02*
14	1.26	5.63	0.001*	17	0.67	2.32	0.04*
				25	0.60	2.91	0.04*
				27	0.72	2.82	0.02*
				28	0.69	2.41	0.04*
Non-social dynamic experimental condition (one sample t-test)							
Left lateral pad				**Right lateral pad**			
	Δ[Hb0$_2$] µM				**Δ [Hb0$_2$] µM**		
Ch	*Mean*	*t*	*p*	**Ch**	*Mean*	*t*	*p*
				15	0.61	3.08	0.01*
				26	0.61	2.42	0.03*
Non-social vs social experimental condition (paired sample t-test)							
Left lateral pad				**Right lateral pad**			
	Δ[Hb0$_2$] µM				**Δ [Hb0$_2$] µM**		
Ch	*Mean*	*t*	*p*	**Ch**	*Mean*	*t*	*P*
14	-0.88	-2.15	0.04*	28	-1.15	-2.91	0.01*

Figure 1

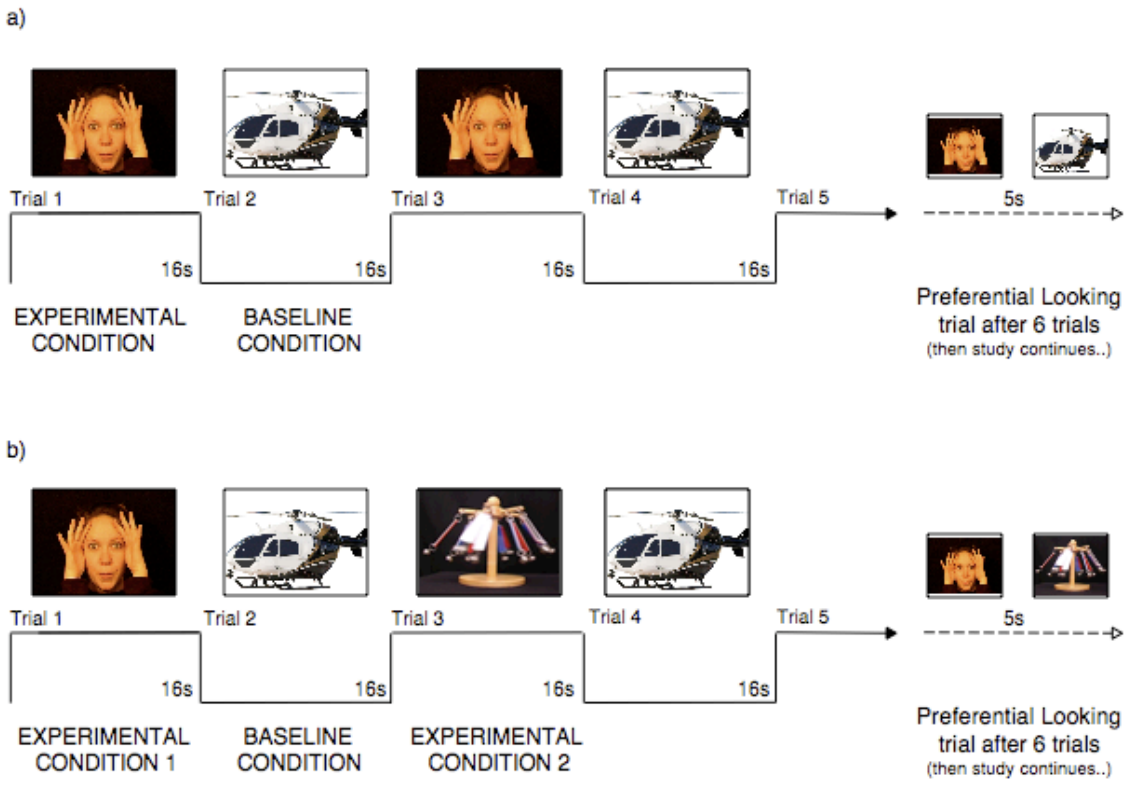

a)
Trial 1
Trial 2
Trial 3
Trial 4
Trial 5
16s
16s
16s
16s
5s
EXPERIMENTAL CONDITION
BASELINE CONDITION
Preferential Looking trial after 6 trials
(then study continues..)
b)
Trial 1
Trial 2
Trial 3
Trial 4
Trial 5
16s
16s
16s
16s
5s
EXPERIMENTAL CONDITION 1
BASELINE CONDITION
EXPERIMENTAL CONDITION 2
Preferential Looking trial after 6 trials
(then study continues..)

Figure 2

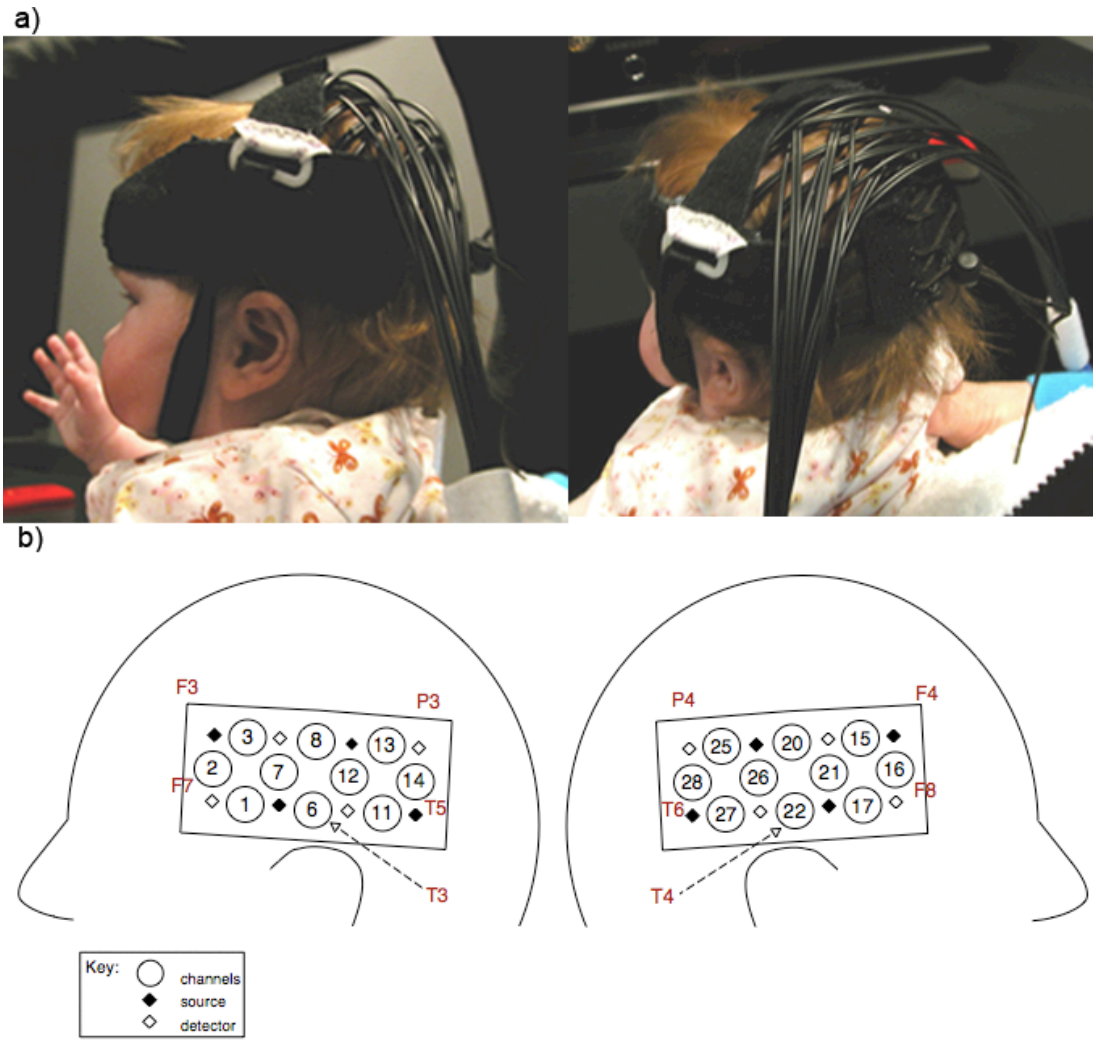
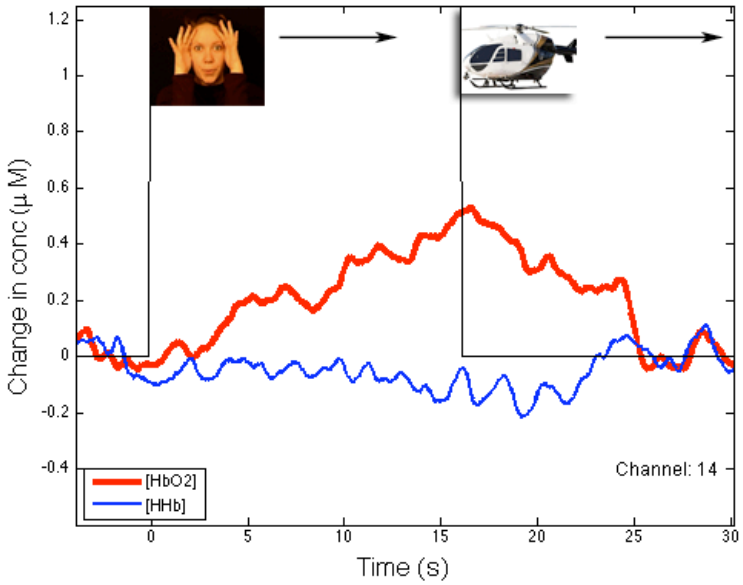


Figure 3
a)



b)

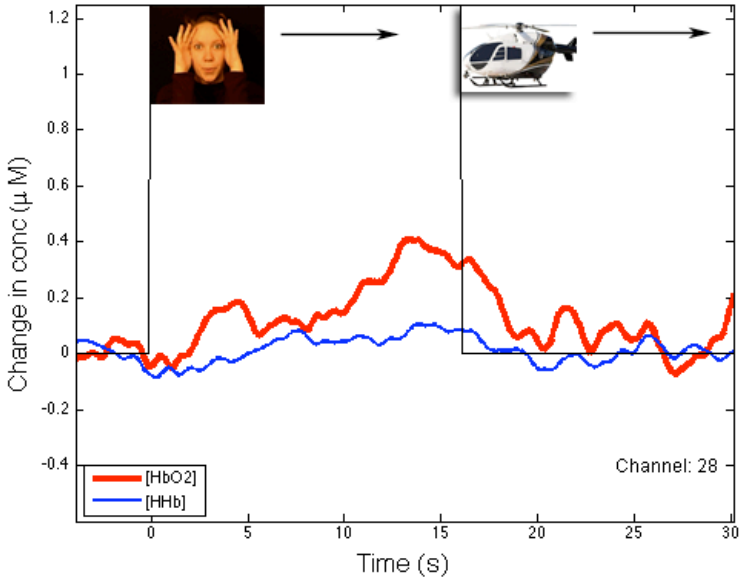
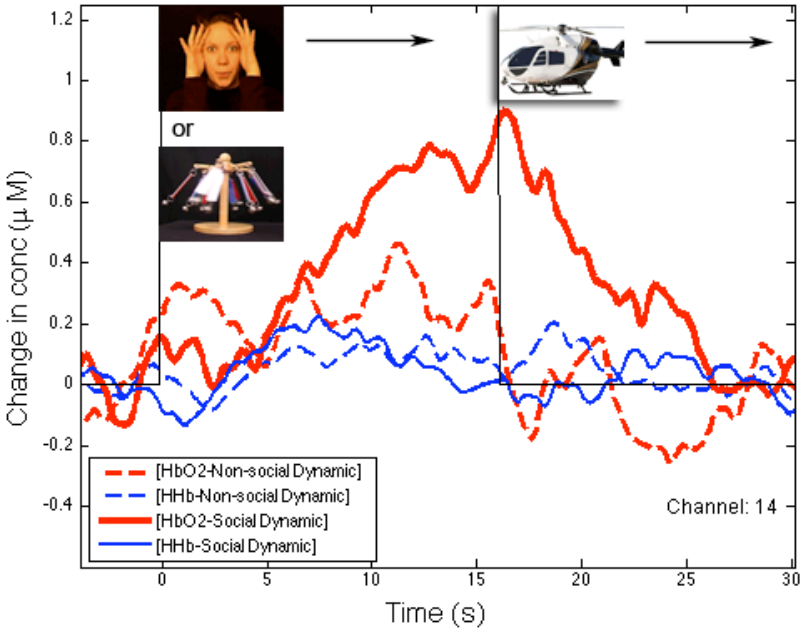


Figure 4
a)


or
Change in conc (μ M)
Time (s)
[HbO2-Non-social Dynamic]
[HHb-Non-social Dynamic]
[HbO2-Social Dynamic]
[HHb-Social Dynamic]
Channel: 14

b)

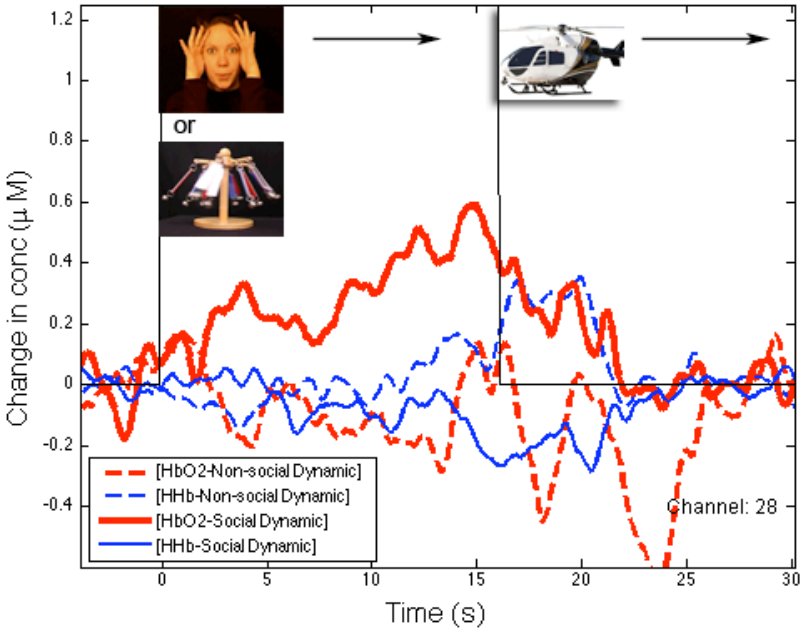
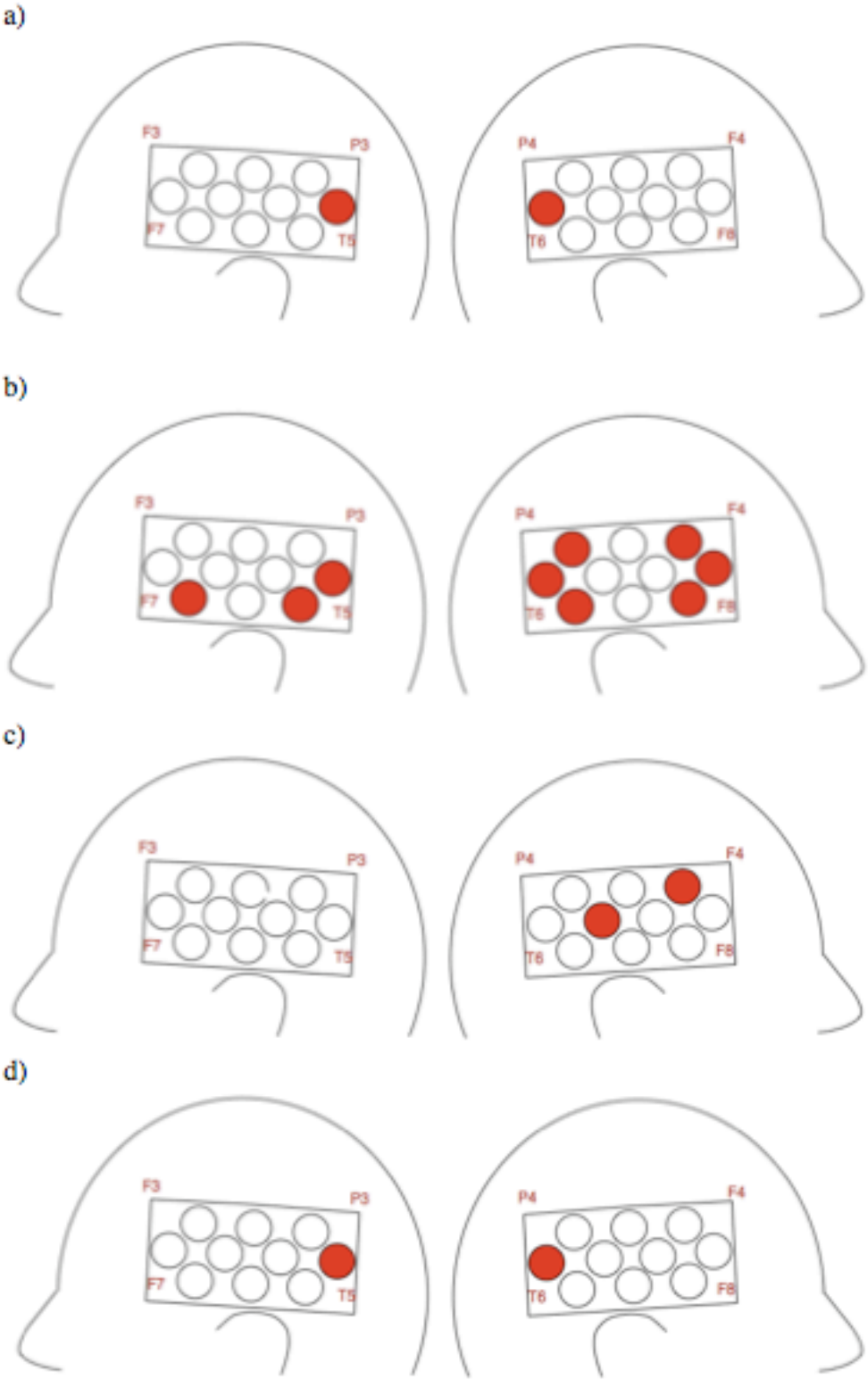

or
Change in conc (μ M)
Time (s)
[HbO2-Non-social Dynamic]
[HHb-Non-social Dynamic]
[HbO2-Social Dynamic]
[HHb-Social Dynamic]
Channel: 28

Figure 5


a)
F3
P3
F7
T5
P4
F4
T6
F8
b)
F3
P3
F7
T5
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F4
T6
F8
c)
F3
P3
F7
T5
P4
F4
T6
F8
d)
F3
P3
F7
T5
P4
F4
T6
F8