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The contribution of facial dynamics to subtle expression recognition in typical viewers and developmental visual agnosia

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ABSTRACT

Facial expressions are inherently dynamic cues that develop and change over time, unfolding their affective signal. Although facial dynamics are assumed important for emotion recognition, testing often involves intense and stereotypical expressions and little is known about the role of temporal information in the recognition of subtle, non-stereotypical expressions. In Experiment 1 we demonstrate that facial dynamics are critical for recognizing subtle and non-stereotypical facial expressions, but not for recognizing intense and stereotypical displays of emotion. In Experiment 2 we further examined whether the facilitative effect of motion can lead to improved emotion recognition in LG, an individual with developmental visual agnosia and prosopagnosia, who has poor emotion recognition when tested with static facial expressions. LG's emotion recognition improved when subtle, non-stereotypical faces were dynamic rather than static. However, compared to controls, his relative gain from temporal information was diminished. Furthermore, LG's eye-tracking data demonstrated atypical visual scanning of the dynamic faces, consisting of longer fixations and lower fixation rates for the dynamic-subtle facial expressions, comparing to the dynamic-intense facial expressions. We suggest that deciphering subtle dynamic expressions strongly relies on integrating broad facial regions across time, rather than focusing on local emotional cues, skills which are impaired in developmental visual agnosia.

1. Introduction

A picture is worth a thousand words. But is a single, frozen picture enough for conveying an emotional expression? In everyday social interactions, facial expressions of emotion are highly dynamic – with diverse fleeting movements, emerging and disappearing over time. Furthermore, facial expressions are rarely stereotypical, rather, they are often subtle and varied. Yet, most studies on emotion perception fail to capture these key characteristics and use static, intense and stereotypical emotion displays from standardized sets (Ekman and Friesen, 1976; Ekman et al., 2002; Izard, 1994; Langner et al., 2010; Van Der Schalk et al., 2011).

Studies examining the unique advantage of dynamic over static displays of emotion have also been strongly influenced by the basic emotion approach (Ekman and Friesen, 1976; Ekman, 1993; Izard, 1994), which highlights stereotypical facial expressions. As a result, little is known about the role of dynamic information in the perception of subtle, non-stereotypical facial expressions. The current study points the spotlight at such faces and examines their recognition in both typical individuals and in a unique neuropsychological case of developmental visual agnosia.

1.1. The dynamic gain effect

Previous studies exploring the role of facial dynamics in expression perception have shown that in comparison to static displays, emotion recognition is facilitated when facial expressions are dynamic (Krumhuber et al., 2013). The beneficial effect driven by visual motion is particularly prominent for subtle facial expressions (Ambadar et al., 2005; Bould et al., 2008), while stronger displays of emotion show no such perceptual advantage (Bould and Morris, 2008; Gepner et al., 2001). The reason for this may be that for intense expressions, static displays are already strong carriers of emotional signals, leaving little room for improvement through the provision of dynamic information (Krumhuber et al., 2013). We refer to the facilitative effect of motion to emotion recognition as the "dynamic gain effect".

The notion that dynamic faces are processed in a different way than static faces is also evident in neuroimaging studies. It has been shown that emotion recognition of dynamic and static facial expressions involves dissociable neural pathways (Kilts et al., 2003). Particularly,

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while static displays of emotion mainly activated a motor, prefrontal, and parietal cortical network (Kilts et al., 2003), the dynamic displays of emotion were found to be correlated with enhanced posterior activation of the occipital and temporal cortices, especially in the right hemisphere. Frontal and parietal sites in the right hemisphere, such as the ventral premotor cortex and intraparietal sulcus, were also activated in response to dynamic facial expressions (Kilts et al., 2003; Sato et al., 2017, 2004). Higher intensities of dynamic facial expressions, which are characterized with a higher degree of visual motion, were also correlated with stronger neural activity in classic motion-responsive areas in the occipital cortex, such as MT+ /V5 and V3a (Gilaie-Dotan, 2016b; Sarkheil et al., 2012). Similarly, expressive intensity increased the magnitude of emotional event-related brain potentials (ERP), suggesting that larger facial movements increase the arousal-value of the expression and improve its visual processing, leading to better discriminability between emotions (Recio et al., 2014).

Different aspects of information may contribute to the enhancement of emotion perception when faces are dynamic rather than static. Ambadar et al. (2005) showed that for subtle expressions, a static expressive face preceded by a static neutral face is perceived just as accurately as the full dynamic sequence. This result suggests that the dynamic gain effect might be attributable to increased sensitivity to changes, rather than the perception of motion signals per se, such as velocity of change.

Conversely, Kamachi et al. (2013) provided support for the notion that participants were affected by the unique temporal characteristics of the facial expression, such as the rate at which the expression unfolds in the face. For example, sadness was most accurately identified when slow pace sequences were presented, anger was most accurately detected from medium pace sequences and happiness was most accurately identified when fast pace sequences were presented. In line with this finding, Bould et al. (2008) demonstrated that the speed at which the emotions emerge is a diagnostic cue to emotion recognition, as slowing down or speeding up the original sequences influenced recognition accuracy across the six emotional expressions.

Finally, Jack et al. (2014) demonstrated that dynamic facial expressions transmit an evolving hierarchy of signals over time, characterized by simpler signals appearing earlier, followed by more complex socially-specific signals that enable emotion discrimination. This finding supports previous results (Bould et al., 2008; Kamachi et al., 2013) by showing that unique temporal characteristics of the dynamic facial expression facilitate emotion recognition and contribute to the dynamic gain effect.

1.2. Dynamic facial expression stimuli in emotion research

While previous research has yielded important insights into the contribution of temporal information to subtle expression perception, the stimuli used had several limitations. For example, some researchers created varying degrees of static subtle facial expressions by digitally morphing a neutral face with an emotional one. They then created multiple still frames sequences in which the face changed from neutral to a peak expression with different degrees of intermediate stages (e.g., see Kamachi et al., 2013; Bould and Morris, 2008). Although the resulting expressions are indeed subtle, this method is limited to the prototypical facial movements of basic emotions. Moreover, dynamic expressions based on morphing may not capture the anatomical richness of actual facial motion trajectories when faces move from neutral to expressive.

Other studies used dynamic video clips of prototypical expressions that were edited and truncated at an early point before the full blown emotion peaked (i.e – Ambadar et al., 2005; Bould et al., 2008). Such displays may differ in shape and temporal dynamics from displays that are genuinely subtle and that would never develop to a full blown prototypical display (Matsumoto and Hwang, 2014).

In a different type of study, Jack et al. (2014) examined dynamic facial expressions using a computer program that randomly selected a set of facial action units (AUs, functionally independent facial movements; Cohn et al., 2007) and combined them with different temporal parameters to generate a random dynamic facial animation. Observers categorized the random facial animations as conveying one of six basic emotions, or "don't know". Then, observers' categorical responses were reverse correlated with the randomly chosen AUs and temporal parameters to produce dynamic facial expression models that best represent each emotional category. Emotional displays in this method differ from previous studies due to the fact that they are not restricted to prototypical AU combinations. However, in this experimental design dynamic faces were presented solely, without the comparison to static faces. Moreover, in this method it is not clear whether facial expressions are subtle or intense. Finally, the use of avatars rather than humans, and the reverse correlation from a multiple choice labeling task to a set of models, tend to reduce the expressions' ecological validity and to focus on internal representations of facial expressions which may differ from those encountered in everyday social interactions.

1.3. The present study

In the current study we addressed prior limitations and examined the role of facial dynamics to emotion perception using a novel set of naturalistic facial expressions that are dynamic, non-stereotypical and subtle (Yitzhak et al., 2017). In fact, recent work with these stimuli has demonstrated that they are perceived as more ecologically valid, and better representing of expressions in real life situations. Following these recent findings, in Experiment 1 we hypothesized that emotion recognition of the subtle stimuli will be most accurate when facial expressions are presented portraying a full dynamic episode (i.e., a dynamic clip starting with a neutral facial expression which gradually turns emotional). Unlike prototypical intense expressions, in which a dynamic clip may be reduced to a single peak image with little cost on emotion recognition, we predicted that the subtle stimuli will be highly sensitive to such a reduction, leading to significant decline in emotion recognition. In other words, we expected the dynamic gain effect for the subtle stimuli to be larger in comparison to that of prototypical intense expressions.

While these predictions are straightforward for healthy participants, in Experiment 2 we aimed to examine the dynamic gain effect in LG, an individual with a rare form of developmental visual agnosia. LG is prosopagnosic, he has deficient facial expression recognition (Ariel and Sadeh, 1996; Gilaie-Dotan, 2016a), and he presents a specific impairment with visual integration (Aviezer et al., 2012a). On the one hand, LG is expected to demonstrate the same dynamic gain effect as do individuals with typical vision. On the other hand, the excess information that needs to be processed when expressions are dynamic (additional time of presentation, change over time) leads to increased visual load and may require higher visual integration abilities – which are impaired in LG. Therefore, it is unclear whether LG would show a normal, reduced, or absent dynamic gain effect in comparison to normally sighted participants. By monitoring LG's eye movements during the emotion recognition task we expected to shed light on his strategies for extracting visual information from facial expressions.

2. Experiment 1 – The role of facial dynamics in the perception of subtle non-prototypical facial expressions

Previous work has shown that the dynamic gain effect, considered as the beneficial effect of temporal dynamics, is driven by two broad diagnostic cues selectively appearing in dynamic (rather than static) form of facial expressions. First, the change from neutral baseline to the emotional face makes facial movements more salient and detectable (Ambadar et al., 2005). Second, specific emotions are characterized by specific temporal signals, such as the expression velocity and specific facial muscular movements accompanying that emotion (Bould et al., 2008; Kamachi et al., 2013; Jack et al., 2014).

In the present study we aimed to examine the dynamic gain effect with a novel set of subtle dynamic facial expressions, portrayed in a non-prototypical manner. These subtle expressions were rated as more ecologically valid than intense stereotypical expressions by naïve observers (Yitzhak et al., 2017).

When expressions are subtle, we expected that observers will be highly sensitive to dynamic information. Specifically, our first hypothesis was that observers will be least accurate when labeling these expressions based on the peak frame alone. Second, we hypothesized that emotion categorization would be more accurate for two static images that are presented sequentially, when the first image is a neutral face and the second is the peak frame of the emotion – an improvement attributed to change perception. Third, we hypothesized that observers would be most accurate when the full dynamic facial expression, providing all the temporal cues, is presented.

By contrast, when expressions are prototypical and intense, we expected emotion recognition to be similarly accurate in all the dynamic conditions (i.e., peak frame, neutral - peak, and full dynamic). Because they are highly stereotypical and intense, these expressions may be well recognized even after the removal of all dynamic cues.

2.1. Method

2.1.1. Stimuli

Dynamic facial displays of the six basic emotions (anger, disgust, fear, happiness, sadness and surprise), and neutral, as portrayed by eight actors (4 female), were taken from two stimulus sets (see Fig. 1): a) The JeFEE (Jerusalem Facial Expression of Emotion) consisting of subtle emotion displays conveyed in a non-prototypical manner (for full details of the development and norms for this set see Yitzhak et al., 2017); b) The ADFES (Amsterdam Dynamic Facial Expression Set; Van der Schalk et al., 2011), consisting of intense emotion displays conveyed in a FACS-based prototypical manner.

From the original video clips of these two sets, we created stimuli for the three presentation conditions: a) Peak frame condition, in which a 3-second still image appeared at the frame of the peak emotional expression. For the ADFES stimuli, peak frames were taken from the static images of the stimulus set. For the JeFEE stimuli, peak frames were determined based on judgements of the emotional intensity of each expression: two judges watched each of the video clips and extracted the frame in which the facial expression reached its peak emotional intensity. When different frames were chosen by these two judges, a third judge determined which frame is more intense; b) Neutral – Peak condition, in which a 1-second still image of a neutral expression was followed by a 2-second still image of the peak image (i.e., the peak image used in the peak frame condition); c) Full dynamic condition, the original video clips from the JeFEE and the ADFES stimulus sets, started with a neutral facial expression and dynamically changed to a full-blown emotion display. The JeFEE average clip length was 10 s and the expressions changed gradually over time, while the ADFES average clip length was 6 s and the expressions changed rapidly.

2.1.2. Participants and design

A group of undergraduate students ($N = 78$, 79% female, mean age $= 24.8$) received partial course credit or payment in exchange for their participation. The study had a 2×3 mixed design. The within-subjects factor was stimulus set (JeFEE, ADFES). The between-subjects factor was the presentation condition (peak frame, neutral – peak, full dynamic). The number of participants in each condition was 25, 24 and 29 respectively. Sample size was determined based on previous studies indicating sufficient power to detect a medium to large behavioral effect (Ambadar et al., 2005; Bould et al., 2008; Kamachi et al., 2013). The experiments reported in this paper were approved by the Hebrew University ethics board and comply with the ethical requirements of the Declaration of Helsinki for human experimentation.

2.1.3. Procedure

After signing consent, participants viewed the displays on a PC screen in the lab and completed an emotion labeling task using a forced-choice question, with all of the 6 basic emotions + neutral as response options. Each group of participants observed one experimental block – peak frame static images, neutral – peak double-static displays or full dynamic stimuli. Within each block, subtle and intense expressions were presented in random order. Participants indicated which emotion label best described the presented expression. For each participant, we calculated the proportion of accurately recognized displays.

Fig. 1. Individual frame examples of (A) intense ADFES emotion displays and (B) subtle JeFEE emotion displays, over time. Both posers present facial expression of disgust.

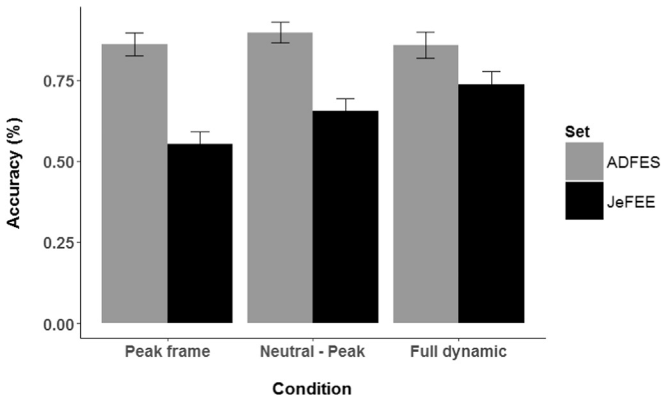

Fig. 2. Results of Experiment 1 – Emotion recognition of intense (ADFES) and subtle (JeFEE) facial expressions in three presentation conditions – peak frame still image (Peak frame), sequence of a neutral expression still image followed by a peak frame still image (Neutral - Peak) and fully dynamic video clip (Full dynamic). For the subtle JeFEE expressions, which are more difficult to recognize, emotion recognition accuracy increased as more dynamic information was available. For the intense ADFES expressions, emotion recognition accuracy did not significantly benefit from increased dynamic information. Error bars represent confidence interval with $\alpha = .05$.

2.2. Results and discussion

A two-way mixed ANOVA was conducted with stimulus set (JeFEE, ADFES) as a within-subjects factor and presentation condition (peak frame, neutral – peak, full dynamic) as a between-subjects factor. As expected, a main effect for stimulus set was found ($F(1,75) = 713.85$, $p < .001$, $\eta_p^2 = .91$), in line with the notion that overall the JeFEE subtle expressions are more challenging to recognize in comparison to the intense ADFES expressions. The main effect of condition was also significant ($F(2,75) = 6.73$, $p = .002$, $\eta_p^2 = .15$), showing a general dynamic gain effect (see Fig. 2).

Interestingly, a significant interaction emerged between stimulus set and condition ($F(2,75) = 45.89$, $p < .001$, $\eta_p^2 = .55$). As seen in Fig. 2, for the intense ADFES expressions, emotion recognition accuracy was similar across conditions ($F(2,75) = 1.34$, $p = .27$). Accordingly, none of the pairwise comparisons of different dynamic conditions in the post hoc analyses were significant (all p'$s_{\text{Tukey}} > .29$). However, for the subtle JeFEE expressions, emotion recognition improved as dynamic information increased ($F(2,75) = 20.94$, $p < .001$, $\eta_p^2 = .36$). The greatest accuracy was achieved for the full dynamic video clips, followed by the neutral – peak condition, whereas the peak frame static condition yielded the least accurate categorization. Post-hoc analyses also revealed significant differences between dynamic conditions (peak frame – neutral-peak: $t = 3.43$, $p_{\text{Tukey}} = .003$; neutral-peak – full dynamic: $t = 2.85$, $p_{\text{Tukey}} = .01$).

Using a novel set of facial expressions, we provide direct evidence for the critical role of dynamic information in the recognition of facial emotion, but only when the expressions are subtle and non-stereotypical. In line with previous studies, our results support two independent sources for the dynamic gain effect. First, the increased accuracy in the neutral – peak condition in comparison to the peak frame condition indicates that emotion recognition improves when the face changes from neutral to emotional, and therefore replicates the findings of Ambadar et al. (2005). Second, only when the full dynamic signals are present emotion recognition does reach its maximal potential. This indicates that human observers are highly sensitive to temporal cues, such as velocity of facial change or muscular activity sequences over time, when recognizing subtle facial emotions. The accuracy improvement in the full dynamic condition over the neutral – peak condition also supports previous findings (Bould et al., 2008; Kamachi et al., 2013; Jack et al., 2014). While previous studies have debated which of these two explanations is key, our unique set of stimuli demonstrates these two components of the dynamic gain effect - salience of change and temporal cues - in one experimental design, and supports the notion that these two components are additive.

One possible limitation for the interpretation that temporal cues are the signals that improve emotion recognition in the full dynamic condition over the peak frame and neutral – peak static conditions is that the dynamic and static conditions also differ in the amount of information they transmit, and not just in the dynamic aspect. In the static conditions participants observed only one or two images, while the dynamic stimuli contained many more images. However, because we used the static image that was most expressive in the peak frame and in the neutral - peak conditions, this alternative explanation seems unlikely.

Another possible limitation refers to the differential role of dynamic information that was found for subtle and non-stereotypical expressions, as opposed to intense and prototypical expressions. Beyond the qualitative difference between these two expression types, the stimuli also differ in their duration: while the duration of the intense expressions was 6 s, the duration of the subtle expressions was 10 s on average. This longer duration, and therefore the increased amount of information in the subtle, over the intense, dynamic expressions, may have contributed to the subtle full dynamic condition superiority. While it is very likely that increased spatiotemporal information would enhance performance for the subtle expressions, for the intense expressions it is an unlikely explanation, as no differences were found between participants' accuracy in the three dynamic conditions for these stimuli (see Fig. 2). Hence, it is reasonable to assume that even extended duration of the intense dynamic expressions would not increase their accuracy rate.

3. Experiment 2 – The role of facial dynamics in a case of developmental visual agnosia

After demonstrating the importance of temporal information for subtle, non-prototypical emotion recognition in healthy individuals, we turned to investigate the dynamic gain effect in LG, an individual with developmental visual agnosia and prosopagnosia (Ariel and Sadeh, 1996). Developmental visual agnosia is a rare syndrome, consisting of unique symptoms of profound visual deficits, which typically include form agnosia, deficient perceptual integration skills and impaired generalized processing of faces, including gender, emotion, and identity information (Ariel and Sadeh, 1996; Duchaine et al., 2003). Prosopagnosia is a condition of face processing impairments that is defined by difficulties in recognizing facial identity. In developmental prosopagnosia, facial expression perception is usually spared (Humphreys et al., 2007; Nunn et al., 2001; Palermo et al., 2011; Sergent and Villemure, 1989; Tranel et al., 1988; Young and Ellis, 1989).

However, although LG was diagnosed with developmental prosopagnosia, his unique condition is characterized with impaired facial expression recognition from static images, even when these are embedded in emotionally expressive bodies (Ariel and Sadeh, 1996; Aviezer et al., 2012a; Gilaie-Dotan, 2016a). This impairment is rooted in broader difficulties with perceptual integration from static information, even for low level visual processes (Brooks et al., 2012; Gilaie-Dotan et al., 2009; Lev et al., 2015). These unique symptoms of visual perception difficulties are part of LG's rare condition of developmental visual agnosia, and they differ from typical patients with developmental prosopagnosia.

Moreover, LG shows normal perceptual integration for biological motion and he successfully integrates sparse dynamic body information such as point light displays (Gilaie-Dotan et al., 2011, 2015). Considering his apparently normal motion sensitivity and normal perception of biological motion with point-light stimuli of moving human figures, in the present study we examined whether dynamic information can facilitate LG's facial expression perception.

On the one hand, based on LG's normal motion processing, there is a reason to believe that LG may overcome his integration difficulties when facial expressions are dynamic rather than static. The theoretical logic behind this prediction is that for some aspects, dynamic facial expressions are qualitatively, rather than quantitatively, different than static facial expressions. As described above, the recognition of facial emotions involves partly dissociable neural pathways for static and dynamic facial expressions (Kilts et al., 2003). Dynamic displays were also found to be correlated with enhanced neural activity and higher physiological activation, in comparison to static facial expressions (Alves, 2013; Sato et al., 2004). Such separable pathways may underlie the finding of Humphreys et al. (1993) who reported a patient with prosopagnosia who was sensitive to facial movements and could use such movements to judge moving light-dot facial expressions accurately. Overall, these findings support the notion that expression is computed separately for moving and for static faces.

On the other hand, LG has severe integration deficits for visual static information (Brooks et al., 2012; Gilaie-Dotan et al., 2009). Aviezer et al. (2012b) have shown that extended duration of face-exposure (2000 ms in comparison to 150 ms) diminished the beneficial effect of priming diagnostic facial features in LG's emotion recognition from the whole face. They suggested that LG's impairment in emotion recognition might result from deficient visual integration across face components. Such visual integration skills are critical, particularly when facial expressions are dynamic, subtle and non-stereotypical. In such expressions a variety of facial movements that are not necessarily easy to interpret independently appear sequentially over time (Yitzhak et al., 2017). Consequently, high levels of cognitive resources, such as visual attention and working memory, are likely recruited in order to visually integrate these changing spatiotemporal emotional cues and decipher the emotion in the face. Accordingly, it is possible that LG's impairment in emotion recognition from dynamic subtle facial expressions will be even more salient in comparison to static faces.

We addressed these contrasting predictions by testing LG's emotion perception of dynamic faces, for both intense and subtle expressions. Moreover, in order to examine the underlying cause for LG's emotion recognition deficits we monitored eye movements during the emotion recognition tasks.

LG's visual scanning pattern of faces was of special interest in our design based on the hypothesis that he may have never learned to successfully process emotional faces due to his developmental visual agnosia (Aviezer et al., 2012b). Specifically, LG may be impaired at visually focusing on diagnostic face components and extracting from them the affective information that is necessary for emotion categorization. If this is the case with LG, we should expect different visual scanning patterns compared to control participants. We also measured LG's fixation duration and fixation rate in different face regions in order to characterize LG's strategy of facial expression visual decoding. These eye-movements are correlated with mental effort (Chen et al., 2011; Zagermann et al., 2016), and thus may demonstrate increased difficulties in recognizing dynamic facial expressions.

3.1. Method

3.1.1. Stimuli

We used the same stimulus sets as in Experiment 1 - the JeFEE for dynamic, subtle and non-prototypical emotion displays; and the ADFES, for FACS based prototypical, intense and dynamic displays. In this experiment we tested only two presentation conditions – a peak frame condition (a 3-seconds still image of the full-blown expression appearing at the frame of the peak emotional expression); and a full dynamic condition (the original video clips from the JeFEE and the ADFES stimulus sets, starting with a neutral facial expression and rising to a full-blown emotion display. Video clip durations were 6 s for the ADFES stimuli and 10 s on average for the JeFEE stimuli). See Experiment 1 for more details.

3.1.2. Participants and design

At the time of testing, LG, an individual with developmental visual agnosia, was a 30 year old male, studying in the university, and was therefore compared to 21 healthy control undergraduate students. Participants with low tracking ratio (< 75%) were excluded, resulting in the exclusion of 6 control participants. The remaining 15 participants (11 female and 4 male, mean age = 23.2) were analyzed as a control group (mean eye tracking ratio = 87.05%, LG's eye tracking ratio = 91.2%). All participants received partial course credit or payment in exchange for their participation. The study had a 2 × 2 × 2 × 3 mixed design, with group (LG, control) as between-subjects factors, and stimulus set (JeFEE, ADFES), presentation condition (peak frame, full dynamic) and face area of interest (AOI– eyes, nose, mouth), as within-subjects factors.

3.1.3. Procedure

Participants viewed the displays on a PC and completed an emotion labeling task using a fixed-choice question, with all of the presented emotions as response options. The experimental conditions were ordered in two blocks, with the peak frame static images presented in the first block, followed by the second block of the full dynamic stimuli. Stimulus presentation within each block was random. Participants indicated which emotion label best described the expression. For each participant, we calculated the proportion of accurately recognized displays per emotion category in each of the sets. Eye-tracking data were collected with an SMI RED-m eye-tracking system, a remote controlled infrared eye camera with an automatic eye and head tracker. The system collects binocular gaze and pupil data while allowing free head movement. Recorded spatial resolution (RMS) is .1° and the sampling rate is 120 Hz. Data processing was performed in SMI BeGaze software. Areas of interest (AOIs) in the observed stimuli were defined according to physiological features of the dynamic faces (see Fig. 3).

3.2. Results and discussion

3.2.1. Emotion recognition

The mean accuracy rates for the peak frame static images of prototypical intense ADFES and subtle JeFEE stimuli were .86 and .51 for controls, respectively, and .66 and .43 for LG. For the full dynamic video clips the mean accuracy rates of prototypical intense ADFES and subtle JeFEE stimuli were .91 and .76 for the controls, respectively, and .75 and .55 for LG. Across all conditions, LG's overall mean accuracy in emotion recognition (.60) was poor in comparison to controls (M = .76, SD = .08). For overall emotion recognition, one-tailed significance test for a case-controls design (Crawford et al., 2010) showed that LG's emotion recognition is significantly below controls, $t(14) = -1.93$,

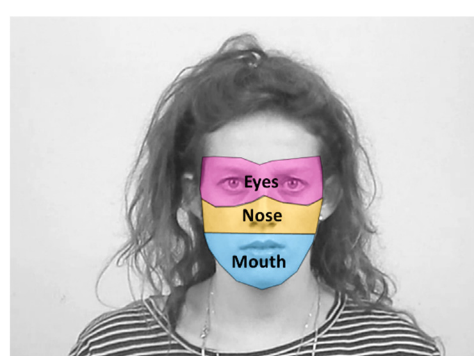

Fig. 3. Face areas of interest (AOI) depicted by different colors on a snapshot from one dynamic subtle facial expression. AOIs are the eye region, nose region and mouth region. AOIs' shape is fixed relative to the face, but dynamic over time and changes according to the facial movements. AOIs' marks and coloring were only visible during data analyses but not during the experimental sessions.

p = .037, Cohen's d = 2.0 (See Fig. 4). In order to compare LG's emotion recognition of specific emotions to control participants' performance we conducted a four-way mixed ANOVA with group (LG, control) as between-subjects factor, and stimulus set (JeFEE, ADFES), condition (peak frame, full dynamic) and emotion (6 basic emotions plus neutral) as within-subjects factors (Corballis, 2009). The group * emotion interaction was not significant ($F(6,84)$ = .40, p = .83), indicating that although LG's emotion recognition deficit can be generalized across emotions, emotion specific attributions cannot be made (for further information, see Fig. S1 in Supplementary material).

To further examine LG's impaired emotion recognition we compared his performance to all of the individual participants of the control group. As can be seen in Fig. 5, in all of the emotion recognition tests (intense vs subtle expressions, full dynamic video clips vs peak frame still images), LG's scores were localized in the low end of the distribution, in comparison to control participants.

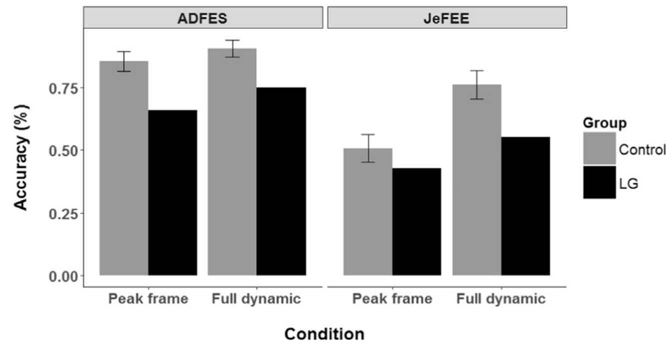

Fig. 4. LG's emotion recognition accuracy in comparison to the controls' mean performance, in different emotion categorization tasks – static peak frame and full dynamic video clips of intense ADFES facial expressions on the left, and static peak frame and full dynamic video clips of subtle JeFEE facial expressions on the right. Error bars represent confidence intervals for control group mean with α = .05.

3.2.2. The dynamic gain effect

In order to assess the effect of dynamic information, we calculated, within participants, the emotion recognition accuracy score for dynamic stimuli minus the emotion recognition accuracy score for still image stimuli. As predicted, when the intense ADFES faces were presented, the facilitative effect of visual motion on emotion recognition (i.e., the dynamic gain effect) for controls was negligible (5%) and only slightly above zero. LG was similar to controls, with a dynamic gain effect of 9% (see Fig. 6). For the subtle JeFEE stimuli, however, the dynamic gain effect for control participants was relatively high − 25% improvement in emotion recognition accuracy on average. However, LG's dynamic gain effect was relatively poor (12%), the lowest in the sample.

The relatively poor contribution of visual motion to LG's emotion recognition for the JeFEE subtle expressions, but not for the ADFES intense expressions is revealing. This may reflect his difficulty in extracting emotional diagnostic information from dynamic subtle stimuli due to heavy load of integration processes that are demanded in this task. As described above, these subtle and non-prototypical expressions convey large variance of subtle emotional cues that appear in different face regions over time. Therefore, higher levels of cognitive resources, such as visual attention and working memory, may be required. Next, we aimed to investigate whether LG's decline in dynamic gain effect and his poor accuracy in emotion recognition from the JeFEE subtle dynamic faces actually reflect a different way of processing these stimuli. Hence, we further explored his eye movements while he visually scanned them.[1]

3.2.3. Gaze location

We first examined which facial regions LG scanned when he tried to decipher dynamic emotional faces, and if his pattern differed from those of controls. This allowed us to examine if LG is impaired at focusing visual attention on diagnostic face regions, and therefore missed affective information that is necessary for emotion categorization.

For this aim we measured participants' relative net dwell time (NDT%, the percentage of time at which an observer's eye enters the AOI until it leaves the AOI) in three face regions – the eyes, nose and mouth. For each participant we calculated a scanning pattern, which is a vector of NDT% in these three facial regions. Next, we compared LG's scanning pattern to the scanning patterns of our control participants. As presented in Fig. 7, the time that LG spent on the eye or mouth regions was similar to the average of the control participants. It seemed that LG spent relatively longer time on the nose region, but this difference was not striking, especially considering the large variability in scanning patterns within participants. Overall, LG's scanning pattern was not unique in comparison to control participants (cf. C3 or C6 in Fig. 7). Thus, the hypothesis that he missed diagnostic cues due to a failure to divert attention to diagnostic facial components seems unlikely.

3.2.4. Fixation duration and fixation rate

While NDT% across AOIs demonstrates *where* one looks, it does not reveal *how* one looks at facial expressions. We measured average fixation duration and fixation rate, as complementary factors that are negatively correlated with each other, and that are known to be correlated with mental effort - the higher the load, the longer the fixations and the lower the fixation rate (Chen et al., 2011; Zagermann et al., 2016).

Using fixation duration as a dependent variable, we conducted a three-way mixed ANOVA with group (LG, control) as between-subjects factor, and stimulus set (JeFEE, ADFES) and emotion (6 basic emotions plus neutral) as within-subjects factors (Corballis, 2009). LG's average fixation duration was significantly higher in comparison to controls, $F(1,14)$ = 8.37, p = .012, η_p^2 = .37. This effect of longer fixations was especially prominent for the JeFEE stimuli, as indicated by a group * set interaction, $F(1,14)$ = 42.32, p < .001, η_p^2 = .75. As can be seen in Fig. 8, the effect was demonstrated in each emotion category.

Further, as seen in Fig. 9, when LG's mean fixation duration is plotted relative to each of the control participants, we can see that for the JeFEE stimuli LG's mean fixation duration was longer than each of the controls'.

For the fixation rate dependent variable (i.e., number of fixations per second) we conducted a three-way mixed ANOVA with group (LG, control) as a between-subjects factor and stimulus set (JeFEE, ADFES) and emotion (6 basic emotions plus neutral) as within-subjects factors (Corballis, 2009). LG's fixation rate was lower in comparison to controls, and this main-effect was near-significant, $F(1,14)$ = 3.42, p = .086, η_p^2 = .20. Although not significant, the trend of lower fixation rate was stronger for the JeFEE stimuli, mirroring the finding with fixation duration. Furthermore, replicating the pattern from fixation duration, this trend was demonstrated in each emotion category (Fig. 10).

In line with the pattern from fixation duration, LG's fixation rate while watching the subtle JeFEE stimuli was the lowest in the sample when compared to each of the control participants (Fig. 11).

These results suggest that the even though LG's emotion recognition improved when displays were dynamic rather than static, his performance remained relatively low in comparison to control participants.

[1] When comparing emotion recognition of the JeFEE subtle faces to other sets of stimuli, like in the present research, it is important to consider that the JeFEE videos have relatively long duration, of 10 s on average. Importantly, in the present study, the subtle JeFEE and intense ADFES clips had different durations (10 s and 6 s, respectively). In order to confirm that the video duration was not a confound in our design we conducted all the eye movements analyses in Experiment 2 both for the whole duration of the videos, and for the first 6 s of the JeFEE videos. The results did not change for the shortened videos, and therefore we can conclude that the clip duration did not confound the results.

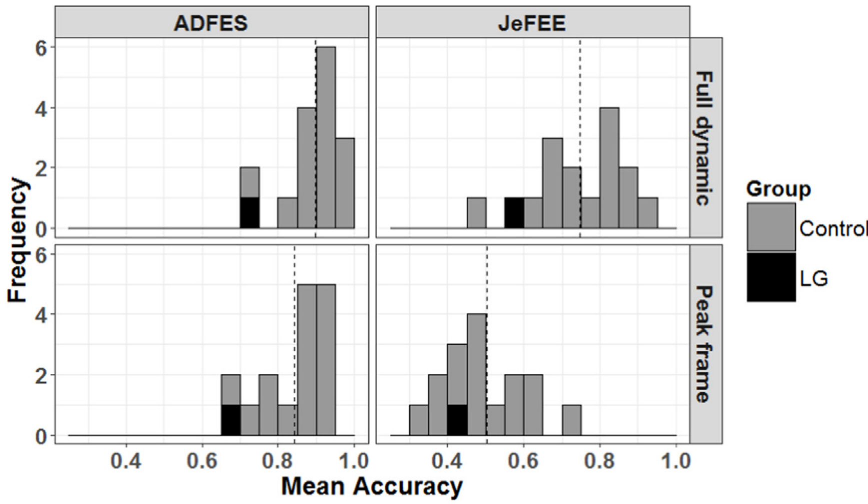

Fig. 5. LG's emotion recognition accuracy (denoted in black) in comparison to control participants (denoted in gray), in different emotion categorization tasks – intense (ADFES, left) and subtle (JeFEE, right), full dynamic (on top) and peak frame (bottom) expressions. Dashed lines represent the mean accuracy across participants.

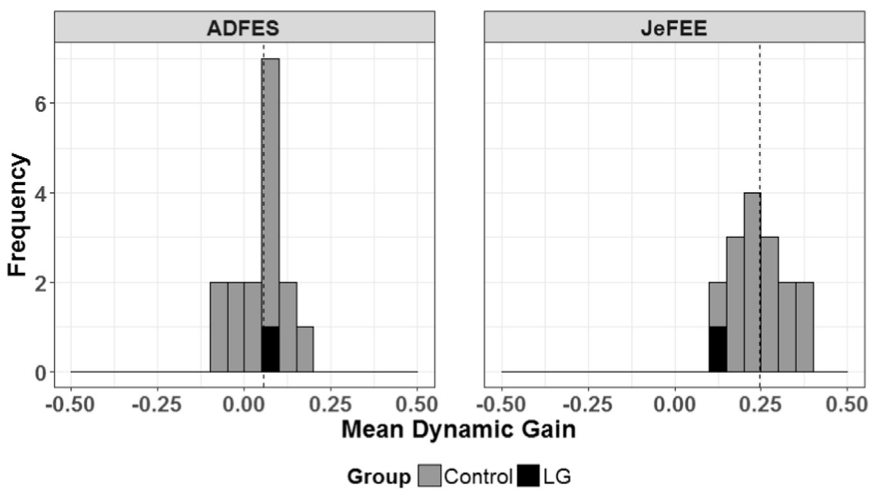

Fig. 6. The dynamic gain effect, calculated as emotion recognition accuracy score for video clip stimuli minus emotion recognition accuracy score for still image stimuli, for intense ADFES (left) and subtle JeFEE faces (right). Dashed lines represent the mean accuracy across participants. LG's dynamic gain effect (denoted in black) was around the average of the controls for the ADFES intense stimuli, and the worst when compared to control participants for the subtle JeFEE stimuli.

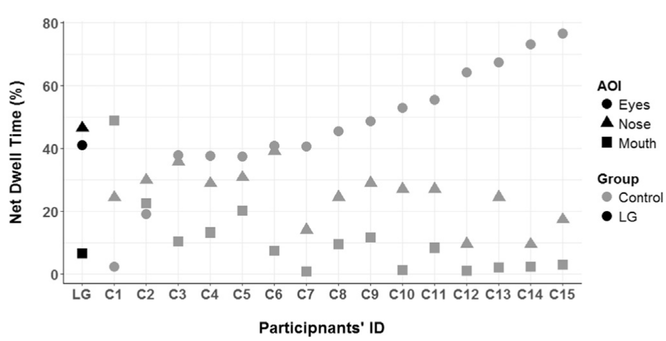

Fig. 7. The net dwell time (%) in three central face regions – eyes, nose and mouth, for LG (in black on the left) and controls (in gray). Considering the variability in scanning patterns among participants, LG's scanning pattern was not unique.

Moreover, while the facilitative effect of visual motion on emotion recognition was similar for LG and controls when facial expressions were intense, for the subtle expressions LG's dynamic gain effect was relatively poor, and he failed to extract the full beneficial effect of motion.

Interestingly, this behavioral performance of dynamic gain effect for subtle and intense expressions reflects a unique processing style: LG has much longer fixations and a relatively lower fixation rate, in comparison to controls, when visually scanning subtle-dynamic expressions. LG's low fixation rate, complimented by his longer fixations, may underlie his reduced ability to accurately be drawn to or interpret subtle dynamic facial expressions.

4. General discussion

In the present study we examined the role of temporal information on facial expression recognition in both typical individuals and in LG, a unique neuropsychological case of developmental visual agnosia. In an attempt to correct the strong research bias for stereotypical highly intense faces, the current research focused on studying the role of motion using a novel set of dynamic, subtle and non-prototypical facial expressions.

In Experiment 1 we provided direct evidence for the critical role of temporal information on the recognition of subtle and non-stereotypical facial expressions. Conversely, facial dynamics did not improve emotion recognition when facial expressions were intense and prototypical. The dynamic gain effect on the perception of subtle emotions may rely on two perceptual processes: salience of change and temporal cues: First, the configural change of the face when expressions unfold from the neutral baseline emphasizes the emotional cues (Ambadar et al., 2005), and enhances emotion recognition. Second, motion cues such as velocity of facial change or muscular activity sequences over time are diagnostic for emotion categorization, and human observers are highly sensitive to these temporal cues (Bould et al., 2008; Kamachi et al., 2013; Jack et al., 2014). Our unique set of stimuli demonstrated these two additive components of the dynamic gain effect in one experimental design.

After establishing the dynamic gain effect with typical participants,

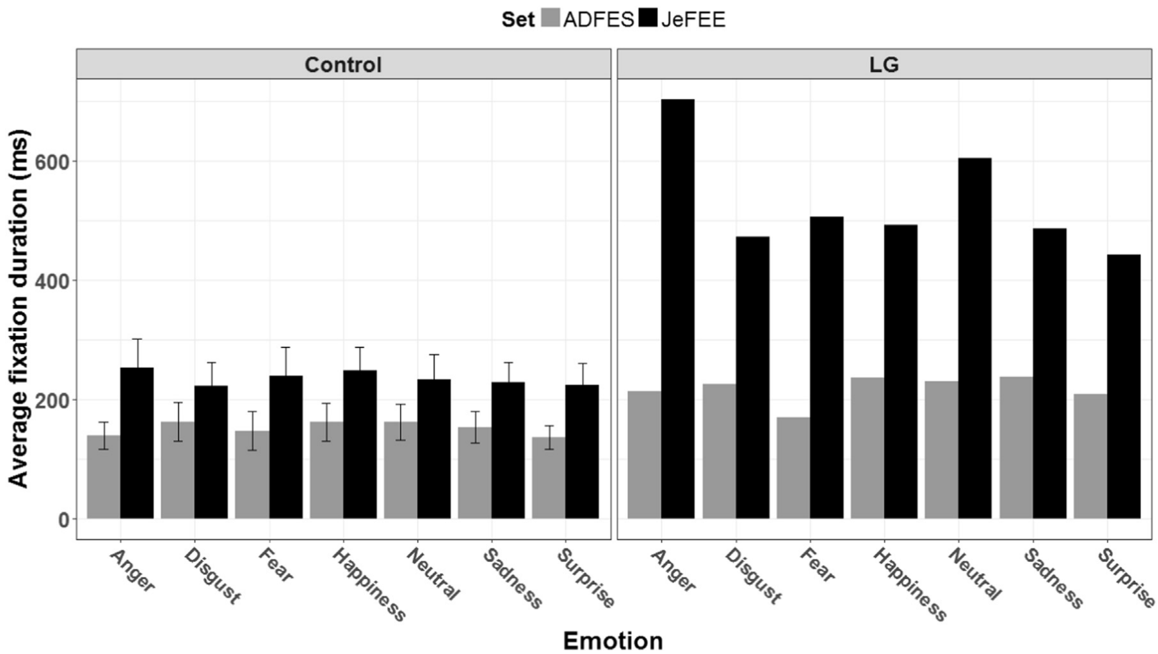

Fig. 8. Average fixation duration of LG (on right) vs controls (on left) in the dynamic subtle JeFEE (in black) and intense ADFES (in gray) faces, across different emotion categories. LG had significantly longer fixations, especially when the subtle JeFEE faces were presented. Error bars represent confidence intervals with α = .05.

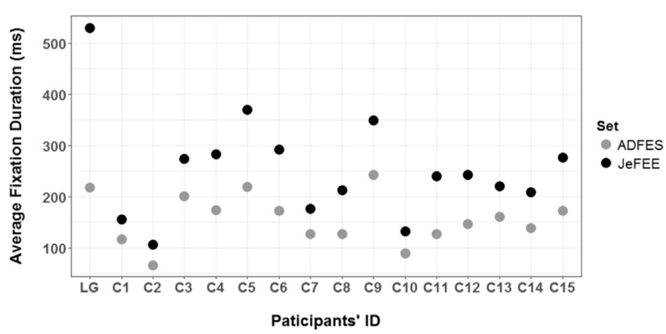

Fig. 9. Average fixation duration of LG vs controls in the dynamic subtle JeFEE and intense ADFES faces, across participants. LG (on the left) had the longest fixations in the sample for the subtle JeFEE dynamic faces.

in Experiment 2 we further examined whether this facilitative effect of motion can lead to improved emotion recognition in LG, an individual with developmental visual agnosia and prosopagnosia, who has poor emotion recognition when tested with static facial expressions (Ariel and Sadeh, 1996; Aviezer et al., 2012b; Gilaie-Dotan, 2016a).

We found that LG's emotion recognition of facial expressions improved when faces were dynamic, but yet remained relatively low in comparison to controls. Regarding the dynamic gain effect, for the intense ADFES faces the facilitative effect of visual motion on LG's emotion recognition was similar to the dynamic gain of controls – dynamic displays of emotion did not have an advantage over static displays. However, for the subtle JeFEE stimuli, LG's dynamic gain effect was relatively poor, as opposed to controls' prominent improvement in emotion recognition when faces were dynamic rather than static.

Interestingly, this behavioral phenomenon of reduced dynamic gain effect for subtle, but not intense, faces reflects a unique visual processing style of the dynamic faces: LG performed longer fixations and his fixation rate was relatively lower, in comparison to controls, especially when facial expressions were subtle and non-stereotypical. The measures of fixation duration and fixation rate are sensitive to processing difficulty, and longer fixations are indicative of high mental effort (Chen et al., 2011; van Diepen et al., 1998; Zagermann et al., 2016). For example, longer fixations are obtained when degrading a picture by lowering its contrast (Loftus, 1985), and when reading words that are less frequent in the language (Inhoff and Rayner, 1986). One possible explanation that was provided for this finding is that as perceptual processing slows, information is acquired more slowly, and longer fixations are needed in order to acquire the same amount of information (Loftus, 1985).

Indeed, the task of recognizing subtle, non-stereotypical expressions is more challenging than recognizing intense stereotypical expressions (Yitzhak, 2017). It is therefore reasonable to assume that LG's mental effort is increased when viewing these expressions, and since he has specific difficulty with emotion recognition, he requires more cognitive resources then typical participants.

We further suggest that LG's reduced dynamic gain effect, and his extremely longer fixations, which were obtained when viewing the subtle expressions, may not be attributed to task difficulty alone. Another factor that might influence LG's processing of the subtle expressions is the visual integration skills that are required to decipher these expressions. When the subtle expressions are reduced to a single static image, emotion recognition dramatically declines. Thus, the diagnostic emotional information in the subtle stimuli does not appear in a single frame, but needs to be integrated over time and over different facial regions. By contrast, for the intense expressions emotional cues in specific facial regions are salient and easy to detect. Therefore, recognition of a local muscular activity may be enough for emotion recognition.

We suggest that deciphering subtle non-prototypica expressions strongly relies on integration over time and across facial regions, rather than on local emotional cues. These integration skills are a key component in LG's visual processing impairment (Aviezer et al., 2012a; Brooks et al., 2012; Gilaie-Dotan et al., 2009; Lev et al., 2015). It is thus plausible that poor integration is the underlying factor in LG's decreased performance, increased mental effort and unique eye-movement patterns during subtle emotion recognition.

A possible impact of LG's visual scanning pattern, which includes a small number of long fixations, is low information sampling rate of the facial expression. LG samples fewer facial components through the video clip, and therefore he may miss diagnostic information. Sampling

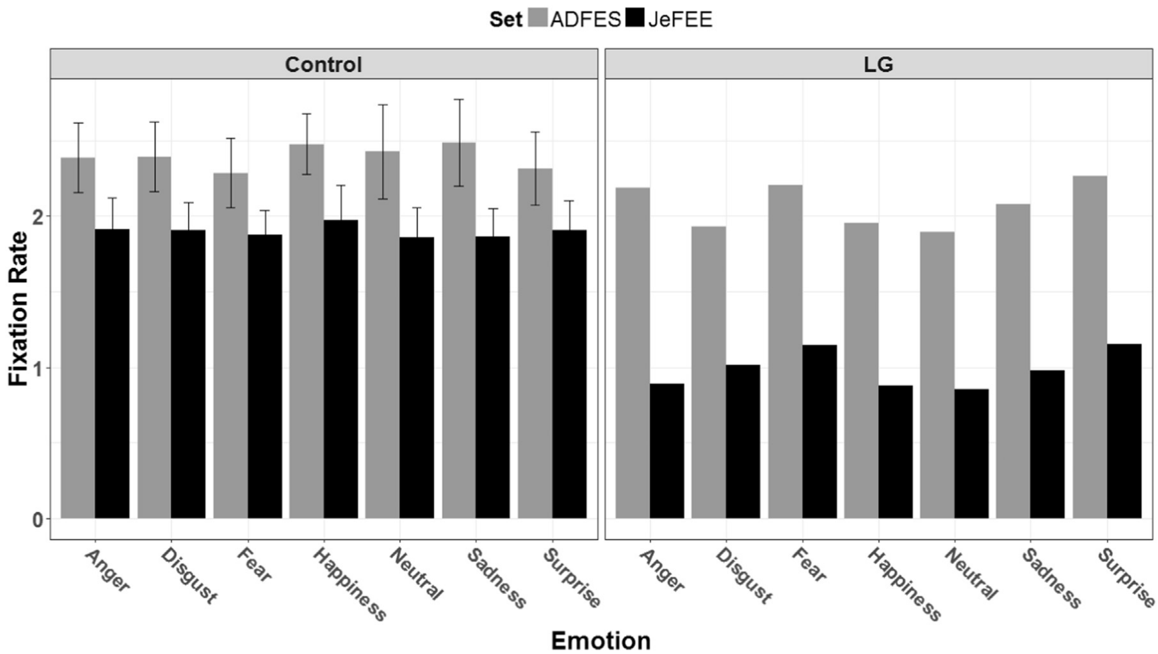

Fig. 10. Fixation rate of LG vs controls in subtle JeFEE and intense ADFES dynamic faces, across different emotion categories. LG had lower fixation rates when the subtle JeFEE faces were presented. Error bars represent confidence intervals with $\alpha = .05$.

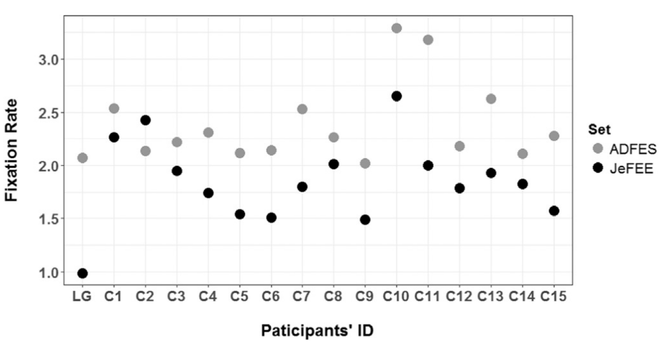

Fig. 11. Fixation rate of LG vs controls in subtle JeFEE and intense ADFES dynamic faces, across participants. LG had the lowest fixation rate in the sample when the subtle JeFEE faces were presented.

rate seems to be specifically relevant for stimuli that change over time, such as dynamic faces. Therefore, LG's unique visual processing profile may be part of the cognitive mechanism that underlies his poor dynamic gain effect for subtle facial expressions.

The use of the JeFEE set of stimuli has clear advantages, especially considering the nearly exclusive focus on prototypical intense facial expressions in emotion research. However, it has some limitations as well. First, the stimuli are isolated faces while real life expressions involve the body and voice (Aviezer et al., 2008; Bänziger and Scherer, 2010; de Gelder et al., 2011). Second, this set contains only displays of the basic emotions, while neglecting multiple portrayals of other affective states (Ortony and Turner, 1990). Third, it relies on actors who pose emotions and not on actual spontaneous facial expressions. Another possible limitation that may be raised is that the JeFEE expressions have relatively long duration (10 s on average), while facial expressions are typically assumed to last shorter durations (Matsumoto and Hwang, 2011). However, these assumptions about the short duration of facial expressions are based on lab experiments where the facial expressions are usually evoked after exposure to a brief presentation of an affective elicitor. With regard to expressions during social interactions, the duration of the expression may extend well beyond a few seconds.

Our findings raise a set of intriguing questions that fall beyond the scope of the current investigation. It would be interesting to examine whether LG's unique scanning profile, and the suggested mechanism for emotion recognition decline, is generalized to other cases of visual perceptual impairments, and maybe even to other neuropsychological patients with impaired emotion recognition (e.g., patients with Huntington's disease or Autism Spectrum Disorder).

Moreover, in developmental prosopagnosia emotion recognition is usually spared (Humphreys et al., 2007; Nunn et al., 2001; Palermo et al., 2011; Sergent and Villemure, 1989; Tranel et al., 1988; Young and Ellis, 1989). However, it has been shown that individuals with developmental prosopagnosia have reduced holistic processing and deficits in deriving the global configuration of faces (Behrmann et al., 2005; Palermo et al., 2011). This is further supported by a recent neuroimaging study showing reduced population receptive field (pRF) size in face selective areas in developmental prosopagnosia, and also linking face recognition ability to pRF size in these face selective brain areas (Witthoft et al., 2016). Limited holistic processing, especially in faces, may have an effect on emotion recognition, particularly when the emotions are conveyed in a subtle and dynamic, rather than in an intense and static fashion. Therefore, it would be interesting to examine whether normal performance in facial expression recognition in developmental prosopagnosia is actually a result of the static and intense stimuli used in earlier research. Alternatively, patients with developmental prosopagnosia may demonstrate emotion recognition deficits, beside their face identity recognition difficulties, when examined with dynamic and subtle facial expressions. Thus, subtle facial stimuli as the JeFFE provide an exciting opportunity to test this issue further and perhaps expose more subtle deficits in facial expression recognition not evident to this day.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2018.04.035.

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