Citation:
Tipples, J and Brattan, V and Johnston, P (2015) Facial Emotion Modulates the Neural Mechanisms Responsible for Short Interval Time Perception. Brain Topography, 28 (1). pp. 104-112. ISSN 1573-6792 DOI: https://doi.org/10.1007/s10548-013-0350-6

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Document Version:
Article (Accepted Version)

Facial emotion modulates the neural mechanisms responsible for short interval time perception

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Abstract

Emotionally arousing events can distort our sense of time. We used mixed block/event-related fMRI design to establish the neural basis for this effect. Nineteen participants were asked to judge whether angry, happy and neutral facial expressions that varied in duration (from 400 to 1600 milliseconds) were closer in duration to either a short or long duration they learnt previously. Time was overestimated for both angry and happy expressions compared to neutral expressions. For faces presented for 700 ms, facial emotion modulated activity in regions of the timing network (Wiener, Turkeltaub, & Coslett, 2010) namely the right supplementary motor area (SMA) and the junction of the right inferior frontal gyrus and anterior insula (IFG/AI). Reaction times were slowest when faces were displayed for 700 ms indicating increased decision making difficulty. Taken together with existing electrophysiological evidence (Ng, Tobin, & Penney, 2011), the effects are consistent with the idea that facial emotion moderates temporal decision making and that the right SMA and right IFG/AI are key neural structures responsible for this effect.

Facial emotion modulates the neural mechanisms responsible for short interval time perception

Personal reflections of emotionally distressing events and positive events often include references to time (e.g., “It felt as if time had stood still”, “time just flew by”). For example, an altered sense of time is frequently referred to during accidents (Arstila, 2012). Experimental research corroborates personal experience: time is reliably distorted for a variety of types of emotional arousing stimuli including affective images (Angrilli, Cherubini, Pavese, & Manfredini, 1997; Dirnberger et al., 2012; Grommet et al., 2011; Lui, Penney, & Schirmer, 2011), sounds (Noulhiane, Mella, Samson, Ragot, & Pouthas, 2007), and fear-conditioned stimuli (Droit-Volet, Mermillod, Cocenas-Silva, & Gil, 2010). In particular, overestimation of time has been recorded when individuals estimate the duration of facial expressions (e.g., Bar-Haim, Kerem, Lamy, & Zakay, 2010; Droit-Volet, Brunot, & Niedenthal, 2004; Thayer & Schiff, 1975; Tipples, 2008). For example, in one study (Droit-Volet et al., 2004) participants were asked to indicate whether angry, happy, sad and neutral facial expressions were displayed for a duration that was more similar to either a standard short or a long duration that they had learnt earlier. Participants responded long more often for angry, happy and to a lesser extent sad facial expressions compared to neutral facial expressions. Furthermore, the bisection point - the comparison duration giving rise to 50% of the long responses - was reached sooner for angry, happy and sad expressions compared to neutral expressions. In other words, emotional expressions were perceived as lasting longer; time was overestimated. Here, we attempted to establish the neural processes responsible for this effect.

Overestimation of time due to emotion can be interpreted in the context of information processing models of interval timing (Gibbon, Church, & Meck, 1984; Treisman, 1963) that specify the operation of a dedicated internal clock. In brief, these models include a pacemaker that sends pulses (or units of elapsed time) to an accumulator. The pulses enter the accumulator via an attention-controlled switch that closes when timing starts at stimulus onset and opens again at stimulus offset when timing ends. The pacemaker is thought to operate at a variable speed and therefore, following the mathematical principles outlined in Scalar Expectancy Theory (Gibbon et al., 1984) effects that are due to an increase in the rate of the pacemaker are predicted to multiply with increases in time. Key evidence for the existence of the pacemaker comes studies that have manipulated arousal (e.g. through the release of dopamine; Buhusi & Meck, 2002) and subsequently reported a multiplicative effect on timing. Facial expressions are typically perceived as arousing (Calder, Ewbank, & Passamonti, 2011) and also lead to an overestimation of time and therefore, are thought to speed the pacemaker in a similar manner to other types of arousal. Further evidence in keeping with pacemaker speeding due to arousal is the finding (Droit-Volet et al., 2004) that overestimation of time for facial expression is larger in magnitude for faces that appear more highly aroused (e.g., angry facial expressions) compared to expressions appearing less aroused (e.g., sad facial expressions). In summary, overestimation of time for emotional stimuli has been interpreted within the context of internal clock models of time perception as reflecting pacemaker speeding due to arousal.

Neuroimaging techniques with high spatial resolution such as fMRI are a further way of testing the idea that emotion affects the operation of an internal clock. If an internal clock exists then there should exist a dedicated neural mechanism for timing (Ivry & Schlerf, 2008) and therefore, we should see modulation of this mechanism during the timing of facial expressions. If emotion modulates the operation of a dedicated internal clock, which neural areas are responsible for this effect? A recent review (Coull, Cheng, & Meck, 2011) and meta-analysis (Wiener et al., 2010) of neural activation studies have helped identify a network of structures which is typically more active during timing compared to a control.

This network includes the SMA, basal ganglia (including the putamen and the caudate nucleus), the cerebellum and the ventral premotor cortex (in the region around the frontal operculum). The junction of the frontal operculum (of the inferior frontal gyrus) with the anterior insula (AI) is one region that is frequently active during time estimation tasks irrespective of task difficulty (Livesey, Wall, & Smith, 2007). According to one model (Craig, 2008, 2009) the AI is the neural substrate responsible for the effects of emotion on time and therefore, is of particular significance for the aims of the current research.

Although there are no datasets on how facial expressions specifically modulate activity within the timing network, recent studies have tested for the effects of emotionally arousing stimuli on activity within timing network (Dirnberger et al., 2012; van Wassenhove, Wittmann, Craig, & Paulus, 2011). One study (Dirnberger et al., 2012) compared the effects of aversive and non-aversive pictures on neural activation during timing. On trials where participants incorrectly judged an aversive image as lasting longer than a non-aversive image, there was increased activation in the amygdala, putamen and insula. A separate study (van Wassenhove et al., 2011) compared neural activation and temporal estimation for looming stimuli that appear to approach the observer, with activation for receding visual stimuli that appear to move away from the observer. Looming stimuli are typically rated as more unpleasant and arousing than receding stimuli and therefore, are suitable for studying the neural mechanisms for temporal distortion due to emotion. For both looming and receding stimuli compared to static stimuli there was increased activation in the insular cortex, anterior cingulate cortex, basal ganglia and dorsolateral prefrontal cortex. Although time was overestimated for looming compared to receding stimuli, the contrast between these conditions did not lead to increased activation in the right anterior insular as predicted by the model proposed by Craig (Craig, 2008, 2009). Nonetheless, the effects are generally consistent with such a role for the insula because, in addition to increased overall activity in the insular cortex, there was also left lateralized activation of the anterior insula for receding compared to looming stimuli. The latter effect is in keeping with the more specific proposal (Craig, 2008) of forebrain emotional asymmetry for the effects of emotion on time. In summary, initial studies of the effects of emotion on the neural activity during timing have revealed activity in the network of structures typically engaged during timing. Further data is needed to clarify the role of insular as a key neural structure responsible for the effects of emotion on time.

Here, we chose the temporal bisection task to examine the effects of facial emotion on neural timing. The temporal bisection task was selected for several reasons. First, a recent study (Tipples, Brattan, & Johnston, 2013) that used this task with face stimuli recorded robust activation in the core timing network structures (e.g., right inferior frontal gyrus, right supplementary motor area (SMA), right pre-SMA and basal ganglia) and therefore, the task is likely to be sensitive to the effects of facial emotion on activity within this network. Second, human performance on the temporal bisection task has been subjected to extensive empirical research into the operation of specific timing processes (for a review see; Kopec & Brody, 2010). Of particular relevance is behavioral evidence (reviewed by; Kopec & Brody, 2010) and electrophysiological evidence (Lindbergh & Kieffaber, 2013; Ng et al., 2011; for a review see; van Rijn, Kononowicz, Meck, Ng, & Penney, 2011) that supports the idea that temporal decision making processes during temporal bisection reach maximum activity prior to the mean duration. In light of these findings, we were interested in whether emotion might also affect temporal decision making by modulating neural activity that reaches a maximum prior to the mean duration. As a further index of temporal decision making difficulty we recorded reaction times. If temporal decision processes are maximally active prior to the mean duration as previous evidence indicates then reaction times should also be slower at this duration.

In summary, we tested for the effects of facial emotion on neural activation within the timing network using the temporal bisection procedure. Furthermore, we tested for modulation by emotion of activity in this network at a duration when temporal decision making processes are thought to operate.

Materials and Methods

Participants

All 19 participants (9 male) were right handed and had normal to corrected-to normal vision. The mean age of the male participants was 23 (*SD* = 1.88) and the mean age of the females was 24 (*SD* = 5.02). Written consent was obtained for all participants, and the study was approved by the York Neuroimaging Centre (YNiC) Ethics Committee.

Stimuli

Digitised photographs of 8 individuals (four male and four female), each individual displaying an angry, happy and neutral expression were selected from the NimStim set of facial expressions (Tottenham et al., 2009). Stimulus presentation and data collection were controlled by E-Prime software (Schneider, Eschman, & Zuccolotto, 2002).

Image acquisition

MRI images were acquired on a GE 3 Tesla HD Excite MRI scanner at the York Neuroimaging Center at the University of York. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage, radio-frequency coil tuned to 127.4 MHz. A T2*-weighted gradient-echo EPI sequence was used to collect a series of 305 brain volumes (TR = 3 s, TE = 25 ms, FOV = 28 × 28 cm, matrix size = 128 x 128, 39 axial slices, slice thickness = 3 mm). After the functional scan, a high-resolution T1-weighted structural volume was acquired using 3D FSPGR (Sagittal Isotropic 3D Fast Spoiled Gradient-Recalled Echo) pulse sequence (TR = 8.03 sec, TE = 3.07 sec; Matrix = 256 mm x 256 mm x 176 mm; FOV = 290 mm x 290 mm x 176 mm, slice thickness = 1.13 mm x 1.13 mm x 1.0 mm; Flip angle 20 degrees) which was used to facilitate the spatial normalisation of the functional data.

Training phase - outside the MRI scanner

Prior to entering the scanner, participants were trained to discriminate short (400 ms) from long (1,600 ms) stimulus durations. In the first block of 8 trials, a pink oval appeared for either a short or long duration in a fixed sequence (e.g., long-short-long-short, etc.). Participants were informed of this sequence and were asked to indicate whether the stimulus appeared for either a short or long stimulus duration by pressing one of two labeled keys on a QWERTY keyboard (the "z" and "m" keys were used). Following a response, visual feedback was given for both correct ("yes") and incorrect ("no") decisions. The feedback appeared in the centre of the screen for 2 seconds and was followed by an inter-trial interval of 1200 msec. In the second block, the pink oval was presented for a further 8 trials in a new random order for each participant. During this phase participants continued to indicate whether the oval appeared for either short or long stimulus durations. Participants continued to receive feedback in this phase. After the training phase participants completed the experimental blocks of trials in the MRI scanner.

fMRI design and procedure

Each scanning session consisted of 24 active blocks comprised of 8 blocks for each expression type (angry, happy, neutral). Active blocks were preceded and followed by passive rest blocks lasting 15 seconds. A mixed-model design was used: expression (angry, happy, neutral) and identity of face was varied between blocks, while the duration of the faces (400, 700, 1000, 1300, 1600) and sex of face (male, female) were varied (on trial by trial basis) within each block. Specifically, on each trial the faces could vary in sex (either male or female) or duration, but (within blocks) the expression and identity remained constant. Within each block there were 10 trials, with the face of individual male and individual female models displayed for each duration (400, 700, 1000, 1300, 1600). All face stimuli were presented in a separate pseudo-randomized order for each participant within each block. The type of expression was also randomised across blocks using a single, pseudo-randomized order. Participants were instructed to respond, using their dominant hand, via a button press, by pressing one button with their right index finger (for short) and another button with their middle finger (for long). Each face was separated by a fixed 1200ms interval during which the screen appeared blank and participants made their response.

fMRI pre-processing

The pre-processing and statistical analyses of MRI data were carried out using SPM 8 software (Wellcome Trust Centre for Neuroimaging, London, UK). The first 9 s of data (the first three volumes) from each scan session to allow for T1 equilibration effects. Standard pre-processing was applied including: slice-timing correction, normalization to a standard brain template in MNI space, smoothing with an 8 mm FWHM Gaussian kernel and removal of low frequency fluctuations using a high-pass filter with a cut-off at 128 s.

General Linear Modeling

At the first-level of analysis each participant's data were subjected to a regression analyses containing terms reflecting the predicted BOLD signal to the three active expression conditions (Angry, Happy, Neutral) and the passive baseline convolved with a canonical hemodynamic response function. Six movement parameters from the realignment corrections were entered as additional regressors of no interest for each scanning run, in order to account for residual movement artifacts after realignment. Three sets of contrast images were created for level 2, random effects analyses. First, to test the comparison Emotion>Neutral we used the following weighted contrasts: Angry (+1), Happy (+1) and Neutral (-2). Second, to test for activity specifically associated with temporal decision making difficulty (see introduction for rationale), we created a weighted contrast to test for increased activity at the intermediate, 700 ms duration: -1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms) -1 (1600 ms). Third, we tested for modulation of the latter contrast by emotion in the form of an Emotion>Neutral x duration (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)) contrast.

Regions of interest analyses and statistical thresholding

The ROIs were selected based on recent reviews (Coull et al., 2011) and a meta-analysis (Wiener et al., 2010) of fMRI studies of time perception and included the bilateral basal ganglia (caudate, putamen, and pallidum), SMA, right frontal Inferior Frontal Gyrus (pars Triangularis) and intersection of the Insula and Inferior Frontal Gyrus (Anterior Insula). The anatomical ROIs for the basal ganglia, SMA and rIFG (pars Triangularis) were created using the Wake Forest University Pickatlas Tool (Maldjian, Laurienti, Kraft, & Burdette, 2003) for SPM8 with the Automated Anatomical Labeling Atlas (AAL; Tzourio-Mazoyer et al., 2002) used to define each region bilaterally.

The ROI mask for the right inferior frontal, anterior insula region was created by defining an 8 mm sphere centered on Talairach co-ordinates ([Right; x=47, y=13, z=13]; [Left: x=−38, y=19, z=−2]) reported in previous research (Wittmann, Simmons, Aron, & Paulus, 2010). All contrasts within the predefined ROIs were evaluated as statistically significant activation if they survived the family-wise error (FWE) correction ($P < 0.05$) for multiple comparisons within small volumes (small-volume correction; SVC) as implemented in SPM 8. To explore other possible regions of activation that were not predicted, the three sets of contrasts described above were analyzed using one-sample t-tests of signal change across the entire brain thresholded at $P< 0.001$ uncorrected at the voxel level and $P< 0.05$ FWE (family-wise error) corrected at the cluster level.

Behavioral data analyses

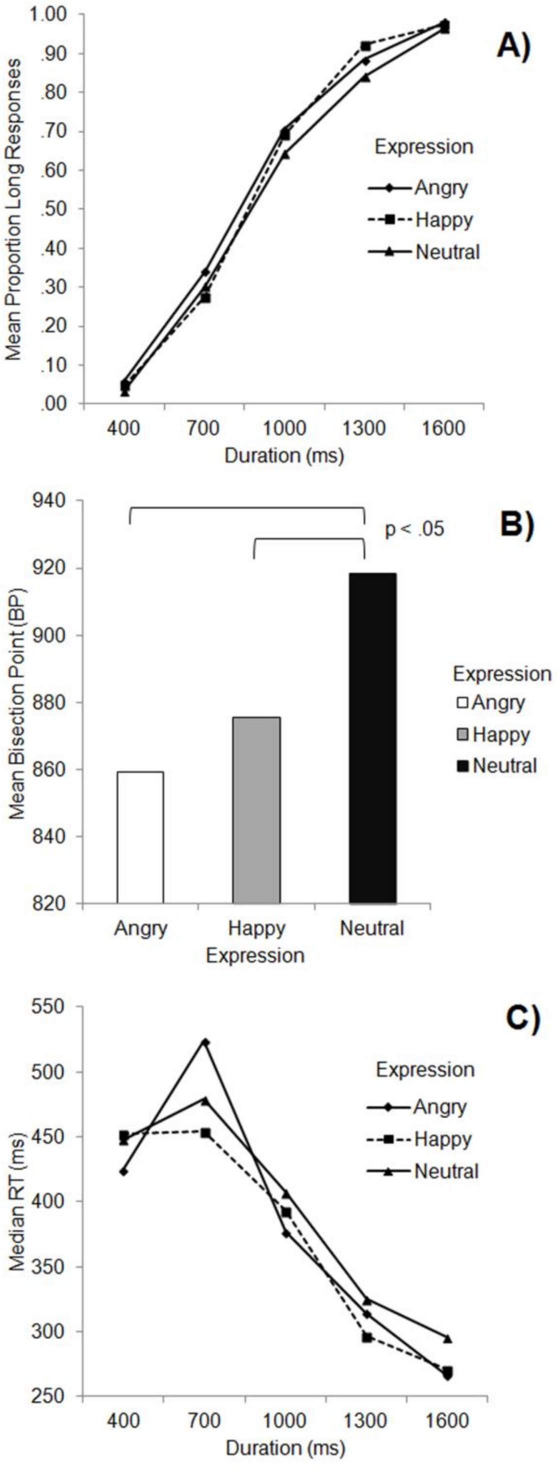

Figure 1. Behavioral data of A) mean proportion of Long responses as a function of expression (angry, happy, neutral) and duration B) the mean Bisection Point (BP) in milliseconds for each expression and C) the median RTs (ms) as a function of expression and duration.

Equipment failure led to the loss of the behavioral data from 2 participants and consequently, analyses of the behavioral data were carried out on the data of the remaining 17 participants. The median RTs, bisection points (BP) and Weber ratios (WR) were calculated for each participant and each expression condition separately. Median RTs were chosen as an index of decision making difficulty with slower median RTs at different durations or for different expressions) indexing more difficult decisions.

The BP and WR indices were calculated from the slope and intercept parameters from the regression of proportion of long responses onto time. The BP refers to the point of subjective equality (.5 point on the psychometric function) and was calculated using the method of least squares from the intercept and slope parameters of regression of p(long) onto stimulus duration (Gescheider, 1997).

The BP is an index of the perception of time that can be used to compare either relative under- or over-estimation of time across conditions (for examples see; Ortega & López, 2008; Wearden, 2008). A relatively low BP value (compared to other conditions or individuals) indicates that participants perceive more time as having passed; time is overestimated. The WR measures temporal sensitivity and is calculated by dividing half the difference between the upper difference limen (*p*long[.75]) and the lower difference limen (*p*long[.25]) by the BP. In short, the BP is an index of perceived duration and the WR is an index of temporal sensitivity or precision.

Bisection and Weber indices of timing

The mean BPs, WRs and median RTs are displayed in Figure 1. The BP and WR values were analyzed using paired sample t-tests for the effects of interest: Angry>Neutral, Angry>Happy, Happy>Neutral. As can be seen in Figure 1a the psychophysical curve was moved to the leftward for angry and happy expressions compared to neutral expressions and the mean BP (Figure 1b) was reached sooner for both angry (M = 859 ms) and happy (M = 875 ms) facial expressions compared to neutral (M = 918 ms) expressions (Angry>Neutral, t (16) = -3.02, p = .008; Happy>Neutral, t (16) = -2.75, p = .01). Although the mean BP value was lower by 19 milliseconds for angry expressions compared to happy expressions this difference was not significant, t (16) = -.74, p = .47. With respect to the WR values, individuals demonstrated good temporal sensitivity: the mean WR values for each expression (angry faces, M = .21; happy faces, M = .21; neutral faces, M = .23) were lower than that reported previously (e.g., Tipples, 2008) and did not differ between the expression conditions (all *p's* > .1).

Reaction time analyses

The median RTs were analyzed in a 3 × 5 (Expression [angry, neutral] × Duration [400, 700, 1000, 1300, 1600] repeated measures ANOVA. There was a main effect of duration, $F(4, 60) = 69.42$, $p< .0001$, $\eta_p^2 = .81$; RTs were slowest at the 700 ms duration (M = 489 ms) compared to all other durations (Bonferroni corrected $p < .016$) and also, there was a linear decrease in RTs from 1000 ms (M = 402 ms) to 1300 ms (M = 319 ms) to 1600 ms (M = 279 ms). As can be seen in Figure 1c, RT slowing at 700 ms was particularly pronounced for angry facial expressions. In support, post-hoc (Bonferroni corrected $p < .016$) t-tests of the simple main expression at the700 ms duration (F (2,30) = 5.63, p = .008, η_p^2 = .27) showed that responses were slower when participants judged the duration of angry (M = 524) compared to both happy (M = 454) and neutral expressions (M = 479). The simple main effect of expression was also significant when faces were displayed for both 400 ms, F (2, 30) = 3.58, p =.04, η_p^2 = .19. For the 400 ms duration, responses were faster when participants judged the duration of angry (M = 424) compared to happy (M = 452) expressions. All other simple main effects did not reach statistical significance.

fMRI analyses

Contrast	Hemisphere	Brain Region	*x*	*y*	*z*	*T*	*P*
Emotion > Neutral	Left	Inferior Occipital Gyrus	-30	-94	-8	7.88	0.001
			-34	-86	-20	7.23	
		Inferior Temporal Gyrus	-48	-50	-26	6.88	
	Right	Cerebellum	36	-76	-32	7.49	0.001
		Fusifrom Gyrus	40	-82	-20	6.84	
		Lingual Gyrus	26	-92	-14	5.83	

Table 1. Whole brain activation for the contrast Emotion>Neutral. All activations survive the P< 0.001 threshold uncorrected at the voxel level and P< 0.05 FWE (family-wise error) corrected at the cluster level (x, y and z co-ordinates are reported in MNI space). Clusters with the largest number of significant voxels are reported for each region.

Whole brain analyses

The neural areas across the whole brain that showed significant activation (FWE-corrected statistical threshold of $p < 0.05$) for the Emotion>Neutral contrast are displayed (with MNI co-ordinates) in Table 1. A one-sample t-test of the Emotion>Neutral contrast images showed significant modulation of BOLD activity within bilateral regions of the ventral occipito-temporal cortices including the right cerebellum and left fusiform gyrus.

Region of Interest analyses

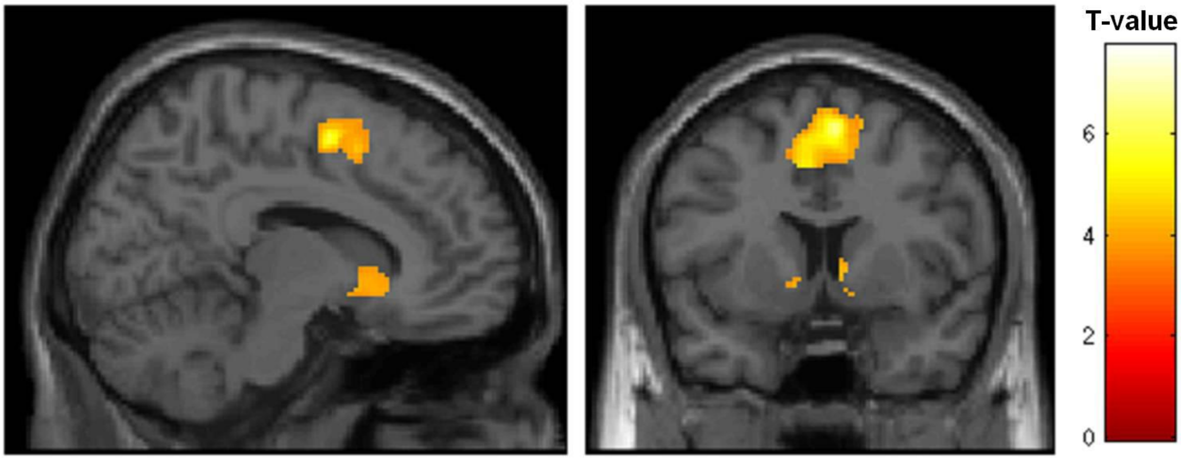

Fig 2

Figure 2. Neural areas within the Regions of Interest (ROIs) (see text) that showed significant activation for the duration contrast (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)). *Left:* sagittal section showing activation of bilateral SMA and right caudate nucleus. *Right:* coronal section showing activation of bilateral SMA, bilateral pallidum and right caudate nucleus. For illustration purposes only, all images are thresholded at $P < 0.001$ uncorrected with an extent threshold of 10 voxels. Activations are projected onto the MNI single subject T1 image.

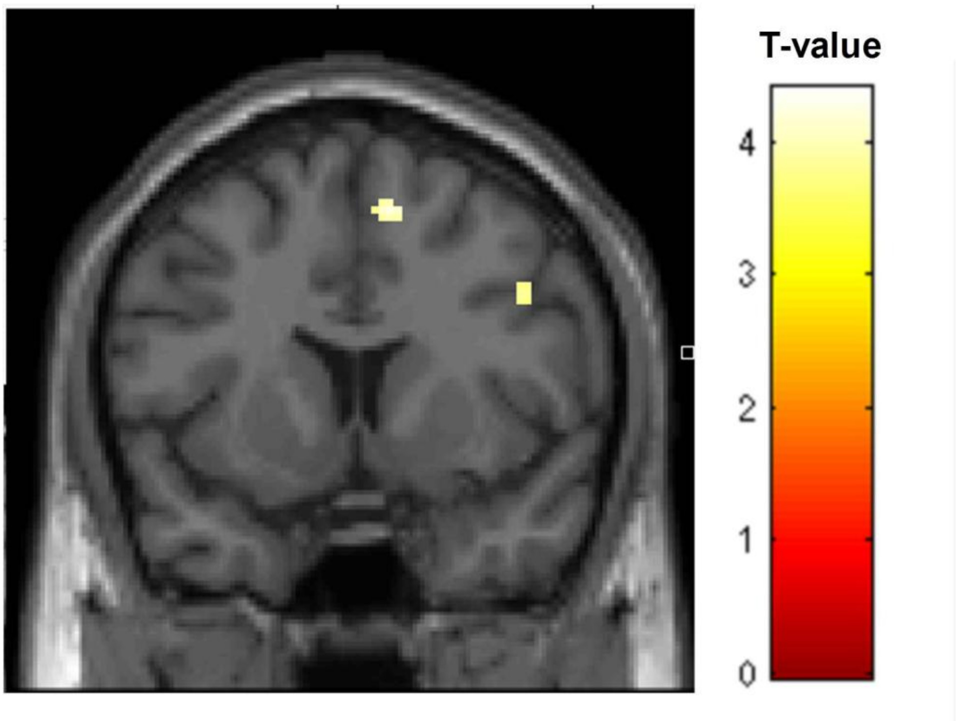

Fig 3

Figure 3. Neural areas within the Regions of Interest (ROIs) (see text) that showed significant activation for the Emotion>Neutral x duration (-1, +4, -1, -1, -1) contrast showing increased activation in the Right SMA and Right IFG/AI. For illustration purposes only, activation has been thresholded at $P < 0.001$ uncorrected with an extent threshold of 10 voxels. Activations are projected onto the MNI single subject T1 image.

Brain Region	*x*	*y*	*z*	*T*	*P*
Left SMA	-10	-4	58	7.73	0.0003
	6	8	60	6.37	0.0027
	0	14	44	5.82	0.0066
Right SMA	10	0	56	5.81	0.0066
	2	22	48	5.14	0.0201
Left Pallidum	-10	4	-4	4.39	0.0143
Right Caudate	8	12	2	4.33	0.0466
	16	20	-8	4.26	0.0523
Right Pallidum	12	6	-4	3.96	0.0310

Table2. Neural areas within the Regions of Interest (ROIs) that showed significant for the duration contrast (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)). All contrasts are statistically significant activations that survive to the SVC for multiple comparisons FWE $p < 0.05$ with a minimum cluster size of 10 voxels (x, y and z co-ordinates are reported in MNI space). SMA = Supplementary Motor Area

Contrast	Brain Region	*x*	*y*	*z*	*T*	*p*=	Cluster Size
Emotion > Neutral	Right SMA	10	12	56	4.4	0.0007	96
		6	4	56	4.21	0.0008	
	Right IFG/AI	44	10	34	3.79	0.0480	17

Table 3. Neural areas within the time and emotion Regions of Interest (ROIs) that showed significant activation for the Emotion>Neutral x duration (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)) contrast. All contrasts are statistically significant activations that survive to the SVC for multiple comparisons FWE $p < 0.05$ with a minimum cluster size of 10 voxels (x, y and z co-ordinates are reported in MNI space). Clusters with the largest number of significant voxels are reported for each region. IFG =Inferior Frontal Gyrus, SMA = Supplementary Motor Area, AI = Anterior Insula

Neural areas within the Regions of Interest (ROIs) that showed significant activation for the duration contrast (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)) and also Emotion>Neutral x duration (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)) interaction contrast are displayed in Figures 2 and 3, respectively. A one-sample t-test for the duration contrast (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)) revealed increased activation of the bilateral SMA, bilateral pallidum and the right caudate nucleus (see Table 2). A one-sample t-test for the Emotion>Neutral X duration (-1 (400 ms), +4 (700 ms), -1 (1000 ms), -1 (1300 ms), -1 (1600 ms)) interaction contrast identified increased activation of the right SMA and the right inferior frontal gyrus/anterior insula (see Table 3).

Discussion

Our key finding is that facial emotion modulates activity within two specific neural regions (the right SMA and right IFG/AI) identified in recent meta-analysis (Coull et al., 2011) and review (Wiener et al., 2010) and also, our own research (Tipples et al., 2013) as playing a central role in short interval time perception. More specifically, the main results are as follows. First, following previous research (Droit-Volet et al., 2004) participants responded long more frequently (time was overestimated) when judging the the duration of both angry and happy facial expressions compared to neutral expressions. Second, for the 700 ms stimulus duration compared to all other durations, reaction times were slowest and neural activity was increased in regions of the timing network (bilateral SMA, caudate nucleus, pallidum and the putamen). Third, emotion modulated activity in 2 regions of the timing network (the right SMA and right IFG/AI) when faces were presented for 700 ms.

Our interpretation of increased activity in the right SMA and IFG/AI at 700 ms specifically, is that emotional arousal modulated activity in the neural regions responsible for temporal decision making. This claim is based on several strands of evidence. First, reaction times were slowest at 700 ms indicating that decision making was most difficult for this duration. Therefore, increased activity at this duration most likely reflects the operation of temporal decision making processes. Second, further evidence that corroborates this conclusion comes from electrophysiological studies of timing that have used the temporal bisection task (Lindbergh & Kieffaber, 2013; Ng et al., 2011). The focus of these studies has been a slow-negative of index of timing called the Contingent Negative Variation (CNV) – an ERP component associated with activity in frontal-central areas including the SMA (Nagai et al., 2004). For example, in one study (Ng et al., 2011) the CNV increased in amplitude to the end of the short duration then remained constant until the geometric mean of the short and long durations before decreasing in amplitude. The interpretation of this effect was that CNV amplitude tracks temporal decision making rather than an accumulation of pulses in an accumulator mechanism (for a discussion see; van Rijn et al., 2011). We have shown that the effects of facial emotion on activity in the right SMA and IFG/AI are present at 700 ms duration before the mean duration. Therefore, in keeping with the explanation given for increased CNV amplitude before the mean duration, we attribute this activation to temporal decision making processes. In summary, the effect of facial emotion and on both reaction times and activity in the SMA and IFG/AI is consistent with the idea that 1) facial emotion modulates temporal decision making and 2) the SMA and IFG/AI are most likely responsible for this process.

An alternative explanation for the effect of facial emotion on SMA and IFG activity is that such activity reflects the operation of an accumulator mechanism. Indeed, this is the interpretation we offered in a recent study (Tipples et al., 2013) where we showed that leftward shifts in the BP (indicating overestimation) were correlated with increased activation in the SMA. Put differently, as time estimates lengthened (across individuals) SMA activity increased – a pattern of climbing activation that we attributed to accumulator activity. A problem with this account is that it does not explain why activity followed the non-linear pattern we have reported here (why does activity peak before the mean duration?) nor does it account for the reaction time slowing at 700 milliseconds. Therefore, our tentative conclusion based on our reaction time results and assessment of our fMRI findings in relation to recent EEG findings, is that facial emotion modulates temporal decision making processes carried out in the right SMA and IFG/AI.

The effect of emotion on activity at the junction of the frontal operculum (of the inferior frontal gyrus) with the AI is consistent with the claim (Craig, 2009) that this region is responsible for the effect of emotion on time. According to this model, the AI integrates visceral information (including bodily arousal due to emotion-eliciting events) emerging from a progression of activity that begins in posterior insula, to form a representation of the present moment (how a person feels 'now' - a Global Emotional Moment). Subjective estimates of elapsed time are based on the accumulation of these moments and consequently are affected by emotional arousal and other changes in body state. Our conclusion that the effects of emotion on neural activity for the 700 ms duration reflects temporal decision making is consistent with this idea because temporal decision making depends on a representation of the elapsed time. Nonetheless, emotion also modulated activity in the right SMA at 700 ms and therefore, this region is also a candidate for the representation of elapsed time. Our speculative hypothesis – based on separate evidence for the (pre-)SMA in response processing (e.g., Forstmann et al., 2008; Hartstra, Waszak, & Brass, 2012) - is that the right IFG/AI represents awareness of elapsed time whereas the SMA is responsible for preparing a response based on this information.

In summary, modulation of a non-linear pattern of activity across time in the SMA and IFG/AI and also reaction time differences indicate that facial emotion moderates temporal decision making and moreover the SMA and IFG/AI are key structures engaged during temporal decision making. A sensible goal for future research will be to establish whether this pattern of activity during timing is found for types of arousal and furthermore, whether such activity can be dissociated from activity due to other processes such as action readiness (Hagura, Kanai, Orgs, & Haggard, 2012) which might mediate the effects of emotion on time.

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