

# Human Amygdala Response to Dynamic Facial Expressions of Positive and Negative Surprise

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Although brain imaging evidence accumulates to suggest that the amygdala plays a key role in the processing of novel stimuli, only little is known about its role in processing expressed novelty conveyed by surprised faces, and even less about possible interactive encoding of novelty and valence. Those investigations that have already probed human amygdala involvement in the processing of surprised facial expressions either used static pictures displaying negative surprise (as contained in fear) or “neutral” surprise, and manipulated valence by contextually priming or subjectively associating static surprise with either negative or positive information. Therefore, it still remains unresolved how the human amygdala differentially processes dynamic surprised facial expressions displaying either positive or negative surprise. Here, we created new artificial dynamic 3-dimensional facial expressions conveying surprise with an intrinsic positive (wonderment) or negative (fear) connotation, but also intrinsic positive (joy) or negative (anxiety) emotions not containing any surprise, in addition to neutral facial displays either containing (“typical surprise” expression) or not containing (“neutral”) surprise. Results showed heightened amygdala activity to faces containing positive (vs. negative) surprise, which may either correspond to a specific wonderment effect as such, or to the computation of a negative expected value prediction error. Findings are discussed in the light of data obtained from a closely matched nonsocial lottery task, which revealed overlapping activity within the left amygdala to unexpected positive outcomes.

*Keywords:* amygdala, dynamic emotion, relevance, novelty, valence, fMRI

*Supplemental materials:* <http://dx.doi.org/10.1037/a0034619.supp>

Since the 1930s and until the end of the 20th century, human amygdala function was typically associated with one emotion: fear. This was based on clear evidence from animal research, human brain imaging, and patient studies that the amygdala is important for fear learning, and more generally for the processing of threat-related information (see Phelps & LeDoux, 2005). The fact that the amygdala is involved in fear is well established and

ultimately led to the view that the amygdala is central to a “defense” or “fear system,” or even by itself is a “fear module” (Ohman & Mineka, 2001), the latter term implying that the domain of specificity of the amygdala is dedicated to fear/threat-related computations. Most meta-analyses of brain imaging studies (see, e.g., Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002; Vytal & Hamann, 2010) found that the amygdala is particularly associated with fear. In fact, the role of the amygdala in fear is unchallenged. However, stating that the amygdala is important for fear processing is not tantamount with saying that its function is solely dedicated to fear. A large body of evidence indicates that the processing domain of the amygdala is not restricted to fear-related information, but also includes negative emotions other than fear, positive information, and even a priori nonvalenced stimuli (see, e.g., Bzdok, Laird, Zilles, Fox, & Eickhoff, in press; Cunningham & Brosch, 2012; Pessoa & Adolphs, 2010; Sander, Grafman, & Zalla, 2003; Sergerie, Chochol, & Armony, 2008).

Various theoretical accounts of amygdala function have tried to elucidate its role in fear versus (a) ambiguity processing (e.g., Whalen, 1998), (b) arousal (e.g., Anderson & Sobel, 2003), or (c) relevance detection (e.g., Sander et al., 2003). For instance, Whalen (2007) proposed that a key reason why a facial expression of fear activates the amygdala is because the source of threat is uncertain. Arguing for a unitary function of the human amygdala, Sander et al. (2003) suggested that such preferential amygdala

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This article was published Online First November 11, 2013.

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This research has been supported by the National Center of Competence in Research for the Affective Sciences, financed by a grant from the Swiss National Science Foundation (51NF40-104897), hosted by the University of Geneva, and an additional grant from the Swiss National Science Foundation to Pascal Vrticka (136480).

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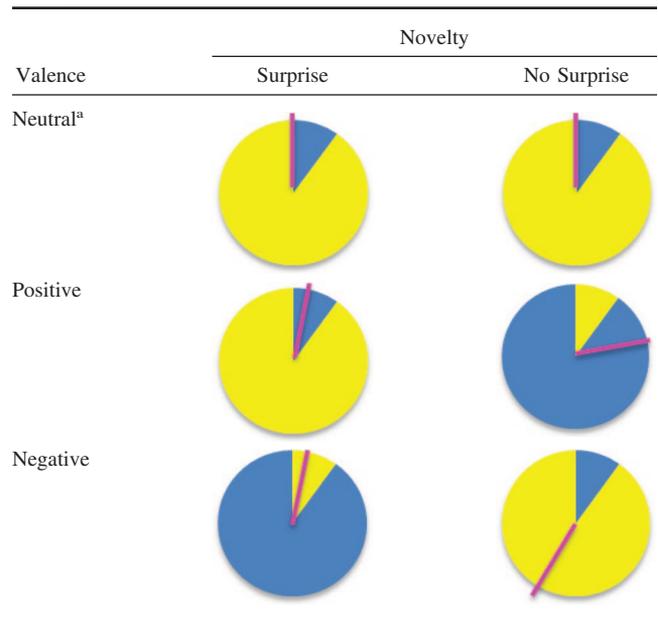
activation to fear happens because an expression of fear is typically appraised as a particularly relevant signal given the individual's current goals, needs, values, and other concerns.

Appraisal theories of emotion typically consider various dimensions that modulate relevance detection, with two key appraisal criteria being (a) novelty and (b) valence (e.g., Delplanque et al., 2009; for a review of appraisal criteria, see Ellsworth & Scherer, 2003). In appraisal theories, novelty is usually associated with suddenness of onset (entailing an orientation response), familiarity (related to previous exposure), and/or predictability (referring to the estimation of the likelihood of an event to occur; see, e.g., Sander, Grandjean, & Scherer, 2005). For instance, appraised stimulus novelty is particularly determinant for distinguishing the emotions of surprise and fear from other emotions. Indeed, in surprise and fear, eliciting events are typically appraised as unexpected, which is not the case for many other emotions.

As another appraisal dimension, appraised stimulus valence, be it in terms of intrinsic pleasantness or motivational valence, is also critical to shape various components of an emotional response (e.g., feeling good or bad), orient behavior (e.g., approach or avoid), and modulate various cognitive functions (Brosch, Pourtois, & Sander, 2010). These two dimensions of "appraised novelty" and "appraised valence" interact in the elicitation of emotions. For instance, Frijda (1988) described in what he referred to as the "law of change" the suggestion that "emotions are elicited not so much by the presence of favorable or unfavorable conditions, but by the actual or expected changes in favorable or unfavorable conditions" (p. 353). Therefore, appraisal theories predict that when a situation is uncertain, both negative (e.g., fear) and positive (e.g., wonderment) emotions are particularly likely to be elicited. In the current study, we therefore investigated the amygdala's response to faces expressing various "novelty" and "valence" appraisal outcomes. Moreover, we included neutral facial expressions as a means to differentiate between relevance in terms of valenced versus nonvalenced stimulus content (see Tables 1 and 2).

Extensive research shows that the amygdala is particularly sensitive to socially relevant stimuli, including faces (Adolphs, 2010). Consequently, the determination of stimulus relevance during social encounters will importantly rely on facial displays of surprise—signaling *novelty*—as well as emotional facial expressions of other emotions such as happiness or anxiety—reflecting *valence*. Much effort has already been devoted to elucidating amygdala involvement in the processing of valenced emotional facial expressions, revealing rather unspecific activation increases, including happiness (e.g., Fitzgerald, Angstadt, Jelsone, Nathan, &

Table 2  
Explanation of Stimulus Conditions During the (Nonsocial) Lottery Task



<sup>a</sup> Neutral no-surprise-containing stimuli were static.

Phan, 2006; see also Cunningham & Kirkland, in press; Sander et al., 2003; Sergerie et al., 2008). In addition, although recent brain imaging evidence accumulates to suggest that the amygdala plays a key role in the processing of novel stimuli (e.g., Balderston, Schultz, & Helmstetter, 2011; Blackford, Avery, Shelton, & Zald, 2009; Weierich, Wright, Negreira, Dickerson, & Barrett, 2010), only little is known about the role of the amygdala in processing expressed novelty detection conveyed by surprised faces, and even less about possible interactive effects of valence and novelty.

Two pioneer functional MRI (fMRI) experiments have investigated amygdala response to static displays of "neutral" surprised faces, either as a function of subsequent valence ratings (Kim, Somerville, Johnstone, Alexander, & Whalen, 2003) or preceded by positive or negative sentences (e.g., "She just found \$500") generating a specific social context (Kim et al., 2004). In both investigations, the amygdala showed a negativity bias, being more strongly activated to more negatively rated or negatively contextually primed surprised faces. These fMRI data suggest that "neutral" surprise as expressed by the human face per se is an ambiguous emotion—at least if presented by means of a static, not contextualized picture—and that the amygdala preferentially processes such surprise if it has a negative connotation. Further corroboration for such negativity bias in the perception of static surprise comes from a series of studies measuring reaction times and corrugator muscle responses to static surprised (vs. happy and angry) faces (Neta, Davis, & Whalen, 2011; Neta, Norris, & Whalen, 2009; Neta & Whalen, 2010). On one hand, participants who tended to rate surprised faces as negative showed increased corrugator activity to surprised faces (and this effect was inverted in participants who rated surprised faces as positive). On the other hand, participants were faster to detect surprised faces presented

Table 1  
Explanation of Stimulus Conditions During the (Social) Face Task

Valence	Novelty	
	Surprise	No Surprise
Neutral	"Typical surprise"	Neutral <sup>a</sup>
Positive	Wonderment	Joy
Negative	Fear	Anxiety

<sup>a</sup> Neutral no-surprise-containing stimuli were static.

within a happy context during an oddball paradigm. Altogether, these behavioral data suggest that the default interpretation of static surprise may actually be negative, which in turn could partly account for the observed negativity bias of amygdala activation to static surprise.

One reason why fear (as a prototypical negative surprise) seems particularly likely to activate the amygdala is because fear is typically elicited by events that are both *novel* (in the sense of unexpected) and of *negative valence*. However, according to the relevance detection account of the human amygdala (Sander et al., 2003), such amygdala response should not be specific to negative valence but also present for emotional expressions that are novel and of *positive valence*. To test this hypothesis, we created a new set of artificial three-dimensional (3D) dynamic facial expressions, displaying surprise with an intrinsic positive (similar to wonderment) and negative (similar to fear) expression. Furthermore, we generated stimuli that did not contain any surprise, but were again intrinsically positive (similar to joy) or negative (similar to anxiety). Finally, we created “neutral” facial expressions that either comprised surprise (similar to a “typical surprise” expression) or did not contain any surprise (neutral)—see Table 1 for a summary of conditions. We made the following three predictions regarding amygdala activation. First, the amygdala should be more activated for emotional versus neutral stimuli (Hypothesis 1). Second, it should also be more activated for expressions containing versus not containing surprise (Hypothesis 2). Finally, among the emotional conditions, the amygdala should display an additive effect of valence and novelty, reflected in higher activity to faces that express both valence and novelty (i.e., wonderment and/or fear) versus faces that express valence (i.e., joy and/or anxiety) or novelty (typical surprise) alone (Hypothesis 3).

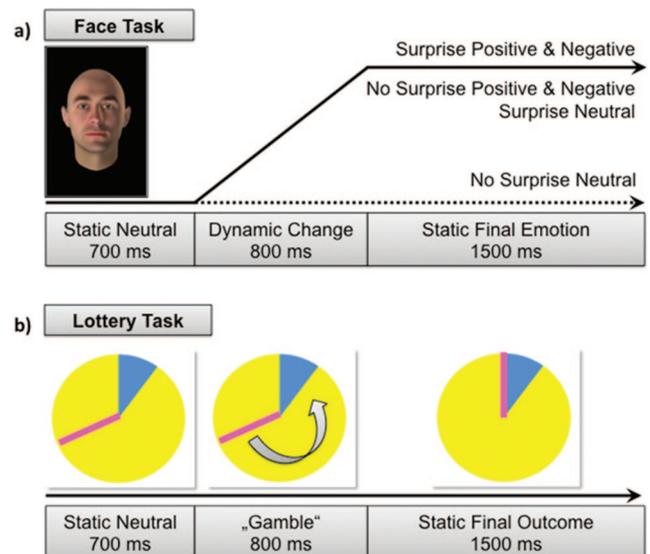
Because the human amygdala is also known to be activated by nonsocial stimuli (Sabatinelli et al., 2011; Sergerie et al., 2008; Vrticka, Sander, & Vuilleumier, 2013), we created an additional control task consisting of a Lottery paradigm where gains, losses, and null trials occurred with different probabilities. This task was created to compare the amygdala response to valence and novelty in a social versus nonsocial context. Two crucial properties were very similar in these two tasks. First, the different degrees of positive and negative surprise (see Table 2) strongly resembled each other. Second, the timing of the Lottery sequence was as closely matched to the emotion generation process in the 3D face movies as possible (see Figure 1). We anticipated amygdala to function in a comparable fashion during (nonsocial) Lottery as in the course of the social (Face) task, again displaying the three predicted activation patterns described above.

## Methods

### Participants

We recruited 20 participants (13 women, mean age  $22.91 \pm 1.86$  years, right-handed), who all had normal or corrected-to-normal vision, no history of neurological or psychiatric disease, and gave informed written consent according to the local ethical committee regulation.

All participants performed both tasks. However, data of the Lottery task from two participants could not be used for data



**Figure 1.** Experimental paradigm. (a) Illustration of the Face task, during which each trial started with a static neutral facial expression for 700 ms, followed by a dynamic expression change period of 800 ms, and another static display of the full blown emotion for 1500 ms. In the neutral no-surprise-containing trials, there was no movement at all. See Methods and Table 1 for more details. (b) Illustration of the Lottery task, during which each trial started with a static display of the probability to either “win” or “lose,” indicated by the yellow or blue parts of the pie, and a purple indicator, forming a wheel of fortune. Subsequently, the indicator started turning during 800 ms, and finally remained static for the remaining 1500 ms at its final position. Here, the final position depicts a “neutral surprise trial,” during which the indicator turned during the lottery phase, but then stopped in between the two colors, thus reflecting neither a “won” nor a “loss.” For the “neutral no-surprise containing” trials, the indicator did not turn at all. See Methods and Table 2 for more details.

analysis (technical failure of either the fMRI scanner computer or the behavioral device registering responses).

### Stimuli and Experimental Conditions

Six experimental conditions were created (see Tables 1 and 2): two dynamic positive and negative surprise-containing (“wonderment” and “fear”), two dynamic positive and negative no-surprise-containing (“joy” and “anxiety”), one nonvalenced condition that was dynamic and contained surprise (“typical surprise”), and one that was static and did not contain any surprise (“neutral”). Examples of face movies can be found online.

For the Face task (Figure 1a and Table 1), 3D movies showing dynamic facial expressions were created using the software FACS-Gen 2.0. This is an animation tool for creating realistic, both static and dynamic 3D facial expressions based on the Facial Action Coding System (FACS; Ekman, 1999; Ekman, Friesen, & Ellsworth, 1972). It provides researchers with control over facial action units (AU), and corresponding informational cues in 3D synthetic faces. The software has been developed by the Swiss Center for Affective Sciences at the University of Geneva (Roesch et al., 2011), and has already been used to generate dynamic facial emotional expressions in previous experiments, some of them

examining the role of the human amygdala in self-relevance processing (Cristinzio, N'Diaye, Seeck, Vuilleumier, & Sander, 2010; Mumenthaler & Sander, 2012; N'Diaye, Sander, & Vuilleumier, 2009). According to the FACS, happiness-related emotional expressions contained the AUs 6 + 12, fear-related emotional expressions the AUs 1 + 2 + 4, and all expressions comprising surprise the AUs 1 + 2 + 5 + 26. Additional minor adjustments on AUs 15, 20, and 27 were necessary to ensure a homogenous mouth-opening (teeth display). We created a total set of 30 identities (15 female) who each expressed five dynamic and one static neutral control state, resulting in 180 trials.

All facial expressions movies begun with a static neutral face (700 ms), which then changed dynamically toward a full-blown emotion during 800 ms, the latter remaining static on the screen for another 1500 ms. In the baseline “neutral” no-surprise-containing condition, the neutral face remained static over the whole 3000 ms period (see Figure 1a).

For the nonsocial Lottery task (see Figure 1b and Table 2), stimuli were created using an algorithm in Eprime 2.0 (Psychology Software Inc., Pittsburgh, PA). Each lottery consisted in a colored pie filled with different proportions of blue or yellow indicating the probabilities of winning or losing a given trial (color mapping was counterbalanced across participants), over which a static pink indicator was superimposed, forming a wheel of fortune. At the beginning of each trial, the pink arrow remained static for 700 ms. Then, the arrow started to spin (between one and three full cycles, randomized and counterbalanced across conditions, always clockwise) for 800 ms. Finally, the pink arrow stopped and remained static for another 1500 ms at its final position. On emotional trials, the indicator stopped either on a blue or yellow background, indicating a “gain” or a “loss.” In “typical surprise”-containing trials, the arrow stopped between the two colors, representing neither a “gain” nor a “loss.” In the baseline “neutral” no-surprise (static) condition, the arrow was present from the beginning but did not rotate during the whole trial. To maintain realism about the probabilities of winning or losing with a given lottery, which is critical to the elicitation of surprise reactions, only 30 trials each were presented for wonderment, fear, and “typical surprise,” but 90 trials each for joy and anxiety. Thirty additional trials contained the static “neutral” condition, which gave rise to 300 trials in total. The smaller portion of the wheel of fortune occupied 25° (i.e., about 7%) in four different positions, counterbalanced across trials (0°–25°, 155°–180°, 180°–205°, or 335°–360°; see Table 2).

## Procedure

The fMRI session was divided into four successive runs. The first two runs comprised the Face task, which lasted approximately 8 min each. The last two runs comprised the Lottery task, which lasted approximately 14 min each. Participants were instructed about both tasks before entering the scanner.

During the Face task (Figure 1a), participants had to respond by button press whether the face they saw was male or female (either button one or two, counterbalanced across participants). All trials were included in the data analysis, as the behavioral gender categorization task was not related to the variables of interest.

During the Lottery task (Figure 1b), participants had to indicate by button press whether the final position of the arrow fell in the yellow or blue portion of the lottery (either Button 1 or 2, coun-

terbalanced across participants via the color-outcome mapping), or in-between (Button 3, “neutral” trials). Only trials with correct responses were included into data analysis, as it was crucial to ensure that participants realized whether they “won,” “lost,” or neither. For the Lottery task, participants were additionally instructed to keep track of their performance, as they would receive a bonus at the end of the experiment if they “won” more often than they “lost.” Eventually, all participants received the bonus, as their “performance” was always exactly 50%.

## MRI Acquisition

MRI data were acquired on a 3 T whole-body scanner (Siemens TIM TRIO), using standard head-coil configuration. For each participant, a structural image was obtained with a MPRAGE T1-weighted sequence (TI/TR/TE/flip = 900ms/1900ms/2.27ms/9°, parallel acquisition (GRAPPA) with acceleration factor 2, FOV = 256 × 256 mm<sup>2</sup>, Matrix = 350 × 263 × 350 mm<sup>3</sup>, Voxel dimensions = 1 × 1 × 1 mm). Functional images (TR/TE/Flip = 2100ms/30ms/80°, parallel acquisition (GRAPPA) with acceleration factor 2, FOV = 205 × 205 mm<sup>2</sup>, matrix = 205 × 205 × 138 mm<sup>3</sup>) covered the whole brain, composed of 36 contiguous 3.84 mm axial slices (in-plane resolution 3.2 × 3.2 mm) parallel to the inferior edge of the occipital and temporal lobes, and acquired continuously for a total of 1,356 images per participant (Face task with 2 × 262 = 524 and Lottery task with 2 × 416 = 832 images—including instructions, etc.). Image quality was verified to exclude prominent signal drop-out in orbitofrontal and medio-temporal areas.

## MRI Analysis

Image processing was performed with SPM8 ([www.fil.ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)) using standard procedures for realignment of the time-series, slice-timing correction, normalization to a standard brain template in MNI space, resampling to 2 mm<sup>3</sup>, and smoothing with an 8 mm FWHM Gaussian kernel. Statistical analysis was performed using the general linear model implemented in SPM8, with a separate regressor for each event type convolved with a 3-s boxcar function comprising the whole duration of the social (Face) or nonsocial (Lottery) trials. For each task, six event types were modeled for each participant (novelty: surprise or no surprise/valence: neutral, positive, or negative), using the four scanning runs at the single-subject level. Movement parameters from realignment corrections were entered as additional covariates of no interest for each scanning run, in order to account for residual movement artifacts after realignment. Statistical parametric maps were then generated from linear contrasts between the different conditions in each participant, for each task separately.

Second-stage random-effect analysis was performed using one-sample *t* tests on contrast images acquired in each subject for each comparison of interest. Because we were specifically interested in amygdala activity, we first anatomically localized bilateral amygdala (region of interest [ROI] selection; Poldrack, 2007) using the Automatic Anatomical Labeling template (Tzourio-Mazoyer et al., 2002) as part of the Wake Forest University School of Medicine PickAtlas software toolbox for SPM (Maldjian, Laurienti, & Burdette, 2004; Maldjian, Laurienti, Burdette, & Kraft, 2004). Activity within the amygdala ROIs was then assessed with

the contrasts best suited to test our three hypotheses by applying small volume corrections ( $p < .05$ ). First, we derived the contrast valenced > neutral ([positive and negative surprise + positive and negative no surprise] > [typical surprise + neutral no surprise]) corresponding to Hypothesis 1. Second, we computed the contrast surprise > no surprise ([positive surprise + negative surprise + typical surprise] > [positive no surprise + negative no surprise + neutral no surprise]) corresponding to Hypothesis 2. And third, we derived the contrast valenced surprise > valenced no surprise ([positive surprise + negative surprise] > [positive no surprise + negative no surprise]) corresponding to Hypothesis 3. Because the latter contrast did not reveal any significant effects, we further decomposed valence and novelty processing in the amygdala. This comprised the contrasts positive surprise > negative surprise and negative no surprise > positive no surprise. When computing these additional contrasts, significant effects were observed for positive surprise > negative surprise trials in both the (social) Face and the (nonsocial) Lottery tasks (see below). We therefore derived a conjunction analysis (inclusive masking of the two contrasts at  $p < .05$ ) to determine whether there were any amygdala voxels that were significantly activated for both comparisons (overlapping activity during the Face and Lottery tasks).

## Results

### Face Task

During the Face task, we observed a significant effect corresponding to Hypothesis 1 within the bilateral amygdala ROIs. For valenced versus neutral faces, there was stronger activation in the right amygdala (93 voxels, peak at  $p = .003$  and  $xyz = 24 -2 -18$ ), and to a weaker degree also in the left amygdala (four voxels, peak at  $p = .036$  and  $xyz = -18 -6 -18$ ). The subsequent contrasts computed to further investigate valence and novelty processing revealed selectively higher activity for positive surprise versus negative surprise in the left amygdala (10 voxels, peak at  $p = .010$  and  $xyz = -22 -8 -12$ ), and to a weaker degree also in the right amygdala (two voxels, peak at  $p = .044$  and  $xyz = 24 -8 -12$ ). See Figure 2a and 2b for these results.

### Lottery Task

During the Lottery task, we did not observe any significant activity within bilateral amygdala ROIs corresponding to our three primary hypotheses. However, the subsequent contrasts to further investigate valence and novelty processing revealed two significant effects. First, we found significantly increased activity bilaterally for negative versus positive no-surprise trials (left: 72 voxels, peak at  $p = .003$  and  $xyz = -24 2 -20$ ; right: 11 voxels, peak at  $p = .025$  and  $xyz = 32 0 -16$ ). Second, we observed significantly increased activity bilaterally for positive surprise versus negative surprise trials (left: 11 voxels, local peak at  $p = .010$   $xyz = -22 -8 -16$ ; right: 16 voxels, peak at  $p = .005$  and  $xyz = 30 -2 -28$ ). See Figure 3a and 3b for these results.

### Conjunction Between the Face and Lottery Tasks

Finally, because amygdala activity was detected at similar locations during both the Face and Lottery tasks for the contrast

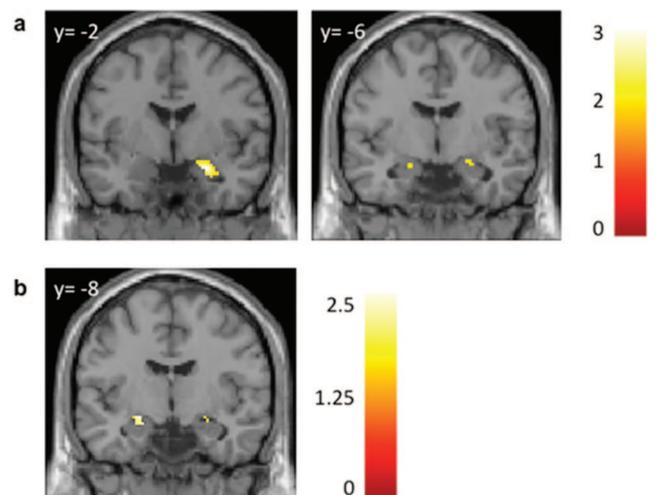


Figure 2. Amygdala activity during the Face task. Significant amygdala activation within anatomical regions of interest was observed during the Face task for the contrast valenced > neutral (a) and positive surprise > negative surprise (b). Functional maps are overlaid on a template single-subject anatomical T1 image.

positive surprise > negative surprise, we generated a conjunction map (inclusive masking) from data obtained during the Face ( $n = 20$ ) and Lottery ( $n = 18$ ) trials. This revealed significant overlapping activity within the left amygdala ( $n = 18$ , five voxels, peak at  $xyz = -24 -8 -16$ ; see Figure 4).

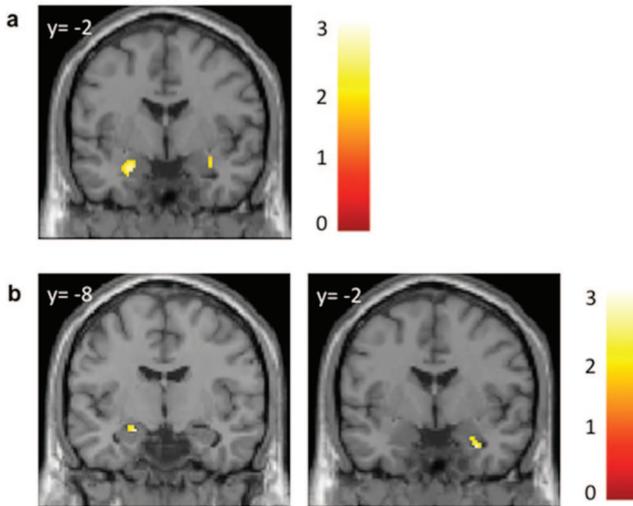
## Discussion

The major aim of this study was to test the hypothesis according to which fearful faces are particularly prone to elicit amygdala activation because they contain both valence-based (i.e., negativity) and novelty-based (i.e., surprise) components. The rationale therefore was that other emotional expressions, which include both valence and novelty cues, should also activate the amygdala, even if the conveyed valence is positive. In consequence, we probed how the human amygdala would respond during the perception of dynamic faces either expressing a valence-based or a novelty-based reaction, a combination of both, or simply a neutral emotion. The general prediction was to observe additive effects of valence and novelty.

A secondary aim was to compare the activation pattern in the (social) Face task to amygdala responses induced by nonsocial self-relevant stimuli also manipulated for their valence and novelty (Lottery task).

### Face Task

When examining amygdala activation during the social (Face) task, the right (and to a smaller extent also left) amygdala was found to respond more to valenced versus neutral dynamic expressions. Furthermore, we observed that left (and to a smaller extent also right) amygdala response was increased for dynamic faces expressing a positive surprise as compared to a negative surprise. Previous fMRI research (Kim et al., 2003, 2004) found the amygdala to be more strongly activated for negatively connoted



**Figure 3.** Amygdala activity during the Lottery task. Significant amygdala activation within anatomical regions of interest was observed during the Lottery task for (a) the contrast negative versus positive no surprise, and (b) the contrast positive versus negative surprise. Functional maps are overlaid on a template single-subject anatomical T1 image.

static surprise, which is consistent with behavioral findings suggesting that static surprise is by default perceived as negative (Neta et al., 2009, 2011; Neta & Whatlen, 2010). Conversely, our data as such is consistent with a recent meta-analysis suggesting that across different tasks, the amygdala overall responds stronger to positive than negative stimuli (Sergeier et al., 2008). This being said, we did not find any evidence in order to support any additive effects of valence and novelty processing during the (social) Face task.

### Lottery Task

When subsequently examining amygdala activity during the nonsocial (Lottery) task, we observed significantly stronger bilateral activity for negative no-surprise versus positive no-surprise, and for positive surprise versus negative surprise conditions. The latter finding was very comparable to amygdala activation found during the Face task. Moreover, there was significant overlap between the left amygdala activation clusters within the same participants ( $n = 18$ ) across the Face and Lottery tasks for the positive versus negative surprise effect. Apart from the similarities observed in amygdala activation between the Face and Lottery tasks, the above reported results per se did not support our hypotheses.

It should be noted here that the Face and Lottery tasks were designed to be comparable with respect to the key variables of interest, novelty and valence, and their temporal dynamics. However, an inherent difference between the two tasks is that the novelty and valence components were irrelevant to the gender categorization during the Face task, whereas participants' attention was directed toward the latter in the Lottery task (outcome monitoring). The reason why we instructed participants to keep track of their gains and losses during the Lottery task is because it is still unclear whether lottery out-

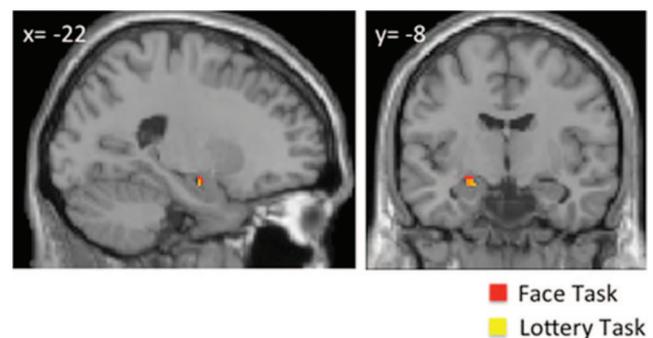
comes are processed when not attended. Implicit processing of facial expressions including surprise, in turn, is well established (see, e.g., Duan, Dai, Gong, & Chen, 2010; Vuilleumier, 2005; Lieberman, 2007).

### Amygdala, Relevance, and Expected Value Prediction (Errors)

The activation increase observed in both the Face and the Lottery task for the positive as compared to the negative surprise condition can be alternatively considered in the light of findings obtained by Yacubian and colleagues (Yacubian et al., 2006). These authors report an fMRI investigation applying a (nonsocial) card-guessing task with different probabilities to either win or lose low or high amounts of money. Participants could bet one or five Euros (representing reward or loss *magnitude*) on either one or four—out of 6—cards (representing reward or loss *probability*) and win the invested money if their bet was placed on the Heart Ace card, which was always present among the 6 cards. Accordingly, the authors calculated positive and negative expected values during the anticipation phase, positive and negative expected value prediction errors during the outcome phase, and measured brain activity for both phases.

Of particular relevance for the present study were Yacubian and colleagues' (2006) findings regarding amygdala activation. For the low gain probability/high reward magnitude trials (investing five Euros on one card), BOLD signal change in the amygdala was higher for loss-related (negative) expected value during anticipation (negativity bias), but higher for gain-related (positive) prediction error during the outcome phase (positivity bias). In other words, when betting a high amount of money with a small probability of winning, the amygdala was activated strongest during loss-anticipation, and strongest when processing an unexpected (surprising) high gain.

Such findings suggest that the human amygdala was critically involved in predicting the worst outcome (five Euro loss), as the latter would entail strongest attention, demand extensive further processing, and require a most extensive adaptive reaction. Yet,



**Figure 4.** Overlapping left amygdala activity across both the face and lottery tasks. Significant overlapping left amygdala activation within anatomical region of interest was observed when comparing brain activity within the same  $N = 18$  participants during both the Face and Lottery tasks (contrast positive surprise > negative surprise inclusively masked at  $p < .05$ ). The functional map is overlaid on a template single-subject anatomical T1 image.

when the final outcome was (unexpectedly) highly positive (five Euro won), the amygdala was again strongly activated, because the anticipated adaptive reaction had to be readapted to the new circumstances, once more requiring strong attention and processing demands. In sum, the amygdala would (a) anticipate the worst outcome (negativity bias), but then (b) update the latter in case of an unexpected positive outcome, thus reflecting the anticipation of a negative outcome and the reaction to a positive surprise (Yacubian et al., 2006).

The amygdala activation pattern that we observed during the Lottery task is very similar to that described by Yacubian and colleagues (2006), although we could not explicitly differentiate between the anticipation and outcome phases in our experiment (due to our different experimental design including dynamic facial expressions of emotion). We found increased activity for (a) negative versus positive no-surprise trials probably reflecting negative expected value, and (b) positive versus negative surprise trials possibly representing a negative expected value prediction error.

In the light of such previous data (Yacubian et al., 2006) and our findings during the Lottery task (see above), we can speculatively apply a similar principle to the perception of facial expressions of emotions, given their dynamic nature.

When exposed to dynamic—as opposed to static—emotional facial expressions, the final outcome of a facial display is, by definition, not yet known at the beginning, because the latter either starts from a neutral (as it was the case in the present experiment), or any other emotional expression (see Sacharin, Sander, & Scherer, 2012). It is therefore very likely that anticipation processes become involved in the predicting brain (Bar, 2011)—with the aim of being ready for the final emotion, as well as to prepare for any potentially arising processing demands as well as adaptive reactions. In so doing, one possibility is that, when the expression is starting to look surprised, the human amygdala is critically involved in the anticipation of a fearful expression (see Kim et al., 2003, 2004). Such explanation is corroborated by behavioral findings indicating that the default interpretation of (static) surprise may be negative (Neta et al., 2009, 2011; Neta & Whalen, 2010). As a consequence, amygdala involvement would be important for computing a prediction error (based on anticipated negative value) if the opposite outcome occurs (i.e., a positive surprise). This is consistent with our main result for surprise-containing expressions, namely that positively surprised faces (wonderment) activated the amygdala to a greater degree than negatively surprised faces (fear). Support for such a prediction error claim also comes from the fact that we found overlapping left amygdala activation for the contrast comparing positive to negative surprise within the same participants across both social and nonsocial tasks. This can be interpreted as suggesting that the left amygdala computed a negative expected value prediction error not only during the Lottery task—where such an interpretation is more straightforward and supported by previous findings (Yacubian et al., 2006)—but indeed also during the Face task.

Our findings of increased amygdala activation to positive versus negative surprise should also be considered from an alternative perspective. Accumulating evidence is showing that—even static—positive faces do activate the amygdala and reveals that both contextual (such as gaze direction, e.g., Adams, Gordon, Baird, Ambady, & Kleck, 2003), as well as personality (such as extraversion, e.g., Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002),

effects can modulate amygdala response to positive faces. Noteworthy, Cunningham and Kirkland (in press) not only showed amygdala sensitivity to positive stimuli as a function of trait happiness, but also found that participants higher on this trait happiness dimension displayed greater amygdala activation to positive than to negative stimuli. Therefore, as discussed earlier, one alternative explanation for our positive versus negative surprise findings during dynamic emotional face perception could be increased amygdala response to the positivity of surprised happy (expressing “wonderment”) faces per se, independently of any prediction error, and future studies directly comparing these two hypotheses are needed.

Furthermore, to better characterize amygdala response to the type of dynamic stimuli that we used, the temporal dynamics of amygdala response could be investigated more in depth in future studies. Indeed, although there is accumulating evidence suggesting that an analysis of the temporal dynamics of human amygdala activation is important (see, e.g., Brosch & Wieser, 2011; Pourtois et al., 2010), only few studies manipulated temporal stimulus aspects to test predictions concerning the specific function of the amygdala. For instance, by manipulating the duration of facial expressions, recent work (Adams et al., 2011, 2012; van der Zwaag, Da Costa, Zuercher, Adams, & Hadjikhani, 2012) demonstrated flipped amygdala responses to clear versus ambiguous threat-gaze combinations. In previous work, our group also tested the hypothesis that the amygdala is critical for relevance detection (Sander et al., 2003) by manipulating facial expression and gaze direction in faces. Consistent with the relevance detection hypothesis, our results suggested a stronger involvement of the amygdala in response to angry versus fearful faces with a direct gaze, but fearful versus angry faces with an averted gaze (Cristinzio, N'Diaye, Seeck, Vuilleumier, & Sander, 2010; N'Diaye, Sander, & Vuilleumier, 2009). Interestingly, another recent fMRI investigation suggests that such self-relevance processing holds true for early, presumably reflexive amygdala responses to facial emotions, but not necessarily for later, presumably more reflective amygdala activity to emotional faces (Adams et al., 2012). Such notion is based on the fact that amygdala activity was observed to be high for (static) fearful faces with an averted gaze only if presented shortly (for 300 ms), but high for (static) fearful faces with a direct gaze if presented for a longer time period (1,000 ms). These results clearly demonstrate the need to better take into account the temporal aspects of stimulus processing when investigating the function of the human amygdala.

Finally, it would also be of interest to obtain more data on specific amygdala subregion involvement in valence and novelty processing as such, and relevance detection more generally. There is previous evidence suggesting that the dorsal amygdala might be more involved in novelty/uncertainty (i.e., higher activity for fearful vs. angry static faces), whereas the ventral amygdala could be more sensitive to valence (i.e., negative vs. positive static emotional facial expressions; see, e.g., Whalen, 1998; Whalen et al., 2001; Kim et al., 2003). Future studies delineating amygdala subregions, particularly by distinguishing between dorsal versus ventral amygdala, are needed to reproduce and further extend such findings.

In conclusion, our data provides first hints on the human amygdala response to dynamic facial expressions of positive versus negative (vs. neutral) surprise, and how this may relate to the

processing of dynamic nonsocial but still self-relevant stimuli. By showing increased sensitivity of the amygdala to positive surprise-containing information, the present study confirms a key role of the amygdala in processing positive outcomes, in particular those that relate to uncertainty. The specific mechanisms underlying such heightened sensitivity to both social and nonsocial stimuli comprising positive surprise still need to be elucidated.

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Received February 1, 2013

Revision received July 1, 2013

Accepted August 2, 2013 ■