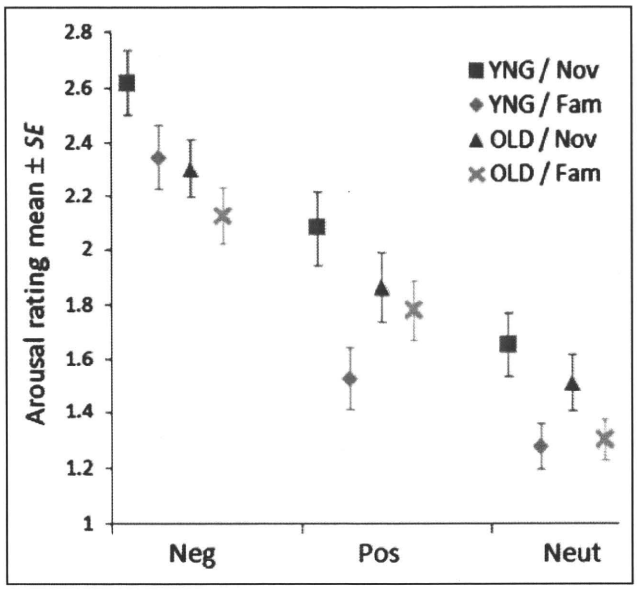

Figure 1. Rating of arousal level of each valence of IAPS pictures. Mean ± *SE* of arousal ratings of IAPS pictures during scanning are plotted in each valence of the stimuli (Neg = negative; Pos = positive; Neut = neutral). YNG = younger group; OLD = older group; Nov = novel condition; Fam = familiar condition.

amygdala responses to novel versus familiar images that were neutral in hedonic valence. To examine age-related differences in amygdala response to novelty and picture arousal level, we conducted Novelty (novel, familiar) × Arousal (high, mid) × Time point (1–8) × Age (young, older) repeated measures MANOVA for amygdala response to valenced images, and Novelty (novel, familiar) × Arousal (mid, low) × Time point (1–8) × Age (young, older) repeated measures MANOVA for amygdala response to neutral images.

FIR Analyses of Age-related Novelty and Valence Effects on the Amygdala Activation

When examining the overall amygdala response, there were no age-related differences in amygdala responses to novelty or valence; there was no Novelty × Age interaction for right amygdala responses [$F(1, 38) = 1.06$, $p = .311$], nor for left amygdala responses [$F(1, 38) = 1.39$, $p = .245$]. There was no Valence × Age interaction for right amygdala responses [$F(2, 37) = 1.79, p = .182$], nor for left amygdala responses [$F(2, 37) = 0.86, p = .430$]. For all participants, both valence [$F(2, 37) = 8.32, p = .001$] and novelty [$F(1, 38) = 5.46, p = .025$] significantly engaged the right amygdala. In addition, both valence [$F(2, 37) = 4.12$, $p = .024$] and novelty [$F(1, 38) = 13.97, p = .0006$] engaged the left amygdala.[1]

To examine age-related differences in the magnitude of the amygdala along its time course, we conducted a Novelty (familiar, novel) × Valence (positive, negative, neutral) × Time point (1–8) × Age (young, elderly) repeated measures MANOVA on the BOLD response within the right and left amygdala ROIs. Time courses are illustrated in Figure 2. The time course patterns in both left and right amygdala were similar; only the data in the left amygdala are shown. There was an age-related difference in the right and left amygdala time course for novelty [Novelty × Time point × Age: right, $F(7.32) = 4.01$, $p = .003$; left, $F(7, 32) = 2.46, p = .039$], such that younger and older individuals showed a different amygdala time course when viewing novel images. In particular, older (vs. younger) individuals have weaker amygdala responses before and after the peak, leading to a narrower and sharper time course (also see Curve Fit Analysis). The overall Valence × Time point × Age interaction was not significant in the right amygdala, $F(14, 25) = 1.65, p = .133$, nor in the left amygdala, $F(14, 25) = 1.45, p = .200$, such that there was no age-related significant difference in the amygdala time course when viewing positive or negative images, although older individuals did appear to show a similar "peakier" response in their amygdala response to negative and positive images when compared to younger individuals.

The four way Novelty × Valence × Time point × Age interaction was not statistically significant in the right amygdala [$F(14, 25) = 0.70, p = .75, \eta_p^2 = .282$], but was marginally significant in the left amygdala [$F(14, 25) = 2.02, p = .061$, $\eta_p^2 = .531$]. From Figure 2, this interaction in the left amygdala appeared to be driven by "peakier" amygdala response in the older group than in the young group, particularly in response to novel positive and neutral images rather than to novel negative images. To check this finding, we added a Valence × Time point × Age stratified repeated MANOVA for left amygdala BOLD response only for the novel pictures; we confirmed this marginally significant three-way interaction [$F(14, 25) = 2.04, p = .058$, $\eta_p^2 = .533$], suggesting that the hemodynamic curves were different for young and older participants, particularly in response to novel positive and neutral images.

Further, we did stratified ANOVAs Novelty (novel, familiar) × Age (young, older) in each time point separately, and found significant Novelty × Age interactions at the time points of 2–4 sec [$F(1, 38) = 5.97, p = .02, \eta_p^2 = .14$],

Table 2. Mean (*SE*) of the Subjective Arousal Ratings of Different Arousal Levels of IAPS Images in Each Age Group

	Age Group	
Images	*YNG*	*OLD*
Valenced		
High arousal	2.31 (0.11)	2.13 (0.10)
Mid arousal	1.98 (0.10)	1.91 (0.09)
Neutral		
Mid arousal	1.64 (0.11)	1.61 (0.10)
Low arousal	1.29 (0.09)	1.20 (0.08)

YNG = young group; OLD = older group.

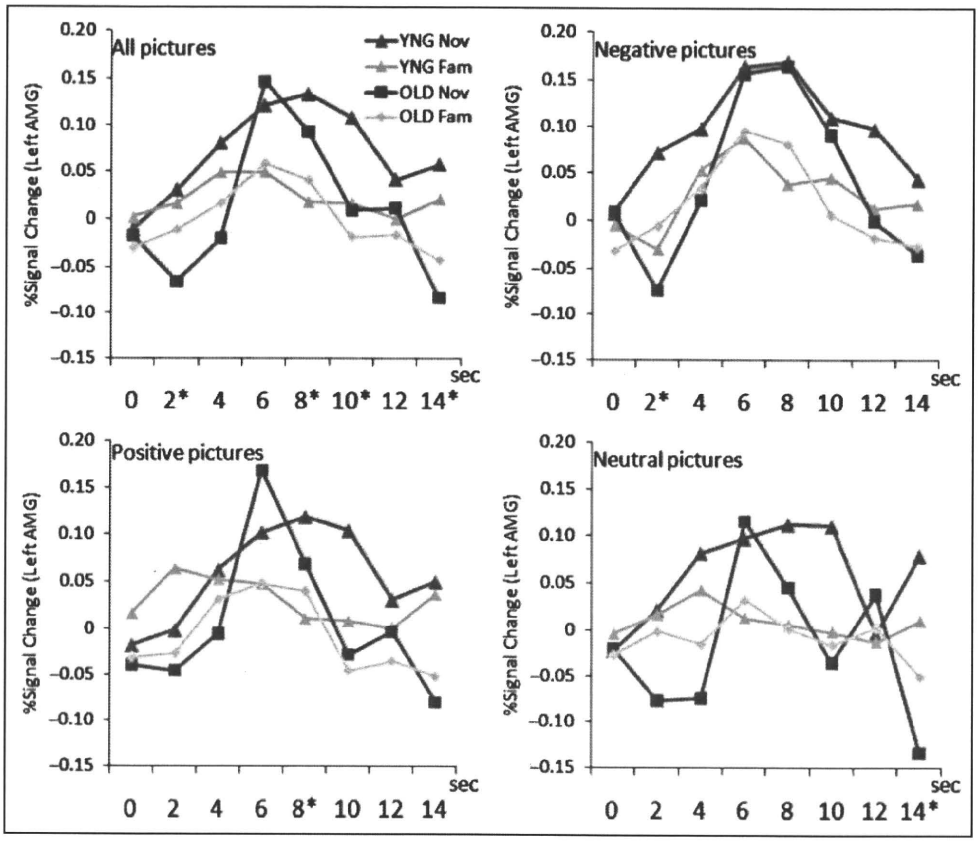

Figure 2. Age-related difference of hemodynamic time course in FIR analysis in the left amygdala. Event-related time course of BOLD response (% signal change) in each condition (Valence × Novelty) in two age groups. The right amygdala also showed a similar pattern so only the time course in the left amygdala was illustrated. Red = young group (YNG); green = older group (OLD). The four lines colored in red and green show response to novel (Nov) and familiar (Fam) images in the young and the older groups (Nov/YNG, Nov/OLD, Fam/YNG, Fam/OLD), which are displayed on each all, negative, positive, and neutral picture condition panels. Asterisk (*) shows significant Novelty × Age interaction ($p < .05$) in each time bin (TR = 2 sec).

8–10 sec [$F(1, 38) = 4.41, p = .04, \eta_p^2 = .10$], 10–12 sec [$F(1, 38) = 3.88, p = .06, \eta_p^2 = .09$], and 14–16 sec [$F(1, 38) = 4.67, p = .04, \eta_p^2 = .11$] in response to all three-valence images in the left amygdala; 2–4 sec in response to negative images in the right amygdala [$F(1, 38) = 5.16, p = .029, \eta_p^2 = .12$]; 2–4 sec in response to negative images in the left amygdala [$F(1, 38) = 10.1, p = .003, \eta_p^2 = .21$]; 8–10 sec to positive images in the left amygdala [$F(1, 38) = 4.27, p = .046, \eta_p^2 = .10$]; and 14–16 sec to neutral images in the left amygdala [$F(1, 38) = 6.72, p = .013, \eta_p^2 = .15$]. Taken together with Figure 2, the analyses appeared to show that the group differences of response to novel pictures occurred in early and late phases in the time course.

Age-related Differences in Amygdala Response to Novel vs. Familiar Neutral Images

To further investigate age-related differences within the amygdala time course in response to novelty, we conducted a Novelty (familiar, novel) × Time point (1–8) × Age (young, elderly) repeated measures MANOVA on the BOLD response to the neutral images, within the right and left amygdala ROIs. There was an age-related difference in the left amygdala time course for novelty [Novelty × Time point × Age: $F(7, 32) = 2.65, p = .028$]. This indicates that, even upon observing only neutral images, older individuals had a narrow and sharper amygdala time course to novelty when compared to younger individuals. In the right amygdala, there was no Novelty × Time point × Age interaction [$F(7, 32) = 1.23, p = .32$].

FIR Analyses of Age-related Novelty and Picture Arousal Effects on the Amygdala Activation

To address the question of whether novelty and picture arousal level interact to produce the neural response in the amygdala, we conducted Novelty (novel, familiar) × Arousal (high, mid) × Time point (1–8) × Age (young, older) repeated measures MANOVA for the right and the left amygdala response to valenced images, and Novelty (novel, familiar) × Arousal (mid, low) × Time point (1–8) × Age (young, older) repeated measures MANOVA for the right and the left amygdala response to neutral images. We found significant Novelty × Arousal × Time point × Age interactions for the left amygdala response to valenced images [$F(7, 32) = 2.43, p = .041, \eta_p^2 = .35$], and to neutral images [$F(7, 32) = 2.82, p = .021, \eta_p^2 = .38$], but not for the right amygdala response to valenced images [$F(7, 32) = 1.73, p = .13, \eta_p^2 = .28$], nor to neutral images [$F(7, 32) = 0.42, p = .88, \eta_p^2 = .09$]. Overall, the results were the same as the analyses with novelty and valence; older individuals showed a peakier amygdala response to novel pictures of higher levels of arousal when compared to younger individuals who showed a more sustained response across ~10 sec. The figures are not shown here, and the details of the findings and figures are available from the first author by request.

Curve Fit Analysis

On inspecting the hemodynamic curves from the FIR analysis, older individuals appeared to have a "peakier" amygdala time course when compared to younger individuals, particularly in response to novel stimuli. This was confirmed by an additional curve fitting analysis, showing that older individuals showed a different amygdala time course in response to novel pictures when compared to young individuals (Figures 3 and 4).

The simplified gamma probability density function hypothesized in the Methods section fits the observed FIR time course data quite well; all adjusted $R^2 > .9$ and all root-mean-squared-error (RMSE) < .05 (suggested by

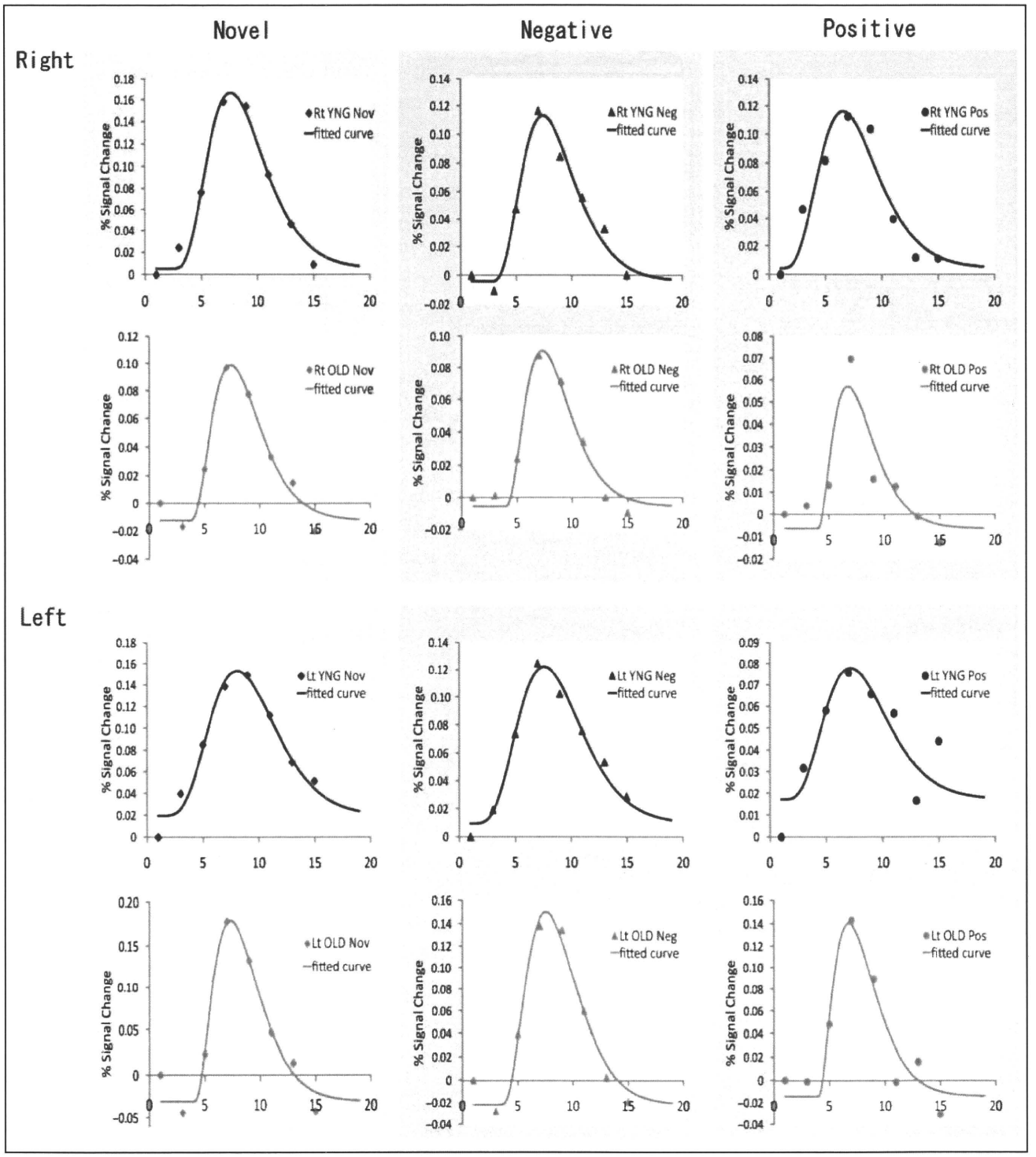

Figure 3. The time course of BOLD response to novel, negative, and positive pictures and fitted curves in curve fitting analyses. Rt = right; Lt = left; red dots and curve = young group; blue dots and curve = older group. The left column = novel condition; middle column = negative condition; right column = positive condition.

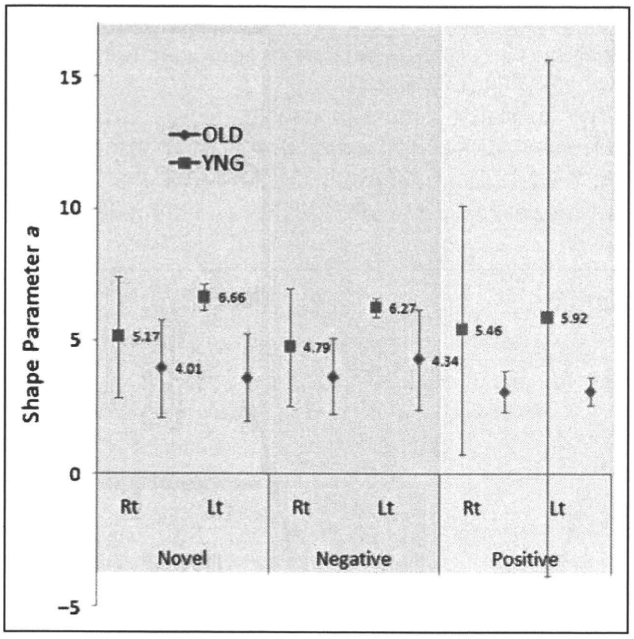

Figure 4. Shape parameter *a* in the curve fitting analyses in the novel, negative, and positive condition in the right/left amygdala. BOLD responses produced by FIR analyses in the right and left amygdala were fitted by gamma probability density function with three variable parameters of delay from time 0, height, and shape (broadness). The graph shows shape parameter *a* in each younger (YNG) and older (OLD) group in novel, negative, and positive condition. Upper = FIR data and fitting line; Lower = estimated value and 95% confidence interval (95% CI) of shape parameter *a* in both groups.

Browne & Cudeck, 1992). Table 3 shows the mean and 95% confidential interval of estimated shape parameter *a* for the BOLD time course in novel, negative, and positive conditions in the right and left amygdala. In these analyses, we found that older individuals had lower estimated *a* than that of the younger group, indicating that the older group had a peakier hemodynamic response to novel and negative pictures in the left amygdala. There was no group difference of parameter *a* in response to positive images in the left amygdala, or to any images in the right amygdala. Also, we did not observe any statistical age-related difference of delay (*d*) and height parameter (*c*).

Additionally, to check if this age-related difference of shape of hemodynamic time course was specific for the amygdala, we compared the hemodynamic time courses for the younger and older groups in other brain areas such as left medial posterior OFC, thalamus, hippocampus, fusiform gyrus, inferior frontal gyri pars triangularis, and inferior frontal gyri pars orbitalis. We also did curve fitting analyses in each ROI on BOLD response to novel stimuli. We did not find any age-related differences of parameter *a* similar to what were observed in the amygdala (Table 4). This suggests that not all hemodynamic responses across whole-brain areas show an age-related difference in time course shape difference, indicating that hemodynamic time course difference in the amygdala was not due to a general change in vasculature with aging.

Table 3. Estimated Mean and Upper/Lower Bound of 95% Confidence Interval of Shape Parameter *a* in Curve Fitting Analysis

	YNG			*OLD*		
	Mean	$LoCI_{95}$	$UpCI_{95}$	*Mean*	$LoCI_{95}$	$UpCI_{95}$
Right AMG						
Nov	5.17	2.94	7.41	4.01	2.21	5.81
Neg	4.79	2.62	6.96	3.70	2.30	5.11
Pos	5.46	0.76	10.17	3.17	2.39	3.95
Left AMG						
Nov	**6.66**	**6.17**	7.14	**3.66**	2.04	**5.27**
Neg	**6.27**	**5.90**	6.63	**4.34**	2.49	**6.19**
Pos	5.92	−3.85	15.70	3.20	2.67	3.73

YNG = younger group; OLD = older group; AMG = amygdala; Nov = novel condition; Neg = negative condition; Pos = positive condition; $LoCI_{95}$ = lower bound of 95% confidence interval; $UpCI_{95}$ = upper bound of 95% confidence interval.

Bold type: YNG mean > OLD $UpCl_{95}$ and OLD mean < YNG $LoCl_{95}$.

For novel conditions, mean *a* = 3.66 in older < $LoCI_{95}$ = 6.17 in younger, mean *a* = 6.66 in younger > $UpCl_{95}$ = 5.27 in older; for negative conditions, mean *a* = 4.34 in older < $LoCI_{95}$ = 5.90 in younger, mean *a* = 6.27 in younger > $UpCl_{95}$ = 6.19 in older.

Functional Connectivity Analysis

Functional connectivity analyses indicated that the amygdala of older individuals had a somewhat different pattern of correlated activity than the amygdala of younger individuals when responding to novelty. Correlation coefficients in novel versus familiar picture conditions were compared between the two groups (Figure 5), and those reported

Table 4. Mean and Upper/Lower Bound of Confidential Interval of Shape Parameter *a* in Curve Fitting Analysis in Affect-related ROIs in the Left Hemisphere

	YNG			*OLD*		
	Mean	$LoCI_{95}$	$UpCI_{95}$	*Mean*	$LoCI_{95}$	$UpCI_{95}$
OFC	5.26	3.02	7.51	4.60	1.89	7.31
Thal	5.16	3.43	6.90	4.51	3.15	5.86
Hc	4.17	2.55	5.80	2.97	1.57	4.37
FG	2.73	2.43	3.03	4.12	2.89	5.36
IFG tri	4.67	3.00	6.34	5.18	3.38	6.98
IFG orb	4.90	3.21	6.59	3.36	1.57	5.15

OFC = posterior orbito-frontal cortex at Brodmann's area 11 to 13; Thal = thalamus; Hc = hippocampus; FG = fusiform gyrus; IFGtri = inferior frontal gyrus (Brodmann's area 45 to pars triangularis); IFGorb = inferior frontal gyrus (Brodmann's area 47 to pars orbitalis); $LoCl_{95}$ = lower bound of 95% confidence interval; $UpCI_{95}$ = upper bound of 95% confidence interval.

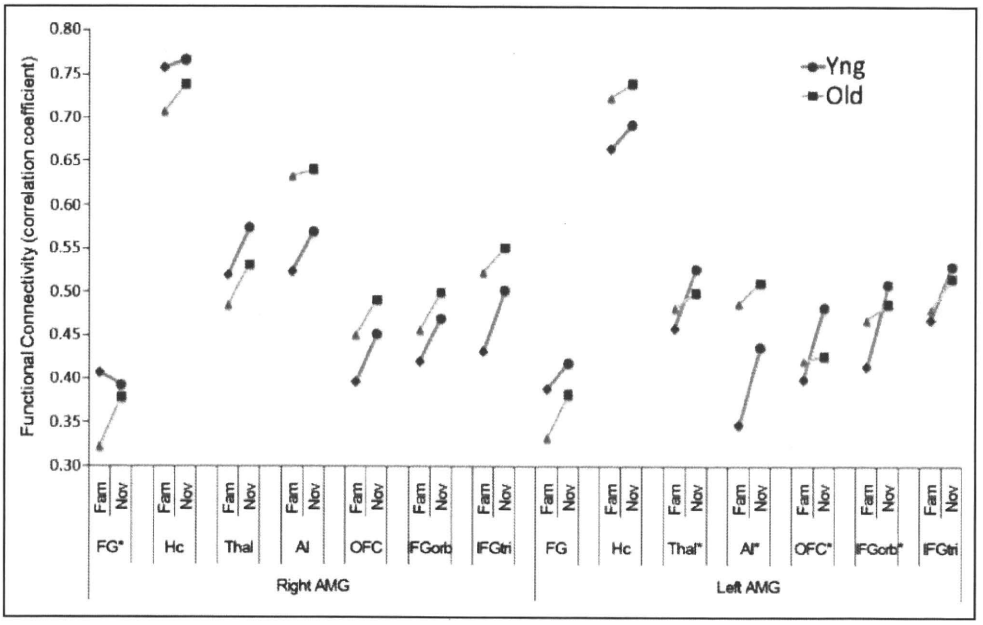

Figure 5. Functional connectivity between amygdala and other ROI. Correlation coefficients of event-related BOLD response between the amygdala and other emotion-related ipsilateral ROIs in novel (Nov) and familiar (Fam) conditions. Contralateral connectivity showed similar pattern so only ipsilateral connectivity was shown. FG = fusiform gyrus; Hc = hippocampus; Thal = thalamus; AI = anterior insula; OFC = orbito-frontal cortex; IFGorb = inferior frontal gyrus (pars orbitalis); IFGtri = inferior frontal gyrus (pars triangularis); AMG = amygdala. Red circle/diamond and line = young group (YNG); green triangle/square and line = older group (OLD). The flesh-colored ROI and asterisk (*) show a connectivity with significant Novelty × Age interaction ($p < .05$).

were significant according to a Novelty (novel, familiar) × Age (young, older) interaction at $p < .05$. Only ipsilateral connections (i.e., right amygdala–right ROIs, and left amygdala–left ROIs) are presented because the patterns of contralateral connections were similar.

To test the interactive effect of valence and age on the functional connectivity in response to novel (vs. familiar) pictures, estimates of functional connectivity in response to novel/negative, novel/positive, novel/neutral, familiar/negative, familiar/positive, and familiar/neutral images were first calculated. Next, these estimates of connectivity (correlation coefficients) were entered into Novelty (novel, familiar) × Valence (negative, positive, neutral) × Age (young, older) repeated ANOVA. The results are presented in the Figure 5. Novelty increased the functional connectivity between the amygdala and almost every ipsilateral ROI; for novel pictures, the right amygdala showed greater functional connectivity with the right hippocampus [$F(1, 39) = 5.56, p = .024$], the right thalamus [$F(1, 39) = 10.95, p = .002$], the right anterior insula [$F(1, 39) = 4.54, p = .039$], right medial/posterior OFC [$F(1, 39) = 8.68, p = .005$], the right inferior frontal gyrus (pars orbitalis) [$F(1, 39) = 8.95, p = .005$], and the right inferior frontal gyrus (pars triangularis) [$F(1, 39) = 15.42$, $p < .001$]. Similarly, the left amygdala showed greater functional connectivity with the left fusiform gyrus [$F(1, 39) = 4.86, p = .033$], the left hippocampus [$F(1, 39) = 8.59, p = .006$], the left thalamus [$F(1, 39) = 12.76, p = .001$], the left anterior insula [$F(1, 39) = 12.24, p = .001$], left medial/posterior OFC [$F(1, 39) = 7.09, p = .011$], the left inferior frontal gyrus (pars orbitalis) [$F(1, 39) = 11.12$, $p = .002$], and the left inferior frontal gyrus (pars triangularis) [$F(1, 39) = 10.84, p = .002$]. Functional connectivity did not vary by the valence of the pictures, and the Novelty × Valence interaction did not reach statistical significance.

Furthermore, we found a significant Novelty × Age interaction for the connectivity between the left amygdala and the left thalamus [$F(1, 39) = 4.31, p = .045, \eta_p^2 = .10$], the left anterior insula [$F(1, 39) = 4.20, p = .047, \eta_p^2 = .10$], left medial/posterior OFC [$F(1, 39) = 5.63, p = .023, \eta_p^2 = .13$], and the left inferior frontal gyrus (pars orbitalis) [$F(1, 39) = 5.04, p = .031, \eta_p^2 = .11$]. In response to novel (vs. familiar) pictures, younger individuals showed greater functional connectivity than did older individuals between the left amygdala and the left thalamus, anterior insula, medial/posterior OFC, and inferior frontal gyrus (pars orbitalis). In contrast, older individuals showed enhanced connectivity between the right amygdala and the right fusiform gyrus; a significant Novelty × Age interaction [$F(1, 39) = 4.91, p = .033, \eta_p^2 = .11$]. This pattern of functional connectivity suggests that the frontal/orbital areas might be involved in sustaining amygdala response in younger individuals.

Both ventromedial prefrontal cortex and ventral anterior cingulate cortex (bilaterally) showed a decrease in activation from fixation baseline in response to positive images (replicating Leclerc & Kensinger, 2008), but we also observed deactivations in response to negative and novel images. Furthermore, the hemodynamic time courses in these two regions were weakly correlated with the amygdala time course ($r = 0.0–0.2$; data not shown). In functional connectivity analysis, correlations between activation and deactivation hemodynamics are difficult to meaningfully interpret from a methodological standpoint,

and so the results of this functional connectivity analysis are not shown here but are available upon request.

DISCUSSION

Our findings clearly indicate that novel stimuli are affectively significant and engage the amygdala in a robust way. This novelty effect was not accounted for by the arousing or valenced nature of the stimuli, as was exhibited even with neutral images. The idea of novelty as a stimulus property with affective salience is consistent with studies in which the amygdala habituates even to very evocative stimuli (e.g., Wright et al., 2001; Fischer, Furmark, Wik, & Fredrikson, 2000), and by animal studies showing that amygdala lesions disrupt normal responses to novelty in primates (e.g., Mason, Capitanio, Machado, Mendoza, & Amaral, 2006; Prather et al., 2001; Burns, Annett, Kelley, Everitt, & Robbins, 1996; for reviews, see Petrides, 2007; Knight & Grabowecky, 1999). Together, these findings shape an emerging view that the amygdala's function is not to represent negativity or valence per se, but rather to mark the salience of a stimulus and modulate other brain areas to increase the processing of that stimulus to gain information for future use (e.g., Ewbank, Barnard, Croucher, Ramponi, & Calder, 2009; Wedig et al., 2005; Anderson & Phelps, 2001; for a discussion, see Barrett & Bliss-Moreau, 2009; Duncan & Barrett, 2007a, 2007b). This view is also consistent with the view that the amygdala is a key brain structure that is involved in evaluating an object for its goal relevance (Sander, Grafman, & Zalla, 2003).

We did not find age differences of the peak magnitude of the hemodynamic response in amygdala to any evocative images, indicating that, at least in one sense, affective processing within the amygdala, including responsiveness to novelty, is preserved in older people. These results are consistent with prior research showing no age-related changes in novelty processing (Wright et al., 2006, 2008), suggesting that salience (Carstensen & Turk-Charles, 1994) or vigilance (Whalen, 2007) is maintained across the lifespan. These findings are in line with the observation that the amygdala is one of the regions which is relatively structurally preserved with aging when compared to many other brain regions (e.g., West, 1996; Moscovitch & Winocur, 1995; Daigneault & Braun, 1993). Our findings differ from those previously published studies that reported reduced amygdala activation to negative images in older individuals, however, for a number of reasons. One of the possible reasons is that we used FIR analyses to examine our event-related BOLD data, whereas prior studies have used an SPM canonical hemodynamic function (e.g., Mather et al., 2004). The remarkable difference of the shape of the hemodynamic time course in older (vs. younger) individuals that we discovered suggests that a canonical hemodynamic function might provide a worse fit to the actual hemodynamic pattern in older individuals, resulting in a lower estimate of activation (i.e., a lower correlation between actual amygdala response and hypothetical gamma curve). This valence effect in aging remains to be tested with future studies.

Importantly, our results demonstrated age-related difference in the shape of the hemodynamic time course of the amygdala, particularly in response to the novel stimuli that have not previously been reported; older people showed "peakier" hemodynamic response when compared to younger individuals. In previous methodological papers, age-related changes of hemodynamic response were inconclusive (e.g., the rise time of the fMRI signal in motor cortex increased with age during a 10-sec hand-squeezing task, Taoka et al., 1998; spatial extent of activation in older people did not differ from that of young people for a photic stimulation task, Ross et al., 1997; no highly consistent age difference exists in the shape of hemodynamic responses in primary sensorimotor cortex, D'Esposito et al., 1999; and sustained event-related BOLD effect even after the peak in the older group, Aizenstein et al., 2004). These methodological studies indicate the age-related time course difference of fMRI hemodynamic responses may depend on the situations and experimental paradigms, is probably brain region specific, and might not be a general property of the aging brain.

There are three possible ways to explain the origins of age-related amygdala time course differences found in the present study. The first is vascular effects of aging, including stiffening of the arterial wall, decreased blood flow, and so on. Considering the blood flow directly influences the BOLD signal, the present data might reflect vascular issues in aged people. The data showed a negative BOLD change in the initial part of the event-related time course, which might be the "initial dip" (Heeger & Ress, 2002; Vanzetta & Grinvald, 1999; Malonek et al., 1997) caused by an increase in deoxyhemoglobin attributable to a brief uncoupling between blood flow and oxygen utilization; this has been reported in patients with arterial stenoses who exhibited larger initial dip in left primary motor cortex (Roc et al., 2006). Therefore, it might be possible that blood flow in the amygdala in aged people increased slowly, and did not catch up the oxygen consumption, which caused an early large negative BOLD signal. And if the increase of the blood flow ended earlier, the BOLD signal would drop earlier, resulting in their sharpened hemodynamic pattern. Nevertheless, considering that we found such a time course difference between age groups only in the amygdala, and not in other affective brain regions, the observed age-related changes in time course difference cannot be due solely to this vascular change with aging. Nonetheless, future studies should consider measuring participants' vascular stiffness and other systemic hemodynamic measurements (arterial pressure, pulse wave, etc.) and relating these to the functional data.

The second explanation for age-related changes in the hemodynamic time course of the amygdala is alteration of neurovascular coupling with age. Neurovascular coupling refers to the processes by which neural activity influences the hemodynamic properties of the surrounding

vasculature (cf. D'Esposito, Deouell, & Gazzaley, 2003). It is still unclear whether neurovascular coupling is altered with aging (see Fabiani & Gratton, 2004; Rosengarten, Aldinger, Spiller, & Kaps, 2003; Buckner et al., 2000). The fact that we did not find age-related differences in the shape of the time course other brain regions, however, suggests that changes in neurovascular coupling might not be the main source of the age-related differences observed in the current study. This issue should be addressed by future studies.

A third possible explanation for age-related changes in the hemodynamics of the amygdala time course is that other brain areas, such as medial posterior OFC and adjacent inferior frontal gyrus (IFGorb), are up-regulating or sustaining the neural response to novel images in younger individuals, such that brains of younger people appear to hold on to novel information longer than brains of older people. This regulatory hypothesis is plausible given that OFC–IFGorb areas are reciprocally connected with the amygdala (Milad & Rauch, 2007; Petrides, 2007; Rempel-Clower, 2007; Bachevalier & Loveland, 2006). A caudal sector of lateral OFC (Brodmann's areas 12 and 13) is mainly interconnected with the amygdala (Carmichael & Price, 1995; Barbas & De Olmos, 1990; Aggleton, Burton, & Passingham, 1980), midline thalamus, and temporal pole (Bachevalier & Loveland, 2006). This connection is very unique because the lateral OFC area receives projections from both the amygdala and the temporo-polar area, whereas the rest of prefrontal cortex appear to have fewer connections with the amygdala and temporal pole (Ghashghaei & Barbas, 2002). Posterior OFC has been known to be involved in novelty processing (Petrides, 2007), along with the prefrontal cortices (Mesulam, 1998). Taken together with the results of the present study, this system is altered in older people.

Whether changes in the amygdala time course are due to the vascular effects of aging, alterations of neurovascular coupling, or reduced amygdala regulation by other brain regions in the affective workspace, these findings are consistent with the "aging brain hypothesis" that improved affective stability in later adulthood is a by-product of biological decline including structural and functional degradation of the amygdala and other affect-sensitive brain areas (Scheibe & Carstensen, 2010; Cacioppo, Berntson, Bechara, Tranel, & Hawkley, 2008). This does not mean that older people lose their capacity to respond to affective salient (including novel) environmental conditions, but rather, that older brains do not show sustained processing in this regard.

Furthermore, our results suggest that a consideration of novelty might play a key role in understanding the affective changes that occur with age. Without the moderating influence of stimulus novelty, there were no age-related differences in amygdala activation for positive versus negative stimuli. By including novelty, however, we were able to observe that positive stimuli were perceived as more familiar (and therefore perhaps not as evocative) in older individuals. This is consistent with the recent observation that younger adults exhibited novelty memory bias for the positive items, whereas older adults did not, such that older adults experienced greater overall familiarity for positive items (Spaniol, Voss, & Grady, 2008). On the surface, this might appear inconsistent with earlier published report, but in fact, previous studies of age-related differences in amygdala responsivity have been inconsistent. Older individuals were observed to show increased amygdala responses to positive IAPS images (Mather et al., 2004), but other studies have shown the opposite (Addis, Leclerc, Muscatell, & Kensinger, 2010). Furthermore, positive facial expressions did not activate the amygdala in older individuals more than in young individuals (Gunning-Dixon et al., 2003; Iidaka et al., 2002).

Finally, our findings on the subjective experience of arousal point to potentially important age-related changes in the subjective salience of visual images. Novel pictures were more subjectively arousing for everyone, reflecting their increased salience, but older individuals found them less arousing than did younger individuals. In addition, older individuals found high arousal pictures less arousing when compared to younger individuals. These differences in subjective arousal very likely reflect age-related reductions in interoceptive information from the body. Older individuals are less interoceptively sensitive (e.g., Khalsa, Rudrauf, & Tranel, 2009), and have blunted physiological reactivity (Levenson, Carstensen, Friesen, & Ekman, 1991). In addition, they are less likely to use information from the body to make decisions under uncertainty (Denburg, Tranel, & Bechara, 2005). According to the concept of "maturational dualism" (Mendes, 2010), these age-related changes in sensory feedback from the body has consequences for age-related changes in subjective experience of affect. Given the amygdala's role in regulating autonomic response, the peakier time course of the amygdala activation in older individuals might be related to these autonomic changes, although this is a point for future research.

Acknowledgments

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Note

1. To clarify whether the effect of stimulus novelty on the BOLD response in the amygdala was mediated by subjective arousal, we conducted mediation analyses in the left and right amygdala with

stimulus novelty as an independent variable, amygdala BOLD response estimated by FIR analysis as a dependent variable, and subjective arousal rating in every event as a mediator. For the right and left amygdala, subjective arousal only partially mediated amygdala response (indirect effects were significant; $z = 7.000$, $p < .0001$ for the right, $z = 6.064$, $p < .0001$ for the left). Nonetheless, stimulus novelty continued to directly predict amygdala response ($z = 1.89$, $p = .058$ for the right, $z = 3.31$, $p = .0009$ for the left). These findings replicate those reported in Weierich et al. (2010), indicating that amygdala responses to novelty were not solely related to the arousing nature of the novel pictures. In addition, we computed a set of correlational analyses to examine whether differences in subjective arousal ratings (novel − familiar) were related to the differences in amygdala BOLD activity in novel (vs. familiar) contrasts. These findings indicated that the difference between subjective arousal in novelty (vs. familiar) and in the amygdala contrasts for novelty (vs. familiar) were related for positive pictures only. The young group showed a larger positive correlation between subjective rating difference scores and right amygdala contrast in response to positive pictures, and a larger negative correlation for neutral pictures, but the older group did not show that pattern. Specifics of the analyses are available from the first author upon request.

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