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Affective priming following unilateral temporal lobectomy: The role of the amygdala

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Affective priming following unilateral temporal lobectomy: The role of the amygdala

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Affective priming following unilateral temporal lobectomy: The role of the amygdala

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Abstract: The way that emotions are processed in the brain has been widely debated. The two leading hypotheses are the cognitive appraisal viewpoint (Lazarus, 1982) and the affective primacy hypothesis (Zajonc, 1980). The former argues that higher cortical structures are needed to evaluate affective stimuli whereas the latter asserts that humans can use information only processed at the subcortical level to influence behavior. The current study tested the presence of this subcortical pathway by using an affective priming task developed by Murphy and Zajonc (1993). Happy and angry faces were presented for 4 ms before the presentation of a neutral stimulus (Chinese Ideograph) that participants were asked to rate based on how much they liked each one. Individuals do not report conscious awareness of primes presented at this suboptimal speed. In a young adult sample, participants rated ideographs preceded by happy primes significantly higher than those preceded by angry primes. Also, the priming effect was only observed in participants who reported a high positive mood. Next, when primes were presented in the left or right hemifield priming was only found in the right hemifield, and was driven by increased ratings for ideographs preceded by happy primes. Patients with epilepsy who have undergone a temporal lobectomy provide a unique opportunity to study emotional processing. In this procedure, not only is the seizure focus (typically the hippocampus) removed, but the amygdala and surrounding areas of the mesial temporal lobe are removed as well. Nine patients post right temporal lobectomy and three patients post left temporal lobectomy completed the study and did not show an effect of priming. However, 21 pre-surgical epilepsy patients were found to give higher liking ratings to ideographs preceded by angry primes as compared to those preceded by happy primes. Overall, these results support the affective primacy hypothesis however they also suggest that patients with temporal lobe dysfunction may process emotional stimuli differentially from controls. In this population, ideographs preceded by angry primes were rated as more liked than those preceded by happy primes. Directions for future studies to clarify the role of the amygdala in emotional processing are discussed.

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Chapter 1 - The Role of the Amygdala in Affective Processing

Emotions are crucial to our everyday existence and social functioning. Affective processing helps us to read the feelings of others and respond appropriately. As a species that lives in groups and depends heavily on cooperation between individuals, being able to quickly interpret both verbal and nonverbal cues provides a distinct advantage to maintaining mutually beneficial relationships. Emotions also provide important cues for our safety. For example, when two individuals are having a conversation and one becomes angry it is crucial for the other to recognize this facial affect and make the proper adjustments to their behavior. If this adjustment is not made it could lead to escalation of the verbal argument or even physical violence.

We are constantly bombarded with a multitude of sensory information so it is vital that we are able to quickly attend to relevant stimuli. One function of emotions is to help provide these attentional shortcuts. In a study by Kubota et al. (2000) participants who were exposed to negative images, such as frightening animals, at speeds so fast they could not consciously detect them (30 ms) showed a greater galvanic skin response (GSR) than when they were exposed to pleasant images. This shows that humans possess the cognitive ability to detect threat extremely quickly. In the case of fear, threatening stimuli trigger a sympathetic nervous system response (as indicated by GSR in this case). While the evolutionary necessity of affective processing is widely understood, the neural underpinnings are not as well known.

1.1 Lesion Studies in Animals

Animal models have shown that there are subcortical pathways that allow for automatic processing of threatening stimuli before standard cortical processing occurs. In a study by Romanski & LeDoux (1992), the role of the thalamo-amygdala and thalamo-cortico-amygdala circuits was examined in rats. A tone was paired with a foot shock and the acquisition of fear conditioning was examined. In this experiment some rats were given lesions to thalamo -amygdala projections, some were given lesions to the thalamo-cortico-amygdala projections, and some were given both lesions. Romanski & LeDoux found that when either pathway was damaged the rats displayed fear conditioning, but when both were damaged they did not show this response. This suggests that there are two pathways for processing threatening stimuli: the cortical route and the subcortical route (Romanski & LeDoux, 1992).

The amygdala is a region of the brain that is critically important in both of these pathways. One of the first studies that elucidated the functioning of this region was conducted by Professor Heinrich Kluver and neurosurgeon Paul Bucy. After removing the temporal lobes of several monkeys they noticed a common pattern of symptoms including the following: “psychic blindness” (a form of visual agnosia), learning and memory impairment, oral exploration of objects, hypersexuality, and an extinction of fear and anger behaviors (Kluver & Bucy, 1939). For example, monkeys who had previously been bitten by a snake with intact amygdalae would avoid the animal, while those with bilateral amygdala damage would casually approach it again. To determine which area of the temporal lobes was responsible for changes in fear and anger behaviors Weiskrantz

(1956) performed more selective lesions and found an association between ablating projections from the amygdala and increased tameness, and a weakening or disappearance of previously conditioned fear responses.

While Weiskrantz's work showed a connection between efferent projections from the amygdala and fear conditioning, later studies showed a direct connection between ablation of the amygdala itself and inappropriate reactions to social stimuli (Meunier, Bachevalier, Murray, Málková, & Mishkin, 1999). In one experiment, fifteen rhesus monkeys were given neurotoxic amygdala lesions, which destroyed the region of interest without harming fibers connecting it to surrounding structures. Most notably, these monkeys demonstrated increased submission, and reduced fear and aggression behaviors (Meunier et al., 1999).

Lesion studies in a variety of animal species have shown that destruction of the amygdala leads to reduced emotionality (see Davis, 1992). Rats with this impairment show decreased fear in the presence of a sedated cat and in fact will sometimes approach the animal, crawl over it, and nibble its ear (Blanchard & Blanchard, 1972). Additionally, wild rats with this ablation show decreased fight or flight behaviors (Kemble et al., 1984). Birds with archistriatum (a region analogous to the human amygdala) lesions become docile and will infrequently try to escape from humans – a behavior that is not seen in non-lesioned animals (Phillips, 1964; Phillips, 1968). Across a variety of animals, destruction of the amygdalae has consistently been shown to lead to these uncharacteristically docile behaviors.

While ablation techniques demonstrate the absence of fear-related behaviors when the amygdala is removed, electrical stimulation of this area corroborates the role of the amygdala in fear-related behaviors. Electrodes stereotaxically implanted in animals have been used to show a correlation between electrical stimulation of the amygdala and a variety of physiological markers of fear such as the following: changes in heart rate and blood pressure (e.g., Anand & Dua, 1956; Pascoe, Bradley, & Spyer, 1989), respiration (e.g., Applegate, Kapp, Underwood and McNall, 1983; Harper, Frysinger, Trelease, and Marks, 1984), sham rage behavior (Allikmets, 1966), and freezing behavior (e.g., Kaada, 1972). Both ablation and electrical stimulation paradigms demonstrate the role of the amygdala in fear-related behaviors in animals. Of interest to the current study are the neural pathways involved in affective processing.

LeDoux's experiments give credence to a dual-pathway of emotional processing. From an evolutionary prospective, a subcortical route could provide a distinct advantage for survival. When threatened with a dangerous stimulus responding quickly can mean the difference between life and death. The time that it takes a rat to process an acoustic stimulus traveling from the thalamus to the amygdala is approximately 12ms, while the time it takes the same stimulus to travel from the cortex to the amygdala is twice as long (LeDoux, 1996). This time advantage is derived from the fact that the message traveling through the subcortical route is routed directly from the thalamus to the amygdala, while the message traveling through the cortical pathway has more "stops" to make along the way. However, the subcortical route is often referred to as the "quick and dirty" pathway;

because while it is faster it has not undergone more complex processing so it only gives a basic message of threat. This means that, for example, a rat who hears a rustling behind it may engage in a fight or flight response. The noise may only be the wind rustling leaves, so the response may not be appropriate for the situation, but overreaction is more beneficial for survival than not responding to a threatening stimulus.

In addition to direct threats such as predators, there are also social indicators of threat that facilitate responding appropriately to dangerous situations. Facial expressions and body language provide important information to individuals in a social group. For example, recognizing a facial expression of fear may provide information that a threat is in the environment, while recognizing anger may indicate that another individual is about to become physically aggressive. Primates serve as a useful animal model for understanding this process because they have been shown to display facial expressions that share similar features to those of humans and that communicate meaningful information to other group members (Preuschoft & van Hooff, 1995; Parr & Heintz, 2009). In one study, young adult rhesus monkeys raised in captivity were shown to initially not be afraid of snakes. However, after only eight minutes of watching a parent (who had been raised in the wild) display fear towards a snake, they also demonstrated fear upon their next exposure to the animal (Mineka, Davidson, Cook, and Keir, 1984). This research highlights the potency of observational learning and how powerful social stimuli are in addition to direct threats.

The proposed subcortical pathway for this kind of affective processing in humans has been theorized to operate through the pulvinar, a nucleus of the thalamus. While this structure is virtually non-existent in rats, it is present in primates. In a study by Jones & Burton (1976) the brains of three squirrel monkeys and three rhesus monkeys were examined and projections from the pulvinar to both the lateral amygdala and frontal cortex were found. This evidence of connectivity between these two regions in primates lends further support to a dual-pathway model of affective processing in humans.

1.2 Lesion Studies in Humans

Research conducted on animals provides foundational information about the amygdala and the neural pathways involved in affective processing but it is limited mainly to conditioned fear paradigms and the subjects are unable to provide verbal feedback regarding their experience. Also, animal models provide only an estimation of how the human brain may function.

Human patients with bilateral amygdala damage provide unique insight into the role of the amygdala. Adolphs, Tranel, Damasio, & Damasio (1994) were among the first to conduct a series of tests on a patient with this rare condition. This study found that, compared to controls, the patient with bilateral amygdala damage showed impairment in recognizing fearful facial expressions but not in recognizing the identity of faces. Also, while she could identify the names of familiar faces and draw happy, sad, angry, and disgusted faces, she could not draw a fearful face (Adolphs et al., 1994). This deficit is consistent with the animal literature because it shows that the amygdala not only responds to direct threat but also social indicators of threat. It also demonstrates that a different neural system is responsible for affective processing independent of that which processes identity.

Since this initial study by Adolphs et al. (1994) there has been work with other patients with bilateral amygdala damage that has both supported this deficit in emotional facial processing (Broks et al., 1998; Calder et al., 1996; Adolphs, Tranel, Damasio, Damasio, 1995; Young, Hellawell, Van de Wal, Johnson, 1996) and work that has shown no impairment in this area (Hamann et al., 1996). One possibility that would account for the variability in these results is the different methodology used. To rectify this problem, many of the investigators who conducted this research collaborated on a single project where participants were asked to identify the level of six basic emotions (happiness, surprise, fear, anger, disgust, and sadness) present in each of 39 faces. A strength of this study was the number of participants involved. While previous reports had presented case studies or data from 2 or 3 patients, this study examined 9 patients and compared them to a more rigorous control group of brain-damaged patients. It was found that as a group the patients with bilateral amygdala damage showed significant impairment in recognizing fear (Adolphs et al., 1999). Perhaps just as interestingly, statistical analysis of the errors made showed that these patients did not consistently mistake fear for one other emotion, but rather mistook it for a variety of emotions. This suggests a specific impairment in fear recognition and not a simple confusion for another emotion.

Further studies, however, have revealed even more complex social constructs that the amygdala is involved in processing. Not only does bilateral amygdala damage impair fear recognition, but also the ability to judge trustworthiness and approachability (Adolphs, Tranel, & Damasio, 1998). More specifically, these patients show impaired judgment in recognition of these qualities in faces but *not* in verbal descriptions of individuals. This indicates a specific role of the amygdala in decoding social information displayed on the face but not necessarily through all other modalities. Also, when taken collectively with previous studies this demonstrates that the amygdala is involved in more than simple fear processing.

Building on this work, it has also been shown that the amygdala may have a more general role in the processing of social emotions rather than just basic emotions. While the basic emotions are widely considered to be happy, sad, angry, afraid, surprised, and disgust, social emotions have also been shown to be reliably detected by healthy adults. Some examples of these are more complex mental states such as: scheming, guilt, thoughtfulness, admiration, flirtatiousness, boredom, interest, and arrogance (Baron-Cohen, Wheelwright, & Jolliffe, 1997). Individuals with Asperger’s Disorder and Autism have trouble identifying these, as well as patients with unilateral and bilateral amygdala damage (Adolphs, Baron-Cohen, & Tranel, 2002). In fact, patients with amygdala damage have more trouble identifying social emotions than basic emotions on the whole (Adolphs, Baron-Cohen, & Tranel, 2002). This may mean that the amygdala is involved in processing select basic emotions as well as more complex social emotions.

The amygdala is also known to play a role in enhancing declarative memory for emotional events. It is well known that in humans emotional memories are more likely to be recalled than neutral memories. The amygdala is situated in close proximity to the hippocampus, which is an area responsible for consolidating episodic memories, and these structures are highly connected. It has been shown that patients with bilateral amygdala damage show poorer long-term memory for emotional declarative material as opposed to controls (Adolphs, Cahil, Schul, & Babinski, 1997). A similar pattern of results has been found in patients with epilepsy who have undergone unilateral temporal lobectomy (Jambaque, Pinabiaux, Dubouch, Fohlen, Bulteau, & Delande, 2009).

Temporal lobectomy patients show deficits in fearful face recognition similar to patients with bilateral amygdala damage. However, because only one amygdala is absent in these individuals, the relative role of the left and right amygdala can be examined. Some studies have found more general impairment in negative affect recognition both in facial and vocal expression for both right and left temporal lobectomy patients (Brierley, Medford, Shaw, & David, 2004), while others have found that patients with right temporal lobectomy but not left temporal lobectomy have impaired recognition of fearful faces (Adolphs, Tranel, Damasio, 2001; Burton, Gilliam, Flynn, Labar, & Conn, 2002). While the role of the left versus the right amygdala is not widely agreed upon in the literature, it is interesting to note the global emotional status of these individuals after surgery. Patients who have had a left temporal lobectomy tend to report a decrease in socialization and an increase in depression post-surgically as opposed to patients who have had a right temporal lobectomy who tend to report increases in general happiness post-surgically (Burton & Labar, 1999).

1.3 Neuroimaging Studies in Humans

Behavioral tasks conducted on patients with either unilateral or bilateral amygdala damage have helped elucidate the role of the amygdalae in affective processing but neuroimaging offers additional insight by showing what stimuli the amygdalae respond to *in vivo*. Additionally, neuroimaging techniques allow us to look at the functioning of the amygdala in healthy individuals, which allows for greater sample sizes.

Some of the first studies using Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI) were conducted in healthy individuals and confirmed findings from the animal and human lesion studies. Fear conditioning training performed with healthy adults, demonstrated activation of the amygdala during both the acquisition and extinction of fear conditioning (Labar, Gatenby, Gore, LeDoux, & Phelps, 1998). Also, participants asked to view fearful faces without making an explicit judgment regarding the affect of the stimuli, showed amygdala activation (Morris et al., 1996; Breiter et al., 1996). Interestingly, in the study conducted by Morris et al. (1996), a positive correlation was found between the degree of fear shown in the face and the blood-oxygen-level-dependant (BOLD) response in the amygdala. This suggests that the amygdalae are responsive not only to facial emotion but the intensity as well.

Subsequent studies have also found a link between the intensity of non-facial visual stimuli and amygdala activation. In one study both negative and neutral scenes were presented to healthy adults and they were asked to rate the emotional intensity of the stimuli. Similar to the facial expression studies, the scenes which were rated as the most emotionally intense also produced the greatest BOLD response in the amygdala (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000). This is important because it shows both that the human amygdala is involved in processing emotional valence/content of complex visual stimuli and that there is a variable response that is dependent on emotional intensity. Further, in a study by Canli et al. (2000), when an unannounced memory test was conducted 3 weeks after initial exposure to the stimuli, the left amygdala activation during encoding was predictive of the participants' memory for the scenes. This finding demonstrates the role of the amygdala in the consolidation of emotional memories.

Additionally, the study by Canli et al. (2000) suggests laterality effects that are somewhat contradictory to lesion studies. As described in the previous section many lesion studies have found either a similar role for the left and right amygdalae in the processing of negative emotion or that the right amygdala is more involved in this processing. However, in the neuroimaging literature the results are still mixed but more consistently show left amygdala activation. For example, during mood induction paradigms a BOLD response in the left amygdala has been found to correspond with both happy and sad mood induction (Schneider et al., 1997). Also, a review by Baas, Aleman, & Kahn (2004) reported the findings of a meta-analysis conducted on 54 fMRI and PET studies in which they found that across studies the left amygdala was more frequently activated than the right amygdala. Perhaps most interestingly they did not find a correlation between laterality of activation and several factors that have been hypothesized to be processed differentially in the left and right amygdala: type of stimuli (pictures/words), instruction set (implicit/explicit), and level of processing (simple/elaborate). Another review (Wager, Phan, Liberzon, Taylor, 2003) also found no laterality effects for positive and negative stimuli and no difference across genders.

While individual studies have found differences in the role of the left and right amygdala, the consistent finding that meta-analyses do not show these effects on a larger scale has caused further speculation regarding whether laterality effects exist or whether they are more complicated than first imagined. One theory is that the amygdala is a relevance detector that plays a role in determining the salience of a stimulus in relation to an individual’s well-being (Wager, Phan, Liberzon, Taylor, 2003). This would explain why positive stimuli also activate the amygdala because detecting stimuli that should be approached is just as necessary as avoiding stimuli that pose a threat. Another theory is that the right amygdala is part of a faster stimulus detection system while the left amygdala is more involved in sustained stimulus evaluation (Wright et al., 2001). This is consistent with the disparity in the lesion studies and neuroimaging meta-analyses. One of the troubles with fMRI research is the temporal resolution. It could be that the right amygdala is just as involved in affective processing as the left but because it processes more quickly the activation may not be captured by the time period sampled (Wright et al., 2001). This is also supported by studies that show faster habituation to complex emotional pictures in the right amygdala than in the left amygdala when measured by fMRI (Irwin et al., 1996) and PET (Fischer et al., 2000). Neuroimaging studies have helped to shape these theories but further behavioral experiments are needed to examine the relative role of the left and right amygdalae.

Chapter 2 - Affective Priming and the Role of the Amygdala

The way that emotions are processed in the human brain has been widely debated in the literature. The two leading hypotheses for affective processing are the cognitive appraisal viewpoint (Lazarus, 1982), and the affective primacy hypothesis (Zajonc, 1980). The cognitive appraisal viewpoint asserts that a person must understand the implications of an emotionally salient stimulus in order to determine if it will threaten its well-being. Thus, information must be processed in higher cortical structures. Whereas, the affective primacy hypothesis asserts that there are subcortical structures that allow humans to quickly assess the valence of a stimulus before it is processed by higher cortical areas. Both hypotheses agree that key structures in emotional processing include the amygdalae and portions of the prefrontal cortex (Lazarus, 1982; Zajonc, 1980; Morris, Ohman, & Dolan, 1999). However, the affective primacy hypothesis (the dual-pathway model) theorizes that humans can use information only processed at the subcortical level, in the absence of higher cortical processing, to influence behavior.

To test this theory Murphy & Zajonc (1993) conducted a study where participants were asked to rate how much they liked neutral stimuli (Chinese ideographs) that were primed by an affective face of happy or angry valence. They found that when the same ideographs were preceded by a happy face they were rated as more likeable than when they were preceded by an angry face. This effect was seen when the faces were only presented for 4ms, a suboptimal presentation time, and then backward masked. This duration of stimulus presentation ensured that the participants did not consciously perceive the stimulus. This was confirmed by participant reports. The assumption underlying this paradigm is that at suboptimal presentation times the stimuli are processed in the amygdalae but not in frontal structures (Murphy & Zajonc, 1993).

Since this initial study, priming has been shown to affect other behaviors in humans. Mirroring the animal work, studies have been conducted that look at the role of affective priming in conditioned fear responses. A study by Ohman and Soares (1998) tested whether fear-relevant (pictures of spiders and snakes) or fear-irrelevant (pictures of mushrooms and flowers) stimuli presented at suboptimal speeds could be used to condition participants to predict a mild electric shock. The participants did not report conscious knowledge of the stimuli but those who received the fear-relevant primes did show an increased GSR before the shock. This is parallel to the findings with rats and indicates that stimuli that are not consciously perceived can affect physiology and fear conditioning. It also demonstrates an effect of priming for only fear-relevant stimuli.

In addition to altering physiological responses, priming has also been shown to affect evaluative judgments beyond liking or not liking. An individual's beliefs regarding a stranger's personality traits have been shown to be influenced by a suboptimally presented affect-arousing photograph (Krosnick, Betz, Jussim, and Lynn, 1992). Additionally, participants in another study judged novel cartoon characters as having more negative traits when the cartoon was preceded by a suboptimally presented prime of a face expressing disgust as compared to when it was primed with either a neutral face or one expressing joy (Niedenthal, 1990). This research shows a link between unconscious perception of a stimulus and its subsequent influence on an evaluative judgment.

One method of discovering the neural processes underlying this effect has been the use of neuroimaging studies. Paradigms using optimal presentation times have shown amygdala activation in response to making evaluative judgments about stimuli. Cunningham, Johnson, Gatenby, Gore, and Banaji (2003) performed a study where participants read the names of famous people and were either instructed to rate the person as “good” or “bad,” or to decide when the person lived (“past” or “present”). They found increased BOLD activation in the amygdala for names rated as “bad” compared with those rated as “good” in both conditions, and also a greater medial and ventrolateral prefrontal cortex (PFC) response for this evaluative judgment as compared to the non-evaluative judgment. Similarly, Hariri, Bookheimer, & Mazziotta (2000) scanned participants in an fMRI while they matched angry or fearful faces to a target face or chose the correct linguistic label for the affect displayed on a face. They found that the perceptual matching task corresponded to bilateral amygdala activation while the linguistic matching task corresponded to activation in the right PFC and relatively diminished activation in the amygdalae (Hariri, Bookheimer, & Mazziotta, 2000). A later study conducted by Hariri and colleagues showed the same effect when this task was applied to pictures of threatening stimuli (Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003). Taken together these studies provide evidence of the involvement of the amygdalae and PFC in making evaluative judgments; more specifically, the Hariri studies show the unique role of the amygdala for making judgments that are not dependent on linguistics and are perceptual in nature.

In line with these studies using optimal presentation times, neuroimaging studies using suboptimal presentation times also demonstrate the unique role of the amygdala in priming. It has been shown that when fearful or happy faces are presented for only 33 milliseconds (msec) and masked by a neutral face, individuals report seeing only neutral faces but show greater bilateral amygdala activation for those primed with fearful faces as compared to those primed with happy faces (Whalen et al., 1998). This BOLD response in the amygdalae in response to emotionally valenced stimuli that are not consciously perceived have been shown in a number of studies (Irwin et al., 1996; Breiter et al., 1996; Cahill et al.,; 1996; Morris et al., 1996). This activation in the absence of PFC activation provides evidence for a subcortical route of emotional processing.

Additionally, a study by Morris, Ohman, & Dolan (1999) expanded upon these studies showing amygdala activation in response to emotionally-valenced primes and looked at what other areas of the brain had activity that covaried with the amygdala while viewing these primes. By examining what voxels were active when the amygdala was active, they found evidence for connectivity between the pulvinar, superior colliculus, and right amygdala during the presentation of suboptimal primes. This was an interesting finding because it is in line with the subcortical route found in animal models. Thus this study provides compelling evidence for a subcortical route of emotional processing in humans.

A route of processing that does not involve consciously perceiving stimuli is also supported by a case study conducted on a patient with spatial extinction due to right parietal lobe damage (Williams & Mattingley, 2004). Visual extinction is a phenomenon in which two stimuli are presented briefly in unison to both visual fields, and the patient shows extinction to the contralesional stimulus. Hence, even though unilateral sensitivity/perception of the stimulus is intact, when presented simultaneously with a stimulus in both hemifields, the patient does not consciously perceive or report the stimulus in the affected side and cannot explicitly report what was seen. Williams and Mattingley created a task to look at whether priming effects were present in a patient with this condition during spatial extinction. In the experimental condition, one face was presented in each hemifield for 160 msec (optimal presentation time). One of these faces had an emotional valence (happy or sad) and one was neutral. The patient was then presented with a target face centrally and asked to rate the affective valence of the target face. In healthy adults a priming effect is seen when the prime matches the target. For instance, if the prime was a happy face and the following target was a happy face the participant would more quickly judge the target as happy than if a non-congruent prime had preceded it (e.g., an angry face). Williams and Mattingly found that the patient with extinction to double simultaneous stimulation exhibited this priming effect both when the face prime was presented to the intact hemifield *and* when the face prime was extinguished. This shows further evidence that affective priming occurs outside of conscious awareness.

Another approach to examining the neural processing involved during affective priming is to observe how the system works without a key component: the amygdala. In patients with unilateral amygdala damage, primes can be projected to either the intact hemisphere or the lesioned hemisphere and the subsequent physiological responses can be monitored. Galvanic skin response, in this case, is used as a quantifiable measure of emotional arousal. Kubota et al. (2000) used pictures of negative animals/scenes and pictures of neutral items/scenes and projected them in either the ipsilesional or contralesional hemifields of patients who had undergone a unilateral temporal lobectomy. When the negative pictures were presented to the intact hemisphere, the patients showed a greater GSR than when the neutral pictures were presented. This effect, however, was only seen under suboptimal viewing conditions (30 msec) and was not seen when pictures were presented to the lesioned hemisphere. This study again points to an important role of the amygdala in unconscious processing of affective material.

In addition to showing overall impairment in unconscious processing of affective stimuli in patients with unilateral amygdala damage, Glascher and Adolphs have also demonstrated differences between right and left lesions (2003). This study followed a method similar to Kubota et al. (2000), but the stimuli were comprised of positive, negative, and neutral pictures and the patients were asked to rate the pictures based on how emotionally arousing they found them to be after the GSR task was completed. They found that patients with right amygdala damage showed a significantly lower GSR in response to negative pictures as compared to a healthy control group. This shows a connection between an intact right amygdala and showing average arousal to a stimulus. They also found that in patients with an intact left amygdala their GSR was more highly correlated with the arousal ratings they gave the pictures than in patients with a lesioned left amygdala. The authors conclude that the right amygdala may provide an overall level of emotional arousal while the left amygdala may distinguish the arousal signaled by a specific stimulus (Glascher, & Adolphs, 2003). This idea is line with a theory presented in Chapter 1 that the right amygdala is responsible for stimulus detection while the left amygdala is more involved in sustained stimulus evaluation.

The most recent study of affective priming in a temporal lobectomy population was completed by Coppens et al. (2007). In this study participants viewed a positive or negative prime (e.g., a kitten, or a picture of an explosion) and then were asked to identify the valence of a target as quickly as possible. A priming effect (faster response times when the prime valence matched the target valence) was found in both the control group and the temporal lobectomy group. Further, no differences were found between these two groups or between the left and right lesion groups. However, the methodology of this study varied from that of previous studies. For example, primes were presented for 250 msec, which is above the threshold for suboptimal viewing. Also, primes were presented centrally so the abilities of the intact hemisphere could not directly be compared to the abilities of the lesioned hemisphere.

Chapter 3 - Summary and Hypotheses

Taken together, the literature reviewed shows compelling evidence for a dual-route model of affective processing in humans. Previous work has shown that a subcortical route involving the pulvinar, superior colliculi, and amygdalae may work in tandem with a cortical route that involves the prefrontal cortices. However, there is evidence that the subcortical route provides a “quick and dirty” assessment of valence that can operate at suboptimal viewing speeds, whereas the cortical route provides more complex processing but cannot react as quickly as the subcortical route. Looking at affective processing in temporal lobectomy patients undergoing temporal lobectomy provides a unique opportunity to examine this system without the anterior portion of the temporal lobe. This means that the amygdala and surrounding areas are removed, which would theoretically disrupt the subcortical route of emotional processing if a dual route of processing exists. Previous studies of temporal lobectomy patients have shown physiological responses following suboptimally presented affective stimuli are dependant on having an intact amygdala in this group, but research has yet to show if an intact anterior temporal lobe is necessary for affective priming to occur. Further, whether the left or right side is responsible for this effect or whether both amygdalae subserve the same function is still not clear.

The aim of the current study is to take the next step in this line of research and examine the role of the left and right amygdala and anterior temporal lobe in an emotional priming task involving an evaluative judgment. A paradigm of affective priming was used in which an emotional face (either happy or angry) was presented for

4ms (suboptimal presentation) and then followed by a neutral target (Chinese ideograph). Primes were projected to either the left or right visual field and participants will be asked to rate on a Likert scale how much they liked a centrally-located target that follows. By presenting stimuli at a suboptimal speed for conscious processing and directing them to one hemi-field at a time it will allow us to look at two things: 1) the role of the left vs. the right anterior temporal lobe, and 2) if evaluative judgments can be influenced by suboptimally presented affective primes in the absence of the ipsilateral amygdala.

If this processing can occur with the subcortical route disrupted it would mean that other structures (possibly higher cortical structures) can serve this function. However, if a priming effect is only seen when projected to the intact anterior temporal lobe then a dual-pathway model of affective processing would be supported. Given strong evidence in the human and animal literature it is hypothesized that the latter will occur. The second issue is whether a difference will be seen in the right temporal lobectomy group and the left temporal lobectomy group. While there is some evidence that the right amygdala is a stimulus detector and the left is involved in more sustained stimulus assessment, this difference has yet to be found in a population with only a right or only a left anterior temporal lobe. Admittedly, the research is sparse in this area. The current study could serve to further clarify laterality differences in this structure. In summary, the following two hypotheses will be tested:

1. A finding that priming is seen for both an intact right or left anterior temporal lobe would provide evidence that both regions can carry out this process.

2. A finding that priming is only seen with an intact right anterior temporal lobe would provide support for the relevance detector theory.

3. A finding that only positive primes influence processing in the left anterior temporal lobe and only negative primes influence priming in the right anterior temporal lobe would provide evidence that the left and right hemispheres carry out different roles in affective processing.

Chapter 4 - Experiments

4.1 - Norming of Neutral Stimuli

Chinese ideographs were rated for valence to ensure that stimuli included in the experiment were judged to be emotionally neutral.

Method

Participants

Thirty-six undergraduate students (ages 18-23, 26 females) at the University of Texas at Austin participated in this experiment in partial fulfillment of the research requirement of their Introduction to Psychology course. Participants did not have knowledge of the Chinese language.

Materials and Apparatus

Four hundred Chinese ideographs were presented to participants on Macintosh desktop computers, using Superlab software by Cedrus.

Procedure

Participants were told that the experiment dealt with predicting, based on their first impression, whether Chinese ideographs have a positive or negative meaning in that language based on visual characteristics alone. They were presented with a series of four-hundred Chinese ideographs which they were asked to rate on a 7-point Likert scale, where 1 indicated a strong negative meaning, 4 indicated a neutral meaning, and 7 indicated a strong positive meaning. Ideographs were presented for 2000 msec or until the participant made a rating. If the participant did not make a rating after 2000msec, a prompt appeared on the screen asking them to do so. Stimuli were presented in 2 blocks, each lasting approximately 7 minutes, with a 5 minute break in between blocks. Stimuli were presented in a randomized order for each participant to control for order effects.

Results

Three-hundred and ninety of the 400 ideographs tested had average valence ratings between 3 and 5 (the range judged as neutral *a priori*). The two hundred and forty ideographs judged as most emotionally neutral were then selected (average rating= 3.996 ± .22, See Appendix A).

4.2 - Experiment 1

The goal of this study was to replicate the findings of Murphy & Zajonc (1993) in a normative sample. Chinese ideographs were preceded by a happy face, an angry face, or a control image presented centrally.

Method

Participants

Fifty-one undergraduate students (ages 18-23) participated in this experiment in partial fulfillment of the research requirement of their Introduction to Psychology course. Individuals with knowledge of the Chinese language were excluded.

Materials and Apparatus

Affective primes were comprised of 20 black and white photographs of 10 different faces (5 male, 5 female; See Appendix B) taken from the Ekman and Friesen Pictures of Facial Affect (1976). Ten photographs displayed happy expressions, while ten photographs displayed angry expressions. Neutral primes and masks were created by randomly rearranging the pixels of one of the affective faces (see Appendix B). Priming stimuli were presented 2^{o} from foveal center and measured 320 x 480 pixels. Participants sat approximately 55 cm from the computer screen.

Two hundred and forty Chinese ideographs previously rated as affectively neutral were used as novel stimuli. Stimuli were presented on a Dell Latitude Laptop computer, using Matlab software by the Math Works.

Procedure

Participants were told to rate how much they liked each Chinese Ideograph based on their “gut reaction” on a 7-point Likert scale, where 1 indicated strongly disliking the stimuli, 4 indicated neither liking or disliking the stimuli, and 7 indicated strongly liking the stimuli. Participants initiated each trial with a button push and a cross-hair was presented two inches below the top of the screen, centered horizontally for 1000ms to ensure participants were focusing their gaze in the horizontal center of the screen. Affective primes were displayed for 4ms centrally, followed by backward masking (10ms). A centrally displayed Chinese Ideograph followed immediately after for 2000ms. If the participant did not make a rating within 2000msec, a prompt appeared on the screen asking them to do so.

A total of two-hundred and forty ideographs were utilized in 4 blocks. Eighty were preceded by positive faces, eighty were preceded by negative faces, and eighty controls were preceded by neutral primes. An equal distribution was used in each block, and all stimuli were randomized. After the task was finished, participants completed the Positive and Negative Affect Scale (PANAS) to assess their current mood. They were then asked if they saw any faces during the experiment in order to determine if they were consciously aware of the primes. Participants were debriefed regarding the true purpose of the study and all participants chose to continue involvement.

Results

Effect of prime

Ideographs preceded by a happy prime had an average rating of 4.10 ±.09, those preceded by an angry prime had an average rating of 3.88 ±.11, and those preceded by a control prime had an average rating of 4.04 ±.09 (See Figure 1).

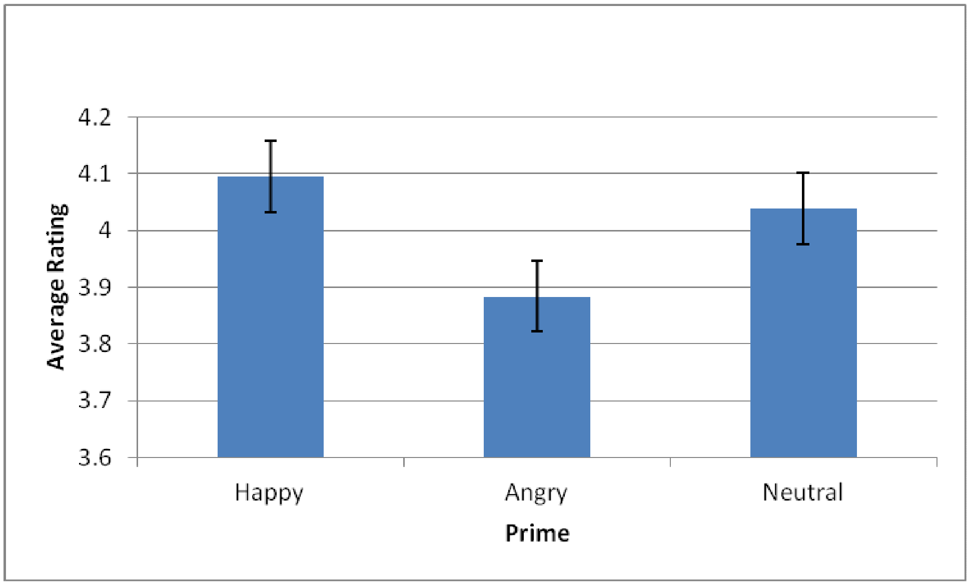


Figure 1. Average affective rating for centrally presented primes.

A repeated measures ANOVA for prime type was significant, F(2,100)=5.98, p=.003, η^2=.11 (observed power = .77). We performed three pairwise comparisons and corrected for multiple comparisons by dividing alpha (.05) by three. Therefore, for these analyses the significance threshold for each pairwise comparison was .017. Using these criteria there were significant differences in ratings following happy vs. angry primes, t(50)=2.70, p=.010, and following neutral vs. angry primes, t(50)=3.03, p=.004. There was no difference in ratings following happy vs. neutral primes, t(50)=1.00, p=.32. Thus, ideographs preceded by happy primes were rated as significantly more liked than those preceded by angry primes. However, happy primes were not rated significantly higher than neutral primes.

Effect of Mood

Average positive mood score on the PANAS was 31.9±7.7, and average negative mood score was 16.6±5.9. A repeated measures ANCOVA using positive mood score and negative mood score on the PANAS as covariates did not show a significant effect of negative mood score F(2,47)=.03, p=.87, η^2.001, but showed a marginally significant interaction between positive mood score and valence F(1,48)=3.95 p=.053, η^2.08.

Given the interaction between valence and positive mood score, a median split analysis was conducted where participants were divided into two groups: high positive mood score (≥33), and low positive mood score (<33). Table 1 shows ratings by prime type in the high and low positive mood groups. A repeated measures ANOVA for prime type was conducted using mood group as a between subjects variable and a marginally significant interaction between prime valence and mood group was found, F(2,100)=2.42, p=.09, η^2=.05. Pairwise comparisons examining primes of the same valence across groups demonstrated no difference in ratings of ideographs preceded by angry primes (t(49)=.05, p=.96) or neutral primes (t(49)=-.36, p=.71), but a trend towards a difference in ratings for ideographs preceded by happy primes t(49)=-1.44, p=.16.

	Positive Mood Group	
Prime Type	High (Ave. ± SE)	Low (Ave. ± SE)
Happy	4.23 ±.09	3.97±.09
Angry	3.88±.10	3.89±.10
Neutral	4.07±.09	4.01±.09

Table 1. Average ratings by mood group.

Repeated measures ANOVAs for prime type were conducted on both the high and low positive mood group. Participants in the low positive mood score group did not rate stimuli with affective primes differently F(2,25)=1.26 p=.29, η^2.05. However, there was a significant effect of prime type in the high mood score group F(2,24)=3.01 p=.004, η^2.20. Again, to correct for multiple comparisons, the adjusted pairwise error rate used for alpha was .017. In the high positive mood group, there were significant differences in ratings following happy vs. angry primes, t(24)=2.78, p=.010 and marginally significant differences following neutral vs. angry primes, t(24)=2.41, p=.02. A trend towards an effect of happy vs. neutral primes was found t(24)=1.74, p=.095. Figure 2 displays the difference in ratings for each prime type by mood group and illustrates how ratings of happy primes drive the interaction between these variables.

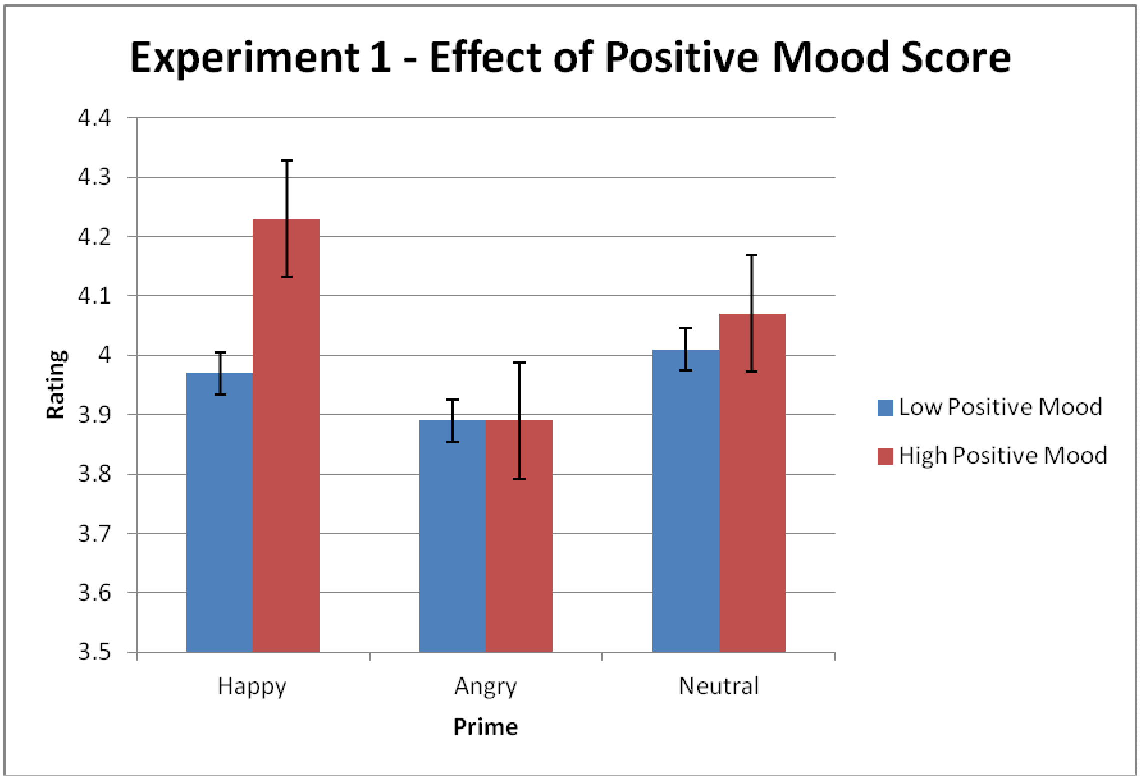


Figure 2. Average affective rating for primes in young adults reporting high and low positive mood.

Discussion

This experiment replicates the findings of Murphy & Zajonc (1993) using central presentation of affective primes. Additionally, it shows that only participants self-reporting high positive mood show the priming effect. The difference in ratings across groups is driven by increased liking ratings of ideographs preceded by happy primes.

4.3 - Experiment 2

In this study affective primes were presented in the left or right visual field and participants were asked to rate centrally presented Chinese Ideographs.

Method

Participants

Fifty-one undergraduate students (ages 18-23) participated in this experiment in partial fulfillment of the research requirement of their Introduction to Psychology course. Individuals with knowledge of the Chinese language were excluded.

Materials and Apparatus

Affective primes were comprised of 20 black and white photographs of 10 different faces (5 male, 5 female) taken from the Ekman and Friesen Pictures of Facial Affect (1976). Ten photographs displayed happy expressions, while ten photographs displayed angry expressions. Neutral primes and masks were created by randomly rearranging the pixels of one of the affective faces (see Appendix B).

Two hundred and forty Chinese ideographs previously rated as affectively neutral were used as novel stimuli. Stimuli were presented on a Dell Latitude Laptop computer, using Matlab software by the Math Works.

Procedure

Participants were told to rate how much they liked each Chinese Ideograph based on their “gut reaction” on a 7-point Likert scale, where 1 indicated strongly disliking the stimuli, 4 indicated neither liking or disliking the stimuli, and 7 indicated strongly liking the stimuli. Participants initiated each trial with a button push and a cross-hair was presented two inches below the top of the screen, centered horizontally for 1000ms to ensure participants were focusing their gaze in the horizontal center of the screen. Affective primes were displayed for 4ms in either the right or left hemifield, followed by backward masking (10ms). A centrally displayed Chinese Ideograph followed immediately after for 2000ms. If the participant did not make a rating after 2000msec, a prompt appeared on the screen asking them to do so.

A total of two-hundred and forty ideographs were utilized in 4 blocks. Ten were preceded by positive faces on the right, ten were preceded by negative faces on the right, and ten were preceded by neutral primes on the right. The same distribution was used on the left. The six conditions were randomized and participants completed four blocks. After the task was finished, participants completed the Positive and Negative Affect Scale (PANAS) to assess their current mood. They were then asked if they saw any faces during the experiment in order to determine if they were consciously aware of the primes. Participants were debriefed regarding the true purpose of the study and all participants chose to continue involvement.

Results

Effect of prime and side of presentation

Average ratings for each prime type are shown in Table 2 below.

	Hemifield of Presentation	
Prime Type	Left (Ave. ± SE)	Right (Ave. ± SE)
Happy	4.03 ±.10	4.28±.11
Angry	4.06±.10	4.11±.10
Neutral	4.18±.10	4.09±.09

Table 2. Average ratings by prime type and side of presentation.

A 2(hemifield of presentation) x 3(prime type) repeated measures ANOVA did not show a main effect of hemifield of presentation (F(2,100)=1.49, p=.23, η^2=.03) or prime type (F(2,100)=1.39, p=.25, η^2=.03). However, there was a significant interaction between hemifield of presentation and prime type, F(2,100)=10.48, p<.001, η^2=.17 (observed power = .99). To examine the origin of this effect and correct for multiple comparisons an adjusted alpha of .017 was used. Significant differences in liking ratings were found following happy vs. angry primes in the right hemifield, t(50)=3.34, p=.002. There was no difference in ratings following happy vs. angry primes in the left hemifield, t(50)=-.54, p=.59. Thus, ideographs preceded by happy primes were rated as significantly higher than those preceded by angry primes, only when presented in the right hemifield. Also, Chinese ideographs preceded by happy primes were given higher liking ratings when presented in the right hemifield than when presented in the left hemifield t(50)=2.9, p=.01.

Effect of mood

Average positive mood score on the PANAS was 29.2±7.4, and average negative mood score was 15.5±4.6. A repeated measures ANCOVA using positive mood score and negative mood score on the PANAS as covariates did not show a significant interaction between hemifield of presentation, prime type, and positive mood score F(1,48)=1.65, p=.20, η^2.07, but showed a marginally significant interaction between hemifield of presentation, prime type, and negative mood score F(1,48)=2.79 p=.07, η^2.11. No other main effects or interactions reached significance in the ANCOVA. Given this trend towards a significant interaction, a median split analysis was conducted where participants were divided into two groups: high negative mood score (>14), and low negative mood score (≤14). Repeated measures 2(hemifield of presentation) x 3(prime type) ANOVAs were conducted on each group. There was a significant interaction between hemifield of presentation and prime type in both the high negative mood group, F(2,26)=6.93 p=.004, η^2.36, and the low negative mood group, F(2,23)=3.97 p=.03, η^2.15. In both groups, ideographs preceded by positive primes were rated significantly higher than ideographs preceded by negative primes only in the right hemifield (high negative mood: t(26)=2.57 p=.02, low negative mood: t(23)=2.22 p.04). Figure 3 displays average ratings for each group.

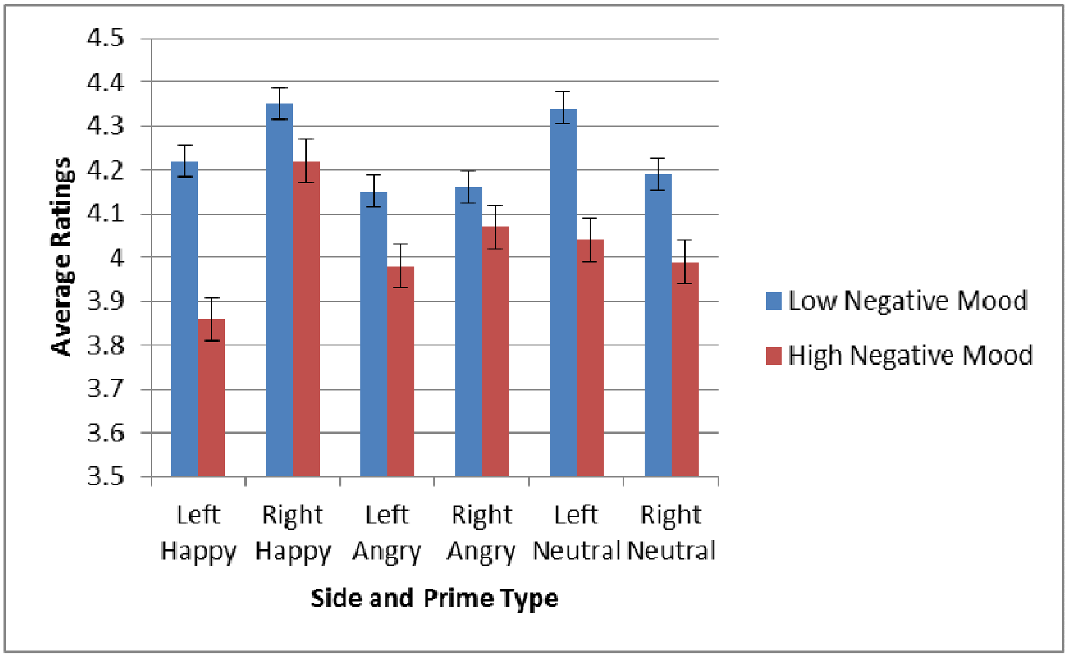


Figure 3: Average ratings by side and prime type in the high and low negative mood groups.

Examination of habituation effects

Imaging studies have shown faster habituation to emotional stimuli in the right amygdala than in the left amygdala (Irwin et al., 1996; Fischer et al., 2000). If habituation is occurring in the right hemisphere, we might not see a priming effect in the left hemifield over the course of the experiment. To test this, priming in the first 60 (out of 240) trials in this group was examined using a 2(hemifield of presentation) x 3(prime type) repeated measures ANOVA. At this point in the experiment each prime had only been presented once on each side of the screen. There was not a main effect of hemifield of presentation (F(1,100)=.08, p=.78, η^2=.002) or prime type (F(1,100)=.63, p=.54,

η^2=.01). However, there was a significant interaction between hemifield of presentation and prime type, F(2,100)=3.29, p=.04, η^2=.06 (observed power = .61). Planned pairwise comparisons (using an adjusted alpha of .017) showed significant differences in ratings following happy vs. angry primes in the right hemifield, t(50)=3.23, p=.002. There was no difference in ratings following happy vs. angry primes in the left hemifield, t(50)=-.67, p=.51. Thus the same pattern of responding was found after 60 trials and after 240 trials.

Discussion

In a sample of young adults, evaluative judgments of neutral stimuli were only influenced by affective primes presented in the right hemispace. Habituation to primes was examined, but was not found to play a significant role in this effect. An interaction between prime type, hemifield of presentation, and negative mood score was found, however, participants self-reporting both high and low negative mood both showed a priming effect.

4.4 - Experiment 3

One question that arose from the previous experiments was why ideograph ratings following neutral primes tended to be higher than the midpoint of the scale (4). In this study the effect of the neutral non-face primes used in experiments 1 and 2 in contrast to neutral face primes was studied. This allowed for examination of the effect that human faces may have in affecting liking ratings when they are used as priming stimuli. In

Experiment 3 ideographs were preceded by either the neutral primes used in the previous two experiments or faces with a neutral expression from the Ekman and Friesen Pictures of Facial Affect (1976).

Method

Participants

Thirty-three undergraduate students (ages 18-23) participated in this experiment in partial fulfillment of the research requirement of their Introduction to Psychology course. Individuals with knowledge of the Chinese language were excluded.

Materials and Apparatus

Neutral primes from the previous two experiments and ten black and white photographs of faces displaying neutral expressions were used. Neutral face primes were taken from the Ekman and Friesen Pictures of Facial Affect (1976) and the same actors used to portray happy and angry faces in the previous experiments were used.

A total of two-hundred and forty ideographs were utilized in 4 blocks. On half of the trials participants rated primes following neutral face stimuli, and on the other half participants rated primes following neutral non-face stimuli. As in Experiment 2, half of the primes were presented in the left hemifield, and half were presented in the right hemifield. After the task was finished, participants completed the Positive and Negative Affect Scale (PANAS) to assess their current mood. They were then asked if they saw any faces during the experiment in order to determine if they were consciously aware of the primes. Participants were debriefed regarding the true purpose of the study and all participants chose to continue involvement.

Results

Table 3 presents the average ratings of the neutral face and non-face primes.

	Hemifield of Presentation	
Prime Type	Left (Ave. ± SE)	Right (Ave. ± SE)
Neutral Face	3.86 ±.15	3.86±.16
Neutral Non-Face	3.82±.17	3.85±.16

Table 3. Neutral face and non-face stimuli: Average ratings by prime type and side of presentation.

A 2 (prime type) x 2 (hemifield) repeated measures ANOVA did not show a significant effect of hemifield of presentation (F(1, 32)=.20 p=.66 η^2 .01), prime type (F(1, 32)=.49 p=.49 η^2 .02), or interaction between these variables (F(1, 32)=.35 p=.56 η^2 .01).

Average positive mood score on the PANAS was 32.4±8.6, and average negative mood score was 15.6±5.5. A repeated measures ANCOVA using positive mood score and negative mood score on the PANAS as covariates did not show a significant interaction between hemifield of presentation, prime type, and positive mood score F(1,32)=2.54, p=.12, $\square^2$.08, or hemifield of presentation, prime type, and negative mood score F(1,32)=1.94 p=.17, $\square^2$.06.

Discussion

No differences in liking ratings between stimuli preceded by neutral face primes and the same neutral non-face primes used in experiments 1 and 2 were found. This suggests that the presence of affective primes in the first two experiments may have affected ratings of the neutral non-face primes.

4.5 - Experiment 4

A procedure identical to study 2 was used in a population of individuals with epilepsy in order to examine whether priming was affected by anti-epileptic medications (which may reduce processing speed) and temporal lobe pathology.

Method

Participants

One hundred and one individuals being treated for epilepsy at Austin Neuropsychology, PLLC and/or Seton Brain & Spine Institute were identified. Patients were called between May, 2011 and April, 2012 to assess interest in participating in the study. For those individuals that could not be reached initially, a minimum of 3 attempts were made to contact them. For those individuals without voicemail, a minimum of 6 attempts were made to contact them on varying days of the week/times. Table 4 details recruitment attempts.

	Number of Patients
Study completers - non-surgical	21
Study completers - post temporal lobectomy	12
At least 3 attempts to contact with no response	36
Declined participation	15
No current phone number available/disconnected phone number	15
Patient not fluent in English	2

Table 4. Recruitment attempts

Twenty-one patients with epilepsy who had not had brain surgery but were taking anticonvulsants to control seizure activity (average number of medications 2.6±1.4) participated in the experiment (11 males, 19 right-handed, average age 44.8±11.9 years). The average age of seizure onset was 23.0±18.4 years and average years of education was 15.3±2.8. Regarding seizure focus, 10 individuals were found to have a left focus, three demonstrated bilateral findings, eight did not have focal findings, and none had exclusively right hemisphere involvement. Participants were instructed that they could not participate in the experiment if they used alcohol or other recreational drugs within 24 hours. None of the participants had prior knowledge of the Chinese language. Presence of mood disorder was recorded post hoc and was defined as having a diagnosis of Depressive Disorder or Bipolar Disorder, significant symptoms of depression (T score greater than 65) on the Minnesota Multiphasic Personality Inventory-II (MMPI-2) at prior neuropsychological testing, or current use of an anti-depressant medication. Records were available for 15 participants and 2 met the aforementioned criteria for presence of a mood disorder.

Procedure

A procedure identical to experiment 2 was used. However, due to a computer programming error mood ratings on the PANAS were only recorded for ten of the participants.

Results

Effect of prime

Average ratings for each prime type are shown in Table 5 below.

	Hemifield of Presentation	
Prime Type	Left (Ave. ± SE)	Right (Ave. ± SE)
Happy	4.12 ±.10	4.19±.11
Angry	4.36±.10	4.39±.10
Neutral	4.35±.10	4.20±.09

Table 5. Non-surgical epilepsy patients: Average ratings by prime type and side of presentation.

A 2(hemifield of presentation) x 3(prime type) repeated measures ANOVA did not show a main effect of hemifield of presentation, $F(1,40)=.06$, $p=.81$, $\eta^2=.003$, or an interaction between hemifield of presentation and prime type, $F(2,40)=1.91$, $p=.16$, $\eta^2=.09$. However, there was a significant effect of prime type, $F(2,40)=6.87$, $p=.003$, $\eta^2=.26$, observed power = .90. Overall, ideographs preceded by angry primes were rated higher than those preceded by happy primes ($p=.002$). However, ideographs preceded by neutral primes were not rated higher than those preceded by happy primes ($p=.04$).

Effect of Mood

Average positive mood score on the PANAS was 32.4±3.8, and average negative mood score was 15.9±6.1. A repeated measures ANCOVA using positive mood score and negative mood score on the PANAS as covariates did not show a significant interaction between hemifield of presentation, prime type, and positive mood score F(1,9)=.42, p=.66, η^2.06, or hemifield of presentation, prime type, and negative mood score F(1,9)=1.34 p=.29, η^2.16.

Effect of other covariates

A repeated measures ANCOVA using gender, number of anticonvulsant medications, seizure focus location, and presence of mood disorder as covariates was used to examine the role of these factors on priming. There was not a significant interaction between hemifield of presentation, prime type, and seizure focus location F(2,20)=.23, p=.80, η^2.02, hemifield of presentation, prime type, and gender F(1,20)=.05, p=.95, η^2.01, or hemifield of presentation, prime type, and presence of mood disorder, F(1,20)=.31 p=.74, η^2.03.

However, there was a significant interaction between hemifield of presentation, prime type, and number of medications, F(2,20)=7.33, p=.004, η^2.42. A median split analysis was conducted where participants were divided into two groups: 1 or 2 anticonvulsant medications, 3 to 6 anticonvulsant medications. Repeated measures ANOVAs for prime type were conducted on each group. A main effect for valence was found in the group taking fewer medications (F(2, 14) = 3.91, p=.045, η^2.=.36), where ideographs preceded by angry primes were rated more highly than ideographs preceded by happy faces p=.01. In the group taking more medications there was a significant interaction between hemifield of presentation and valence (F(2, 14) = 4.46, p=.04, η^2.=.47), where ideographs preceded by angry or neutral primes in the left hemispace were rated more highly than ideographs preceded by happy primes (t(5)=3.33, p=.02 and t(5)=3.83 p=.01, respectively). The average ratings by prime type and hemifield for both groups are presented in Figure 4.

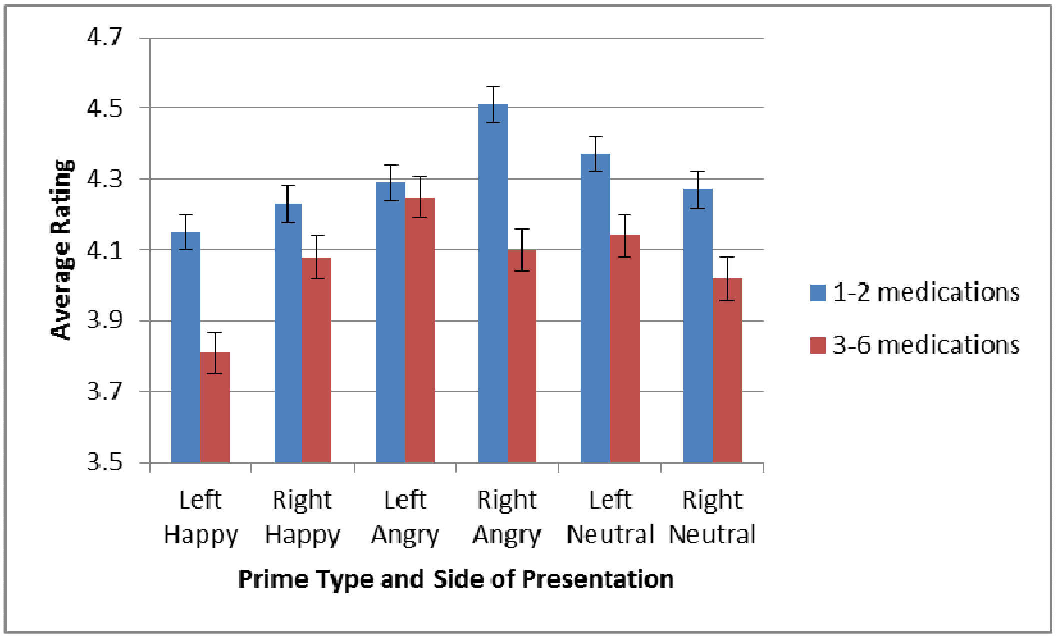


Figure 4: Average ratings by prime type and side of presentation in patients taking 1 to 2 anticonvulsant medications and those taking 3 to 6 medications

Discussion

In a sample of patients with epilepsy, ideographs preceded by angry primes were rated as significantly more liked than ideographs preceded by happy primes. This effect was not influenced by side of presentation (as in the young adult sample), seizure focus location, gender, or presence of a mood disorder. However, patients taking more medications were found to only show the above mentioned priming effect in the left hemispace.

4.6 - Experiment 5

A procedure identical to experiment 2 and 4 was used in a population of individuals with epilepsy who underwent unilateral temporal lobectomy for pharmacologically refractory complex partial seizures. In this procedure, not only is the seizure focus (typically the hippocampus) removed, but the amygdala and the temporal tip (anterior temporal cortex) are removed as well. Therefore, in this population we can see how emotions are processed in the absence of one amygdala. Participants at least three months post-surgery were permitted to participate.

Method

Participants

Twelve patients with epilepsy who underwent a unilateral temporal lobectomy participated (9 right temporal lobectomy, 3 left temporal lobectomy). Recruitment is detailed in Experiment 4. Post-surgical brain imaging (CT/MRI) was reviewed in order to quantify extend of the resection. Nine patients had complete removal of the amygdala, one had partial removal of the amygdala, and imaging data was unavailable for two patients. Complete removal of the hippocampus was seen in seven patients. Resections extended on average 42.5 ± 9.9 mm from the temporal tip mesially (range: 27.8-61.5 mm) and 47.9 ± 8.4 mm from the temporal tip laterally (range: 32.0 – 57.0 mm). Participants included 4 females and 8 males average age 45.8± 13.7 years old. All participants were taking anticonvulsant medications. Eleven subjects were left hemisphere dominant for language and one right hemisphere dominant confirmed by preoperative Wada testing. Patients completed the Wechsler Adult Intelligence Scale III, Wechsler Adult Intelligence Scale IV, or the Wechsler Abbreviated Scale of Intelligence and the average full scale IQ was 105±17, average verbal index was 104±14, and average performance/perceptual reasoning index was 105±17. They were instructed that if they used alcohol or other recreational drugs within 24 hours of the experiment they could not participate. None of the participants had prior knowledge of the Chinese language.

Method

A procedure identical to experiment 2 was used. However, due to a programming error mood ratings on the PANAS were not saved for the first seven participants.

Results

Due to the small sample size in the left temporal lobectomy group, the surgical samples were analyzed separately to more clearly examine the effect of right temporal lobectomy surgery.

Right temporal lobectomy patients

Average ratings for each prime type are shown in Table 6 below.

	Hemifield of Presentation	
Prime Type	Left (Ave. ± SE)	Right (Ave. ± SE)
Happy	4.40 ±.10	4.40±.11
Angry	4.43±.10	4.49±.10
Neutral	4.45±.10	4.26±.09

Table 6. Right temporal lobectomy epilepsy patients: Average ratings by prime type and side of presentation.

A 2(hemifield of presentation) x 3(prime type) repeated measures ANOVA did not show a main effect of hemifield of presentation (F(1,16)=.89, p=.37, η^2=.10) or prime type (F(1,16)=1.40, p=.28, η^2=.15), or an interaction between hemifield of presentation and prime type (F(1,16)=1.98, p=.17, η^2=.20). An ANCOVA using gender, presence of a mood disorder, and number of anticonvulsant medications as covariates did not show a significant interaction between hemifield of presentation, valence, and gender, F(1,7)=.47, p=.64, η^2=.11, hemifield of presentation, valence, and presence of mood disorder, F(1,7)=.03, p=.97, η^2=.004, or a hemifield of presentation, valence, and number of anticonvulsant medications, F(2,10)=.32, p=.74, η^2=.06.

Left temporal lobectomy patients

Average ratings for each prime type are shown in Table 7 below.

	Hemifield of Presentation	
Prime Type	Left (Ave. ± SE)	Right (Ave. ± SE)
Happy	4.00 ±.10	4.30±.11
Angry	4.15±.10	4.21±.10
Neutral	4.32±.10	4.29±.09

Table 7. Left temporal lobectomy epilepsy patients: Average ratings by prime type and side of presentation.

A 2(hemifield of presentation) x 3(prime type) repeated measures ANOVA did not show a main effect of hemifield of presentation ($F(1,4)=1.11$, $p=.40$, $\eta^2=.36$) or prime type ($F(1,4)=3.06$, $p=.16$, $\eta^2=.61$), or an interaction between hemifield of presentation and prime type ($F(1,4)=.47$, $p=.66$, $\eta^2=.19$). Covariates were not examined due to the small sample size.

Discussion

In a sample of patients who have undergone a temporal lobectomy, no effect of priming was seen. Gender, presence of a mood disorder, and number of anticonvulsant medications were also not shown to moderate a priming effect.

4.7 - General Discussion

Young Adult Sample

Overall, a priming effect was found in the young adult sample where ideographs preceded by suboptimally presented happy primes were given significantly higher liking ratings than ideographs preceded by angry primes presented centrally. This represents a replication of the results found by Murphy & Zajonc (1993). Interestingly, in our sample this priming effect was also influenced by mood. Only in the participants with self-reported high positive mood was there a significant priming effect. In particular, ratings of ideographs preceded by angry and neutral primes did not differ among the high and low positive mood groups. Instead ideographs preceded by happy primes showed a trend towards being rated as liked more by participants in the high positive mood group. This is a novel finding and suggests that baseline positive mood appears to have a significant impact on the potency of positive primes.

Following this study, hemifield presentation of primes was introduced and a significant effect of side of prime presentation was found. When primes appeared in the right hemispace the aforementioned priming effect was found, however, when primes appeared in the left hemispace, this was not found. It was not predicted that an effect of side of presentation would be seen in a population with intact amygdalae. Given the brief nature of the prime presentation (4 ms) and backward masking of primes it is possible that one hemisphere primarily processed stimuli presented in the contralateral hemispace. If this is the case, these results do not support the relevance detector hypothesis at first glance. If the right hemisphere was responsible for stimulus detection we would expect to see priming in the left hemispace. However, this may be complicated by habituation effects. Imaging studies have shown faster habituation to emotional stimuli in the right amygdala (Irwin et al., 1996, Fisher et al., 2000). Therefore if habituation is occurring in the right hemisphere (left hemispace) over the course of the experiment, this effect may diminish over many trials. To test this, priming in the first 60 (out of 240) trials in this group was examined. Here the same pattern of responding was found; participants consistently rated ideographs preceded by happy primes higher than those preceded by angry primes only on the right side. Therefore, even controlling for possible habituation effects the relevance detector hypothesis is not supported by our findings.

These results may however lend support to the theory that the left and right hemispheres play differing roles in affective processing. It seems that the priming effect was primarily driven by higher ratings of ideographs preceded by happy primes (rather than lower ratings of ideographs preceded by angry primes), which points towards greater responsiveness to positive stimuli presented to the left hemisphere. Studies examining mood after temporal lobectomy have found that patients with an intact left amygdala tend to report greater increases in global happiness while patients with an intact right amygdala tend to report increases in depressive symptoms (Burton & Labar, 1999). This suggests that the left amygdala is more involved in processing positive emotions. Alternatively, Glascher and Adolphs (2003) conducted a study that found that the right amygdala may be involved in providing an overall level of emotional arousal, while the left may distinguish the valence of the arousal. So it may not be that the left or right amygdalae are responsible for responding to particular emotional input; they may just serve different functions.

One question that arose from the previous experiments was why ideograph ratings following neutral primes tended to be higher than the midpoint of the scale (4). The effect of the neutral non-face primes in contrast to neutral face primes was studied. This also allowed for examination of the effect that human faces may have in affecting liking ratings when they are used as priming stimuli. In the absence of emotionally-valenced primes there were no differences found across stimulus type or hemifield of presentation and mood was not a predictor of liking ratings. In fact, ratings for all stimuli were lower than the midpoint of the scale, whereas ratings in the previous two experiments were above the midpoint of the scale. This suggests that the presence of emotionally-valenced stimuli increases arousal. Therefore, there may be a carry-over effect when neutral primes are presented in close temporal proximity to affective primes.

Epilepsy Patients- Non-Surgical

In the non-surgical epilepsy population there was an effect of suboptimally presented primes, however, it was not in the direction predicted and hemisphere of presentation was not found to moderate the effect. In this population, ideographs preceded by angry primes were given higher liking ratings on average than ideographs preceded by happy primes. This effect was not predicted by gender, current mood, presence of a mood disorder, or location of seizure focus. When number of medications was taken into account, patients taking one or two anticonvulsant medications showed the above described effect, however, patients taking 3 or more medications were found to rate ideographs preceded by angry primes higher than those preceded by happy primes preferentially in the left hemispace. This may not necessarily reflect an effect of medication, but may instead be more tied to the fact that patients taking more medications have seizures that are less controllable and therefore typically display greater neurological pathology and greater cognitive impairment. If this is the case, then these results suggest that more pathology in the left hemisphere may disrupt priming in the right hemispace. Hence in the group taking more medications and displaying greater left hemisphere (or bilateral) disruption, primes may affect behavior more when presented to the right hemisphere (left hemispace).

Overall, the findings in this population show that suboptimally presented primes are affecting evaluative judgments but not as we would expect. It is further puzzling that the factors used as covariates did not predict these effects. For example, it was postulated that since anticonvulsant medications sometimes slow down processing speed primes may need to be presented for a longer duration in this population to influence evaluative judgments. This does not seem to be the case. The difference found in ratings based on prime type had a large effect size, suggesting that primes are in fact having an impact on behavior.

Also, in this population both current mood and presence of a mood disorder did not predict priming. This may be explained by a couple limitations of the study though. First, current mood data was only collected from ten non-surgical participants. Having this information for a greater number of participants might elucidate the relationship between mood and priming in this sample. Also because presence of a mood disorder was examined retrospectively, multiple indicators were used (e.g., past diagnosis of Major Depressive Disorder, elevation on the depression scale of the MMPI-2) and current data was not accessible for all participants. For example, if a participant showed an elevation in depression symptoms on the MMPI-2 they could have been tested the week before participating in the current experiment or two years before. Also, treating mood as a categorical variable rather than a continuous one markedly reduces power and may have made it more difficult to detect an effect if one was present.

Recent studies suggest that mood disorders significantly affect priming. Dai & Feng (2011) demonstrated, using a priming paradigm, that individuals with depression show dysfunctional distracter inhibition and facilitation for negative stimuli. In a study examining gaze behavior and subsequent memory for affective faces, stably dysphoric individuals showed greater breadth of attentional focus and greater recognition of angry faces than nondysphoric individuals (Wells, Beevers, Robinson, Ellis, 2010). In other words, individuals with depressive symptoms pay more attention to negative stimuli. Symptoms of depression are present in 40% - 60% of individuals with epilepsy (Grabowska-Grzyb, Jedrzejcak, Naganska, & Fiszer, 2005), and are associated with reduced quality of life (Kanner, 2003; Boylan et al., 2004). These individuals are also five times more likely to commit suicide than controls (Matthews & Barbaras, 1981). It stands to reason that greater incidence of depression in this population may be associated with greater attentional bias for negative stimuli. One study also found that patients with depression showed an attentional bias and rated ideographs primed by sad faces **higher** than ideographs primed with neutral faces, even after significant depressive symptom remittance (Dannlowski et al., 2006). This last study is particularly relevant to the current study because it demonstrates that presence of a mood disorder has been shown to correlate with higher ratings of negative stimuli as was found in this experiment. Reduced inhibition for negative stimuli has been shown to correlate with depression and anxiety self-report scores (Goeleven, De Raedt, Baert, & Koster, 2006). While mood was measured in the current study, the questionnaire used (the PANAS) does not adequately assess depression and anxiety symptoms. Therefore, future studies should collect current measures of these symptoms using questionnaires such as the Beck Depression Inventory and the Beck Anxiety Inventory. Past research would suggest that scores on these symptoms may moderate the priming effect.

Epilepsy Patients – Post Temporal Lobectomy

In both the patients who underwent a right temporal lobectomy and the patients who underwent a left temporal lobectomy, affective primes were not shown to influence evaluative judgments of neutral stimuli. Gender, presence of a mood disorder, and number of anticonvulsant medications were not found to moderate any potential effect. There are two possibilities: 1) Removal of either the left or right anterior temporal lobe disrupts affective priming, or 2) There was not a sufficient sample size to detect the effect. With three participants in the left temporal lobectomy group the latter is likely.

Given the findings in the young adult sample, it would be expected that patients with an intact left amygdala (who underwent a right temporal lobectomy) would show priming in the right hemispace. However, this was not found. Closer examination of differences between the young adult and patient population may offer insight. Although the average age for the epilepsy sample was 46 years old whereas the average age of the undergraduate sample was 19 years old, previous studies examining younger adults and middle aged adults found that the priming effect actually increases with age (Hess, Waters, & Bolsted, 2000). So this variable is likely not accounting for the disparity. An alternative hypothesis is that, as explored in the non-surgical population, symptoms of anxiety and depression moderate the priming effect and cannot be seen given the inadequate measure of symptoms and small sample size.

Limitations & Future Directions

As discussed previously, the small sample size of the surgical epilepsy group likely made it more difficult to detect an effect of priming if one was present. In the non-surgical group incomplete current mood data also may have made it more difficult to detect an effect of this variable if one was present. Overall, future studies should include measures of current depression and anxiety symptoms to examine whether these symptoms are moderating the priming effect.

Another limitation of our sample was the lack of non-surgical epilepsy patients with an exclusively right seizure focus and the lack of patients post left temporal lobectomy. Without these samples, we were unable to adequately compare patients pre and post surgery. Looking at changes across these groups, or conducting a longitudinal study comparing individuals pre and post temporal lobectomy surgery would give greater insight into the role of the left and right anterior temporal lobes. This might also inform clinical practice in terms of providing more information about the effect of this surgery, and how patients' emotional cognition changes as a result.

Conclusion

Overall, the findings of Murphy and Zajonc (1993) were replicated and extended, demonstrating that mood moderates affective priming. More specifically, this body of work suggests that baseline positive mood has a significant effect on the potency of positive primes. A study utilizing neutral face primes also showed that it is not simply the presence of human face primes that affects behavior. There is a unique effect of faces displaying positive or negative emotion that influences evaluative judgments. In a sample of patients with epilepsy who had temporal lobe sclerosis or anterior temporal lobe removal the effect of priming was not as clear-cut. In the non-surgical sample patients rated ideographs preceded by angry faces as more liked than those preceded by neutral or happy faces. It is unclear what is driving higher ratings of negative stimuli in the non-surgical group, but high rates of depression in individuals with epilepsy and temporal lobe dysfunction in this population may contribute. Future studies exploring these possibilities will offer insight into the roles of the left and right amygdala as well as the effect of mood on attentional bias and emotional priming.

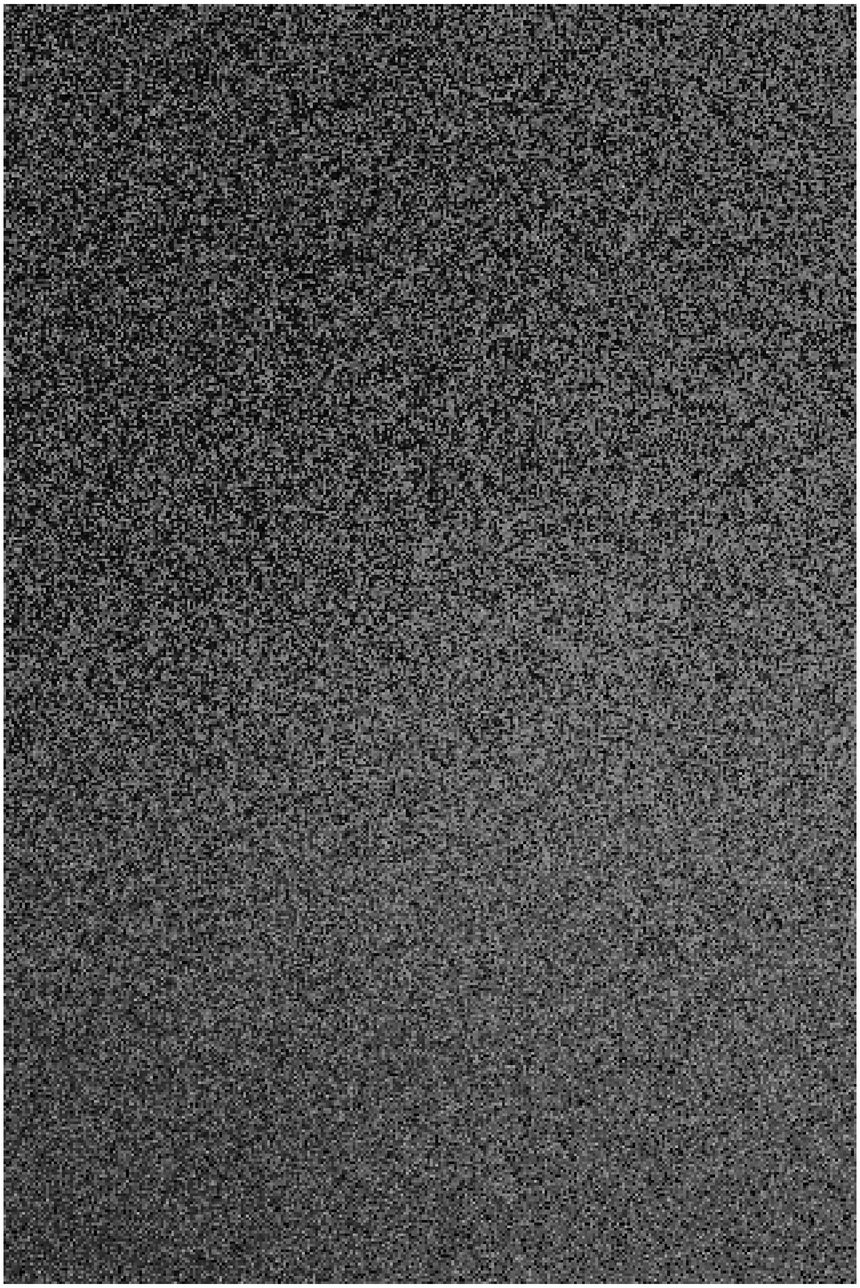
Appendix A.

禪黃薯狼冬翼酒風柳妻白鯨西蠟波
水善醋傘醜鮪兆樹毒塔虎賊茶芋尾甜
燕經神日夏糖強絃停石胃刺駒星春辣
南歌蛇奴天罪銀絲蝦羊鯊影性海
悟鮭根河環富韻犀翎紅鼠雨兔氣
謎紫純獎囚陶毒詩松鴿雉梨桃爪
紙蠔牛梟爐橙油海橡北夜新針
鼠山蛾蚊麋月猴媽謙鏡瓜肉楓鵲
慾愛蓮獅光謊豹懶笑燈湖梯吻王踢
劫跳妒玉島瘋香冰夫馬家重恨手鎚
灰好金神薑鬼蒜霜蛙友狐禽福叉恕
力足飛花拳魚火猛貂羽懼運肥速隼
信仙貴出口入口能麋姊兄蛋鰻吃東鴨
鼓龍鴿疑門驢狗神深債死舞鱷狂蟹
棉螺巧爪圓栗棋買蝶腦書骨船藍花
血盲刃黑鳥大蜂熊豆竹球斧悟秋
吉杏錨活酸零

Appendix B.


MO1-4
JM1-4
NR1-6
MF1-6
A1-6
PE2-12
JB1-9
EM4-7
JB1-9
GS1-8
PE2-21
JB1-23
GS2-8
EM5-14
WF3-4
MO2-11
MF2-5
JM5-3
NR2-7
A1-14

Appendix C.



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