Tactile-emotion synesthesia

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We discuss experiments on two individuals in whom specific textures (e.g., denim, wax, sandpaper, silk, etc.) evoked equally distinct emotions (e.g., depression, embarrassment, relief, and contentment, respectively). The test/retest consistency after 8 months was 100%. A video camera recorded subjects' facial expressions and skin conductance responses (SCR) were monitored as they palpated different textures. Evaluators' ratings significantly correlated with the valence of synesthetes' subjective reports, and SCR was significantly enhanced for negative synesthetic emotions. We suggest this effect arises from increased cross-activation between somatosensory cortex and insula for 'basic' emotions and fronto-limbic hyperactivation for more subtle emotions. It may represent an enhancement of pre-existing evolutionarily primitive interactions between touch and emotions.

Keywords: Synesthesia; Emotion; Multisensory; Synaesthesia; Tactile.

INTRODUCTION

Synesthesia is an involuntary experience in which stimulation of one sensory modality causes unusual activation in a second, unstimulated modality. Two of the most common forms include the perception of color while listening to sounds or while responding to graphemes; tone- and grapheme-color synesthesia, respectively (Baron-Cohen, Burt, Smith-Laittan, Harrison, & Bolton, 1996; Cytowic, 1989; Simner et al., 2006). For over a century after its discovery by Francis Galton (1883) it was considered an unreliable 'fringe' phenomenon but in the last 7 years there has been a tremendous resurgence of interest (Dixon, Smilek, Cudahy, & Merikle, 2000; Mattingley, Rich, Yelland, & Bradshaw, 2001; Nunn et al., 2002; Palmeri, Blake, Marois, Flanery, & Whetsell, 2002; Ramachandran & Hubbard, 2001a, 2003a; Simner & Ward, 2006).

We previously suggested that at least in some synesthetes, the evocation of color is an authentic sensory effect based on cross-activation between early sensory areas; it is not a high level cognitive one (Ramachandran & Hubbard, 2001a, 2001b). We proposed that the effect was caused by a gene mutation causing defective pruning of axons between the color area V4 and the number grapheme area - which lie adjacent to each other in the fusiform gyrus. We put forth five bits of evidence favoring this 'sensory' hypothesis. First in some grapheme-color synesthetes - whom we have dubbed 'lower' synesthetes – the vividness of perceived color decreases monotonically as the luminance contrast is reduced and disappears at 10% contrast even though the grapheme itself remains clearly visible. Such dependence on elementary physical parameters such as contrast would be hard to account for on the hypothesis that synesthesia is merely a set of memory associations. Second, the synesthetically induced color can lead to perceptual texture segregation because of the color difference; e.g., if 2 s are embedded in an array of randomly scattered 5 s, the 2 s are more readily detected by synesthetes than by normal individuals (Ramachandran & Hubbard, 2001a; Palmeri et al., 2002). Third, some synesthetes report that individual numbers can have different colors in different parts

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which would be consistent with errors in cross-wiring but not with high level memory association. Fourth, the colors produced by graphemes can drive the perception of apparent motion in displays in which no normal person can see motion (Kim, Blake, & Palmeri, 2006; Ramachandran & Azoulai, 2006; Ramachandran & Hubbard, 2002). Fifth, we showed further evidence for this cross activation hypothesis with fMRI studies in subjects with grapheme-color synesthesia (Hubbard, Arman, Ramachandran, & Boynton, 2005), highlighting concurrent activation in V4 and the grapheme area. This 'sensory' hypothesis is also now supported by diffusion tensor imaging, showing that there is an actual increase of axons between fusiform gyrus and color area V4 in 'projectors' (synesthetes who experience the color projected into space; lower synesthetes according to our terminology) and additional white matter tracts in the superior parietal lobule of all grapheme-color synesthetes (Rouw & Scholte, 2007), exactly as we had predicted (Ramachandran & Hubbard, 2001a).

We suggested that synesthesia, far from being a curiosity, might provide an opportunity for studying elusive aspects of the mind – such as metaphor. For instance the same 'defective pruning' genes that cause grapheme-color synesthesia when expressed in the fusiform gyrus may – if expressed more diffusely in the cortex – confer a propensity toward linking seemingly unrelated concepts represented in brain maps ('metaphor'; Ramachandran & Hubbard, 2001b), explaining the much higher incidence of synesthesia

in artists, poets and novelists (Mulvenna, 2007; Ward, Thompson-Lake, Ely, & Kaminski, 2008). Finally, if the mutant gene is expressed patchily instead of diffusely, one would predict (Ramachandran & Hubbard, 2001b, 2003b) that if you have one form of synesthesia you are more likely to have another, and that is indeed the case (Ramachandran & Hubbard 2001b; Simner et al., 2006).

In addition to intramodal and higher cognitive forms of synesthesia, more exotic types have been described involving complex interactions between sensory modalities. In particular, individuals like 'The man who tasted shapes', experience tactile sensations when tasting different foods (Cytowic, 1993). In concordance with the recent finding of increased connectivity in grapheme-color synesthesia, we have theorized this rare form of 'tasting shapes' is due to cross activation between taste – represented in the insula and the postcentral gyrus representation of the hand (Ramachandran & Hubbard, 2001b).

These ideas do not imply synesthesia can be explained entirely by sensory cross-activation nor that top-down influences are without involvement. Indeed, our group was the first to show such effects, e.g., a 'Navon' figure – a large 2 made of small 5 s – can be seen either as red or as green depending on what a grapheme – color synesthete attends to (Ramachandran & Hubbard, 2001b). We showed also that an ambiguous grapheme can change color depending on surrounding context (CAT vs. THE; see Figure 1) suggesting that the



Figure 1. Synesthetic color changes depending on the context of the middle letter.

linguistic categorization of the grapheme can determine the color evoked. Furthermore, in another less common form of synesthesia each grapheme is reported to be either male or female (ordinal linguistic personification); hardly the sort of thing that lends itself to simple phrenological account (Ramachandran & Hubbard, 2005). It is not inconceivable, however, that the 'binarizing' of the world into polar opposites such male/female, good/evil, etc. is a way of simplifying cognitive processing and may be mediated by specific brain regions (Ramachandran & Hubbard, 2005). As Freud said, 'anatomy is destiny'. This 'binarizing' model, however, cannot explain the 'ordinal linguistic personification effect' of Simner and Hubbard (2006) in which different complex personality types are evoked by graphemes and/or phonemes. We would suggest however that even personality types - despite their apparent diversity and complexity - may have a simple underlying taxonomy and may be based on combinations of a relatively small number of simple attributes.

Based on such considerations, one could make the case that it is precisely because synesthesia lies at the elusive interface between sensory and higherlevel conceptual processes that it might provide a valuable experimental lever for probing higher level thought processes (such as metaphor and language). The link between synesthesia and metaphor (Ramachandran & Hubbard, 2001b) may seem tenuous at first since the former involves seemingly arbitrary links between sensations (e.g., a blue '5'), whereas the latter is not arbitrary (e.g., saying 'Juliet is the sun'; you can't say 'Juliet is green'). Why would a general increase in crosswiring increase the propensity to non-arbitrary conceptual metaphor? There are two answers to this. First, many metaphors are in fact arbitrary: e.g., when we say 'loud tie', 'green with envy', etc. (although they may respect anatomical constraints; see Ramachandran & Hubbard, 2001b, 2003b). Second - and more important - words themselves have only a finite set of attributes. A word such as 'Juliet' has a penumbra of associations, e.g., woman, warm, nurturing, radiant, Italian, etc., and so does a sun - warm, radiant, nurturing, solar system, sky, huge, etc., so that you have two partially overlapping halos such as 'warm, nurturing, radiant' which constitute the metaphor ('Juliet is the sun'). But they also have non-overlapping attributes and associations (woman, Italian, huge, solar system, etc.; you don't say Juliet is huge). With more diffuse expression of the synesthesia gene there

would be a much bigger halo of associations around each word and therefore a wider overlap, multiplying the opportunity for metaphor. This might explain the purported creativity of synesthetes (Domino, 1989; Rich, Bradshaw, & Mattingley, 2005; Ward, Yaro, Thompson-Lake, & Sagiv, 2007) and also explain so-called variants like ordinal linguistic personification which may begin life as essentially random associations of the kind we all make from time-to-time. For instance, the link between (say) a number 7 and a 'lean and hungry looking man' may occur more frequently and vividly in synesthetes because excess cross-activation resulting from stronger penumbras. And once such an arbitrary association is made the same excess connections may lead to a form of 'auto-kindling' further strengthening the association of personalities and numbers far in excess of what might occur in a non-synesthete. In short, what are vaguely felt, almost unconscious, fluctuating propensities in all of us (e.g., '8 is sexy and tall woman', etc.) may after the first exposure - become permanently entrenched and emerge into consciousness in synesthetes (Ramachandran & Brang, 2008).

We now report two individuals with an unusual new form of synesthesia in which nearly all tactile textures (e.g., velvet or wax) consistently and reliably evoke highly specific, and strong emotions. Of course even in normal individuals certain textures would be expected to be associated with emotions (e.g., a furry blanket with 'comfort'). What was remarkable about the two synesthetes we studied was the intensity of the induced emotional states as well as the arbitrary yet highly specific nature of the evoked emotion. For example there is no obvious reason one would expect denim to evoke depression and disgust. To our knowledge this form of synesthesia has not been reported or previously studied to establish its characteristics or, indeed, its authenticity. We report three experiments and offer speculations on the anatomical basis of this form of synesthesia.

CASE DESCRIPTIONS

AW (22 years old) and HS (20 years old) are both female, right-handed university students who have no history of neurological or psychiatric disorder. Each time these individuals touch a particular texture with their hands, they automatically and consistently experience a particular emotion; something they report have experienced from as far back in

early childhood as they can remember. Certain types of textures evoke raw or primal emotions such as joy or disgust, whereas others generate subtle nuances of emotion such as jealousy or guilt. In the case of subject AW, the most extreme sensations arise from the texture of denim, causing feelings of depression and disgust, and silk, generating the experience of perfect happiness and contentment (Table 1). With subject HS, the most acute sensation is gained from soft leather, which she personally describes as 'making my spine crawl' (Table 2). The intensity and quality of each emotion experienced is consistent over time for any given texture (e.g., denim always causes extreme disgust). In both subjects there are textures that elicit no sensation (human skin or paper).

In addition to experiencing emotions from tactile input, AW possesses a 'calendar line' (the form of synesthesia she was originally identified for) – a well known form of synesthesia in which days and months are experienced in terms of specific and predictable spatial locations (Sagiv, Simner, Collins, Butterworth, & Ward, 2006). In some individuals, as is the case with AW, important events become highlighted on these perceptual calendars such as birthdays and other significant dates. During object

palpation, AW experiences a specific emotion as well as a number (e.g., while touching a particular type of cotton she experiences the number 4). These experiences are automatic for AW and have, according to her, occurred since childhood, consistent with descriptions given by other synesthetes. Indeed, it has been shown that individuals with one form of synesthesia likely possess one or more additional forms (Ramachandran & Hubbard, 2001b; Simner & Holenstein, 2007; Simner et al., 2006). Anecdotally, she reports that as a child she argued with her parents over her refusal to wear jeans to school (denim evokes the worst emotion for AW, causing disgust and self-loathing).

AW's emotional inductions through tactile input are mediated best by her little finger and forefinger, as was revealed through our experimentation. Emotions can be evoked from both the hands and feet, yet input from the hands produces markedly more intense emotions. Oddly, experienced emotions differ depending on whether the stimulus is palpated by the hands or by the feet (e.g., ceramic evokes calmness via her hands a feeling of power when placed on the foot). This is presumably due to differential connectivity patterns between somatosensory S1 and SII for the feet and hands (Whitsel,

TABLE 1
Emotions experienced by synesthete AW, generated by touching specific objects are shown above

Specific Texture	Emotion Experienced in First Test	Emotion Experienced in Second Test
Bok Choy	Disgust	Disgust
Corduroy	Confusion, walking into a room and not knowing why	Frustrated, lost, a bit confused
Denim	Depression, disgust	Depressed, worthless
Leather	Receiving criticism	Embarrassed
Moist soil	Content, happy	Content, like a sunny day where things are good
Textured glove	Willies, wanted to get up and run	Creepy, like being followed
Multicolored toothpaste	Anxious	Anxious
Orange peel	Like an electrical shock	Like an electrical shock
Paper	No emotion	No emotion, neutral
Plastic paper clip	Funny, disgusting, like touching a worm	Disgusting, but not bad, like touching a worm
Ridged plastic	Laughter	Funny
Rough textured plastic	Disgusted, didn't like it	Disgusted, not content
Sand paper (grade 120)	Telling a white lie	Guilty, but not a bad guilt
Sand paper (grade 180)	Relief	Relief
Sand paper (grade 60)	Guilty	Guilty
Silk sleeping bag	Happiness, safety	Happy, amazingly happy
Skin	No emotion	No emotion
Smooth metal	Calmness	Calm
Tennis ball	Content, memory of having fun with dad	Content, memory of dad playing guitar
Tylenol gel caps	Jealousy	Jealous
Vanilla Pudding	Content, like sitting quietly with friends	Happy, content
Water (room temperature)	No emotion	No emotion
Water (warm)	Waking up in the morning and disoriented	A little on the anxious side
Wax	Embarrassment	Embarrassed and frustrated

Emotional induction is automatic and involuntary, and subjects can offer no basis for emotional pairings between stimuli.

TABLE 2
Emotions experienced by synesthete HS, generated by touching specific objects are shown above

Specific Texture	Emotion Experienced in First Test	Emotion Experienced in Second Test
Bok Choy	Irritated	Uncomfortable and annoyed
Corduroy	Disappointed	Unpleasant, felt bad
Denim	Mostly neutral, no real emotion	Neutral, no emotion
Dry leaves	Distasteful, did not want to touch	Disgust, made her feel withered
Fleece	Disgust	Disgust
Lush leaf	Calm, peaceful	Curious, happy
Moist soil	A little uncomfortable	Made her feel damp and gritty
Paper	No emotion	Neutral, no emotion
Plastic paper clip	No emotion	No emotion
Rayon	Relaxed, comfort	Comforted
Ridged plastic	Cool, happy	Kind of fun, happy
Rough textured plastic	No emotion	No emotion
Sand	Safe, happy	Fluttery, lighthearted, happy
Silk	Laughter	Laughter
Silk sleeping bag	Relaxing	Calm and neutral
Skin	No emotion	No emotion
Smooth metal	Sedated, calm	Relaxed
Soft leather	Extremely scared, makes her spine crawl	Afraid and repulsed
Tennis ball	Нарру	Нарру
Textured glove	Creepy, cool, weird	Excited, intriguing
Tylenol gel caps	Fun but weird	Нарру
Water (room temperature)	Calm, felt like wet air	Calming, soothing
Water (warm)	Calm, but less so than room temperature	Mildly calm
Wax	Disgust	Disgust

Petrucelli, & Werner, 1969). When AW experiences tactile sensations on areas other than hands or feet (e.g., the face) she will not experience a direct induction of an emotion. Instead, if she knows what emotion typically induced by that item, she will experience a vague and blunted, associative preference or aversion for the texture. For example, denim palpated by AW's hands induces depression and self-loathing. When denim is pressed against AW's face she feels a mild foreboding of discomfort without a specific emotion.

HS does not experience any other forms of synesthesia beyond tactile-emotion synesthesia and was identified through a survey in her class. She reports these experiences have occurred since early childhood, are automatic, and cannot be ignored. In general, HS's emotional descriptions are more basic than AW's, staying clustered around a core primary emotion (e.g., joy, relaxation, fear, disgust, discomfort); she rarely describes an object as causing complex emotions like jealousy. It is also possible HS is less introspective about her emotions than AW making her less sensitive to subtle emotional gradations of synesthesia. HS reports that the temperature of an object will modulate the emotion experienced (cold stones are mildly comforting while warm

stones contain an element of disgust). Induction of emotion occurs only through tactile input of the hands for HS; maximal emotional induction occurs through the tips of the forefinger and thumb, as well as the palm of her hand.

Interestingly, there is a small visual component present in both AW's and HS's experience of emotions through palpation. While the emotions are present and consistent without visual input, emotional intensity can be modulated by this additional information (though vision by itself was ineffective at causing emotional experiences). As mentioned previously, AW experiences depression and disgust for denim. This feeling is intensified if the denim is blue and she subjectively reports that when her parents forced her to wear jeans, she would wear black denim to dull the intensity. HS reports that the strength of an emotion is amplified by the size of the object. Small, cold, smooth stones are often mildly comforting, whereas large stones provoke more intense comfort.

Both synesthetes have developed methods of coping with the world in situations involving emotionally negative textures. For example, if forced to touch an emotionally aversive texture, AW will sing to try and ignore the emotion, or

hold silver in her opposite hand and focus on the calming effect of the smooth metal. Both individuals also enjoy the freedom and ease of changing their mood for the better by simply touching a 'positive' texture after experiencing a negative emotion that has been induced naturally (e.g., a fight or bad day) or through another texture. Finally, switching rapidly across different textures from an array is reported to be 'emotionally draining'.

EXPERIMENTAL INVESTIGATION

To investigate the stability of these experiences we tracked the subjects test-re-test consistency of evoked emotions (e.g., denim eliciting disgust) over an 8-month period. In addition we surreptitiously recorded subjects' facial expressions during the palpation of different textures. As another test of authenticity, we measured the impact of tactile input on autonomic arousal using sympathetic skin conductance response (SCR). The brain mechanisms underlying the generation of SCR are regulated by those involved in emotional processing (Buchel, Morris, Dolan, & Friston, 1998), suggesting this technique as a valid measure of subjects' emotional arousal. Since SCR's cannot be 'faked', the technique is often used as part of a 'lie detector' battery. Lastly, subjects rated the valence (pleasant, neutral, or unpleasant) and magnitude (1-10) of each tactile sensation.

Participants

Two tactile-emotion synesthetes and 18 non-synesthetic control volunteers participated in this study (8 females, mean age: 20.4 years, range 18–26). All gave informed consent and had normal or corrected to normal vision and none had any history of psychiatric or neurological disorder.

Stimuli and procedure

In the first portion of this study, participants were seated alone in a room and instructed to follow instructions delivered by the monitor in front of them. Skin conductance was recorded from the left hand, with a pair of Ag-AgCl electrodes (0.8 cm diameter) attached to the palmar surface of the medial phalange of the index and middle fingers, and filled with a 0.050 molar NaCl paste. Subjects

were instructed to touch 10 items one time each (soil, paper, water, denim, sand, leather, ridged plastic, silk, rubber, smooth plastic) located on a table adjacent to their right hand. Each trial lasted 10 s, with 2 min between trials.

Subjects' facial expressions during this task were recorded by a video camera (hidden from view during synesthetes' testing to avoid emotional expressions generated for the benefit of experimenters). Skin conductance was not analyzed from this session, but only present so as not to tip subjects off we were observing their facial expressions. Experimenters also left the room during this session telling subjects that we did not want our presence to interfere with SCR recording (and to create an environment where subjects felt comfortable reacting naturally to textures).

Four evaluators who were blind to the purpose of the experiment were asked to rate both the valence (pleasant, neutral, or unpleasant) and magnitude (1–10) of the facial expressions while the subjects palpated various textures. Evaluators could not see the object being touched and scored videos in a randomized order, sequentially by trial number (scoring the first trial of all 20 subjects before moving on to the second trial).

Following completion of this task, subjects' SCR activity was recorded in a second session of object palpation, this time with the experimenter present in the room and the video camera turned off. The order of items was randomized between synesthetes, and non-synesthetic volunteers were matched to the item order of AW or HS (9 subjects each). Again, each of the 10 textures was palpated in one trial only, for 10 s with 2 min between trials. After this session, subjects completed a questionnaire assessing the valence (pleasant, neutral, or unpleasant) and magnitude (1–10) of each object palpated.

In addition to this testing session, on two different occasions over an 8-month period the synesthetic subjects were asked to touch a range of textures (24 items) and report any specific experience. With very few exceptions, the items palpated were the same physical items used in both sessions. The subjects were not told ahead of time that they would be retested. As synesthetes reported a visual component to the tactile-induced emotions, all textures used in each of these tasks were visible to the subjects during testing. In addition, subjects actively palpated the textures in these studies (as opposed to being passive recipients).

RESULTS AND DISCUSSION

Facial affect

In synesthetes, results showed a highly significant (r = .77, p < .001) correlation between the facial expression (as assessed by independent reviewers) and the subjects own introspective ratings of valence and magnitude (Figure 2). In non-synesthetic individuals, no such correlation was present (r = -.10, p = .19; Figure 3). This provides strong evidence that synesthetes' experiences were not of confabulatory origin. In addition, synesthetes compared to controls produced significantly more pronounced facial expressions [F(1, 199) = 94.55, p < .0001]; interater reliability yielded an average correlation of r = .68 between reviewers for all subjects' facial expressions.

Skin conductance response

SCR activity during object palpation reflected a range of emotional experiences, both negative and positive, in the two synesthetes. In both subjects, the magnitude of the SCR was strongly correlated with subjective intensity ratings (0-10) for neutral and negative emotions (r = .74, p < .01), but not for positive emotions (r = -.28, p = .49). This is not surprising given that even in normal individuals, SCRs for pleasant emotions are usually weaker and less reliable than for aversive stimuli (MacDowell & Mandler, 1989). This may because the amygdala responds preferentially to aversive stimuli (LeDoux, Cicchetti, Xagoraris, & Romanski, 1990) and sends its output through the hypothalamus to increase SCR. Controls' SCR showed no correlation with subjective intensity ratings (r = .05). p = .52). The correlation between the subjective

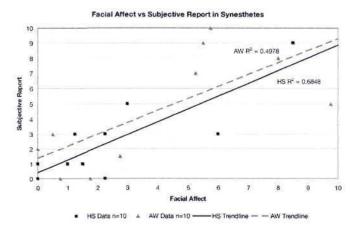


Figure 2. Magnitude of synesthetes' facial expressions (x-axis) plotted against subjective internal report (y-axis), (r = .77, p < .001).

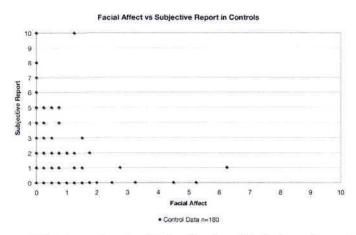


Figure 3. Magnitude of controls' facial expressions (x-axis) plotted against subjective internal report (y-axis), (r = -1.10, p = .19).

magnitude of the emotion and the SCR further supports the authenticity of the synesthetically induced emotions.

Consistency testing

Consistency for the reported emotions across the two sessions was 100% although different words were sometimes said to describe the same emotion. For example, in one session AW reported grade 120 sandpaper elicited a emotion similar to 'telling a white lie' and in the subsequent session stated 'guilty, but not a bad guilt, like you know you had to do something wrong to get something better in the long run'. This illustrates the stability of the phenomenon but also provides circumstantial evidence that the evoked emotions are not liguistically mediated. If mediated by language or memory alone, it is unlikely that she would have used a completely different terminology to describe the same emotional experience during the re-test trials.

GENERAL DISCUSSION

Correlations among the surreptitiously recorded facial expressions, self-reported intensities of the emotions, and the SCR all suggest that Tactile-Emotion synesthesia is a highly reliable and automatic perception. This phenomenon shows remarkable consistency in the specificity of emotions evoked across trials spread across months.

In both subjects, emotional induction occurs mainly through appendages that have more acute tactile discrimination (hands and feet in AW, hands only in HS), as revealed by experimental investigation. The fact that the body location matters strongly suggests, once again, that this phenomenon is not confabulatory. Furthermore, when different textures are simultaneously applied to the face and hand, the emotions are dulled in both subjects. In addition, AW's emotional experiences vary depending on the limb that is used (ceramic tile on her feet elicits a feeling of power, while on her hands comfort) rendering it unlikely that this is a learned association. If during childhood AW established a strong accidental association between ceramic and comfort, this association should not differ if touched with either the hands or feet.

Subjective reports of tactile-induced emotions were shown consistent over 8 months in both synesthetes. Correlations between subjective reports and facial affect confirm this phenomenon activates emotionally intense expressions, as judged by blind evaluators. Furthermore, the synesthetes' reports of strong emotional effects during tactile palpation were correlated significantly with SCR activity (reflecting autonomic arousal) which is automatic and cannot be faked. Indeed, even when normal individuals are instructed to imagine positive or negative events, no differences between the emotions are seen in SCR activity (Haney & Euen, 1976).

Our study reports the first experimental investigation of synesthesia between tactile sensations and induced emotional experiences. These findings have important implications for the perceptual nature of synesthesia and its interactions with higher cognitive functions, in addition to having implications for tactile perception in general. Given its obvious evolutionary advantage there are probably pre-existing connections between touch and emotion that would normally be adaptive e.g., soft fur = pleasant, and sandpaper = aversive since it is potentially abrasive. Painful tactile stimuli send information through both fast-conducting myelinated afferent fibers (alpha-fibers) signaling pain, and slow-conducting unmyelinated C-fibers. providing information to the limbic system mediated by the anterior cingulate and insula (Olausson et al., 2002; Ploner, Gross, Timmermann, & Schnitzler, 2002). Tactile sensations beneficial to a species survival (e.g., soft furs for warmth, and smooth textures for 'nonabrasive') and those which are harmful (e.g., jagged stones) may be connected to limbic pleasure and aversion centers, respectively. A derangement of these connections caused by a gene that causes hyperconnectivity (as in the case of grapheme color synesthesia; Ramachandran & Hubbard, 2001a; Rouw & Scholte, 2007) would explain the curious and arbitrary parasthesia-like emotions being evoked by touch in AW and HS. There may also be additional selective enhancements with the frontal structure leading to the extraordinary specificity some of the emotions (e.g., 'jealousy' or 'white lie'). We propose that in the context of pain, alpha fibers developed at least partially as a predictive mechanism for alerting you to tactile sensations that could potentially cause damage over the long term. Holding an abrasive rock or sandpaper will not cause immediate pain and thus will not activate unmyelinated c-fibers. However, this texture will slowly damage or abrade the skin until a threshold for pain is reached. Through the alpha fibers linking with emotional limbic areas, primates may have developed a mechanism for unconsciously

predicting the potentially damaging long-term effects of a particular object (which is then translated into a conscious experience of raw emotions). Over time, these established pathways were expanded to include more subtle gradations across multiple sensory modalities giving rise to many of the emotions humans experience. We suggest that it is these pathways that regulate subtle tactile preferences in all individuals. However, the fact that stimuli such as fleece could evoke disgust, denim, or pain, suggests that we are dealing not just with enhancement of pre-existing associations but connections that are randomly enhanced and abnormal in other ways as well. This would be analogous to the tingling electric shock-like feeling (parasthesiae) that occur even in normal people when the ulnar nerve is tapped. The tapping creates an unnatural pattern of 'junk' impulses that the brain interprets as idiosyncratic quale that cannot be labeled in any ordinary manner. The observation suggests the priority of pattern - coding over place -coding in the nervous system.

What are the underlying physiological mechanisms? As already alluded to, we suggest that different tactile textures evoke highly selective activity in secondary somatosensory cortex (SII), which in turn is known to provide an input to the insula (Robinson & Burton, 1980). Efferents from the insula then project to limbic/emotional brain areas including the anterior cingulate (Mishkin, 1979). A heightened cross activation between SII cortex and the insula, with output to the cingulate, may lead to tactile–emotion synesthesia while an additional enhancement of connections with frontal cortex may evoke more subtle nuances unique to social primates (e.g., jealousy, guilt, etc.). We are currently exploring these mechanisms with neuroimaging.

The heightened cross activation between SII/ insula/fronto-limbic structures could come about as a result of two distinct mechanisms, both of which might be caused by a gene mutation. First, there could be an actual increase in axonal connections as seen in the fusiform gyrus of graphemecolor synesthetes (Ramachandran & Hubbard, 2001a; Rouw & Scholte, 2007). Second there could be disinhibition of feedback modulation based on transmitter imbalance (Armel & Ramachandran, 1999; Grossenbacher & Lovelace, 2001). This latter hypothesis is supported by our recent observation that synesthetes temporarily lose their synesthesia with SSRI's which cause increased serotonin S1 receptor activation and reciprocally lowered activation of serotonin 2A (5HT2A) receptors and increased levels of norepinephrine (Brang & Ramachandran, 2008). Based on this observation we have suggested that 5HT_{2A} receptors might be the 'synesthesia receptors' of the brain, that work in conjunction with reduced levels of norepinephrine. We propose that the cross-activation in synesthesia is caused by a mutation of gene HTR2A on chromosome 13q.

In addition to these two mechanisms, we propose that because of the enhanced cross-activation (caused by the diffuse expression of genes that cause hyperconnectivity or disinhibition) associations that are made fleetingly by all of us become entrenched – automatic or obligatory – in synesthetes due to a form of 'auto-kindling'.

In summary these findings support our original conjecture that synesthesia in general, including tactile – emotion synesthesia, can help us link phenomenology, genetics, brain anatomy, pharmacology, and metaphor ('I am touched by your kindness') in a precise enough manner that they might provide a new approach to understanding higher brain functions that have hitherto eluded physiological analysis. In addition they would provide a valuable antidote to the retreat back to the dark ages of classical associationist psychology championed recently by some researchers as an explanation for all types of synesthesia.

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REFERENCES

Armel, K. C., & Ramachandran, V. S. (1999). Acquired synesthesia in retinitis pigmentosa. *Neurocase*, 5, 293–296.

Baron-Cohen, S., Burt, L., Smith-Laittan, F., Harrison, J., & Bolton, P. (1996). Synaesthesia: prevalence and familiality. *Perception*, 9, 1073–1079.

Buchel, C., Morris, J., Dolan, R. J., & Friston, K. J. (1998). Brain systems mediating aversive conditioning: An event-related fMRI study. *Neuron*, 5, 947–957.

Brang, D., & Ramachandran, V. S. (2008). Psychopharmacology of synesthesia; The role of serotonin S2a receptor activation. *Medical Hypothesis*, 70(4), 903–904.

Cytowic, R. E. (1989). Synesthesia and mapping of subjective sensory dimensions. *Neurology*, 6, 849–850.

Cytowic, R. (1993). The man who tasted shapes: A bizarre medical mystery offers revolutionary insights into reasoning (1st ed.). New York: Putnam.

Dixon, M. J., Smilek, D., Cudahy, C., & Merikle, P. M. (2000). Five plus two equals yellow. *Nature*, 406(6794), 365–365.

- Domino, G. (1989). Synesthesia and creativity in fine arts students: An empirical look. Creativity Research Journal, 2, 17–29.
- Haney, J. N., & Euse, F. J. (1976). Skin conductance and heart rate responses to neutral, positive, and negative imagery: Implications for covert behavior therapy procedures. *Behavior Therapy*, 7, 494–503.
- Hubbard, E. M., Arman, A. C., Ramachandran, V. S., & Boynton, G. M. (2005). Individual differences among grapheme-color synesthetes: Brain-behavior correlations. *Neuron*, 45(6), 975–985.
- Galton, F. (1883). Inquiries into human faculty and its development. London: Dent & Sons.
- Grossenbacher, P. G., & Lovelace, C. T. (2001). Mechanisms of synesthesia: Cognitive and physiological constraints. Trends in Cognitive Sciences, 5(1), 36-41.
- Kim, C.-Y., Blake, R., & Palmeri, T. J. (2006). Perceptual interaction between real and synesthetic colors. Cortex, 42, 195–203.
- LeDoux, J. E., Cicchetti, P., Xagoraris, A., & Romanski, L. M. (1990). The lateral amygdaloid nucleus: Sensory interface of the amygdala in fear conditioning. The Journal of Neuroscience, 10(4), 1062–1069.
- MacDowell, K. A., & Mandler, G. (1989). Constructions of emotion: Discrepancy, arousal, and mood. *Moti*vation and Emotion, 13(2), 105–124.
- Mattingley, J. B., Rich, A. N., Yelland, G., & Bradshaw, J. L. (2001). Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia. *Nature*, 410(6828), 580–582.
- Mishkin, M. (1979). Analogous neural models for tactual and visual learning. Neuropsychologia, 2, 139–151.
- Mulvenna, C. M. (2007). Synaesthesia, the arts and creativity: A neurological connection. Frontiers in Neurology and Neuroscience, 22, 206–222.
- Nunn, J. A., Gregory, L. J., Brammer, M., Williams, S. C. R., Parslow, D. M., Morgan, M. J., et al. (2002). Functional magnetic imaging of synesthesia: Activation of V4/V8 by spoken words. *Nature Neuroscience*, 5, 371–375.
- Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B., Starck, G., et al. (2002). Unmyelinated tactile afferents signal touch and project to insular cortex. *Nature Neuroscience*, 9, 900–904.
- Palmeri, T. J., Blake, R., Marois, R., Flanery, M. A., Whetsell Jr, W. (2002). The perceptual reality of synesthetic colors. *Proceedings of the National Academy* of Sciences, 6, 4127.
- Ploner, M., Gross, J., Timmermann, L., & Schnitzler, A. (2002). Cortical representation of first and second pain sensation in humans. *Proceedings of the National Academy of Sciences*, 19, 12444–12448.
- Ramachandran, V. S., & Azoulai, S. (2006). Synesthetically induced colors evoke apparent-motion perception. *Perception*, 35(11), 1557–1560.
- Ramachandran, V. S., & Brang, D. (2008). Synesthesia. Scholarpedia, 3(6), 3981.
- Ramachandran, V. S., & Hubbard, E. M. (2001a). Psychophysical investigations into the neural basis of

- synaesthesia. Proceedings: Biological Sciences, 1470, 979-983.
- Ramachandran, V. S., & Hubbard, E. M. (2001b). Synaesthesia: A window into perception, thought and language. *Journal of Consciousness Studies*, 12, 3–34.
- Ramachandran, V. S., & Hubbard, E. M. (2002). 'Synesthetic colors support symmetry perception and apparent motion'. Psychonomic Society Abstracts, 7, 79.
- Ramachandran, V. S., & Hubbard, E. M. (2003a). Hearing colors, tasting shapes. Scientific American, 5, 52–59.
- Ramachandran, V. S., & Hubbard, E. M. (2003b). The phenomenology of synaesthesia. *Journal of Con*sciousness Studies, 10, 49–57.
- Ramachandran, V. S., & Hubbard, E. M. (2005). Do qualia, metaphor, language, and abstract thought emerge from synesthesia? In J. L. van Hemmen, & T. J. Sejnowski (Eds), 23 problems in systems neuroscience (pp. 432–473). New York: Oxford University Press.
- Rich, A. N., Bradshaw, J. L., & Mattingley, J. B. (2005). A systematic, large-scale study of synaesthesia: Implications for the role of early experience in lexical-colour associations. *Cognition*, 98(1), 53–84.
- Robinson, C. J., & Burton, H. (1980). Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of M. fascicularis. The Journal of Comparative Neurology, 1, 69-92.
- Rouw, R., & Scholte, H. S. (2007). Increased structural connectivity in grapheme-color synesthesia. *Nature Neuroscience*, 6, 792–797.
- Sagiv, N., Simner, J., Collins, J., Butterworth, B., & Ward, J. (2006). What is the relationship between synaesthesia and visuo-spatial number forms? *Cognition*, 101(1), 114–128.
- Simner, J., & Holenstein, E. (2007). Ordinal linguistic personification as a variant of synesthesia. *Journal of Cognitive Neuroscience*, 19(4), 694–703.
- Simner, J., & Hubbard, E. M. (2006). Variants of synesthesia interact in cognitive tasks: Evidence for implicit associations and late connectivity in crosstalk theories. *Neuroscience*, 143(3), 805–814.
- Simner, J., & Ward, J. (2006). Synaesthesia: The taste of words on the tip of the tongue. *Nature Neuroscience*, 444, 438–438.
- Simner, J., Mulvenna, C., Sagiv, N., Tsakanikos, E., Witherby, S. A., Fraser, C., et al. (2006). Synaesthesia: The prevalence of atypical cross-modal experiences. *Perception*, 8, 1024–1033.
- Ward, J., Yaro, C., Thompson-Lake, D., & Sagiv, N. (2007). Is synaesthesia associated with particular strengths and weaknesses? UK Synaesthesia Association Meeting.
- Ward, J., Thompson-Lake, D., Ely, R., & Kaminski, F. (2008). Synaesthesia, creativity and art: What is the link? *British Journal of Psychology*, 99(Pt 1), 127–141.
- Whitsel, B. L., Petrucelli, L. M., & Werner, G. (1969). Symmetry and connectivity in the map of the body surface in somatosensory area II of primates. *Journal* of Neurophysiology, 32(2), 170–183.