CHAPTER 45

SYNESTHESIA AND CONSCIOUSNESS

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Introduction

We have learnt much from studying selective deficits in neurological patients and what they tell us about normal brain function. This neuropsychological approach has been useful in the study of perception, attention, memory, and thought. However, interest in positive symptoms or phenomena such as synesthesia, hallucinations, and phantom limbs can be equally instructive.[1] Like deficits, positive symptoms could provide some useful clues concerning likely components and organization of the underlying cognitive or neural mechanisms and therefore facilitate the generation of new hypotheses. Additionally, they provide test cases for established theories of cognition. A good theory should be able to predict both negative and positive deviations from normal function when certain parameters are changed. Indeed, scientists are becoming increasingly convinced that there is much we could learn from synesthesia about normal function. While early synesthesia research focused primarily on documenting the phenomenon and verifying the genuineness of the subjective reports, current synesthesia research goes beyond this. Today, we are concerned with explaining the extraordinary perceptual experiences of synesthetes and considering what synesthesia may reveal about perception and cognition more generally (e.g. Cohen Kadosh, Gertner, and Terhune 2012; Sagiv and Ward 2006). In this chapter we will make the case for considering synesthesia as a model problem in the scientific study of consciousness and highlight some of the promising directions such a project could take.

[1] In neuropsychology, positive symptoms are characterized not by losing some ability or function but rather by adding or altering perception or cognitive processes in some way. For example, perceiving a stimulus in the wrong visual field (allesthesia), perceiving something that is not really there (e.g., hallucinations) or remembering something that did not really happen (e.g., déjà vu). This may or may not be accompanied by negative symptoms (i.e., deficits of perception, memory, etc.).

Consciousness

The problem of consciousness is one of the most challenging ones scientists are facing. It is usually divided into two major components—awareness and arousal (Zeman 2005). We will focus here on the problem of awareness or contents of consciousness (rather than levels or states of consciousness)—understanding our subjective, private experiences and how they emerge. This includes our thoughts, feelings, intentions, what we perceive, and the sense of authorship of our own actions.[2] The scientific study of consciousness examines the relationship between these subjective experiences and behavior, cognitive processes, brain structure and function, the course of development, as well as genetic, environmental, and cultural constraints. Scientists trying to understand consciousness are faced with many questions and problems. These include, for example, what distinguishes conscious from unconscious processing? How might we understand intentions, agency, free will, thought, and the relationship between attention and awareness? What determines the nature of our experiences, and what is the relationship between perception and reality? The study of consciousness is therefore an interdisciplinary endeavor and touches on many aspects of human cognition and brain function. It is not our intention to provide here a thorough introduction to the scientific study of consciousness (for an introduction, see Blackmore 2010; Revonsuo 2010; Zeman 2002).

Trying to understand consciousness follows a long tradition of attempts to address the mind-body problem. Chalmers' (1995) formulation of the problem—why should brain activity give rise to subjective experience in the first place?—has generated extensive debates (for a brief outline of the early debates, see Searle 1997). Such "*why*" questions are notoriously hard to answer[3] and scientists have always been better at describing *what*, *when*, and *how* things happen instead. Indeed considerable progress has been made understanding a number of key problems in the scientific study of consciousness: Identifying the neural correlates of consciousness (e.g., Frith, Perry, and Lumer 1999; Rees and Frith 2007), understanding the role of attention (e.g., Koch and Tsuchiya 2007; Lavie 2007), or how information is accessed (e.g., Block 2011) or integrated (e.g. Robertson 2003; Tononi 2007). Here we will focus on insights generated by empirical research.

Given the elusive nature of consciousness and the difficulty of providing a definition that encapsulates all aspects of consciousness, many studies have focused on specific,

[2] Following Searle (2000), we do not provide a precise, analytical definition of consciousness at the outset, and settle for this commonsense working definition for now.

[3] Richard Feynman (1983) once noted that explaining *why* something happens leads to an infinite series of questions (Why does A happen? Because of B; why is B true? Because of C; what explains C then? And so on). Therefore, we cannot usually give a full and comprehensive answer to "why" questions unless we do so within a framework in which some things are taken to be true (BBC2, 15 July 1983; *Fun to Imagine 2: Stretching, Pulling and Pushing*; <http://www.bbc.co.uk/archive/feynman/>).

circumscribed aspects of consciousness. Considerable progress has been made through the fractionation of consciousness into well-defined features or functions (such as visual awareness, bodily awareness, or the feeling of willing). It is sensible to start with a modest project—trying to understand how a single uni-modal perceptual experience arises. The problem of seeing the color red, for example, has been a particular favorite in philosophical debates on consciousness. Once we can provide an account of seeing red, we can try to extend our explanation to more complicated visual experiences and to other domains of human experience. We might then ask ourselves what synesthesia can bring to this debate, or indeed, how a general notion of consciousness might inform us about the nature of synesthesia.

Synesthesia as a Model Problem for Understanding Experience

Seeing red may be a pure form of awareness, but focusing on this simple problem may come at a price. There may be features of perceptual awareness that are more readily noticed when looking beyond simple color vision. For example, active exploration of the environment, thought to be crucial in perceptual awareness, is more easily appreciated when considering tactile perception rather than visual perception (Noë 2004). Similarly, we can understand better the role of attention in consciousness within more natural settings, when varying perceptual load or manipulating the focus of attention (Kuhn, Amlani, and Rensink 2008).

We argue that synesthesia can serve a useful function in the scientific study of consciousness, since it could provide a new perspective on the problem and is a test-case for current theories. It is not immediately apparent why a relatively uncommon perceptual phenomenon should be useful at all in understanding perception or more broadly—consciousness. So let us try to clarify this. First, synesthesia is phenomenologically-defined. It is characterized by an atypical perceptual experience and like any other type of experience it can be compared with instances in which it does not arise (while the subjective reports of participants' conscious experience serve as a dependent variable; Baars 2003). The perceptual experiences of synesthetes (i.e., those who experience synesthesia) may be unusual, but its existence raises the same general problems: How do such experiences arise? What is their neural basis? How does attention modulate synesthetic experience? A second feature that makes synesthesia a particularly useful case study is the impressive variety of types of synesthesia, involving different combinations of sensory modalities and different types of experience. This provides us with a large number of observations and many opportunities to test our theories of brain function and the associated mental states. It also presents an opportunity to open up the debate on individual differences in subjective experience of the world around us. The third, practical reason that makes synesthesia valuable is that synesthetes are usually healthy and cooperative research participants and that synesthesia is more common than previously thought. This makes the condition easier to study than, for example, studying the perceptual anomalies in certain neurological or neuropsychiatric patients.

This chapter outlines why consciousness scientists and scholars should be interested in synesthesia, and why synesthesia researchers should be interested in consciousness. It delineates some the areas where synesthesia research is likely to contribute to our understanding of consciousness.

Approaches to Studying Synesthesia

Contemporary synesthesia studies are concerned with explaining how the phenomenon arises and exploring what it tells about perception and cognition more generally. Essentially, we are taking the neuropsychological approach. In neuropsychology, study of the deficits associated with circumscribed brain damage tells us something more generally about the relationship between cognition and brain function. In the same way one can study the deviations from the norm in healthy individuals with synesthesia (or in those who have acquired synesthesia). Cases of synesthesia are radically different than what we are used to, and so force us to reconsider our ideas about perception. New observations from such cases may help us generate new hypotheses about normal cognition and expose implicit assumptions. What we take for granted may not always be true. Indeed if there is anything that we have learned about consciousness it is that appearance and intuitions can be misleading.

One challenge in the study of synesthesia is assessing and quantifying the subjective reports of synesthetes. This has become somewhat easier in recent years as more cases of synesthesia have come to light. Prevalence estimates using different methodologies had varied widely. Recent studies taking into account both participants' self-reports and objective indices such as high consistency in their descriptions over time (e.g., the correspondences between specific letters and colors tend to be very stable) have typically lead to conservative estimates. After eliminating some of the sampling confounds that plagued earlier reports, Simner et al. (2006) were able to show that the prevalence of grapheme-color synesthesia (i.e., colored letters or digits) is close to 1.4%, and more than 4% of the population reported one of several common variants of synesthesia. One limiting factor in estimating the prevalence of synesthesia is the lack of agreement on a precise definition.[4] There is a growing consensus that better understanding of the underlying neurobiological mechanisms could inform the way in which we categorize synesthesia variants (Sagiv, Ilbeigi, and Ben-Tal 2011; Simner 2012) in addition to the phenomenological and behavioral characteristics. Patterns of inheritance of different variants as well as their co-morbidity may also prove useful in assessing the relationship

[4] For a discussion of the problem of defining synesthesia, please see Simner (2012), Eagleman (2012), Cohen-Kadosh and Terhune (2012), McPherson (2007), and Sagiv, Ilbeigi, and Ben-Tal (2011).

between different forms of synesthesia (e.g., Novich, Cheng, and Eagleman 2011). We will discuss here a number of synesthesia variants and related phenomena, highlighting their relevance for the study of consciousness (regardless of whether or not all these variants will end up being classified as types of synesthesia in their own right, as, for example, in the case of grapheme personification; see later and Amin et al. 2011). One of the principal factors that make defining synesthesia so difficult is our growing appreciation of the sheer variety of different ways in which synesthetes—and indeed all of us—might experience the world around us. This brings us to our first issue—individual differences.

Individual Difference in the Way We Perceive the World

The possibility that we literally see things differently from one another has intrigued scholars at least since John Locke's (1690/1979) discussion of the "inverted spectrum" argument. Is it possible that while we agree on the names of colors, we experience them differently? Behavioral measures can helps us rule out some possible transformations of individuals' color space (Palmer 1999a), but in general comparing experiences remains very challenging because we simply cannot get into other people's heads. Nevertheless, we can still say with confidence that some people do experience the world differently. Some notable examples can be traced back to the neurophysiology of sensory systems. Color blindness is one such example (e.g., Palmer 1999b). Dichromats—individuals missing one of the three types of cone photoreceptors—cannot discriminate between certain colors that the rest of us experience as very different. Conversely, a minority of women endowed with four types of cone photoreceptors seem to have a richer color experience (Jameson, Highnote, and Wasserman 2001). Similarly, genetic variations in taste receptors influence the sensitivity to bitter tastes (e.g., Des Gachons, Beauchamp, and Breslin 2009).

Variability in subjective experience of visual stimuli has also been recently linked to variability in the cerebral cortex. Schwarzkopf, Song, and Rees (2011) showed that V1 size negatively correlates with the subjective experience of object size, as indicated by the magnitude of two visual illusions. Anomalous functional organization of the cerebral cortex also underlies conditions such as congenital prosopagnosia (Behrmann et al. 2007). Individuals who are unable to tell the difference between two or more faces that look radically different to most of us, will not only score lower on behavioral face recognition tests, but obviously, will also have a very different experience in many everyday situations looking at faces. The examples described here are all concerned with differences in the *intensity* or magnitude of perceptual experience (or inability to detect a stimulus difference, at the extreme low end of the spectrum). Indeed, some progress has been made in quantifying individual difference in the intensity of stimuli (Bartoshuk et al. 2004). However, evidence concerning possible individual differences in the *quality* of experiences (not merely the intensity) has been rather limited.

Synesthesia provides us with one example of qualitatively different experiences. Synesthetes don't only perceive more than the rest of us, but they also differ among themselves on the quality of that additional experience. For example, for AD (a synesthete)—the letter C is yellow, and P is blue, while for CP (another synesthete)—the opposite is true—she perceives the letter C in blue while P is yellow (Sagiv and Robertson 2005). Synesthetes are living examples of a mixed-up spectrum of sorts. Their experience of colored surfaces (e.g., a red pepper) may be similar, but there are certain other sets of stimuli (e.g., black and white graphemes) that induce different color experiences for these individuals.[5] Thus, different colored-grapheme synesthetes have a different correspondence between colors and common objects (which are shared with the rest of the population) and between colors and graphemes (which are not). We know this because (a) they can report how their synesthetic color experience compares with color experiences we are all familiar with, and (b) because we have objective measures corroborating the self-reports. Demonstrations of the perceptual reality of synesthetic colors include, for example, the finding that colored-grapheme synesthetes can perform better than non-synesthetes on some visual search tasks by utilizing their synesthetic colors (Palmeri et al. 2002; Ramachandran and Hubbard 2001a). Such superior performance is difficult to fake, increasing our confidence in the reality of their experience. Furthermore, the advantage certain synesthetes gain in some behavioral tasks involving graphemes (namely texture segregation and crowding experiments), correlates with the degree to which the synesthetic colors engage early visual areas in different synesthetes (Hubbard et al. 2005). This heterogeneity is also present in the variability of the spatial reference frames within which different synesthetes perceive their synesthetic colors, i.e., projected externally in the synesthete's peri-personal space or perceived in the synesthete's mind's eye (Dixon, Smilek, and Merikle 2004; Ward et al. 2007). These differences affect the saliency of synesthetic colors.

In many types of synesthesia the correspondence between trigger for the synesthetic experience (inducer) and the synesthetic experience itself (concurrent) are idiosyncratic to the individual,[6] for example, recall the cases of AD and CP who have opposite colors for the letters C and P. Each of those correspondences provides us with a further

[5] At the very least we can say that the *relational structure* of the experiences they report differs, if one is forced to make the argument without any reference to the quality of experience whatsoever (c.f. Dennett 1991, 1999).

[6] Mirror touch synesthesia (Blakemore et al. 2005) presents an exception to this rule. There, the synesthetic experiences are more predictable: An individual *seeing* another individual receiving *tactile* stimulation to their hand, will experience a corresponding tactile experience on their own hand (not in a seemingly random, different body part). However, even mirror-touch synesthetes show a difference in the way they map the right and left sides of the observed body onto their own (Banissy and Ward 2007; Banissy et al. 2009). Some synesthetes consistently experiencing a specular mapping (left mapped to right—resembling a mirror reflection) while others map anatomically (the left is mapped to the left) as if adopting the other person's perspective or reference frame.

demonstration of qualitatively different subjective experiences when comparing two synesthetes with the same type of synesthesia, be it colored graphemes, lexical-gustatory synesthesia (i.e., words trigger tastes; Jones et al. 2011; Ward and Simner 2003), colored touch (Ludwig and Simner, 2013), colored music (e.g., Ward, Huckstep, and Tsakanikos 2006), or the visualization of spatial patterns induced by letters (Jonas et al. 2011), numbers (e.g., Sagiv et al, 2006; Tang, Ward, and Butterworth, 2009), or time units (Brang et al. 2011; Jarick et al. 2011; Smilek et al. 2007). Hence even among synesthetes there are individual differences. Indeed, one thing that synesthesia teaches us about our conscious experience is that we cannot take it for granted that others see the world in the same way. Such individual differences have implications for philosophical frameworks for understanding consciousness. Experience appears to vary independently of the stimulus and associated behavior in synesthesia. This has led some to claim that a purely behavioral functionalist framework may not be sufficient to account for synesthesia (Gray 2002, 2003; c.f. Noë and Hurley 2003). Indeed for a complete understanding we would have to take into consideration, not only a very detailed history of the stimuli to which individual synesthetes have been exposed, but also neurobiological constraints (Sagiv, Ilbeigi, and Ben-Tal 2011). As we fine tune our understanding of the neural basis of conscious perception in general and synesthesia in particular, we may be able to predict with greater accuracy how synesthetes' experiences might be different from those of non-synesthetes.

The Neural Correlates of Consciousness and Synesthesia

Now that scientists have established that synesthesia is not confabulatory in origin, attention has turned to trying to understand how such experiences arise in some individuals but not in others, and what these experiences have in common with other forms of ordinary and extraordinary forms of perception. One key project concerns the neural basis of synesthesia. In particular, studying the neural correlates of synesthetic experience seems to be a special case of the general quest for the neural correlates of consciousness (NCC)—identifying the minimal sets of neural mechanisms, activation of which is sufficient to give rise to a subjective experience of one sort or another. We will comment on this body of work here. It is not our intention to provide here a comprehensive review of neuroimaging studies of synesthesia (for a review see Rouw, Scholte, and Colizoli 2011, and other dedicated chapters in this volume), but rather to comment on the associated methodological issues, highlight a number of lines of research with implications for understanding consciousness, and identify directions for future research.

From a methodological point of view, the same advice concerning the NCC in general applies to the study of neural correlates of synesthetic experiences in particular (for a review see Frith, Perry, and Lumer 1999; Rees and Frith 2007). First we must be careful to distinguish between brain activations associated with processing of the stimuli, activations associated with the associated behaviors, and the NCC. For example, stimuli may be processed to some degree and affect behavior in the absence of any awareness. Hence it is important to establish both necessity and sufficiency for particular activations to be associated with conscious experience (for a review, see also Kanwisher 2001). Paradigms particularly suited to identifying the NCC require a change in subjective experience while the stimulus remains constant. We must also keep in mind different aspects of candidate NCCs, including, not only the location where activation is observed, but also the time-course and patterns of activity, as well as interactions between different areas. Caution must be applied in establishing causality in the absence of direct evidence (e.g., from brain stimulation or lesion studies).

However, studying the neural correlates of conscious synesthetic experience entails one more unique problem. We must also distinguish between the neural correlates of the *synesthetic experience* and the neural correlates of awareness of the *inducing stimulus*. This is challenging to achieve using within-subject designs since, when the evoking stimulus is unattended, the synesthetic experience is unlikely to arise (Sagiv, Heer, and Robertson 2006). Between-subject designs provide a relatively straightforward means for keeping the stimulus exactly the same, while comparing groups with and without synesthetic experiences. However, caution must also be applied in classifying and grouping synesthetes. Some synesthesia variants now have widely-used accepted labels; these may give us a false sense of confidence that we are dealing with a relatively uniform well-understood sort of experience. Time and again, we have discovered that there could be distinct sub-types within such groups. Researchers would be wise to first interview and listen carefully to what synesthetes have to say before classifying their experiences based on questionnaires that may sometimes contain terms that researchers and participants interpret in different ways (e.g., "the mind's eye"). Finally, researchers should keep in mind that brain activations associated with the type of synesthesia of interest may be "contaminated" by those associated with other variants of synesthesia also present in the same individual. Indeed, it is not uncommon for synesthetes to have multiple variants (e.g., Simner et al. 2006).

One common finding is that synesthetic experiences are associated with activations in sensory cortices thought to be necessary for processing and awareness of the stimuli normally associated with such experiences. For example, synesthetic taste experiences activate, among other areas, the primary gustatory cortex (Jones et al. 2011) located in the insula (Small 2010). Reassuringly, such activity is also observed during gustatory hallucination (Henkin, Levy, and Lin 2000). Similarly, synesthetic color is associated with the activations of V4/V8 (e.g., Nunn et al. 2002)—the brain's color center (Zeki and Bartels 1999). This may seem like a straightforward finding but in fact it carries significance for understanding the idea of "essential nodes" supporting conscious experience—areas that are necessary for such experiences (and may or may not have other functions). For example, we have long suspected that V4 is necessary for color vision (e.g., Zeki 1990), but in order to demonstrate it is necessary for color consciousness, we will need to show that there could be no color experience without V4. If we could find an example of color experience without V4 activation, this could be potential evidence against necessity. Evidence from patients with Charles Bonnet syndrome suggests that they too show V4 activation while hallucinating colors (ffytche et al. 1998). Studies of synesthetic color experience show a similar pattern of V4 activation (Hubbard et al. 2005; Nunn et al. 2002), providing further converging evidence to support the idea that V4 is indeed necessary for supporting the subjective experience of seeing color.

However, the picture is more complicated than this. Not all synesthesia studies have replicated this finding. Rouw et al. (2011) attribute this to lack of power in some cases (Aleman et al. 2001; Paulesu et al. 1995) or to the different experimental paradigm and analyses used by others (Weiss, Zilles, and Fink 2005; Rich et al. 2006). These inconsistencies may also be due to phenomenological heterogeneity and possible clustering of different subtypes of synesthetes (see our discussion of individual differences) that may have led to averaging out of some effects (Dixon and Smilek 2005). In any case, this merits further investigation and may lead to new insights into individual differences in synesthesia and functional organization of the sensory cortex in synesthetes.[7]

Is synesthetic color experience associated with additional activations outside the primary sensory cortices? Involvement of posterior parietal regions is a relatively consistent finding in the neuroimaging literature of colored-grapheme synesthesia (Rouw, Scholte, and Colizoli 2011). Authors of these studies propose that such activations reflect binding and attentional processes. This is consistent with behavioral studies showing that attention to the evoking stimulus is indeed required for awareness and binding of the synesthetic colors associated with graphemes. Indeed Sagiv, Heer, and Robertson (2006) predicted that this would be necessary for synesthesia to arise. However, using TMS to the parietal lobule, Esterman et al. (2006) were only able to reduce the magnitude of the synesthetic Stroop effect (where synesthetes struggle to process graphemes presented in colors that conflict with their synesthesia) but not to knock out synesthetic color experience altogether. Further research will be necessary in order to determine whether parietal involvement is essential for the experience of a synesthetic color at all, or at least for the experience of the synesthetic color as bound to the surface of the inducing stimulus (see also, Robertson 2003; Treisman 2005).

Does the experience of synesthesia depend on structural anatomical brain features present in synesthetes but not in non-synesthetes? Let us turn our attention next to brain connectivity. For more than a century, scientists have suspected that synesthesia is the consequence of a neural short circuit—that somehow parts of the brain were communicating in an atypical way (Marks 1975). Both Pedrono (1882) and de Rochas (1885) suggested a form of cross-activation in sensory brain areas. The idea has been

[7] Note that there is an implicit assumption in most discussions of the neural basis of synesthesia that, apart from the linkage between inducer and concurrent experience, the functional organization of the cerebral cortex is otherwise very similar. While we find this parsimonious and quite likely, it is worth noting that it is possible that the same factors that have led to the development of synesthesia have also resulted in slight differences in the functional organization (e.g., greater involvement of areas normally supporting imagery in perception of external stimuli).

revived and elaborated in the modern synesthesia literature (e.g. Hubbard, Brang, and Ramachandran 2011; Ramachandran and Hubbard 2001b). In 2007, Rouw and Scholte provided the first direct observation of localized cortical hyperconnectivity in developmental synesthetes using diffusion tensor imaging (DTI) to image white matter. However, Hänggi, Wotruba, and Jäncke (2011) argue that connectivity may be globally-altered.[8] Although substantial progress has been made in mapping the functions of different cortical areas in the past two decades, the effects of various patterns of cortical connectivity on cognition, brain function, and consciousness are not as well understood (but see, e.g., Hasenkamp and Barsalou 2012). Synesthesia provides us with an opportunity to examine this issue from a different angle, especially given the growing interest in connectivity in developmental conditions (e.g., Rippon et al. 2007; Stevens 2009).

Finally, synesthesia has considerable untapped potential to tell us more about the relationship between brain function, plasticity and conscious experience. Some additional areas of particular interest include, for example, plasticity and rehabilitation after brain damage (e.g., Ro et al. 2007) and acquiring new experience via sensory substitution devices, e.g., providing input from electronic visual sensors via an array of tactile stimulators or complex auditory signal instead, (e.g., Kupers et al. 2006; Proulx 2010; Ward and Wright, in press). This is sometimes described as a synthetic form of synesthesia.

Representation and Construction of the Perceived World and the Social World

Information coming from different sensory modalities is combined in order to make sense of the world around us. However, this process often goes beyond sensory integration; quite often processing in one sensory channel can influence the processing in another. For example, in the cinema, we perceive the sound of actors' voices as coming from the actors' lips on the screen even though the loudspeakers may be elsewhere in the room (i.e., visual input can influence sound localization; for a review, see Macaluso and Driver 2005). More puzzling is the observation that sensory interactions could happen when only one sensory modality is stimulated—as is the case in synesthesia.[9] Indeed, synesthesia exemplifies well

[8] Note, however, that while a certain degree of (anatomical) hyperconnectivity between sensory areas may be sufficient to enable individuals to experience synesthesia, it is probably not necessary. Cohen Kadosh et al. (2009) have been able to induce synesthesia using post-hypnotic suggestion within a time-course that is simply too short to allow any new axons to grow. It is an open question whether the procedure has increased functional connectivity, or facilitated the experience of synesthetic color via an entirely different route. Synesthesia can also be induced by fast-acting hallucinogenic drugs (Hartman and Hollister 1963) or anesthetics (Gregory 1988, 203).

[9] It should be pointed out that this is not unique to synesthesia. Behavioral as well as neuroimaging studies have demonstrated this in the general population. For example, Conrad (1964) showed that in a letter recall task, participants' errors and confusions reflected the letters' acoustic similarities, even

the conclusions that we construct our perceived world, that our representations of the perceived world are not mere copies of the external world, and that the visual system does not operate like a simple camera. In fact, we could go as far as to say that perception is a fantasy that happens to coincide with reality much of our waking time (Frith 2007). In other words, perception is an inferential process. We make inferences about what is out there in the world based on the best-available input and prior experience, but these inferences can sometimes be wrong, resulting in perceptual illusions (Gregory 1980).

It seems that perception in synesthetes is perhaps even less constrained by the physical world. Note, however, that because synesthetic correspondences are usually consistent over time, synesthetes can utilize these additional percepts in order to make sense of the world around them (Sagiv, Ilbeigi, and Ben-Tal 2011). For example, when trying to identify the voice of a speaker, they could be aided by the visual impression that it evokes, in additional to the auditory experience of the voice itself. Like the rest of us, synesthetes explore the world with their senses; however, their perceptual experiences seem to be richer. There may be other ways in which perception and mental imagery vary in the general population and it is important to keep in mind that we may not all construct the perceived world in a similar manner.

Studying synesthesia may also yield insights into the construction of our social reality. In order to navigate in this social world—to understand others and predict their behavior—we must infer their mental states—their thoughts, feelings, intentions (e.g., Frith and Frith 2007), i.e., we must engage in "mentalizing." Amin et al. (2011) recently proposed that grapheme personification (thinking about letters and numbers as if they had gender, personality, and even mental states), may represent a case of benign hypermentalizing, and tentatively suggested that this may be a form of "social synesthesia." Whether one accepts this as a type of synesthesia in its own right (Simner and Holenstein 2007) or not, is less important than the interesting opportunity to look at social cognition and second-person approaches to understanding consciousness from a new angle. It raises fascinating questions about the role of the self in understanding others, not only by mirroring, but also via self-projection (for a discussion, see Sobczak-Edmans and Sagiv, Chapter 12, this volume).

Additionally, synesthesia can also raise interesting questions concerning agency and thought processes. For example, Dronkers et al. (2004) described a case of "ticker-tape" synesthete, who visualizes every word she hears. These letters and words don't have colors, but they are printed in a very particular font in front of her, like subtitles. Intriguingly, she also visualizes her own thoughts in a similar manner and describes the experience of reading her own thoughts as if she was a passive observer. She only knows what her thoughts are, after reading them. Observations of such benign, yet anomalous

though those letters were visually-presented. Calvert et al. (1997) showed that silent lip reading—a purely visual stimulus—activates primary auditory areas. Furthermore, Blakemore et al. (2005) found that some of the somatosensory activations found in synesthetes when they saw someone else being touched, are also present in the non-synesthete control group although they did not report any tactile experiences. Nevertheless, in synesthesia such cross-modal interactions are common.

forms of self-knowledge are rare. Indeed pathological failure to recognize one's own thoughts provided in a written format are even rarer (ffytche, Lappin, and Philpot 2004 describe a case of visual command hallucinations in a patient with pure alexia). Both cases, however, offer us an opportunity to re-examine the problems of sense of subjectivity and authorship of our own thoughts (Frith and Gallagher 2002)

Conclusion and Future Directions

We reviewed here the case for looking at synesthesia as a model problem for the scientific study of consciousness. We have described some of the areas in which synesthesia could inform our understanding of consciousness, for example, looking for the latter's neural correlates. There are two areas in which synesthesia's contribution could be transformative. One is the appreciation and study of individual differences in conscious experience. The second is the course of development of conscious perception. Contemporary discussions on consciousness largely focus on the common experience of adults and for the most part ignore individual differences and the experiences of infants and children. We must take development seriously if we are to understand consciousness. Understanding the role of learning and the environment in the development of the different cognitive/perceptual styles seen in synesthetes may well inform general as well as remedial educational strategies (Simner and Hubbard, Chapter 4, this volume), as we understand the strengths as well as weaknesses associated with different types of synesthesia (e.g., Ward, Sagiv, and Butterworth 2009). Finally, understanding whether we could cultivate, enhance, or generate synesthesia may offer a way of opening the doors of perception to everyone.

Acknowledgments

We thank Julia Simner for helpful comments on an earlier version of this manuscript.

References

Aleman, André, Geert-Jan M. Rutten, Margriet M. Sitskoorn, Geraud Dautzenberg, and Nick F. Ramsey. 2001. Activation of striate cortex in the absence of visual stimulation: An fMRI study of synesthesia. *Neuroreport* 12 (13):2827–2830.

Amin, Maina, Olufemi Olu-Lafe, Loes E. Claessen, Monika Sobczak-Edmans, Jamie Ward, Adrian L. Williams, and Noam Sagiv. 2011. Understanding grapheme personification: A social synaesthesia? *Journal of Neuropsychology* 5 (2):255–282.

Baars, Bernard J. 2003. Treating consciousness as a variable: The fading taboo. In *Essential Sources in the Scientific Study of Consciousness*, ed. Bernard J. Baars, William P. Banks, and James B. Newman, 1–10. Cambridge, MA: MIT Press.

Banissy, Michael, Roi Cohen Kadosh, Gerrit Maus, Vincent Walsh, and Jamie Ward. 2009. Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia. *Experimental Brain Research* 198:261–272.

Banissy, Michael J. and Jamie Ward. 2007. Mirror-touch synesthesia is linked with empathy. *Nature Neuroscience* 10 (7):815–816.

Bartoshuk, Linda M., Valerie B. Duffy, Barry G. Green, Howard J. Hoffman, Chia-Wen Ko, Laurie A. Lucchina, Lawrence E. Marks, Derek J. Snyder, and James M. Weiffenbach. 2004. Valid across-group comparisons with labeled scales: The gLMS versus magnitude matching. *Physiology & Behavior* 82 (1):109–114.

Behrmann, Marlene, Galia Avidan, Fuqiang Gao, and Sandra Black. 2007. Structural imaging reveals anatomical alterations in inferotemporal cortex in congenital prosopagnosia. *Cerebral Cortex* 17 (10):2354–2363.

Blackmore, Susan J. 2010. *Consciousness: An Introduction*. 2nd ed. London: Hodder Education.

Blakemore, Sarah-Jayne, Davina Bristow, Geoffrey Bird, Chris Frith, and Jamie Ward. July 2005. Somatosensory activations during the observation of touch and a case of vision–touch synaesthesia. *Brain* 128 (7):1571–1583.

Block, Ned. 2011. Perceptual consciousness overflows cognitive access. *Trends in Cognitive Sciences* 15 (12):567–575.

Brang, David, Ursina Teuscher, Luke E. Miller, Vilayanur S. Ramachandran, and Seana Coulson. 2011. Handedness and calendar orientations in time-space synaesthesia. *Journal of Neuropsychology* 5 (2):323–332.

Calvert, Gemma A., Edward T. Bullmore, Michael J. Brammer, Ruth Campbell, Steven C. R. Williams, Philip K. McGuire, Peter W. R. Woodruff, Susan D. Iversen, and Anthony S. David. 1997. Activation of auditory cortex during silent lipreading. *Science* 276 (5312):593–596.

Chalmers, David J. 1995. Facing up the problem of consciousness. *Journal of Consciousness Studies* 2 (3):200–219.

Cohen Kadosh, Roi, Limor Gertner, and Devin B. Terhune. 2012. Exceptional abilities in the spatial representation of numbers and time: Insights from synesthesia. *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry* 18 (3):208–215.

Cohen Kadosh, Roi, Avishai Henik, Andres Catena, Vincent Walsh, and Luis J. Fuentes. 2009. Induced cross-modal synaesthetic experience without abnormal neuronal connections. *Psychological Science* 20 (2):258–265.

Cohen Kadosh, Roi and Devin B. Terhune. 2012. Redefining synaesthesia? *British Journal of Psychology* 103 (1):20–23.

Conrad, R. 1964. Acoustic confusion in immediate memory. *British Journal of Psychology* 55 (1):75–84.

de Rochas, A. 1885. L'Audition Colorée. *La Nature.* Pt. 1, 306–307, 406–408; Pt. 2, 274–275.

Dennett, Daniel C. 1991. *Consciousness Explained*. London: Penguin.

——. 1999. Intrinsic changes in experience: Swift and enormous. *Behavioral and Brain Sciences* 22 (06):951.

Des Gachons, Catherine Peyrot, Gary K. Beauchamp, and Paul A. S. Breslin. 2009. The genetics of bitterness and pungency detection and its impact on phytonutrient evaluation. *Annals of the New York Academy of Sciences* 1170 (1):140–144.

Dixon, Mike J. and Daniel Smilek. 2005. The importance of individual differences in grapheme-color synesthesia. *Neuron* 45 (6):821–823.

Dixon, Mike, Daniel Smilek, and Philip Merikle. 2004. Not all synaesthetes are created equal: Projector versus associator synaesthetes. *Cognitive, Affective, & Behavioral Neuroscience* 4(3):335–343.

Dronkers, Nina F., Rachel Edelson, Jenny Ogar, David Wilkins, and Joseph T. Elder. 2004. Letteral invision: A speech-to-text form of synesthesia. Paper presented at the 4th American Synesthesia Association Meeting, University of California, Berkeley, USA, 5–7 November.

Eagleman, David M. 2012. Synaesthesia in its protean guises. *British Journal of Psychology* 103 (1):16–19.

Esterman, Michael, Timothy Verstynen, Richard B. Ivry, and Lynn C. Robertson. 2006. Coming unbound: Disrupting automatic integration of synesthetic color and graphemes by transcranial magnetic stimulation of the right parietal lobe. *Journal of Cognitive Neuroscience* 18 (9):1570–1576.

ffytche, Dominic H., Robert J. Howard, Michael J. Brammer, Anthony David, Peter Woodruff, and Steven Williams. 1998. The anatomy of conscious vision: An fMRI study of visual hallucinations. *Nature Neuroscience* 1 (8):738–742.

ffytche, Dominic H., Julia M. Lappin, and Michael Philpot. 2004. Visual command hallucinations in a patient with pure alexia. *Journal of Neurology, Neurosurgery & Psychiatry* 75 (1):80–86.

Frith, Chris D. 2007. *Making Up the Mind: How the Brain Creates our Mental World*. Oxford: Blackwell.

Frith, Chris D. and Uta Frith. 2007. Social cognition in humans. *Current Biology* 17 (16):R724–32.

Frith, Christoper, and Shaun Gallagher. 2002. Models of the pathological mind. *Journal of Consciousness Studies* 9:57-80.

Frith, Chris, Richard Perry, and Erik Lumer. 1999. The neural correlates of conscious experience: An experimental framework. *Trends in Cognitive Sciences* 3 (3):105–114.

Gray, Jeffrey. 2003. How are qualia coupled to functions? *Trends in Cognitive Sciences* 7 (5):192–194.

Gray, Jeffrey A., Susan Chopping, Julia Nunn, David Parslow, Lloyd Gregory, Steve Williams, Michael J. Brammer, and Simon Baron-Cohen. 2002. Implications of synaesthesia for functionalism: Theory and experiments. *Journal of Consciousness Studies* 9 (12):5–31.

Gregory, Richard L. 1980. Perceptions as hypotheses. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 290 (1038):181–197.

——. 1988. *Odd Perceptions*. New York: Routledge.

Hänggi, Jürgen, Diana Wotruba, and Lutz Jäncke. 2011. Globally altered structural brain network topology in grapheme-color synesthesia. *The Journal of Neuroscience* 31 (15):5816–5828.

Hartman, Alan M. and Leo E. Hollister. 1963. Effect of mescaline, lysergic acid diethylamide and psilocybin on color perception. *Psychopharmacologia* 4:441–451.

Hasenkamp, Wendy and Lawrence W. Barsalou. 2012. Effects of meditation experience on functional connectivity of distributed brain networks. *Frontiers in Human Neuroscience* 6:38.

Henkin, Robert I., Lucien M. Levy, and Chin S. Lin. 2000. Taste and smell phantoms revealed by brain functional MRI (fMRI). *Journal of Computer Assisted Tomography* 24 (1):106–123.

Hubbard, Edward M., A. Cyrus Arman, Vilayanur S. Ramachandran, and Geoffrey M. Boynton. 2005. Individual differences among grapheme-color synesthetes: brain-behavior correlations. *Neuron* 45 (6):975–985.

Hubbard, Edward M., David Brang, and Vilayanur S. Ramachandran. 2011. The cross-activation theory at 10. *Journal of Neuropsychology* 5 (2):152–177.

Jameson, Kimberly A., Susan M. Highnote, and Linda M. Wasserman. 2001. Richer color experience in observers with multiple photopigment opsin genes. *Psychonomic Bulletin & Review* 8 (2):244–261.

Jarick, Michelle, Candice Jensen, Michael J. Dixon, and Daniel Smilek. 2011. The automaticity of vantage point shifts within a synaesthetes? Spatial calendar. *Journal of Neuropsychology* 5 (2):333–352.

Jones, Catherine L., Marcus A. Gray, Ludovico Minati, Julia Simner, Hugo D. Critchley, and Jamie Ward. 2011. The neural basis of illusory gustatory sensations: Two rare cases of lexical-gustatory synaesthesia. *Journal of Neuropsychology* 5 (2):243–254.

Jonas, Clare N., Alisdair J. G. Taylor, Sam Hutton, Peter H. Weiss, and Jamie Ward. 2011. Visuo-spatial representations of the alphabet in synaesthetes and non-synaesthetes. *Journal of Neuropsychology* 5 (2):302–322.

Kanwisher, Nancy. 2001. Neural events and perceptual awareness. *Cognition* 79 (1–2):89–113.

Koch, Christof and Naotsugu Tsuchiya. 2007. Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences* 11 (1):16–22.

Kuhn, Gustav, Alym A. Amlani, and Ronald A. Rensink. 2008. Towards a science of magic. *Trends in Cognitive Sciences* 12 (9):349–354.

Kupers, Ron, Arnaud Fumal, Alain Maertens de Noordhout, Albert Gjedde, Jean Schoenen, and Maurice Ptito. 2006. Transcranial magnetic stimulation of the visual cortex induces somatotopically organized qualia in blind subjects. *Proceedings of the National Academy of Sciences of the United States of America* 103 (35):13256–13260.

Lavie, Nilli. 2007. Attention and consciousness. In *The Blackwell Companion to Consciousness*, ed. Max Velmans and Susan Schneider, 485–503. Malden, MA, USA: Blackwell Publishing.

Locke, John. 1979. *An Essay Concerning Human Understanding*. Oxford: Clarendon Press. (Originally published 1690.)

Ludwig, Vera U. and Julia Simner. 2013. What colour does that feel? Tactile–visual mapping and the development of cross-modality. *Cortex* 49: 1089–1099.

Macaluso, Emiliano and Jon Driver. 2005. Multisensory spatial interactions: A Window onto functional integration in the human brain. *Trends in Neurosciences* 28 (5):264–271.

Marks, Lawrence E. 1975. On colored-hearing synesthesia: Cross-modal translations of sensory dimensions. *Psychological Bulletin* 82 (3):303–331.

Noë, Alva. 2004. *Action in Perception*. *Representation and Mind*. Cambridge, MA: MIT Press.

Noë, Alva, and Susan Hurley. 2003. The deferential brain in action: Response to Jeffrey Gray. *Trends in Cognitive Sciences* 7 (5):195–196.

Novich, Scott, Sherry Cheng, and David M. Eagleman. 2011. Is synaesthesia one condition or many? A large-scale analysis reveals subgroups. *Journal of Neuropsychology* 5 (2):353–371.

Nunn, Julia A., Lloyd J. Gregory, Michael J. Brammer, Steven C. Williams, David M. Parslow, Michael J. Morgan, Robin G. Morris, Edward T. Bullmore, Simon Baron-Cohen, and Jeffrey A. Gray. 2002. Functional magnetic resonance imaging of synesthesia: Activation of V4/V8 by spoken words. *Nature Neuroscience* 5 (4):371–375.

Palmer, Stephen E. 1999a. Color, consciousness, and the isomorphism constraint. *The Behavioral and Brain Sciences* 22 (6):923–43.

——. 1999b. *Vision Science: Photons to Phenomenology*. Cambridge, MA: MIT Press.

Palmeri, Thomas J., Randolph Blake, René Marois, Marci A. Flanery, and William Whetsell. 2002. The perceptual reality of synesthetic colors. *Proceedings of the National Academy of Sciences of the United States of America* 99 (6):4127–4131.

Paulesu, Eraldo, John Harrison, Simon Baron-Cohen, John D. Watson, Laura Goldstein, Jon Heather, Richard S. J. Frackowiak, and Chris D. Frith. 1995. The physiology of coloured hearing A PET activation study of colour-word synaesthesia. *Brain* 118 (3):661–676.

Pedrono. 1882. De l'Audition Colorée. *Annales d'Oculistique* 88:224–237.

Proulx, Michael J. 2010. Synthetic synaesthesia and sensory substitution. *Consciousness and Cognition* 19 (1):501–503.

Ramachandran, Vilayanur S. and Edward M. Hubbard. 2001a. Psychophysical investigations into the neural basis of synaesthesia. *Proceedings.Biological Sciences/the Royal Society* 268 (1470):979–983.

——. 2001b. Synaesthesia—a window into perception, thought and language. *Journal of Consciousness Studies* 8:3–34.

Rees, Geraint and Chris Frith. 2007. Methodologies for identifying the neural correlates of consciousness. In *The Blackwell Companion to Consciousness*, ed. Max Velmans and Susan Schneider, 553–566. Malden, MA: Blackwell Publishing.

Revonsuo, Antti. 2010. *Consciousness: The Science of Subjectivity*. Hove: Psychology Press.

Rich, Anina N., Mark A. Williams, Aina Puce, Ari Syngeniotis, Matthew A. Howard, Francis McGlone, and Jason B. Mattingley. 2006. Neural correlates of imagined and synaesthetic colours. *Neuropsychologia* 44 (14):2918–2925.

Rippon, Gina, Jon Brock, Caroline Brown, and Jill Boucher. 2007. Disordered connectivity in the autistic brain: Challenges for the 'new psychophysiology'. *International Journal of Psychophysiology* 63 (2):164–172.

Ro, Tony, Alessandro Farnè, Ruth M. Johnson, Van Wedeen, Zili Chu, Zhiyue J. Wang, Jill V. Hunter, and Michael S. Beauchamp. 2007. Feeling sounds after a thalamic lesion. *Annals of Neurology* 62 (5):433–441.

Robertson, Lynn C. 2003. Colour my i's blue. *Nature* 410:533–534.

Rouw, Romke, H. Steven Scholte, and Olympia Colizoli. 2011. Brain areas involved in synaesthesia: A review. *Journal of Neuropsychology* 5 (2):214–242.

Sagiv, Noam, Jeffrey Heer, and Lynn Robertson. 2006. Does binding of synesthetic color to the evoking grapheme require attention? *Cortex* 42 (2):232–242.

Sagiv, Noam, Alireza Ilbeigi, and Oded Ben-Tal. 2011. Reflections on synesthesia, perception, and cognition. *Intellectica* 55 (1):81–94.

Sagiv, Noam and Lynn C. Robertson. 2005. Synesthesia and the binding problem. In *Synesthesia: Perspectives from Cognitive Neuroscience*, ed. Lynn C. Robertson and Noam Sagiv, 90–107. New York: Oxford University Press.

Sagiv, Noam, Julia Simner, James Collins, Brian Butterworth, and Jamie Ward. 2006. What is the relationship between synaesthesia and visuo-spatial number forms? *Cognition* 101 (1):114–128.

Sagiv, Noam and Jamie Ward. 2006. Crossmodal interactions: Lessons from synesthesia. *Progress in Brain Research* 155:259–271.

Schwarzkopf, D. Samuel, Chen Song, and Geraint Rees. 2011. The surface area of human v1 predicts the subjective experience of object size. *Nature Neuroscience* 14 (1):28–30.

Searle, John R. 2000. Consciousness. *Annual Review of Neuroscience* 23:557–578.

——. 1997. *The Mystery of Consciousness*. New York: New York Review of Books.

Simner, Julia. 2012. Defining synaesthesia: A response to two excellent commentaries. *British Journal of Psychology* 103 (1):24–27.

Simner, Julia and Emma Holenstein. 2007. Ordinal linguistic personification as a variant of synesthesia. *Journal of Cognitive Neuroscience* 19 (4):694–703.

Simner, Julia and Edward M. Hubbard. 2013. Synesthesia in school-aged children. In *The Oxford Handbook of Synesthesia,* ed. Julia Simner and Edward M. Hubbard, 64–82. Oxford: Oxford University Press.

Simner, Julia, Catherine Mulvenna, Noam Sagiv, Elias Tsakanikos, Sarah A. Witherby, Christine Fraser, Kirsten Scott, and Jamie Ward. 2006. Synaesthesia: The prevalence of atypical cross-modal experiences. *Perception* 35 (8):1024–1033.

Small, Dana M. 2010. Taste representation in the human insula. *Brain Structure and Function* 214 (5):551–561.

Smilek, Daniel, Alicia Callejas, Mike J. Dixon, and Philip M. Merikle. 2007. Ovals of time: Time-space associations in synaesthesia. *Consciousness and Cognition* 16 (2):507–519.

Sobczak-Edmans, Monika and Noam Sagiv. 2013. Synesthetic personification: The social world of graphemes. In *The Oxford Handbook of Synesthesia,* ed. Julia Simner and Edward M. Hubbard, 222–238. Oxford: Oxford University Press.

Stevens, Michael C. 2009. The developmental cognitive neuroscience of functional connectivity. *Brain and Cognition* 70 (1):1–12.

Tang, Joey, Jamie Ward, and Brian Butterworth. 2008. Number forms in the brain. *Journal of Cognitive Neuroscience* 20 (9):1547–1556.

Tononi, Giulio. 2007. The information integration theory of consciousness. In *The Blackwell Companion to Consciousness*, ed. Max Velmans and Susan Schneider, 287–299. Malden, MA: Blackwell Publishing.

Treisman, Anne. 2005. Synesthesia: Implications for attention, binding, and consciousness—a commentary. In *Synesthesia: Perspectives from Cognitive Neuroscience*, ed. Lynn C. Robertson and Noam Sagiv, 239–254. New York: Oxford University Press.

Ward, Jamie, Brett Huckstep, and Elias Tsakanikos. 2006. Sound-colour synaesthesia: To what extent does it use cross-modal mechanisms common to us all? *Cortex* 42 (2):264–280.

Ward, Jamie, Ryan Li, Shireen Salih, and Noam Sagiv. 2007. Varieties of grapheme-colour synaesthesia: A new theory of phenomenological and behavioural differences. *Consciousness and Cognition* 16 (4):913–931.

Ward, Jamie and Noam Sagiv. 2007. Synaesthesia for finger counting and dice patterns: A case of higher synaesthesia? *Neurocase* 13 (2):86–93.

Ward, Jamie, Noam Sagiv, and Brian Butterworth. 2009. The impact of visuo-spatial number forms on simple arithmetic. *Cortex* 45 (10):1261–1265.

Ward, Jamie and Julia Simner. 2003. Lexical-gustatory synaesthesia: linguistic and conceptual factors. *Cognition* 89 (3):237–261.

Ward, Jamie and Thomas Wright. In press. Sensory substitution as an artificially acquired synaesthesia. *Neuroscience and Biobehavioral Reviews*.

Weiss, Peter H., Karl Zilles, and Gereon R. Fink. 2005. When visual perception causes feeling: Enhanced cross-modal processing in grapheme-color synesthesia. *NeuroImage* 28 (4):859–868.

Zeki, Semir. 1990. A century of cerebral achromatopsia. *Brain* 113 (6):1721–1777.

Zeki, Semir, and Andreas Bartels. 1999. Toward a theory of visual consciousness. *Consciousness and Cognition* 8 (2):225–259.

Zeman, Adam. 2002. *Consciousness: A User's Guide*. New Haven, CT: Yale University Press.

——. 2005. What in the world is consciousness? *Progress in Brain Research* 150:1–10.