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Ploeger, A.; van der Hoort, B.

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Evolutionary Psychology as a Metatheory for the Social Sciences: How to Gather Interdisciplinary Evidence for a Psychological Adaptation

Annemie Ploeger
University of Amsterdam

Björn van der Hoort
Karolinska Institutet

Evolutionary psychology has been proposed as a new metatheory for the social sciences (Buss, 1995). Evolutionary psychology is an approach that emphasizes the evolutionary background of psychological phenomena (e.g., cognition, motivation, perception), with the expectation that knowledge about this background enhances our understanding of the working of the present human mind. This proposal has met with both enthusiasm and criticism. An important criticism is that it is hard, if possible at all, to find empirical evidence for a hypothesized psychological adaptation. This criticism has been addressed with the proposal to build a nomological network of evidence around a hypothesized psychological adaptation (Schmitt & Pilcher, 2004). In this article, we show that it is possible to use this nomological network of evidence to support the hypothesis that face recognition is an adaptation. We reviewed the literature on face recognition from different disciplines (psychology, medicine, neuroscience, genetics, primatology, and anthropology) and conclude that there is an extensive network of evidence for the proposed hypothesis. We argue that building a nomological network of evidence is a promising way to address several criticisms of evolutionary psychology, and that such a network can serve as a metatheoretical framework for the social sciences.

Keywords: evolutionary psychology, face recognition, metatheories

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Evolutionary psychology has been proposed as a new metatheory for psychological science (Buss, 1995; Cosmides & Tooby, 2013), or even broader, for all social sciences (Duntley & Buss, 2008; Ploeger, 2010). Evolutionary psychology is an approach that emphasizes the evolutionary background of psychological phenomena (e.g., cognition, motivation, perception), with the expectation that knowledge about this background enhances our understanding of the working of the present human mind. Its tenet is that the human mind is an information-processing device that consists of specialized problem solving mechanisms, evolved by natural selection. These mechanisms, or adaptations, are considered to be domain-specific, rather than domain-general (Barrett & Kurzban, 2006; Cosmides & Tooby, 1994). Specialized mechanisms will outperform a single general mechanism, because generality is detrimental to both effectiveness and efficiency. Different problems require different solutions. For example, the heart is specialized to pump blood throughout the body, but the uptake of oxygen is carried out by a separate organ. There is no more reason to expect that two organs are alike as it is to expect that two cognitive functions are alike.

Evolutionary psychology has met with both enthusiasm and criticism. It has been a fruitful approach, with numerous empirical studies that confirmed evolutionary based hypotheses (for examples, see Buss & Reeve, 2003; Cosmides & Tooby, 2013). In addition, evolutionary psychologists have published widely in the main journals in psychology (for recent examples, see DeScioli & Kurzban, 2013; McCullough, Kurzban, & Tabak, 2013; Tybur, Lieberman, Kurzban, & DeScioli, 2013). However, some scholars argued that we will never know how cognition evolved, because we cannot perform evolutionary experiments on human cognition, and the fossil record provides little information about how the mind evolved (for an overview of criticisms of evolutionary psychology, see Hagen, 2005).

To deal with these criticisms, Ketelaar and Ellis (2000) argued that evolutionary psychology is a fruitful approach in the light of the Lakatosian philosophy of science. According to this philosophy of science, most researchers center their work around a general theory (e.g., evolutionary theory; see Figure 1 in Buss, 1995, for an example), which they assume to be correct, although they do not directly test it. This general theory is called the *hard core* of assumptions that most researchers share. The hard core is surrounded by hypotheses that can be empirically tested. When these hypotheses are confirmed, they form a *protective belt* around the hard core. The validity of the hard core is judged by the performance of the protective belt, rather than by direct attempts to falsify the hard core. The hard core is considered to be fruitful and progressive when it results in the generation of new predictions and empirical studies to test these predictions. Ketelaar and Ellis argued that evolutionary psychology is a very progressive hard core, because it resulted in a wide array of new predictions and empirical tests.

In addition, Schmitt and Pilcher (2004) developed a nomological network of evidence to guide the evaluation of evidence for the existence of a psychological adaptation (i.e., to estimate the validity of the hard core by judging the fruitfulness of the protec-

Annemie Ploeger, Department of Psychology, University of Amsterdam; Björn van der Hoort, Department of Neuroscience, Karolinska Institutet.

Correspondence concerning this article should be addressed to Annemie Ploeger, University of Amsterdam, Department of Psychology, Weesperplein 4, 1018 XA Amsterdam, The Netherlands. E-mail: a.ploeger@uva.nl

tive belt). This network distinguishes eight types of evidence from various research fields (see Figure 1). Each type of evidence increases the likelihood of the existence of a psychological adaptation. The quality and quantity of each type of evidence is called 'evidentiary depth' and the number of types of evidence is called 'evidentiary breadth.'

We argue that this nomological network of evidence is a major tool in establishing evolutionary psychology as a metatheory for the social sciences. A metatheory is defined by a set of assumptions that shape how researchers generate theories and test hypotheses (Ketelaar & Ellis, 2000) and that integrates and unifies theories and findings from different disciplines (Buss, 1995; and see Wallis, 2010). The nomological network of evidence clearly shows that the enterprise of evolutionary psychology is interdisciplinary, covering a wide array of fields. The different fields have been chosen because they cover the different subdisciplines that so far have been involved in evolutionary theorizing (Schmitt & Pilcher, 2004). It is very possible that new boxes can be added in the future (e.g., sociology, economics, law; for suggestions, see Duntley & Buss, 2008), or that one box needs to be broken down in different boxes (e.g., cross-species comparisons and fossil findings from the Phylogenetic evidence box). The nomological network of evidence also shows that evolutionary psychology is far from just another new subdiscipline in psychology—it overarches all disciplines in psychology, and it connects them to the other social sciences, and to the life sciences. To show that this nomological network is a useful tool for evaluating the evidence for the existence of a psychological adaptation, we worked out a specific example: we estimate the evidentiary depth and breadth for face recognition as a psychological adaptation.

The evidentiary breadth is estimated by the number of different boxes of Figure 1 that can be filled with evidence. Having only one filled box would be a "minimal" level of evidentiary breadth, two or three filled boxes is considered "moderate" evidentiary breadth, four or five filled boxes "extensive," and more than five filled boxes "exemplary" evidentiary breadth (Schmitt & Pilcher, 2004). Researchers are encouraged to fill all the eight boxes with evidence, but this can be costly, time-consuming, and sometimes simply impossible (e.g., fossil evidence for psychological phenomena such as face recognition). It happens frequently that researchers rely on only one box of evidence. This research can be a good starting point for an evolutionary explanation of a psychological phenomenon, but the nomological network of evidence encourages researchers to look for other modes of evidence or to start collaborations with researchers from other disciplines.

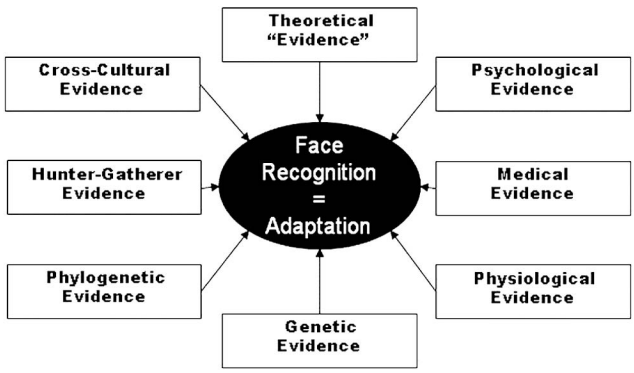

Figure 1. The proposed framework for evaluating the evidence for a psychological adaptation. Each box in this schema will be discussed in a separate section. Evidence from the various scientific disciplines will be combined to asses the evidentiary breadth and depth of the hypothesis that face recognition is an adaptation (Schmitt & Pilcher, 2004).

The other factor, evidentiary depth, refers to the quality of the evidence. Evidentiary depth depends on the average number of studies per box, the use of different modes of measurement, the use of proper controls, and the quality of sampling. "Minimal" depth would be found if boxes only show single studies with single modes of measurement and poor controls. The next level, "moderate" depth, means that at least two studies exist per box with more than one mode of measurement and good controls. "Extensive" evidentiary breadth is found when most boxes have numerous studies with more than one measuring method and high levels of controls. Furthermore, a high sampling quality should have been used. The highest level of evidentiary depth is the "exemplary" level with dozens of studies using the best controls and sampling techniques. It would be nice to have very strict guidelines of what counts as "exemplary" (e.g., a minimum number of studies in each box), but it is possible that one very high-quality study is enough to support the evolutionary explanation, whereas several low-quality studies may not be enough. As Schmitt and Pilcher (2004) emphasize, the nomological network of evidence is only a tentative guideline, but nevertheless it is based on traditional norms for evaluating the validity of empirical findings.

In this article we chose face recognition as a psychological adaptation to show the value of the nomological network of evidence. The evolutionary hypothesis of face recognition proclaims that individuals that possess a specialized mechanism for face recognition will be more likely to survive and reproduce than those without such a mechanism. In the literature, face recognition, face discrimination, and face detection are distinguished as separate psychological constructs. Actual face recognition is generally measured in a forced choice recognition paradigm using test faces to test the recognition of learned faces and new faces. Facial discrimination is the raw ability to discriminate between two faces. During a test session a subject would have to indicate whether two faces are identical. Face detection is the ability to detect the presence of a face per se. Subjects indicate whether a certain visual stimulus is a face. Face detection does not require intracategorical identification of faces, and therefore is not sufficient to solve the evolutionary problem of recognizing group members. Moreover, different neural processes seem to underlie face recognition and face detection; recognition requires a cortical route, but a subcortical route is sufficient for mere detection of faces (Johnson, 2005).

Importantly, in contrast to discrimination and detection, face recognition requires memory storage. Psychological research on both recognition and discrimination will be discussed in this article, because both require visual information processing of faces. The term 'face processing' will be used to refer to all face specific processing. Thus, it incorporates detection, discrimination, and recognition of faces. Another important clarification is that this article is not about perception and/or mimicking of facial expressions. Whether the use and recognition of facial expression in humans (and other primates) is an evolutionary adaptation is another research question and will not be discussed in this article.

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Face recognition is a well-studied subject within several disciplines. We have tried to fill in all the boxes in the nomological network for the hypothesis that face recognition is an adaptation. We emphasize that the aim of this paper is not to review all the existing evidence—this would become a book—but to show that a nominal network of evidence can be used to confirm the hypothesis that face recognition is a psychological adaptation.

Theoretical Evidence

Theoretical "evidence" is the starting point for all evolutionary research. The theory is usually based on general principles of evolutionary biology, and serves as a heuristic to develop new hypotheses and empirical tests. Common theories used by evolutionary scientists are evolution by natural selection (or inclusive fitness theory), and sexual selection theory. The theory we apply to face recognition is evolution by natural selection. The basic theory is that people who are better at recognizing faces have better chances to survive and reproduce than people with less of this capability. When this capability is heritable, more people in the next generation will possess it. Over generations, face recognition, just like having two eyes, two ears, and one nose, will be a stable trait in the population. The hypothesis that follows from this theory is that face recognition is a universal trait in human populations. In addition, when recognizing faces was more important in ancestral times than recognizing other things (e.g., chairs), we expect that people on average tend to recognize faces more easily than other things (e.g., have faster RTs when seeing faces vs. chairs). We also expect that face recognition develops quickly in children. When face recognition is an ancient capability, we expect to find the same or a rudimentary capability in nonhuman primates.

The importance of face recognition lies in the social nature of human behavior. A first reason why face recognition is important, is kin recognition. For example, feeding your own offspring increases your fitness. However, giving food to any child you encounter would not be an efficient strategy. Therefore, it is necessary to identify your offspring. One way to achieve this is through face recognition. Second, identifying conspecifics is necessary for maintaining hierarchy in a group. You need to recognize the position of each individual in the hierarchy in order to adjust your behavior. Third, our ancestors had to remember who helped them and who cheated on them to successfully adjust their behavior. A well-known strategy for individuals to behave in social groups is called tit-for-tat (Axelrod, 1984). Initially you help all your fellow group members, but when an individual of the group defects, the best strategy is to defect at a next occasion with that individual.

This behavior is seen in a number of different species. For example, bats tend to share blood with a group member that was unlucky during the nightly hunt, but only when that group member showed similar behavior in the past. Therefore, it is important for bats to recognize who helped them and who did not. Bats recognize group members by means of odor (De Fanis & Jones, 1995). Instead of odor, humans tend to rely on visual face recognition to identify defectors (e.g., Verplaetse, Vanneste, & Braeckman, 2007; Vanneste, Verplaetse, Van Hiel, & Braeckman, 2007). The need for identification of group members has likely been present as long as humans exist. This importance of face recognition in human social behavior has led some authors to hypothesize that face recognition is a likely psychological adaptation (e.g., Pascalis & Kelly, 2009).

We stress the importance of starting the development of a nomological evidence with a coherent theory. This is important for advocates of evolutionary psychology, because their underlying theory is often implicit or not directly testable. It is also important for the establishment of a metatheory, because the goal of a nomological network of evidence is not just to provide a new minitheory or hypothesis, but to use a unifying theme, that is, evolutionary theory, to integrate different hypotheses and research findings. In the next sections, we provide empirical evidence for the evolutionary hypothesis of face recognition from different subdisciplines, thereby integrating a large body of literature, and showing the value of building a nomological network of evidence.

Psychological Evidence

If face recognition is a psychological adaptation we expect to find a functionally specialized cognitive mechanism. We expect to find specialized face effects, which we summarize below. The alternative would be that face recognition is part of a general object recognition ability. In addition, if recognition is a psychological adaptation we expect that the ability to recognize faces is present in newborns and/or that there is a critical period for the acquisition of face recognizing abilities.

Face Recognition as a Functionally Specialized Mechanism: Face Effects

In the literature, there is ample evidence that suggests that there is something special about the recognition of faces, because of the existence of so called face effects (for reviews, see Crookes & McKone, 2009; McKone, Crookes, Jeffery, & Dilks, 2012). These face effects indicate that face recognition as a cognitive process is separable from mere object recognition.

Perhaps the most cited finding regarding face perception is the *inversion effect*. People tend to be much slower in both discrimination and recognition of upside-down faces compared with right side-up faces. Importantly, this effect is more pronounced for faces compared with objects (Diamond & Carey, 1986). A special form of the inversion effect is the *Thatcher effect* (named after face stimuli of Margaret Thatcher used in the original experiment; Thompson, 1980). Distortion of first-order relations in the face, generally by rotation of the eyes and the mouth, results in perception of a grotesque image. However, this effect on perception is only obtained when the distorted face is watched in an upright fashion.

Another often-cited face effect is the so-called *part–whole effect*. It is much easier to recognize a whole face compared with a part of that face (e.g., the eyes), when the whole face was learned. Again, this effect is much smaller in object recognition (Tanaka & Farah, 1993). A third effect is called the *composite effect*. When a test face is composed of an upper and lower half of two different faces, then subjects tend be slower when both halves are aligned compared to when they are not aligned (Young, Hellawell, & Hay, 1987).

The three effects described above are called *holistic effects*, because they all suggest that an important difference between face and object processing is the holistic nature of face processing. A

whole face (in a proper upright configuration) seems to be more informative than the sum of its parts. This holistic processing is disrupted for inverted faces and is specific for faces.

A second set of psychological effects is called *face-space effects*, because they can be explained by the face-space theory of face perception (Johnston & Ellis, 1995; Valentine, 1991). According to this theory each face corresponds to a certain point in a multidimensional face-space, in which dimensions code physical characteristics that differ between individual faces. The more two faces are alike the closer they are in face-space. Moreover, faces in the center of face-space are the most average faces.

A very robust finding that can be explained by the face space theory is the *distinctive face effect*. Distinctive faces tend to be more easily recognized compared to typical faces (Valentine & Bruce, 1986). Typical faces are located more centrally in face space where the number of faces is more dense. This makes it harder to recognize typical faces. However, when the similarity between distinctive faces is the same as the similarity between typical faces than a *reverse distinctive face effect* is observed (Davidenko, 2004). The effect is now reversed because subjects benefit from more practice in processing average faces.

A second face-space effect is the *caricature effect*: Recognition of caricature faces is better than recognition of veridical faces. In caricatures distinctive features are more pronounced rendering them more isolated in face-space and therefore more easily recognized (Rhodes, Brennan, & Carey, 1987).

A third face space effect is the *other-race effect*. Recognition of other-race individuals is poorer than individuation of same race individuals (Kelly et al., 2007; Valentine, 1991). Face-space is tuned to recognize the most frequent encountered (own race) faces, causing other-race faces to be densely clustered in the periphery of face-space. Since the other-race faces share the same within race similarity, the recognition of other-race faces is poorer.

An important finding favoring the hypothesis that expertise is necessary for face recognition is that professional dog judges show inversion effects for dog recognition (Diamond & Carey, 1986). Even more impressive, this effect is as large as the inversion effect for face recognition. This would indicate that experience is fundamental for the inversion effect. However, this effect has never been replicated by follow-up studies. Robbins and McKone (2007) used the exact same experimental set up as the Diamond and Carey study (e.g., experts with 20 years of expertise with a certain breed) and found no larger dog inversion effect in experts compared to novices. This finding is consistent with the face specificity hypothesis.

Face Recognition in Newborns

Several findings suggest the ability of newborns to selectively process faces (for a review, see Simion, Leo, Turati, Valenza, & Dalla Barba, 2007). Newborns tend to look longer to a spatial configuration that represents a face (Johnson & Morton, 1991; Valenza, Simion, Cassia, & Umiltà, 1996), they look longer to faces that make eye-contact (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000; Rigato, Menon, Johnson, Faraguna, & Farroni, 2011), and they look longer to attractive faces (Slater et al., 1998, 2000). Moreover, newborns (1–6 days old) are able to discriminate between a once seen face and a new face (Pascalis & de Schonen, 1994; Turati, Macchi Cassia, Simion, & Leo, 2006). Furthermore, one of these studies found an inversion effect for this discriminative ability in neonates (Turati et al., 2006). These findings show that newborns have face processing abilities to discriminate between faces and objects, and between individual faces. These results seem to imply that babies are born with the ability to recognize faces, without the need of much experience.

Face Recognition: Critical Period

Apart from face perception in newborns, another strong argument in favor of the evolutionary hypothesis would be a critical period for the acquisition of face perception skills. Evidence from different fields suggests that such a critical period exists. For example, the other-race effect is absent in 3-month-olds; they perform equally for different races on face recognition tasks. However, three months later a small other-race effect is present and at the age of 9 months this effect is as large as it is for adults (Kelly et al., 2007). Another important argument in favor of the critical period hypothesis is that a relatively short inability to see faces due to an innate cataract (removed at 2–6 months of age) induces prosopagnosia (selective permanent deficit to recognize faces) despite excessive experience with facial stimuli later in life (Le Grand, Mondloch, Maurer, & Brent, 2004). Prosopagnosia will be further discussed in the section on medical evidence. These findings suggest a differential critical period; an early critical period for core face processing and a more extended period for the fine-tuning of face space.

To conclude, holistic face effects show that there is something special about faces: holistic processing. The main question is: Is holistic processing a face specific mechanism or is it a general mechanism that becomes specialized in faces because of extended expertise? Experts seem to show holistic processing for objects in at least some degree, however the performance never becomes face-like. Thus, adults seem to perform face-specific cognitive functioning. Furthermore, all holistic face effects are also present in 3-month-olds. The size of these effects is not increasing by age, when controlled for restrictions effects. Age has a positive effect on performance on face tasks but this improvement is probably attributable to improvement of general cognitive functions. Thus, face-specific cognitive functions mature early in infancy.

Newborns have a preference for faces over objects, which might be caused by general structural properties of face stimuli, such as more features in the wider part of an object (congruency) and more features in the upper part of an object (top-down asymmetry).

The combination of an evolved preference for faces and an evolved mechanism for holistic processing (whether it is face specific or not) could together probably solve the evolutionary problem of face recognition.

Conclusion

To sum up, we have gathered empirical evidence from different subdisciplines in psychology to support the evolutionary hypothesis that face recognition is an adaptation. There is ample evidence for specialized face effects, and for the hypothesis that newborns are able to recognize faces. For metatheoretical purposes, it shows that it is possible (and necessary) to collect evidence from different fields in order to substantiate the metatheory (i.e., to create a protective belt around the hard core).

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Physiological Evidence

In this section the physiological evidence for the evolutionary hypothesis is reviewed. Using brain imaging techniques several studies have addressed the issue of face specificity on a neural level. We expect to find specific brain areas, neural circuits, or other functionally specialized neural responses associated with face recognition. Both evoked response potential (ERP) studies and functional MRI (fMRI) studies will be reviewed.

ERP Evidence

One of the earliest findings in neuroscience regarding specialization of the brain for face perception is the electrophysiological marker N170. The N170 has a larger amplitude for human faces compared with objects and animal faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Surprisingly, this negativity is larger for inverted compared with upright faces. ERP studies show that the amplitude of the N170 increases progressively with age (Taylor, McCarthy, Saliba, & Degiovanni, 1999). However, a face-specific ERP component is already measured in 6-month-old babies, but it is much smaller in amplitude and has a longer latency compared to the adult N170 (de Haan, Pascalis, & Johnson, 2002). It is very hard to associate any cognitive function with an ERP. Therefore, it is hard to dissociate general cognitive functions from face specific functioning. However, an interesting finding is that in contrast to the N170, the object selective ERP does not show a developmental change (Taylor et al., 1999). This suggests different developmental patterns for face recognition and object recognition abilities. Furthermore, intracranial electrophysiological experiments with epileptic patients show that the N170 is originated from brain areas that are known to be face selective form fMRI studies (Allison, Puce, Spencer, & McCarthy, 1999). The face specificity of the N170 is in line with the face-specificity hypothesis.

However, ERP studies have also revealed results in favor of the expertise hypothesis in experiments with Greebles. Greebles are three-dimensional objects with similar first-order relations; they all share the same number and location of appendages, but with different second-order relations; the size and form of the appendages differs. Subjects become expert in Greeble discrimination and recognition within 10 hours of practice. Greeble experts showed a face-like N170 in response to a Greeble and this N170 is also affected by inversion (Maurer, Grand, & Mondloch, 2002). Furthermore, a general finding is that the N170 of a face is reduced if a second face is presented simultaneously and the same effect is seen for Greeble experts: The N170 of a face is reduced when a Greeble is simultaneously presented. This effect has also been shown for car-experts, with a distractor car reducing the N170 of a face (Gauthier, Curran, Curby, & Collins, 2003). In line with the expertise hypothesis, the amount of interference caused by distractor cars correlates with level of expertise. Assuming that the N170 reflects a well-defined cognitive function (e.g., holistic processing), car experts use similar mechanisms to process faces and cars. However, an alternative explanation is that distractor studies measure the (in)ability to ignore irrelevant information, comparable with the Stroop task, and that experts are easier distracted by their object of expertise (McKone et al., 2012).

Early visual experience is necessary for the establishment of normal neural networks for face recognition as shown by an ERP study (Mondloch et al., 2013). Adults with visual cataract as a newborn have an abnormal (increased) N170 response to face stimuli, which is indicative for a critical period for face processing and thus a strong argument against the expertise hypothesis.

fMRI Evidence

fMRI studies revealed three face selective regions in the human brain. The inferior occipital gyri, referred to as the occipital face area (OFA), the lateral fusiform gyrus, referred to as the fusiform face area (FFA), and the superior temporal sulcus (STS). These three areas together have been called the *core system* of face perception (for a review, see Haxby, Hoffman, & Gobbini, 2000; for recent empirical evidence, see Rossion, Hanseeuw, & Dricot, 2012) as opposed to an *extended system* in which memory and emotional content are associated with the identity of the face. The OFA gets most input from occipital areas and forms the basis of processing facial features. The STS is committed to facial expressions and eye gaze. The FFA processes invariant face characteristics, and the perception of unique identity of faces. The rest of this section is about the role of the FFA.

Specificity of function of the FFA is an important argument for the evolutionary hypothesis. The FFA responds twice as strongly to face tasks compared with other within-category object recognition (e.g., Greebles, hands, birds and cars) (Kanwisher, McDermott, & Chun, 1997; for a review, see Kanwisher, 2010). Thus, a face specific brain area seems to exist. However, the expertise hypothesis predicts an important role for the FFA in processing objects of expertise. According to the expertise hypothesis an important difference that explains a lot of the face-specificity of the FFA is that faces are processed on a within-category basis in which second-order spatial relations are critical. The FFA would not be face specific per se, but merely specialized in holistic processing. Moreover, the only factor that distinguishes faces from other object classes is the amount of experience the brain has with them. However, it is important to note that the face specificity hypothesis does not deny shaping of the brain by experience.

To study these competing hypotheses, again Greebles have been used. It has been shown that subjects become expert in Greeble discrimination and recognition within 10 hours of practice. These Greeble experts show a higher FFA response to (new and old) Greebles in both active and passive viewing conditions (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). This suggests that the ability to become expert in a category and to increase FFA activation is not bound to a critical period and is not specific for faces. Gauthier et al. (1999) further argue that expertise induces some form of automaticity since Greeble experts show a composite effect that is absent in Greeble novices and the size of this composite effect is correlated to FFA activity, indicating that the FFA is involved in holistic processing. The automaticity of the FFA is confirmed by the finding that FFA activity in response to faces is similar for active and passive viewing conditions (Kanwisher et al., 1997). Tarr and Gauthier (2000) concluded that the FFA automatically processes objects for which a subordinate-level of expertise is gained. They therefore suggest to rename the FFA into the 'flexible fusiform area" to emphasize the role of expertise in FFA activation.

However, researchers arguing for the specificity hypothesis interpreted these results differently. Greebles look like animate figures (but not like faces) and subjects are trained to give indi-

vidual Greebles a name, which could further encourage animate interpretations (Kanwisher, 2000). Furthermore, only three of eight studies showed a significant higher FFA activity for experts compared to novices in response to object of expertise stimuli (Mc Kone et al., 2012). Moreover, in all of these studies the FFA activation induced by objects of expertise is still much smaller than the FFA activation induced by faces (Gauthier, Skudlarski, Gore, & Anderson, 2000). Thus, even after gaining expertise the FFA is still more selective for faces than for any other object classes. An alternative explanation for the object of expertise effect of FFA is that experts are more motivated (because of higher affinity with the stimuli), and a subsequent attentional bias could yield an increased FFA response to objects of expertise. Indeed, the FFA can be modulated by attention (Wojciulik, Kanwisher, & Driver, 1998). Furthermore, expertise effects were found to be larger outside the FFA than within the FFA (Gauthier et al., 2000). Interestingly, the parahippocampal place area (PPA) is very sensitive to expertise, but this area is not activated by faces (Epstein, Harris, Stanley, & Kanwisher, 1999). Moreover, the expertise effect was only found during location-discrimination tasks but not during identity-discrimination tasks (Grill-Spector, Knouf, & Kanwisher, 2004). Thus, the increase of FFA activity in Greeble studies can be explained by an attentional bias. Furthermore, despite the increased activity of the FFA found in Greeble studies, FFA activity for faces is always at least twice as high for faces compared with any other object class (including Greebles; Kanwisher et al., 1997). Thus, the FFA seems to be specialized in face processing, although the evidence does not exclude a role for the FFA in processing other objects of expertise.

The development of the FFA has been reviewed by Grill-Spector, Golarai, and Gabrieli (2008). They concluded that face selective areas (especially the right FFA) are expanding at least until adolescence. However, based on a recent review it can be concluded that face-selective activity in the FFA (and the rest of the core face processing network) does not change during development but remains stable from as early as 7 years old to adulthood (Haist, Adamo, Han Wazny, Lee, & Stiles, 2013). Only activity in the extended network decreases. This finding is a strong argument against the expertise hypothesis.

To conclude, brain areas that belong to the core system of face perception are the fusiform face area (FFA), the occipital face area (OFA), and the superior-temporal sulcus (STS), with the FFA being especially important for face recognition and individuation. The face-specificity of the FFA has been questioned in literature, because FFA-activity of Greeble experts increases when watching Greebles. This leaves open the possibility that there are specialized brain areas involved in face recognition, but that these areas can be used for other within-category discrimination as well.

Conclusion

In general, the physiological data support the evolutionary hypothesis of face recognition. The discussion of competing hypotheses clearly shows that the protective belt of empirical support is very important for the evaluation of the evolutionary hypothesis. As soon as more evidence in favor of the expertise hypothesis is gathered, the evolutionary hypothesis (i.e., the hard core or the metatheory) needs to be reconsidered.

Medical Evidence

In this section the medical evidence for the evolutionary hypothesis of face recognition is reviewed. We discuss evidence related to prosopagnosia and double dissociations. We expect to find disorders that are specifically associated with face recognition.

Prosopagnosia

An often used argument in favor of the face specificity hypothesis and the evolutionary hypothesis of face recognition is the existence of prosopagnostic patients. Prosopagnosia is the isolated inability to recognize faces (for a fascinating introduction, see Fine, 2012). Typically, patients can still detect faces, their parts, and their expressions, indicating that respectively face detection, first-order processing, and emotional processing are intact. Furthermore, prosopagnostics still have knowledge about the people they cannot recognize, thus it is not a memory problem. However, patients cannot identify the faces of other people because somehow the brain mechanism underlying face recognition is disrupted. To circumvent the inability of face identification, prosopagnostics often develop alternative strategies, such as focusing on other aspects of an individual's appearance like posture and clothing. These strategies sometimes fail. For example, the man who joined the marines could not use his 'focus on clothing' strategy anymore.

Both congenital (Behrmann & Avidan, 2005) and acquired (Barton, 2008) prosopagnosia have been described in literature. Acquired prosopagnosia is generally caused by a stroke or a tumor in bilateral or unilateral right-side occipital and temporal face processing areas (OFA, FFA and STS; for a review on neuroimaging data, see Fox, Iaria, & Barton, 2008). Because strokes and tumors are rarely restricted to these brain areas, loss of face recognition is generally accompanied with loss of other cognitive functions, such as object agnosia and alexia.

Compared with acquired prosopagnosia, a congenital form is much more prevalent (Kennerknecht et al., 2006). Congenital prosopagnostics have never been able to recognize faces in their lives. Within this group a developmental form and a true hereditary form exist. Developmental prosopagnosia can be caused by an infection (e.g., meningitis) or severe epilepsy during early development (for reviews, see Dalrymple, Corrow, Yonas, & Duchaine, 2012; Susilo & Duchaine, 2013). As with prosopagnosia caused by a stroke or a tumor, other cognitive functions are generally also affected.

However, developmental prosopagnosia can also be caused by a cataract in newborns, which prevents proper visual input until the cataract is removed several months after birth. Cognitive deficits in these subjects are generally restricted to face recognition. After normal visual input is regained these infants are unable to recover face recognition throughout their lives. Apparently, the plasticity of the brain is not sufficient to outgrow prosopagnosia. This finding is in line with a critical period hypothesis on the development of face recognition. Furthermore, it is against the expertise hypothesis, because the amount of encountered faces after the cataract has been removed is still massive. According to Nelson (2001) all subjects with developmental prosopagnosia have damage extended beyond typical face processing areas and perform worse on object recognition tasks as well, but their face recognition deficit is always much more pronounced.

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The other congenital form is true hereditary prosopagnosia. This type of prosopagnosia has been described in seven families (Grüter et al., 2007). Most people with this condition are only slightly handicapped by the condition in every day life, and they might not even be aware of it because they successfully apply alternative strategies (e.g., focusing on clothing or hair). Studies revealed that hereditary prosopagnosia affects about 2% to 2.5% of the population (Kennerknecht et al., 2006; Kennerknecht, Ho, & Wong, 2008). Interestingly, this prevalence is constant over different races. However, a familiar form of combined prosopagnosia and within object agnosia has also been reported (Duchaine, Germine, & Nakayama, 2007). Therefore, we have to be careful with making firm conclusion about face specificity based on research on prosopagnosia.

Despite the extended descriptions of prosopagnostic patients, some researchers still claim that prosopagnosia is never truly face-specific but rather caused by deficits of more general cognitive functions. To counter the alternative explanations of prosopagnosia, researchers conducted a series of experiments on prosopagnostic patient Edward (Duchaine, Yovel, Butterworth, & Nakayama, 2006). Edward is unable to recognize faces, but like most prosopagnostics has normal face detection skills. Empirical results revealed that Edward performed similar to controls on the top-down faces recognition trials. In contrast, his recognition of upright faces was significantly worse compared to controls. Furthermore, no inversion effect was found for Edwards face recognition skills. These results indicate that a face specific deficit underlies Edward's prosopagnosia.

Duchaine et al. (2006) also included a Greeble experiment with Edward. The expertise hypothesis predicts that Edward would perform equal to controls on early training sessions because expertise levels are not reached yet, but with prolonged training would perform worse than controls. However, Edward performed similar to controls both before and after Greeble training. This finding argues against the expertise hypothesis of face recognition.

Double Dissociations

A double dissociation in face recognition would support the face specificity hypothesis. The most important double dissociation in the face-specificity debate is formed by isolated prosopagnosia and isolated object agnosia. Multiple case studies of apperceptive and associative object agnosia without prosopagnosia have been reported (McMullen, Fisk, Phillips, & Maloney, 2000; Germine, Cashdollar, Duzel, & Duchaine, 2011). Despite the fact that most object agnostics are generally not tested on within-category object recognition, there are some very convincing cases that form a direct double dissociation between face recognition and within-category object recognition and thereby support the face specificity hypothesis. For example, case RM kept his expert car recognizing abilities after he lost his face recognizing abilities. He was able to recognize more cars than any control (Sergent & Signoret, 1992). The same deficit restricted to faces was found for case WJ who was still able to recognize his sheep as good as sheep-expert controls, despite severe prosopagnosia (McNeil & Warrington, 1993). The opposite pattern was found in case CK. He lost his within-category object recognition of toy soldiers and planes while he was able to recognize faces (Moscovitch, Winocur, & Behrmann, 1997).

A third less well described double dissociation is formed by prosopagnosia and hyperfamiliarity for unknown faces. A case is known of a 21-year-old woman who experienced hyperfamiliarity for new faces after a focal left-temporo-occipital venous infarct (Vuilleumier, Mohr, Valenza, Wetzel, & Landis, 2003). Interestingly, acquired prosopagnosia is generally caused by unilateral right-side (or bilateral) tempero-occipital damage. The authors hypothesized that the observed hyperfamiliarity is caused by an imbalance between right side and left side cortical activity. A decrease in left side activity would shift the balance toward the right, thereby increasing the feeling of familiarity. This double dissociation is in line with the face-selectivity hypothesis because the familiarity is face specific.

Conclusion

To sum up, the medical part of the protective belt clearly supports the evolutionary hypothesis of face recognition. We found evidence for prosopagnosia and double dissociations.

Phylogenetic Evidence

In this section the phylogenetic evidence for the evolutionary hypothesis of face recognition is reviewed. We expect to find evidence for specialized face recognition in other species, especially in other primates that are phylogenetically close to human beings. We discuss behavioral and physiological evidence only for nonhuman primates, although there is evidence in other animals, such as sheep (e.g., Kendrick et al., 1995), pigeons (e.g., Ryan & Lea, 1994), and bees (e.g., Pascalis, Kelly, & Caldara, 2006).

Behavioral Evidence

Nonhuman primates show high-level face identification of conspecifics in studies using pictures of faces (Pascalis, Petit, Kim, & Campbell, 1999), but do they also use similar cognitive mechanisms? Some characteristics of human face recognition mechanisms have also been found for nonhuman primate face recognition. For example, an inversion effect was present in chimpanzees (Parr, Dove, & Hopkins, 1998), which later was shown to be face specific in rhesus monkeys (Parr, Winslow, & Hopkins, 1999). However, this inversion effect could not be replicated in their own follow-up studies (although recently Dahl, Rasch, Tomonaga, & Adachi, 2013 found evidence for the inversion effect in chimpanzees). A possible explanation for this lack of replication could be that follow-up studies used very small sets of facial stimuli. Therefore, primates might have used different perceptual strategies, such as focusing more on small parts of the face instead of holistic processing. This strategy shift explains why no inversion effect was found, because the inversion effect is thought to affect holistic processing, but not bottom-up serial processing.

An experiment circumvented the influence of overexperience with facial stimuli by using stimuli that were never seen before (Adachi, Chou, & Hampton, 2009). The results further suggest that humans and other primates share similar face recognition systems. Rhesus monkeys were habituated to upright and inverted faces to a point at which they looked equally long to both stimuli. After this habituation period, thatcherized faces (i.e., faces with inverted eyes and mouth) were shown on some trials in both an upright and

an upside-down fashion. The macaques in this study looked longer to upright thatcherized faces compared to inverted thatcherized and nonmanipulated faces. This Thatcher effect demonstrates that monkeys, like humans, use configural (holistic) processing for face recognition, which is affected by inversion. In line with these findings, it was found that, as in humans, feature configuration is more important than features themselves for face processing in macaque monkeys (Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004). However, the Thatcher effect is not present in rhesus monkeys, although it has been found in chimpanzees (Weldon, Taubert, Smith, & Parr, 2013). The Thatcher effect has also been demonstrated in squirrel monkeys (Nakata & Osada, 2012). Overall, it appears that humans and other primates use similar brain mechanisms to recognize faces.

An interesting finding concerning the constancy of face-space-effects across primate species is a study with humans. Six-month-old babies are able to discriminate between monkey faces. However, this ability is diminished at 9 months of age (Pascalis, de Haan, & Nelson, 2002). This poorer recognition for other species is called *the other-species effect* and is also found in adults. Monkeys also show an other-species effect. Interestingly, this effect follows the same developmental pattern that is found in humans: the effect is not present in very young monkeys (Dufour, Pascalis, & Petit, 2006).

To investigate the existence of a critical period for this fine-tuning of face-space (which would be in line with the evolutionary hypothesis), experience with faces before testing at various stages of development should be prevented. In a study by Sugita (2008), macaque neonates were removed from their parents at birth and raised by humans for 6 to 24 months. The human care-givers were wearing masks throughout the experiment and the macaques had no contact with conspecifics, thus the macaques had no experience to faces whatsoever. After this facial stimuli deprivation these monkeys still showed a preference for faces over objects. This suggests that the preference for faces found in newborns remains without the need for experience with faces. The macaques also showed no preference for monkey faces over human faces, indicating that the absence of the other-species effect in neonates can be extended by deprivation of facial stimuli. Taken together, these behavioral findings suggest a similar face processing system across primates.

Physiological Evidence

An evolutionary hypothesis of face perception would predict anatomical homologies between the face processing systems of humans and other primates. As described above, the human brain consists of three separate face specific areas: the fusiform face area (FFA), the occipital face area (OFA) and the superior temporal sulcus (STS). The FFA is thought to be committed to true face identification, the OFA is engaged with more low-level mechanisms such as processing different face parts, and the STS is related to changeable aspects of face perception such as eye gaze. In an fMRI study on macaques, three face selective areas were found in the inferiotemporal cortex of these primates (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). As in humans, these face areas were found to be organized along the anterior–posterior axis. By computational techniques the macaque brain can be stretched and matched to the human brain. This technique showed that the middle face area of macaques was located quite closely to the fusiform face area in humans. Moreover, the middle face area in macaques and the FFA in humans are both the largest face selective brain areas, which is a first indication of homology between both face recognition systems.

However, macaques showed a face-specific face area anterior to the middle face area, but in the human neither the OFA nor STS is located anterior to the FFA. This finding suggests that there might be additional face regions in the human brain correlating to this anterior face area in the macaque (Tsao, Möller, & Freiwald, 2008). Intracranial electrophysiological recordings in the human brain (Allison, McCarthy, Nobre, Puce, & Belger, 1994) indeed suggest such an anterior area. The first MRI study that actually mapped the anterior portion of the human temporal lobe also tested macaques with the same stimulus material (Tsao et al., 2008). Therefore, comparisons between both face-processing mechanisms could be made. The researchers found five face selective face areas in the macaque in a specific configuration, which was highly reproducible across individuals and contained one posterior, two middle, and three anterior brain areas along the anterior-posterior axis. The exact functions of these different areas remain unclear, but electrophysiological recording showed that the two middle face areas are face-specific (similar to the FFA in humans).

Conclusion

Humans are not alone in recognizing conspecifics by the visual perception of faces. Other primates are also very skilled in face perception. They show similar holistic effects to those found in humans. Furthermore, analogies of the neural substrate of face perception in humans have been found in monkeys. This part of the protective belt also clearly supports the evolutionary hypothesis of face recognition.

Genetic Evidence

Based on the evolutionary hypothesis of face recognition, we expect that variation in face recognition is strongly related to variation in the underlying genetics. Genetic evidence, mentioned in the section on medical evidence, is provided by the case of hereditary prosopagnosia. It has been shown that a hereditary subtype of prosopagnosia exists (for a review, see Grüter, Grüter, & Carbon, 2008). Inheritance follows an autosomal dominant pattern. Such a pattern is suggestive for a single gene mutation. Therefore, it should be interesting to track down such a prosopagnosia gene. However, additional psychological tests are also needed to make sure that this form of prosopagnosia is not accompanied by object agnosia. If it is not, then this would be a very convincing argument in favor of the evolutionary hypothesis.

A general approach to distinguish between the influence of nature and nurture on cognitive mechanisms is to study monozygotic and dizygotic twins. Dizygotic twins share 50% of their genetic material, whereas monozygotic are genetically identical. In an fMRI study, it was shown that the activation patterns elicited by faces is more similar in monozygotic twins than in dizygotic twins (Polk, Park, Smith, & Park, 2007). However, such a difference between monozygotic and dizygotic twins was not found for other stimuli (words and chairs). This finding indicates that genes play a larger role in face processing compared to processing of other visual stimuli.

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Conclusion

Genetic evidence is limited but present. For example, a hereditary form of prosopagnosia exists, which follows an autosomal dominant hereditary pattern. Furthermore, identical twins have more similar face processing brain anatomy than dizygotic twins. Different activation patterns between monozygotic and dizygotic twins are not found for words and objects. This suggests a larger role for genetics in face processing compared with processing of other visual stimuli. Because the genetic evidence in favor of the evolutionary hypothesis of face recognition is still limited, we recommend future studies on this topic, to build a stronger protective belt around the hard core (i.e., the metatheory).

Cross-Cultural Evidence

Based on the evolutionary hypothesis of face recognition, we expect that specialized face recognition is part of our universal human nature, so will be found cross-culturally. However, there are not many studies concerning cross-cultural research in face recognition. This is probably because most researchers assume universality of face recognition and its underlying mechanisms. One study showed that both East Asians and Western Caucasians show the inversion effect (Vizioli, Foreman, Rousselet, & Caldara, 2010). In addition, both groups showed the same magnitude of the N170 amplitude.

However, several studies suggest different strategies in face recognition across cultures. Eastern cultures focus on the area around the nose, whereas Western cultures focus more on discrete locations (Blais, Jack, Scheppers, Fiset, & Caldara, 2008). This finding is in line with the conclusion given by Nisbett and Miyamoto (2005) that Eastern cultures process information in a more holistic manner and Western cultures in a more analytical manner.

Conclusion

Cross-cultural evidence for the evolutionary hypothesis of face recognition is limited. Therefore, we recommend future studies on this topic, to build a stronger protective belt around the hard core (i.e., the metatheory).

Hunter-Gatherer Evidence

Based on the evolutionary hypothesis of face recognition, we expect to find specialized face recognition in hunter-gatherer societies. However, as far as we know, there has been no research on face effects in hunter-gatherer societies. Conclusions concerning the evolutionary hypothesis of face recognition cannot be drawn based on what we know about hunter-gatherers. Here we also think that because most researchers assume universality of face recognition, this research question has not been addressed yet. We argue that it is important to study nonwestern societies to be able to draw firm conclusions about the universality of psychological phenomena. For example, Henrich, Heine, and Norenzayan (2010) reviewed the evidence for universal claims about visual perception, fairness, cooperation, spatial reasoning, categorization and inferential induction, moral reasoning, reasoning styles, self-concepts and related motivations, and the heritability of IQ, and found unexpected differences between cultures. They argue that psychologists tend to study people from Western, Educated, Industrialized, Rich, and Democratic (WEIRD) societies, which may not be representative for all societies. Evolutionary psychologists are among the first to study the existence of human universals in a wide range of societies (see, e.g., Barrett et al., 2013; House et al., 2013).

Conclusion

Hunter-gatherer evidence for the evolutionary hypothesis of face recognition is absent. Therefore, we recommend future studies on this topic, to build a stronger protective belt around the hard core (i.e., the metatheory).

Discussion

The aim of this article was to show that the nomological network of evidence for a psychological adaptation (Schmitt & Pilcher, 2004) gives us a valuable framework for evolutionary psychology as a metatheory for the social sciences. This article reviewed interdisciplinary evidence for face recognition as a psychological adaptation, along this framework (see Figure 1).

Based on the criteria of the various levels of evidentiary breadth and depth mentioned in the Introduction, evidentiary breadth is regarded "extensive," because at least four boxes (psychological, physiological, medical, and phylogenetic) are filled with proper evidence in favor of the evolutionary hypothesis. Overall evidentiary depth is also regarded as "extensive" because boxes generally contain various studies, using different modes of measurement and using proper control conditions. However, it is unclear how to deal with the existence of counterevidence. In addition, it is hard to decide which evidence falsifies the evolutionary hypothesis. For example, evidence for objects of expertise using similar cognitive mechanisms as faces does not falsify the specificity hypothesis, because the specificity hypothesis does not exclude brain plasticity. Furthermore, dissimilarities in the neural substrate of face recognition in humans and monkeys do not falsify the evolutionary hypothesis, because the hypothesis predicts both similarities and dissimilarities.

Nevertheless, we are in favor of the approach developed by Schmitt and Pilcher (2004). We argue that the proposed framework can serve as a metatheory for the social sciences for several reasons. First, it is the first comprehensive framework that shows that we need evidence from several sources to confirm or falsify hypotheses. Second, this framework does not only unite the social sciences, but it clearly shows that we need to cross the borders even further toward the life sciences. It encourages scientists to include the collection of data in the field of genetics, medicine, physiology, paleontology, and primatology in their research programs. Third, although it does not provide very strict guidelines for the confirmation or falsification of hypotheses, it does provide a strong heuristic for doing interdisciplinary research. By providing criteria for both evidentiary breadth and depth, it guides researchers in their decisions about evolutionary hypothesis. We highly recommend that all social scientists consider Schmitt and Pilcher's nomological network of evidence to extend their research programs and make them truly interdisciplinary.

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